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MORPHOLOGICAL AND PALEOBOTANICAL STUDIES OF THE NYSSACEAE, I
A SURVEY OF THE MODERN SPECIES AND THEIR FRUITS

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THE LIVING SPECIES OF the genus *Nyssa* L. are native in eastern North America and in eastern Asia. This widely disjunct distribution is a familiar pattern to students of plant geography, for many other woody genera have a similar range. It is generally accepted that such genera are the remnants of an ancient mesophytic forest that extended throughout most of the northern hemisphere during Tertiary times (Li, 1952). In the case of *Nyssa,* this wide former distribution cannot be doubted, for fossil *Nyssa* remains are found in various Tertiary strata across Europe, Asia, and North America. Since these remains include fruits, pollen, and wood, as well as leaves, it may be said fairly that *Nyssa* has one of the best fossil records of any modern genus of trees.

The fossil fruits of *Nyssa* are particularly interesting because they are frequently found in an excellent state of preservation and because they exhibit a diversity of form that makes it possible to compare them with fruits of the most closely related living species of *Nyssa*; yet the fossils are often sufficiently different from their modern counterparts that one can study some of the evolutionary changes which have taken place within the genus. One of the world's best sources of fossil *Nyssa* is the early Tertiary brown coal of Brandon, Vermont. The largest, most distinctive fruits to be found in this richly fossiliferous deposit are those of *Nyssa*; they are present in such abundance that they were collected as "beechnuts" by 19th century miners. Moreover, the Brandon nyssas are so variable in size and shape that one investigator assigned them to 10 genera and to more than 50 fossil "species."

The investigations to be described here began with the most recent excavation of the Brandon deposit by Barghoorn and associates during 1947 and 1948, at which time many hundreds of *Nyssa* fruits were collected, cleaned, and separated into tentative morphological categories. Preliminary comments on these fruits may be found in the descriptions of the Brandon lignite and its flora by Barghoorn (1950) and by Barghoorn and Spackman (1949). Microtome sections were prepared from many of these specimens, and fruits of modern *Nyssa* species were collected for comparative purposes, as it was intended that *Nyssa* should form an important part of a general morphological and systematic study of the Brandon fruits and seeds. This collection, together with photographs, bibliographical materials, and observational notes, was subsequently turned over to the author of this paper, who has continued the study of *Nyssa* as a graduate research program under the guidance of Professor Barghoorn.

As the investigation progressed it became apparent that the evolutionary significance of the Brandon nyssas could not be evaluated without first studying the external and internal structure of related modern fruits. It became equally apparent that a treatment of fossil *Nyssa* should include a critical survey of as many *Nyssa* remains as possible, and not just those from Brandon. No such survey has been attempted since the appearance of Kirchheimer's admirable monograph more than 20 years ago (1938), although the *Nyssa* record has been greatly increased since then, especially as a result of palynological research. Therefore the present work has been broadened to include both morphological and paleobotanical research on *Nyssa* and closely related genera, with special emphasis on the morphology of the fruits. It should be added that *Nyssa* and allied genera include some of the most primitive living members of the Umbellales. It is to be hoped that the research reported here will not only aid in understanding the relationships between the taxa studied, but will also shed some light on the origin of this order of angiosperms.

The present paper will deal with the living species of *Nyssa* and their fruits; the fossils will be treated in a later report.

FAMILY CHARACTERISTICS

The genus *Nyssa* and the related monotypic genera *Camptotheca* Decne. and *Davidia* Baill. may be treated systematically as a single family Nyssaceae or as two subfamilies, Nyssoideae and Davidioideae, within the Cornaceae *sensu lato*. In any case, the affinity with Cornaceae and other families of the Umbellales is well supported by morphological and anatomical evidence and has been recognized for many years.

The criteria that have been used for separation of Nyssaceae from the Cornaceae are not altogether satisfactory. Hutchinson (1959, p. 94) cites the presence of imbricate petals as a key character for recognizing Nyssaceae; however petals of the cornaceous genera *Griselinia* Forst. f. and *Melanophylla* Baker also are said to be imbricate in the bud (Harms, 1898; Horne, 1914), and in the case of the nyssaceous *Camptotheca* the overlapping of petal edges is often so slight as to be scarcely perceptible. Wangerin distinguished Nyssaceae from Cornaceae on the basis of "Diplostemonie der Blüten, doppeltes Integument des Ovulums und Ausbildung des Pollens" (1910, p. 7). The last two of these distinctions may now be discounted; the similarity of pollen grains in the two families has been pointed out by Erdtman (1952, p. 290), and the absence of a second integument has been noted by Horne (1909, 1914) and by Titman (1949).

Wangerin's use of diplostemony as a distinguishing feature of Nyssaceae retains some validity; it is evident when flowers of all species are examined that there is a tendency for stamens to occur in two series in staminate flowers; however this tendency is somewhat obscured in some species by a marked variability in the numbers of floral appendages. In any case, the number of stamens is greater in flowers of Nyssaceae than in Cornaceae *sensu stricto*, whether or not two series are detectable.

The flowers of Nyssaceae have features in common with those of other members of the Umbellales, e.g., an inferior ovary and a solitary seed in each locule, but the nyssaceous genera are unlike most others in the order in that there are two kinds of flowers, staminate and hermaphrodite.[1] In *Nyssa* and *Camptotheca* the staminate and hermaphrodite flowers are borne on separate inflorescences, and in *Nyssa* the two different kinds of inflorescence are borne on separate plants. The *Davidia* inflorescence is unique in that a single hermaphrodite flower arises from a densely capitate inflorescence in which all other flowers are staminate.

This report will include morphological observations and distributional data not only for all species of Nyssaceae but, to some extent, for the cornaceous genus *Mastixia* Blume as well. *Mastixia* is customarily treated as the only genus of the subfamily Mastixioideae of the Cornaceae, and inclusion of it in the present work is not meant to imply any disagreement with that treatment; however, there is no doubt that the mastixioids, as members of the Cornaceae, have some degree of relationship with Nyssaceae. Moreover, there are two compelling reasons for giving some attention to *Mastixia* in seeking clues to evolutionary trends in the Nyssaceae. First, with regard to its secondary xylem, *Mastixia* is the most primitive genus of Cornaceae and, along with *Davidia*, of the order Umbellales (Adams, 1949; Li and Chao, 1954; Rodriguez, 1957, p. 274); therefore it is not unreasonable to look to this genus for other primitive characters. Secondly, *Mastixia*, like *Nyssa*, has an excellent fossil record, against which evolutionary concepts eventually may be tested.

FIELD AND HERBARIUM STUDIES

The author has made continual use of the Nyssaceae preserved in the Gray Herbarium and the herbaria of the Arnold Arboretum and the New England Botanical Club throughout the course of this investigation. *Nyssa* collections were also examined in the herbaria of the following institutions: the New York Botanical Garden; the Royal Botanic Gardens, Kew; the Indian Botanic Garden, Calcutta; and the U.S. National Museum. In addition, an important collection of *Nyssa javanica* specimens was sent on loan

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[1] The term "hermaphrodite" is used here to emphasize that both gynoecium and androecium are present; however the fertility of the androecium in these flowers has never been critically investigated. Judging from the material examined by the author, pollen is usually produced by hermaphrodite flowers of some Nyssaceae (e.g., *Camptotheca acuminata*), but in other species (*Nyssa aquatica, N. ogeche*) pollen is produced infrequently or not at all. In hermaphrodite flowers of *N. sylvatica* some anthers contain apparently normal pollen, and others are abortive.

from the Rijksherbarium, Leiden. The distribution maps presented in this paper are based on information obtained from these collections. It will be understood that the localities could not be plotted so precisely for Asiatic Nyssaceae as for the American species, since specimens collected in remote parts of Asia are often accompanied only by the collector's number, or by place-names known only locally. In the case of Chinese collections this difficulty was overcome by enlisting the aid of Dr. Shiu-ying Hu, who was able to establish approximate localities through her familiarity with the geography of China and with the travels of botanists who have collected there. For regions outside China, the *Times Atlas* and *Atlas van Tropisch Nederland* were consulted. Although a few of the localities still remain unknown to the author except in a general way, e.g., "North Burma" and "Tonkin," the ranges for Asiatic Nyssaceae as shown here are far more accurate than any previously available in the literature.

Fruits of all the American species of *Nyssa* were collected from living trees during a field trip conducted especially for that purpose in August, 1959. The trip included visits to the lower Apalachicola River in Florida, to the Okefenokee Swamp in Georgia, to the Dismal Swamp in Virginia, and to several other localities where *Nyssa* grows in abundance. Flowers and developing fruits of *N. sylvatica* and flowers of *Davidia involucrata* were collected in preservative at the Arnold Arboretum, and preserved flowers of some of the other species were graciously supplied by Drs. W. P. Adams, Clyde Connell, R. K. Godfrey, and Carroll E. Wood, Jr.

Research on *Nyssa* was interrupted during part of 1960–61 when the author accepted a foreign study fellowship in India; however the trip provided an unexpected opportunity to see *N. javanica* in one of its native habitats, the eastern Himalaya. Accordingly, in May of 1961, when the trees had come into flower, a visit was made to the Darjeeling Hills and specimens obtained were preserved in fixative. Mr. G. C. Sen, Curator of the Lloyd Botanic Garden, Darjeeling, gave assistance in planning this collecting trip; acknowledgment is gratefully extended to him. Acknowledgment is also due to the authorities of the various herbaria for the loan of specimens and facilities, and to the Botany Department, University of South Carolina, for several courtesies.

SURVEY OF THE SPECIES

It seems advisable to discuss specific similarities and differences among the Nyssaceae before entering into a detailed descriptive treatment of their fruits. Information regarding the present distribution and habitat of each species is included as a possible aid in the interpretation of the fossil record. It will be seen that four of the species of *Nyssa* — *N. sylvatica*, *N. aquatica*, *N. ogeche*, and *N. javanica* — differ markedly from each other in many ways, including the appearance of their fruits; on the other hand, *N. sylvatica*, *N. sinensis*, and the putative species *N. biflora* and *N. ursina* are very similar, and it is not possible to assign an unattached fruit to any one of these species with certainty. Since the emphasis of this paper is on fruits, the latter group will be discussed under one heading, "the *Nyssa sylvatica* complex."

The Nyssa sylvatica Complex

NYSSA SYLVATICA Marshall. This common tree of the eastern United States is usually recognizable by its branching habit; most of the very crooked branches leave the trunk almost at right angles, sometimes giving the tree a pyramidal aspect when growing in the open. It frequently attains a height of more than 20 meters; the largest known living tree of this species is 85 feet[2] (Dixon, 1961), and even taller trees have been reported in the past (Anon., 1942). On the other hand, this species and other members of the genus can produce vigorous shoots from the roots and lower stem, resulting in shrubby growth and the formation of thickets. The leaves of *N. sylvatica*, like those of other species of *Nyssa*, are alternate, simple, pinnately-veined, estipulate, and commonly crowded at the ends of branches; they turn red in the fall, and for this reason *N. sylvatica* is sometimes planted as an ornamental tree. Leaf margins are almost always entire, but some leaves with a few coarse teeth may occur on any individual, and are fairly common on seedlings and sprouts. Papillae are often visible on the leaf surfaces, probably caused by the sclereids that are present within the mesophyll (Metcalfe and Chalk, 1950, p. 750). For further details regarding the vegetative parts of *N. sylvatica* and of other American nyssas, the reader is referred to the works of Rickett (1945) and Sargent (1893, 1922).

Flowers of *Nyssa* are first visible in the Arnold Arboretum during the latter part of May, when the young leaves are not yet fully developed. Certain trees bear staminate flowers in short racemes; others bear hermaphrodite flowers in clusters of two, three, or four on slender peduncles.

The range of *Nyssa sylvatica* includes all of the eastern United States from Kennebec County, Maine, south to Lake Okeechobee in Florida, west to the Brazos River in Texas, and north to the Great Lakes, where the species also occurs in the southern part of Canada (MAP 1). It is a familiar tree in the mixed mesophytic forest of the Appalachian Plateaus, the oldest and most complex type of deciduous forest in North America. In the Cumberland Mountains of eastern Kentucky, believed by Braun (1950) to be the region where the American mixed mesophytic forest is best developed, *N. sylvatica* is one of about 35 species comprising the canopy. *Nyssa* is scattered here and there throughout the region, a few individuals occurring in most stands regardless of exposure or altitude, yet contributing little to the total vegetative cover (Braun, p. 52–53). The species is typically one of "high presence-low cover" in other forested areas as well (see, for instance, Braun's tables, p. 139, 167, 246, etc.; also McIntosh, 1959); however, local concentrations of these trees may occasionally be found in unusually wet places (Baldwin, 1961).

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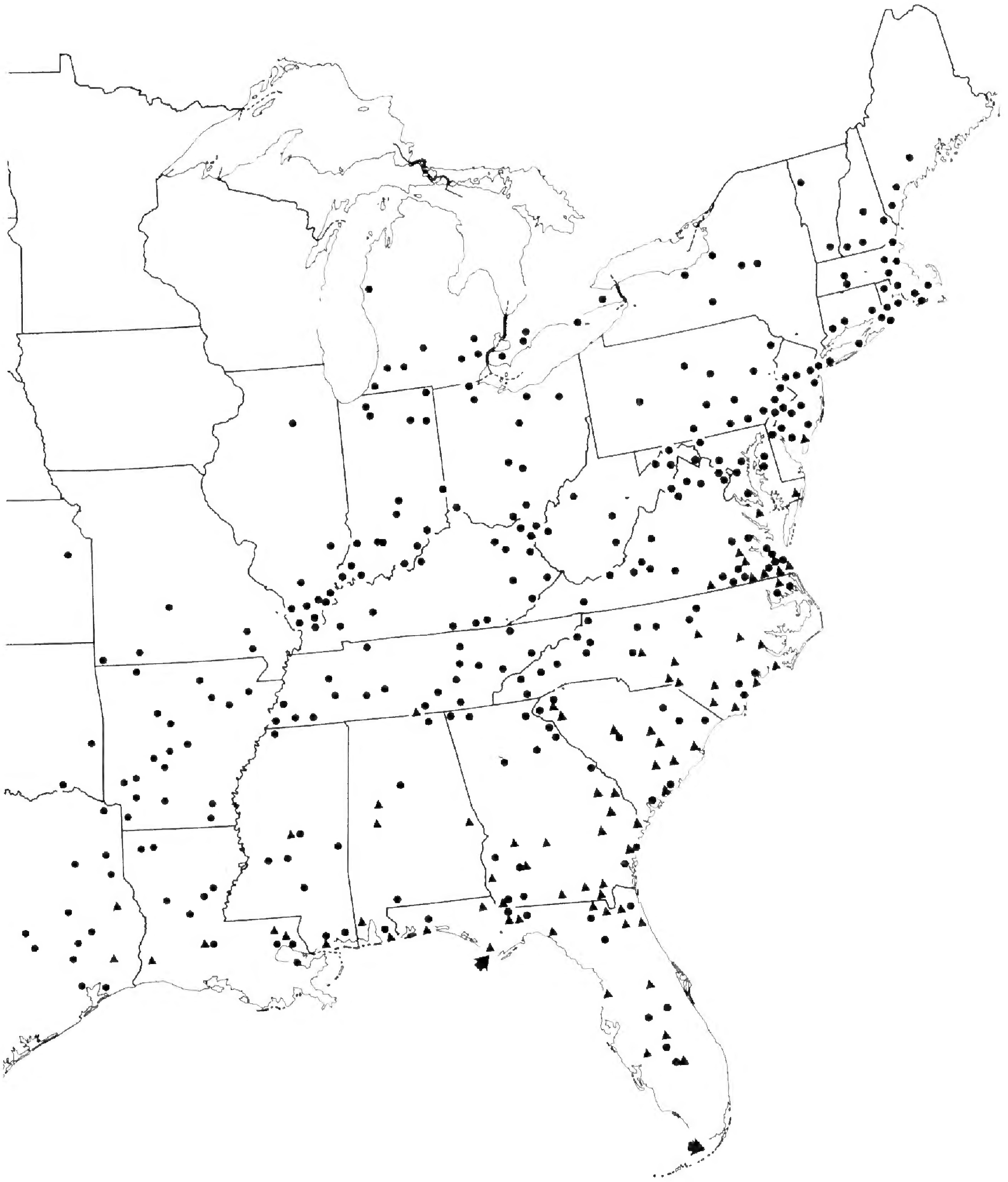
[2] English units of measurement will be used in this paper when necessary to preserve the reports of other authors, data from herbarium sheets, etc., in their original form.



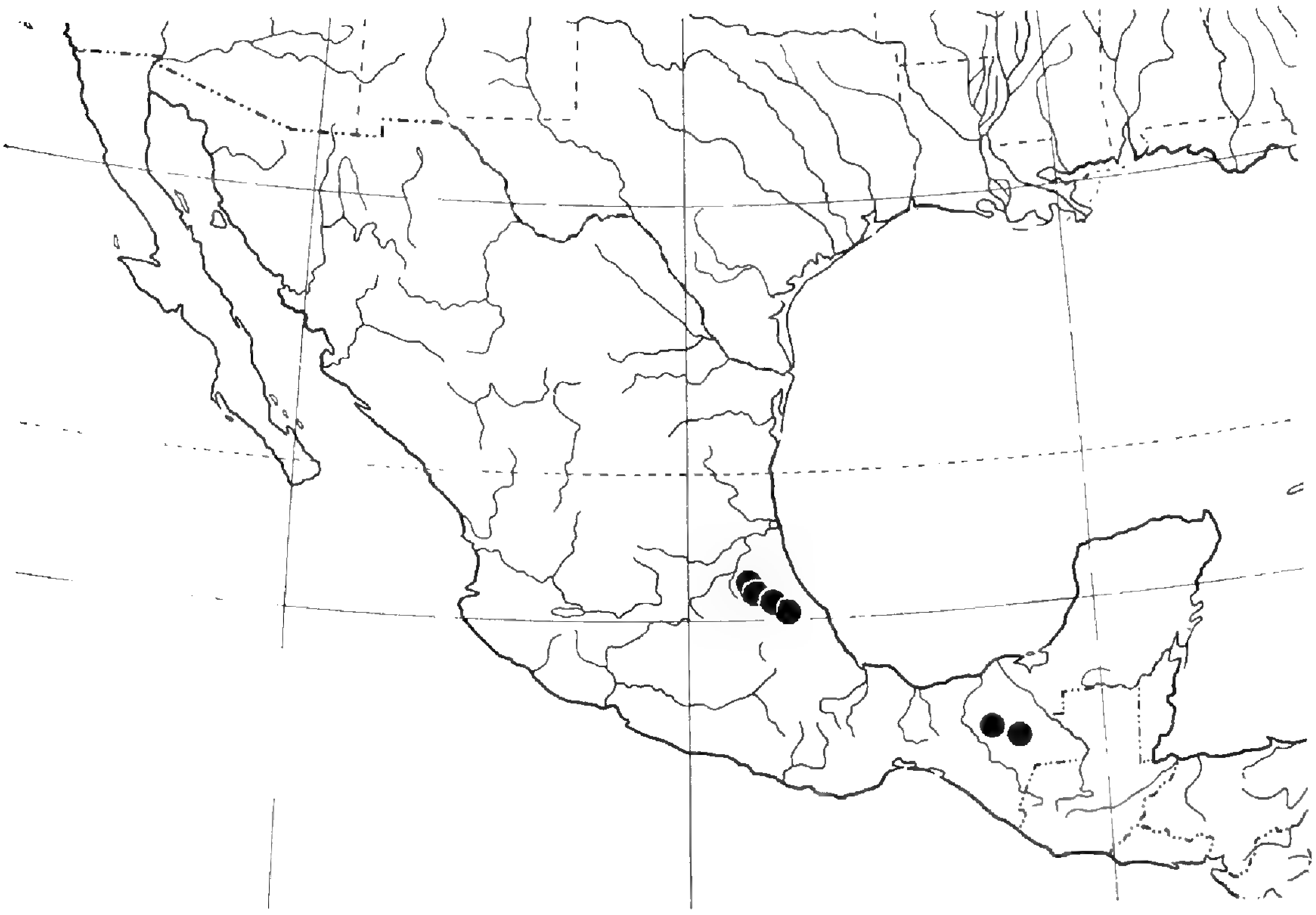
MAP 1. Distribution of the *Nyssa sylvatica* complex in U.S. and Canada. County records for *N. sylvatica* are represented by black circles, for *N. biflora* by triangles. Arrows show localities from which "*N. ursina*" has been collected.

The juicy ripe fruits of *Nyssa sylvatica* are very attractive to birds, which are probably the most important agents of dispersal. During the present investigations gnawed endocarps have been collected, suggesting that rodents may also participate in dispersing the species. Pollination is presumably effected for the most part by the hosts of bees and other insects that visit the flowers, but Wodehouse reports the collection of air-borne pollen about 500 feet from a tree (1935, p. 446).

In 1944 Miranda reported the first collections of *Nyssa sylvatica* in Mexico. In subsequent papers, Sharp and Hernandez X. (1945) and Miranda and Sharp (1950) described the localities in which *Nyssa* has been found. The sites are located in highlands of Hidalgo, Puebla, and Chiapas (Map 2), areas of considerable phytogeographical interest because they support a vegetation resembling that of the eastern United States yet containing elements with other geographical affinities. *Nyssa* has been collected here at altitudes up to 6200 feet, but it is most plentiful between 3300 and 5000 feet, where it is associated with *Liquidambar* in forests in which mixed species of *Quercus*, *Platanus lindeniana*, *Pinus strobus*, or *Liquidambar* may be dominant, depending upon the locality. In most of the Mexican sites, *N. sylvatica* is a tree in the upper layer of the forest, but in the vicinity of Huachinango, Puebla, it has been found only in the form of sprouts and small trees. Sharp and Hernandez X. suggest that this may be due either to periodic burning or to the activities of woodcutters.

In handling a large number of herbarium specimens of *Nyssa sylvatica* one becomes impressed with the great range of variability in the size and shape of the leaves. This amount of variation led Fernald (1935) to distinguish four varieties (var. *biflora* (Walt.) Sarg., var. *dilatata* Fern., var. *caroliniana* (Poir.) Fern., and var. *typica* which must now be called var. *sylvatica*). The author has attempted to recognize these varieties in the course of his herbarium studies and field work but has found it impractical because of the many intergradations and lack of clear geographical segregation to distinguish more than two — var. *sylvatica* and var. *biflora*.

In 1893 Sargent reduced *Nyssa biflora* Walt. to varietal rank under *N. sylvatica*, but in 1905 (Man. 709) he treated it as a distinct species. In



Map. 2. Distribution of *Nyssa sylvatica* in Mexico. Data from Sharp and Hernandez X. (1945). (Copyright, Goode Base Maps.)

many modern floras this practice is also followed, but Rehder, in his *Bibliography of Cultivated Trees and Shrubs* (p. 485), maintains *N. sylvatica* var. *biflora*. In the interest of brevity, the name *N. biflora* will be used throughout the present work, although the taxon is not considered equivalent in rank to *N. sylvatica* and its real status must remain somewhat uncertain until the results of more observations are evaluated.

NYSSA BIFLORA Walter. There are large numbers of trees of *Nyssa* growing in upland swamps and wet bottomlands of the Coastal Plain of the southeastern United States (MAP 1) that are clearly allied with *N. sylvatica* yet sufficiently different in some respects to be treated as a separate taxon, *N. biflora*. These trees are commonly found in great abundance in saturated soil and in standing water, where they often develop enlarged bases. Their leaves are smaller and more leathery than those of *N. sylvatica*,[3] and are of a different shape.

The leaf of *N. biflora* is commonly narrower in outline and more gradually tapered at the base, and sometimes more rounded at the apex as well. The fruiting peduncle is usually not so long as in *N. sylvatica*. *N. biflora* with fruits on long peduncles is not uncommon, and *N. sylvatica* with fruits on relatively short peduncles may be found. A difference in the number of hermaphrodite flowers borne on each peduncle is notable. In *N. sylvatica* two, three, or four flowers occur — a single flower is quite rare. In *N. biflora* although the number of flowers is usually two, as the name implies, solitary flowers are not unusual, and clusters of three may be found, but not clusters of four.

Trees of *Nyssa biflora* flourish in water of sufficient depth to discourage the growth of most other woody plants. *Taxodium* and sometimes *Nyssa aquatica* are associated with it within the swamp forest, but there are no other dominant trees, and the density of each of these species is extremely great. Pure stands of *N. biflora* may also occur, according to Hall and Penfound (1939) who described a virgin swamp forest of southeastern Louisiana in which only this species was important. The individual trees averaged 83 feet in height and were estimated to be 200 years old. In the shallower water at the edges of such swamps species of *Acer*, *Planera*, *Fraxinus*, *Salix*, *Quercus*, *Pinus*, *Magnolia*, *Ilex*, *Cyrilla*, *Zenobia*, and other genera may be found in association with *N. biflora*, depending upon local conditions (Wells, 1942; Penfound, 1952).

The different habitat occupied by *Nyssa biflora*, combined with the somewhat different range of variability in leaf and fruiting characters, mark it as something apart from *N. sylvatica*; however it is not always possible to assign individual plants to either taxon. There are numerous trees of *Nyssa* growing in more or less wet places of the Coastal Plain and adjacent regions bearing leaves intermediate in size and shape between the broad obovate form agreeing with *N. sylvatica* and the narrow oblanceolate form agreeing with *N. biflora*. Such trees may also bear fruits in clus-

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[3] Philpott (1956) has described the anatomical differences that accompany this difference in leaf shape and texture. For dimensions of *Nyssa* leaves, see Rickett (1945).

ters of two and three on stalks of varying length. This situation has led some workers to treat *N. biflora* in a rank below that of species. Rickett (1945) has preferred to treat both *N. biflora* and *N. sylvatica* as species, suggesting that hybridization occurs between the two. A satisfactory solution to this problem would require an intensive investigation of genetic [4] and environmental [5] factors. It is quite possible that an investigation of this kind would show that we are dealing with a stage in speciation, in which part of a very variable population has become adapted to a separate ecological niche, the swamp, but has not yet become entirely isolated from the older gene pool by the formation of reproductive barriers.

The problem of specific limits and distinctions within the *Nyssa sylvatica* complex is made even more intricate by the occurrence in western Florida of shrubby forms that are extreme in the small size, narrow elliptic shape, and leathery texture of their leaves. The fruits of these plants are frequently smaller and much more globular and fleshy than those usually encountered in *N. biflora,* and fruiting peduncles are the shortest in the genus. Hermaphrodite flowers are mostly in pairs, and staminate flowers are few on short peduncles. These shrubby nyssas were first discovered in swamps of the Apalachicola River delta by Small (1927), who described them as a new species, *N. ursina.* No additional localities for *N. ursina* were reported until quite recently, when Monachino and Leonard (1959, p. 184) found a specimen among some forty-year-old collections from the Florida Keys. Mr. Monachino kindly sent this material to the author for inspection. It is a fruiting specimen with fleshy fruits on short peduncles and small leathery leaves like those encountered on the Apalachicola delta.

A number of collections were made in the *Nyssa ursina* region as a part of the present investigation. The shrubby nyssas are very plentiful in standing water near the towns of Port St. Joe and Apalachicola, and they do, indeed, have a very different appearance from the tall trees of *N. biflora* found in virgin swamp forests. The most striking plants of all were seen growing in a bog with *Sarracenia* about two miles east of Overstreet, in Gulf County. These plants were very much branched, as if they had been pruned, and, although only about three feet tall, were in full fruit. In this locality the nyssas were clearly growing as separate plants; in many other localities the *Nyssa* growth was taller, 10 or 12 feet, and occurred in dense

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[4] *Nyssa* has never been a subject for genetic research, nor have the chromosomes been counted for any species save *N. sylvatica.* Dermen (1932) obtained a count of $2n = 44$ from root tips of this species at the Arnold Arboretum. As a matter of curiosity the author attempted to count the chromosomes in developing anthers of *N. biflora* supplied by R. K. Godfrey (*RKG 58248*). From the meiotic figures obtained, the chromosome number cannot be reported with any greater accuracy than $n = 22 \pm 1$.

[5] One might well wonder whether the morphological differences that distinguish *Nyssa biflora* from *N. sylvatica* could be brought about by the swamp environment rather than by genetic factors. The author was able to locate a fruiting *N. biflora* growing under cultivation on dry ground in the arboretum of Brookgreen Gardens in South Carolina. Although this tree reportedly had been grown from seed in the garden, it showed all of the *N. biflora* characteristics. One must infer that these characters are inherent.

thickets not easily separable as individuals. From the town of Apalachicola northward through Franklin County to Sumatra, Florida, nyssas with leaves intermediate between the extreme *N. ursina* form and the usual *N. biflora* form are in evidence; north of this transition zone there are full-sized plants of *N. biflora* and none referable to *N. ursina*.

Not all botanists who have observed the plants in the field are in agreement with Small's concept of *Nyssa ursina* as a distinct species. Professor R. K. Godfrey, of Florida State University, and Dr. W. P. Adams, now of DePauw University, have expressed the opinion in conversations with the author that the dwarfed, branching habit and the peculiarities of leaf form and peduncle length exhibited by *Nyssa* in the Apalachicola delta region are the result of periodic fires. The pruned appearance of the plants found growing near Overstreet does suggest that some factor, perhaps fire, has disrupted the normal apical growth of the branches. Moreover, the existence of intergradations between the extreme *N. ursina* characters and the usual *N. biflora* characters makes somewhat doubtful the concept of two separate species. It is relevant to add here that the globular drupes supposedly characteristic of *N. ursina* may occasionally be found elsewhere. Mr. Frank C. MacKeever collected such specimens from a tree on the island of Martha's Vineyard in Massachusetts and brought them to the attention of the author. The fruits on MacKeever's *MV 306* were quite plump and fleshy when collected, and they contain short, ovoid stones like those found in many fruits from the Apalachicola River delta; however, the fruiting peduncles and leaves of the Martha's Vineyard tree are those of *N. sylvatica*. Possibly globular fruits occur on *N. sylvatica* in other localities; the character is not readily detectable on dried herbarium specimens, which would account for the fact that such fruits have not previously been reported. Certainly a careful study of variation in *N. sylvatica* and *N. biflora* under different ecological conditions is needed before it will be possible to clarify the status of *N. ursina* satisfactorily.

NYSSA SINENSIS Oliver. The Chinese *Nyssa* is so similar in general vegetative and floral characteristics to *N. sylvatica* that its close relationship to the American species cannot be doubted. Notwithstanding, there are a number of morphological differences that clearly separate the two as distinct species. The Chinese species includes individuals with much larger leaves, often with more arcuate secondary nerves, than those usually produced by *N. sylvatica*. Young leaves, shoots, peduncles, and pedicels are more pubescent in the Chinese species, a condition which may persist into maturity. A dense pubescence is commonly noticeable on stalks of staminate inflorescences; less frequently so on fruiting peduncles and on petioles and midribs of leaves. Perhaps the most striking difference between *N. sinensis* and its American counterpart is in the occurrence of pedicels on the peduncles of hermaphrodite inflorescences; such structures are present only occasionally on American members of the *N. sylvatica* complex, but they are universal in the Chinese species. Where this character is most pronounced the pedicels are paired on the peduncle, suggesting that the inflorescence has originated from a dichotomous branching system. The young pedicel is subtended in most cases by a bract which is deciduous early in the development of the fruit, leaving a scar. Hermaphrodite flowers are mostly four to a cluster, and peduncles bearing five are found.[6] A further difference, of special interest in connection with the present work, is the common occurrence of two styles and a bilocular ovary in *N. sinensis*; the condition occurs only with great rarity in *N. sylvatica*.

Nyssa sinensis is widely distributed in hilly regions of the Yangtze Valley and in provinces of southern China. Specimens in the herbarium of the Arnold Arboretum and the Gray Herbarium have been collected from southern Kiangsu, southern Anhwei, northern Kiangsi, and eastern Szechuan; also from Kweichow, Hunan, Chekiang, Kwangsi, Kwangtung, Yunnan (MAP 3). According to Wang (1961, p. 123, 143), the species also occurs in western Szechuan and in southern Fukien, and Merrill (1938, p. 58) reported a specimen collected in the northern part of Tonkin (Vietnam). The westernmost collections so far have been made in the Shweli Valley of western Yunnan and in upper Burma. The Chinese species, like the nyssas of North America, may occur as tall trees (up to 30 m.) in the forest canopy or as shrubby growth along the banks of streams (Wilson, 1914; Hu, 1927).

MAP 3. China, showing distribution of *Nyssa sinensis*.

Throughout much of its range, *Nyssa sinensis* is a member of the crown layer of the Chinese mixed mesophytic forest, a forest formation described

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[6] Clusters containing five flowers are not plentiful in *Nyssa sinensis*, but they are certainly not so rare as in American members of the complex. In the course of inspecting a far greater number of American nyssas in the herbarium and in the field, only one five-flowered cluster was encountered. Wangerin's statement that the pistillate flowers of *N. sylvatica* occur in clusters of two to eight (1910, p. 9, 11), repeated by Rickett (1945), is in error.

in detail in a recent monograph by Wang (1961). The formation resembles the mixed mesophytic forest of eastern North America in that it contains a large number of species of deciduous broad-leaved trees belonging to distantly related families; further resemblances are the homogeneity of the forest over broad geographic areas and the lack of dominance of any one species or group of species; however there is a signal difference in the floristic richness of the two regions. As Wang has pointed out (p. 236–237), the American mixed mesophytic forest, interpreted as broadly as possible, contains no more than 30 genera of dominant trees; whereas its Asiatic counterpart contains more than 60, including all but three of the 30 American genera. This richest of all deciduous forests extends for 2000 kilometers along the lower and upper Yangtze Valley and its watersheds. In the lower Yangtze Valley, a region of intense cultivation, remnants of the natural forest are found only in certain protected areas. (This explains the clustering of collection localities at some places on MAP 3.) There the mixed mesophytic formation covers the mountain slopes from altitudes of 500 to 1500 meters. The upper Yangtze region is one of higher elevations, in which the zone of deciduous forest is usually restricted to levels above 1500 meters, where it lies below a higher coniferous forest; at lower levels in this region, the constituents of the deciduous forest are mixed with evergreen broad-leaved trees (Wang, p. 120). It was within the upper Yangtze mixed mesophytic forest that living *Metasequoia* was discovered, and *N. sinensis* was one of the many deciduous broad-leaved trees found in association with this "living fossil" (Chu and Cooper, 1950). The Tsinling mountain range marks the northern limit of the mixed mesophytic forest and the beginning of a forest in which deciduous oaks predominate. To the south there is no boundary of any kind; deciduous trees become more and more intermixed with evergreen broad-leaved trees at increasing distances from the Yangtze Valley, until the evergreen trees predominate. It may be added that the Asiatic mixed mesophytic forest is also found in parts of Korea and Japan; however, *N. sinensis* has never been reported from either of these countries.

Collections of *Nyssa sinensis* have been obtained from several localities in the predominantly evergreen forest that lies to the south of the Chinese mixed mesophytic forest. This is a subtropical forest, dominated by evergreen species of *Castanopsis*, *Quercus*, and *Pasania*, along with *Schima* and lauraceous trees. The average temperature is not below five degrees Centigrade for any month, and no month is without rain. Total annual rainfall is 1300–1900 mm., somewhat higher than in the mixed mesophytic forest. Elevations are higher and conditions slightly more temperate in the areas where *Nyssa* and other deciduous trees are found as minor constituents (Wang, p. 142–146).

It is of considerable interest to compare the climatic conditions to which the Chinese nyssas and their New World counterparts are subjected. There are, as one would expect, numerous resemblances between the climate of the mixed mesophytic forest region of Asia and the climate of the equivalent North American forest region, but nowhere is the Chinese species exposed to the rigorous winters endured by *Nyssa sylvatica* in the northeastern United States. Furthermore, the growing season is much shorter in the heart of the American mixed mesophytic forest than in similar forest areas of China. The growing season in the Cumberland Mountains of Kentucky is about 180 days (U.S. Dep. Agr. Yearbook, 1941); whereas there are 230–280 frost-free days in the Chinese mixed mesophytic forest (Wang, p. 96). This fact accounts, at least in part, for the greater richness of the Chinese forest. Climatic conditions at the southern part of the range of *N. sinensis* may be compared with those prevailing in parts of Florida and in the highlands of eastern Mexico, the two southernmost regions in the range of *N. sylvatica.*

Perhaps at some future date it will be possible to test the success of the Chinese *Nyssa* in our American climate, but at present there seem to be no trees of this species in the United States. It has, however, been introduced into England at least twice. There are references in the literature to a single plant grown in Veitch's nursery at Coombe Wood from seed sent in 1902 by E. H. Wilson (Bean, 1950). Evidently this plant is no longer in existence; however there is a small *N. sinensis* now growing behind the arboretum office at the Royal Botanic Gardens, Kew, introduced as seed sent from Nanking in 1935. This plant, set outdoors in 1960, seemed to have endured its first winter fairly well at the time the author inspected the plant in early June, 1961. It bore a few staminate flowers, but was only about eight feet high and the expanded leaves were not as big as those usually seen on herbarium specimens of *N. sinensis.* The leaves of this species, like those of *N. sylvatica,* turn red in the fall.

Other Species of Nyssa

There are three other species of *Nyssa* — *N. javanica, N. aquatica,* and *N. ogeche* — in which close interspecific affinity is not evident.

NYSSA JAVANICA (Blume) Wangerin. This is the only species of *Nyssa* in which both hermaphrodite flowers and staminate flowers are borne in capitate clusters. Staminate flowers are numerous, and each is on a pubescent pedicel subtended at its base by three small bracts.[7] Hermaphrodite flowers are sessile and fewer in each head, but similarly associated with basal bracts. Branched inflorescences, with heads on each of two or three branches, occur occasionally in *N. javanica* but in no other species of *Nyssa.* The leaves are more leathery than those of *N. sinensis,* and they often develop a prominent "drip-tip." A distinguishing feature of *N. javanica* to be given special attention in this paper is the relatively smooth surface of the woody endocarp in contrast to the ribbed or winged stones found in the fruits of other members of the genus. Two styles are present,

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[7] Some authors refer to "a bract and two bracteoles"; however a thorough comparative morphological study of the nyssaceous inflorescence has not yet been undertaken; therefore the present author prefers to use "bract" as a general term for all these subtending appendages, regardless of their apparent rank.

but one or both may be broken off from herbarium specimens. As a result, the styles were formerly described as solitary. When the first intact specimens were encountered, they were described as a new species, *N. bifida* Craib. This species was later treated as a synonym of *N. javanica* in Wasscher's (1935) revision of *Nyssa* in the Netherlands Indies. Other synonyms of *N. javanica* are *N. sessiliflora* Hook. f. & Thoms. and *N. arborea* Koord. Further details of description and synonymy may be found in Wangerin's monograph (1910) and in Wasscher's revision (1935, 1948).

Prior to the publication of Wasscher's treatment, Parker (1929) attempted to separate the Indian nyssas into three species. His distinction between *N. javanica* and *N. bifida* is no longer tenable, but special interest attaches to his *N. megacarpa*. This name was based on three specimens, one bearing extremely large fruits (*Parker 2308*, collected "on Nwalabo at 1050 m.," Tavoy District, Burma). The species was said to differ from "*N. bifida*" not only in the size of fruits, but in the relatively glabrous appearance of the underside of the leaf and the fewer number of lateral nerves; a very slight difference in the length of staminate pedicels was also mentioned. All of these supposed specific differences described by Parker are well within the range of variation for *N. javanica*, except for the size of the fruits on his Tavoy specimen. With regard to the shape and markings of the endocarp and the outward appearance of the skin, these fruits are like any *N. javanica* fruits, but they are at least twice as large as most, and more than three times as large as some. Unquestionably they are the most massive modern *Nyssa* fruits that are known, and are the basis of references which have sometimes been made to "*Nyssa megacarpa*" in papers dealing with large fossil fruits of Nyssaceae. It would be more correct if reference were made instead to "*Parker 2308*" in order not to obscure the fact that the unusually large fruits were all taken from one tree.[8]

Parker was not the first to observe that some fruits of the *Nyssa javanica* type are larger than others. Koorders and Valeton (1900; p. 98, 101) reported that there were among the fruiting specimens of "*N. sessiliflora*" collected by Koorders at Takoka, in Java, a few that bore fruits of twice the usual size. Koorders and Valeton explained that the large-fruited specimens and the more plentiful small-fruited specimens were indistinguishable with regard to their foliar characters; otherwise they might have been treated as distinct species. Perhaps future botanical investigation based on larger collections will permit the confident recognition of varieties or even closely related species within the complex now known as

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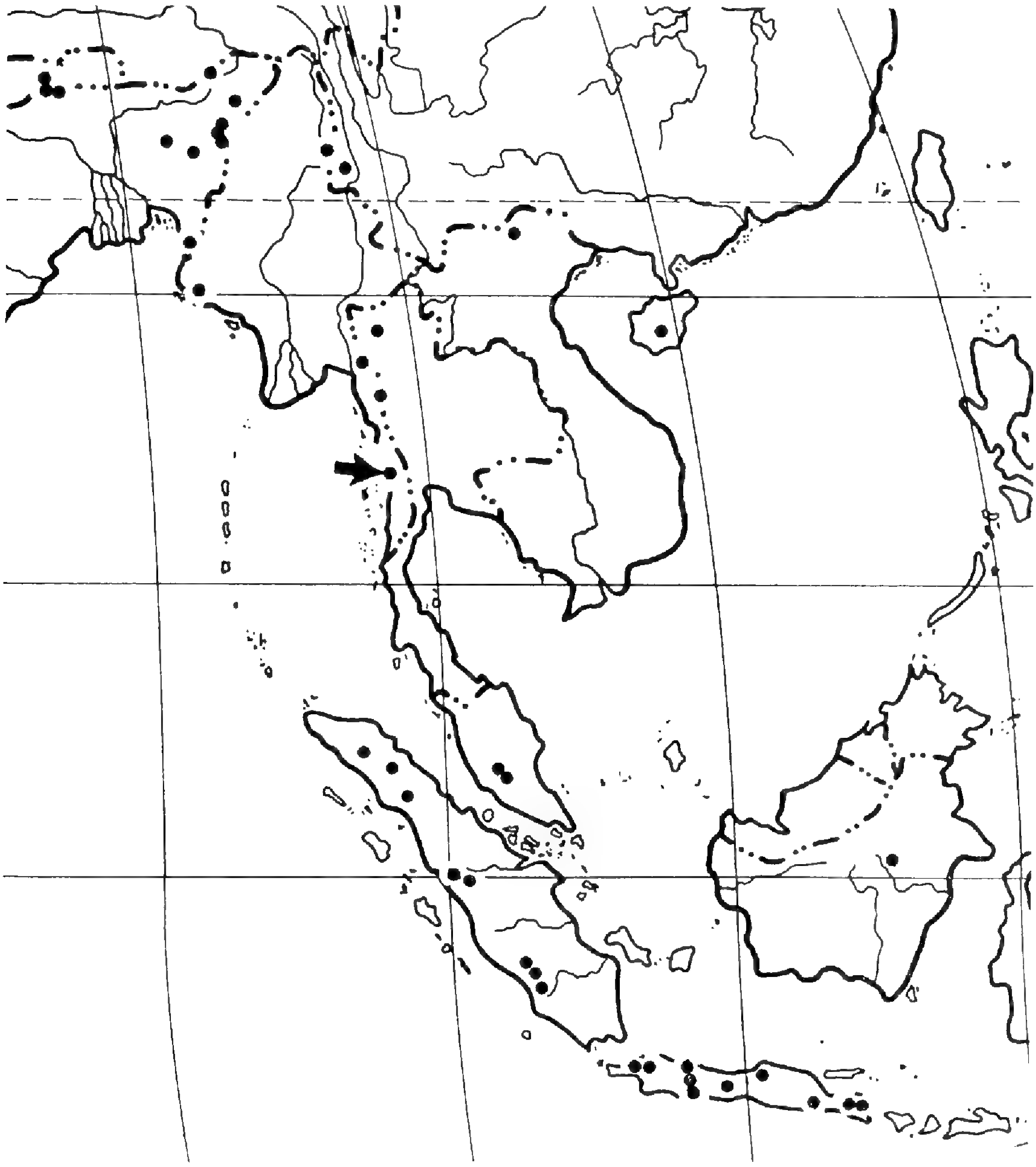
[8] There are duplicates of *Parker 2308* in the Kew herbarium and in the herbarium of the Arnold Arboretum. One of two fruits accompanying the Kew sheet was removed for study by Kirchheimer, and photographs of the endocarp appear in some of his publications (1943, 1957). There were three additional fruits with the Arnold Arboretum sheet, the endocarp from one of which is now in the paleobotanical collection of Harvard University. The two other specimens cited by Parker in his description of *Nyssa megacarpa* (*Lace 4634, Kurz 1562*) are staminate flowering branches.

N. javanica; for the present, however, it seems preferable to deal with *N. javanica* as one very variable species.

Within the monsoon region, *Nyssa javanica* is widely distributed (MAP 4). Tall trees (reported up to 40 meters) of this species are found in wet montane forests of Sikkim, northern Bengal, and Assam; westward into Yunnan, Kwangsi and Hainan; and southward through mountainous parts of Burma, Thailand, Malaya, Borneo, Sumatra, and Java; thus *N. javanica* is the only species in the family to reach the equator. Herbarium labels indicate that the species can occur at a wide range of altitudes. Koorders and Valeton (1900) stated that it could be found all over Java at elevations of 700–1300 meters, but they reported some localities as low as 100 meters. Collections from the eastern Himalaya are often



MAP 4. Distribution of *Nyssa javanica*. Arrow indicates locality where "*N. megacarpa*" was collected. (Copyright 1939, Goode Base Maps.)

taken from levels of 1500–2000 meters. Throughout its range this species grows under conditions of high humidity and very high seasonal rainfall to which other species of *Nyssa* are not exposed. Bor (1938) described a forested region just east of Bhutan in which *N. javanica* is present. He listed *Nyssa* as a dominant member of a *"Phoebe-Beilschmiedia-Engelhardtia* formation," a type of evergreen subtropical forest with numerous lauraceous trees, occupying elevations of 1200–2000 meters between a lower tropical forest and a higher temperate forest. Bor estimated the annual rainfall at this level to be 4000–5000 mm. (p. 134). Temperatures are said to be equable and humidity high; "frost is not unknown." Cowan (1929) described similar wet subtropical forests near Sikkim where *N. javanica* is associated with *Engelhardtia*, *Castanopsis*, *Schima*, *Betula*, and many other trees.

Trees of this species were examined by the author in a forest near Darjeeling, West Bengal. At an altitude of about 1500 meters, *Nyssa javanica* was fairly common, but widely scattered, and the individual trees would have been quite difficult to locate except for their lustrous, light green foliage, occasionally tinged with red, that set them off from other, darker canopy trees. Although the blades were fully expanded, it is likely that these leaves were still relatively new; this species, unlike most of its forest associates, undergoes a brief seasonal loss of foliage even in the southern part of its range (Koorders and Valeton, 1900). The crowns were high up on straight clean boles, making the collection of specimens rather difficult. Many of the upper branches left the trunks almost at right angles, reminiscent of *N. sylvatica*; the trees also resembled *N. sylvatica* in the appearance of the bark, which was light gray in color and divided into patches by numerous cracks, and in the frequent growth of sprouts from the bases of trunks. According to Gamble (1902), this species was once "in considerable use" in the Darjeeling Hills as a building timber; however the native collector who accompanied the present author asserted that it has no value now except as firewood and as "grass for cows" (i.e., branches are lopped off, and the foliage fed to domestic animals).

NYSSA AQUATICA Linnaeus. This is a very well-marked species, easily distinguishable from other nyssas by means of floral and foliar characters. The leaves are larger than those of the *Nyssa sylvatica* complex and there are coarse, mucronate teeth irregularly distributed along many of the leaf margins, a character not nearly so common in other American nyssas, and rarely, if ever, seen in the Asiatic species. Staminate flowers are in heads and hermaphrodite flowers are solitary. The hermaphrodite flowers develop into fruits differing in certain respects from any others in the genus, a matter to be taken up later in this paper.

In its distribution and habitat, *Nyssa aquatica* (MAP 5) is very similar to *N. biflora*. The two species frequently occur together in swampy regions of the Coastal Plain as far north as the Dismal Swamp in Virginia. *Nyssa aquatica* is the more common of the two, however, on the flooded alluvial plains of the Mississippi River, its major tributaries, and other southeastern rivers. *N. biflora* is more characteristic of acid coastal "pinelands" (Braun, 1950; Penfound, 1952). Applequist (1959b) has studied statistically the relationship between soil and site factors and the growth of both species. Forests composed almost entirely of *N. aquatica* are not unknown (Penfound and Hall, 1939), but more often *Taxodium* is present as a major associate. Although the trees thrive in standing water, it has been shown that periodic droughts are necessary for the continuation of this type of forest; seeds of *Nyssa* and *Taxodium* may survive long periods of submergence (Applequist, 1959a), but germination does not occur, nor are seedlings established, under water (Shunk, 1939; Demaree, 1932).

With a maximum height of 110 feet (Dixon, 1961), *Nyssa aquatica* is the tallest of American species of the genus. In dense stands the trunks are clear for two-thirds their height, and the crowns are quite narrow. In standing water these trees may develop a peculiar arching root growth as well as swollen bases.

NYSSA OGECHE Marshall. Although *Nyssa ogeche* has several characters in common with *N. aquatica* — relatively large leaves, capitate staminate inflorescences, solitary hermaphrodite flowers, and the swamp habitat — the two are easily separable in either the flowering or fruiting condition. The flowers of *N. ogeche* are covered with a dense tomentum and the fruits are borne on very short hairy peduncles. Leaves of this species are perhaps the most variable in the genus. On a single herbarium sheet one may find broad leaves oval to elliptic in outline, along with narrow oblanceolate leaves, and others with somewhat cordate bases. The leaf margins are usually entire, but the narrower leaves are sometimes toothed, especially on sprouts, which are very plentiful in this species. Leaves with tapering bases and rounded mucronate apices are perhaps most common. The hairy covering on young leaves is longer persistent in *N. ogeche* than in other species, and the underside of a mature leaf usually bears numerous unbranched trichomes, particularly along the midveins.

Nyssa ogeche, limited in distribution to eastern Georgia, northern Florida, and the southernmost part of South Carolina[9] (MAP 5), has by far the most restricted range of any firmly established species of *Nyssa.* Within this limited geographical area, the species is locally abundant, appearing in swamps and along streams in the form of small trees less than 10 meters high, the smallest in the family, or shrubs with several stems. *Nyssa ogeche* is commonly associated with *Taxodium* and with *N. biflora,* but not so often with *N. aquatica.* The reason for this has not been established; however Oertel (1934) presented some data indicating that *N. aquatica* is often found in less acid soils than the other aquatic nyssas. Along the banks of the lower Chipola and Apalachicola rivers, the growth of *N. ogeche* is sufficiently dense to provide a major source of nectar to commercial apiaries, even though the flowering season for this species lasts no more than two weeks (Wood, 1958; Rahmlow, 1960a, 1960b). Because of the

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[9] In addition, the U.S. National Herbarium has one specimen collected at Mobile, Ala., by C. Mohr (*s.n.*) in 1890.

value of this species to beekeepers, the Agricultural Extension Service of the State of Florida has, in recent years, encouraged the planting of thousands of seedlings at appropriate sites in western Florida (personal communication from J. D. Haynie, Extension Apiculturist, Gainesville).

Comment must be made here regarding the name *Nyssa acuminata*, which Small (1903) applied to shrubby plants of coastal Georgia, believing them to be a different species from *N. ogeche*. Small listed the shrubby habit, narrower leaves, and smaller fruits of these plants as distinguishing characters. Later Eyles (1941) examined Small's collections of *N. acuminata* and compared them with other collections from the same general vicinity (between Warsaw and Townsend, McIntosh County) and from other parts of Georgia. As a result of these comparisons, Eyles concluded that Small's *N. acuminata* did not differ enough to be considered a species and that it might better be treated as a variety of *N. ogeche*. Small's type specimens were again examined as a part of the present study, and the problem of *N. acuminata* was kept in mind during the field work. At several places in western Florida shrubby growth agreeing in all characters with *N. acuminata* was found intermixed with and intergrading with trees of indisputable *N. ogeche*. Therefore, the author prefers to regard *N. acuminata* as falling within the range of variation of *N. ogeche*, rather than as a distinct entity.

Camptotheca and Davidia

Both of these genera were discovered by Father Armand David during his second major journey of exploration in China (1868 to 1870). The first collection of *Camptotheca* was made on Lu-Shan, in northern Kiangsi,[10] and *Davidia* was later found in western Szechuan. Only one species is maintained in each genus.

CAMPTOTHECA ACUMINATA Decaisne. The leaves of this species have entire margins and acuminate tips, and are very variable in size. Specimens can be found to match either *Nyssa sylvatica* or *N. aquatica* in dimensions and outline. The globular capitate inflorescences may be solitary, or there may be two to several on branching stalks. The distal head in the branching system is composed of hermaphrodite flowers and is the first to mature. Judging from the appearance of fruiting herbarium specimens, the other, proximal branches of the system drop off as fruits ripen at the distal end, leaving a single cluster of fruits attached to one crooked stalk. The heads are very dense with sometimes more than 50 flowers and a greater number of hairy bracts tightly crowded together. It is surprising that almost all the flowers in many of these heads set fruit. The flat elongated fruits, often described as subsamaroid, are in marked con-

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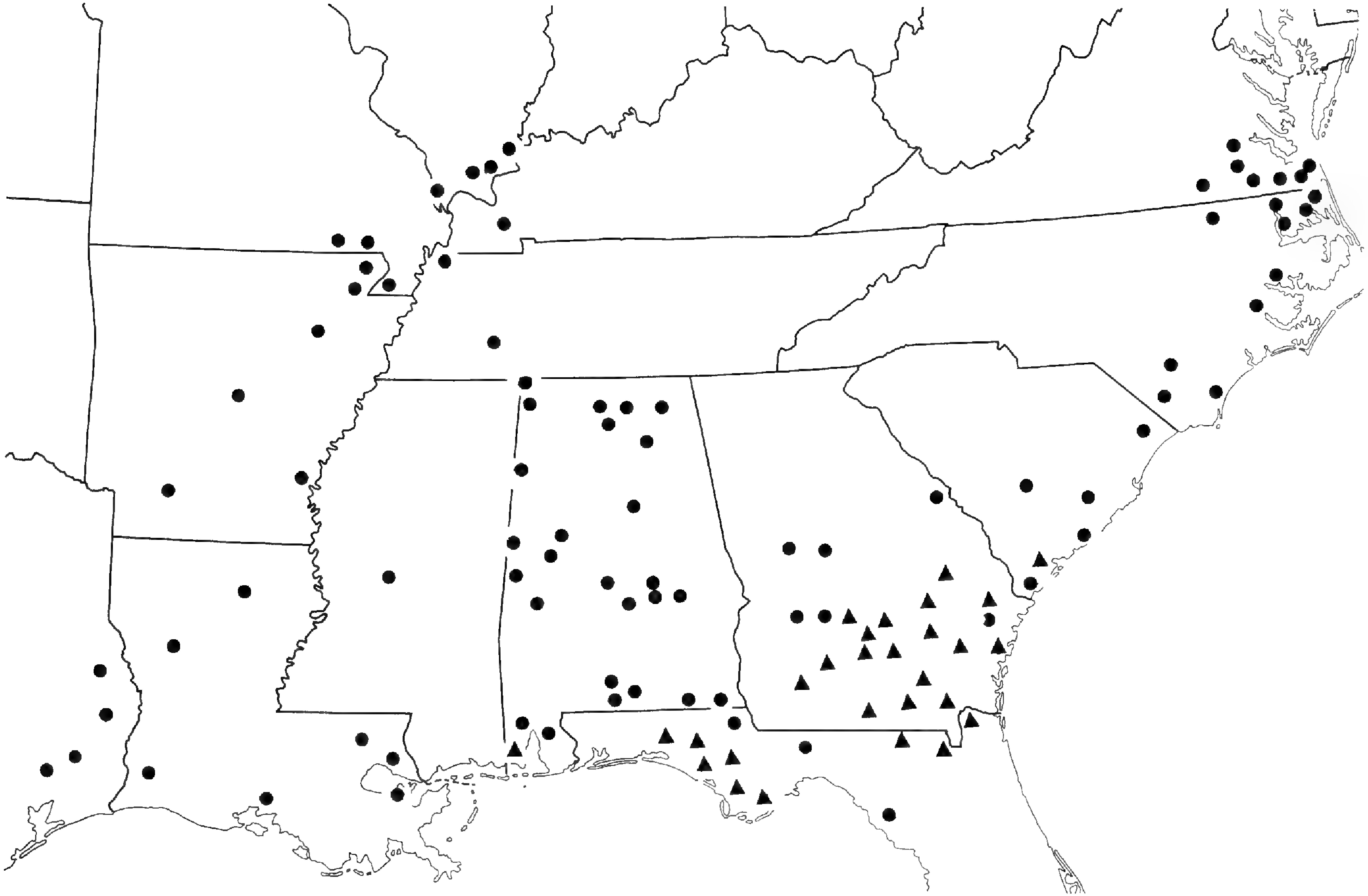
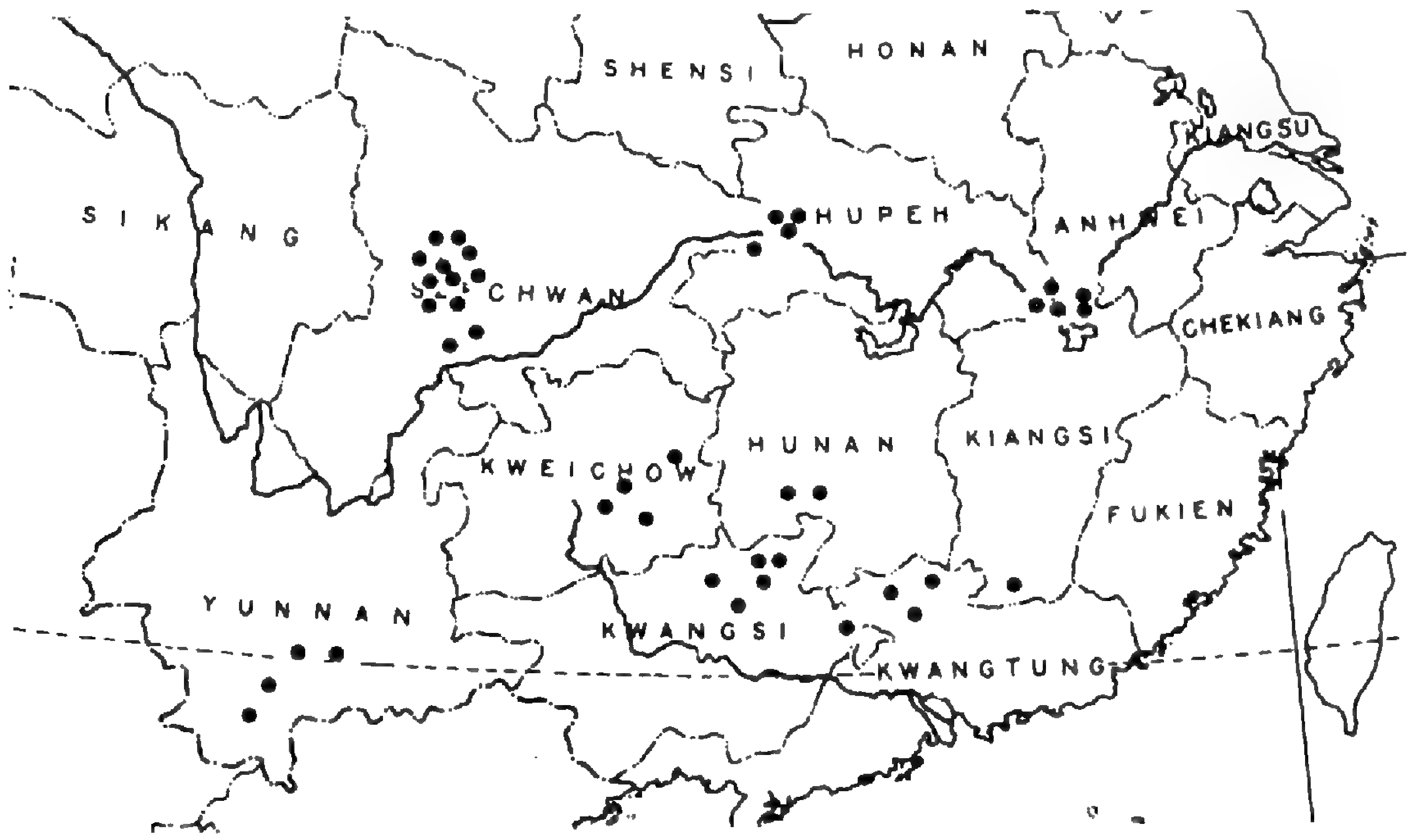
[10] In the original description of *Camptotheca*, Decaisne (Bull. Soc. Bot. Fr. 20: 157. 1873) gave Tibet as the type locality. This error was subsequently corrected by Franchet (Plantae Davidianae 1: 357. 1884), a correction that passed unnoticed by Harms (1898) and by Wangerin (1910).



MAP 5. Distribution of *Nyssa aquatica* (circles) and *N. ogeche* (triangles). Several Alabama localities for *N. aquatica* taken from Harper (1928, p. 284); all others based on author's herbarium studies.

trast to the oval fruits of other Nyssaceae. This character is used as a major distinction in keys to the family. Markedly conical anthers and the occurrence of three styles are other distinctive characters of *Camptotheca.*

Since Father David's first collection in Kiangsi, additional collections have been made in that province and in Hupeh, Szechuan, Kweichow, Hunan, Yunnan, Kwangsi, and Kwangtung (MAP 6). According to Wang (1961, p. 106), *Camptotheca* also occurs at Tientai-Shan in northern Chekiang, a locality from which *Nyssa sinensis* has been reported. A comparison of the distribution maps shows a great similarity in the geographic ranges of *N. sinensis* and *Camptotheca acuminata.* Wang (p. 237) has listed *Camptotheca* together with *Nyssa* as a constituent genus of the mixed mesophytic forest formation. However, notes on herbarium labels show that *Camptotheca* is generally restricted to lower altitudes than *N. sinensis.* In the Gray Herbarium and the herbarium of the Arnold Arboretum there are no specimens of the latter species for which an altitude below 500 meters has been noted; whereas collections of *C. acuminata* from levels below 500 meters are common. One may conclude from the data available that *Camptotheca* does not usually grow above 1000 meters except in Yunnan, where it may reach 1800 meters. Within this altitudinal range, it is found in wooded areas, sometimes attaining a height of 25 meters, or along open streams, frequently growing in thickets. Because of its rapid growth and regeneration, *Camptotheca* is widely planted in China beside irrigation ditches, and its branches are used for firewood (conversation with Dr. S.-Y. Hu). The Chinese also cultivate it as an ornamental (Steward, 1958).



MAP 6. China, showing distribution of *Camptotheca acuminata.*

DAVIDIA INVOLUCRATA Baillon. The foliage of *Davidia involucrata* bears little resemblance to that of other Nyssaceae. The leaves are cordate with serrate margins, long slender petioles, and prominently branching venation approaching the palmate condition. Pendulous flowering heads are produced on short lateral shoots along with a few leaves. These heads are solitary on long peduncles, on which there are also two (sometimes three) large, white, unequal bracts. The bracts, in contrast to the foliage leaves, are sessile, membranaceous, and most often without marginal teeth. An inflorescence is made up of numerous closely united staminate flowers, devoid of sepals and petals and giving the appearance of a single flower bearing hundreds of stamens. The stamens, purple in color and quite long, make a very striking display in combination with the white bracts. Solitary hermaphrodite flowers arise from otherwise staminate inflorescences. These flowers are of considerable importance to any comparative study of nyssaceous fruits because they retain an apparently primitive multilocular condition.

Although *Davidia* is also a genus of the mixed mesophytic forest formation, it is mostly confined to elevations of 1600–2500 meters and is consequently not found in the lower Yangtze region. In the upper Yangtze area it is sometimes locally abundant; Wang (1961, p. 112) describes a forest in eastern Szechuan in which *Davidia*, *Euptelea*, and *Fagus* are the most plentiful elements. *Davidia* has also been collected in western Szechuan and from localities in Hupeh, Kweichow, Sikang, and western Yunnan (MAP 7). In the latter province it reportedly reaches an altitude of 3000 meters. In its native habitat, *Davidia* grows to a height of 20 meters, with about 10 meters of clean trunk below the crown. (Cultivated in the open, it assumes an attractive pyramidal form.) When these trees are in bloom, the fluttering of their white bracts in the forest canopy is said to be an extremely attractive sight. E. H. Wilson, who on several occasions observed the flowering of *Davidia* in the Chinese forests, and who played the major role in its introduction to western gardens, wrote (1913): "To my mind *Davidia involucrata* is at once the most interesting and beautiful of all trees of the north-temperate flora."

The taxon *Davidia involucrata* var. *vilmoriniana* (Dode) Wangerin[11] includes those individuals bearing glabrous mature leaves, as distinguished from the hairy-leaved type originally collected by Father David. The typical variety and var. *vilmoriniana* have been observed growing together in the wild state (Bean, 1950), but the latter is said to be more hardy.

The Genus Mastixia

No attempt to deal with individual species of *Mastixia* Blume will be made here: systematically the genus is still not very well known, and some of the putative species have been collected only once or twice. Danser (1934) listed nine species in his revision of the Cornaceae of the Netherlands Indies; no doubt there are additional species growing in other parts of the *Mastixia* range, but the total number probably would not exceed 15.

Members of this genus are evergreen trees 10–35 meters tall with typical

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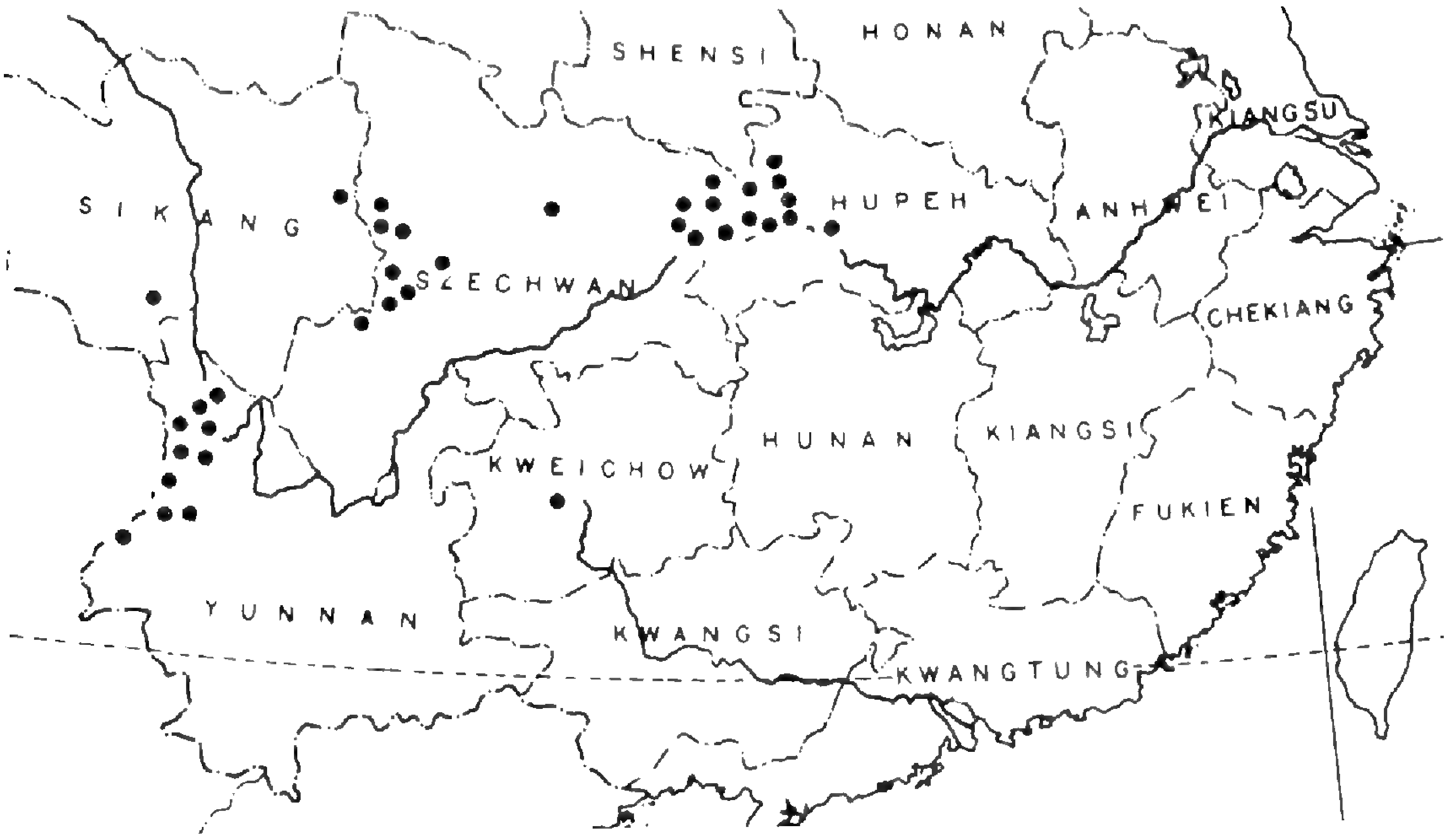
[11] This name has been cited "var. *vilmoriniana* (Dode) Hemsley" by most authors, but Wangerin's (1910) combination antedates Hemsley's (1912).



MAP 7. China, showing distribution of *Davidia involucrata*.

rain forest leaves — leathery blades, entire margins, and prominent acuminate tips. Both alternate and opposite arrangements are common, often on the same plant. The flowers are all hermaphrodite, borne in many-branched, often trichotomous, panicles with a bract at each node. The anatomy of the *Mastixia* stem is of special interest with respect to the phylogeny of the Umbellales: secretory canals are present in the pith, suggesting a relationship with the Araliaceae, and the vessel members are of a very primitive type.

The distribution of *Mastixia* has been discussed in detail by Kirchheimer. His map (1943, p. 17) of the range of this genus includes northern New Guinea, Indonesia, and the Philippine Islands; the southeast Asiatic mainland from Malaya north to Vietnam and the eastern Himalaya; also Ceylon and the southern part of the Indian peninsula. There are other localities of which Kirchheimer was not aware in the Solomon Islands (Merrill and Perry, 1940, p. 527); Yunnan (Merrill, 1937); and Hainan (Merrill and Chun, 1940, p. 153). Many of the collections have been made in wet tropical highlands at elevations up to 2000 meters (a comparison of collectors' notes reveals that some of these were found in the same forests with *Nyssa javanica*). Kirchheimer has pointed out, however, that some species of *Mastixia* are more characteristic of lowland rain forests, and that these species may be encountered near equatorial coasts as well as on higher ground; in this respect, *Mastixia* is unique among the Cornaceae.

MORPHOLOGY OF THE FRUITS

Laboratory Methods

Endocarps were prepared for gross examination by boiling in water or in dilute caustic soda to remove the outer fleshy layers of the fruit. Microtome sections were used for the finer observations. Before sectioning it was necessary to soften the woody tissues by soaking for a week or longer in hydrofluoric acid. The specimens were imbedded in celloidin (Mallinckrodt's "Parlodion") whenever it was desirable to include softer parts of the fruit in the sections. Procedures for imbedding in celloidin may be found in a paper by Wetmore (1932) and in standard manuals on microtechnique. Some of the fruits, especially those picked when not fully ripe, did not soften much, even after prolonged soaking in HF, and sections were cut with considerable difficulty; however such sections were adequate for the study of cellular arrangement and vascular patterns, even if they were not always as pleasing a subject for photographic presentation as one might have desired. Sections were cut at various thicknesses, depending upon the hardness of individual specimens, but most sections were cut at 20–30 μ. The celloidin method does not yield a continuous ribbon of serial sections; each slice must be handled separately, a rather laborious procedure; therefore complete series were maintained only for regions of particular interest within the fruit, such as the placental region. From other parts of the fruit only every third or fifth section was taken, depending upon the size and importance of the specimen. Staining with iron alum and hematoxylin was carried out in individual Syracuse watch glasses whenever necessary; frequently enough detail could be seen in sections of mature fruits without staining.

Initial observations on mature fruits raised morphological questions that could be answered only by examining younger material. Flowers of all species and young fruits of *Nyssa sylvatica* were dehydrated with a butyl alcohol series, imbedded in "Tissuemat," and sectioned on a rotary microtome. A number of different staining procedures were used but Popham's schedule for staining shoot apices (Popham *et al.*, 1948) yielded very pleasing results.

Flowers and young fruits were also studied after bleaching and clearing whole specimens. Sodium chlorite proved to be an effective bleaching agent (Barghoorn, 1948), and material treated with this compound could be cleared quite easily by transferring subsequently to water, chloral hydrate, alcohol, and finally xylene or toluene for appropriate intervals (Arnott, 1959). Vascular patterns in flowers were visible at low magnifications after this method had been applied; in developing fruits the extent of lignification of the endocarp could also be seen through the transparent outer fleshy layers. Flowers of some species had a dense coating of epidermal hairs that obstructed the view of internal features, and it was then necessary to tease the surface with a camel's-hair brush before any observations could be made. It was found that flowers could be imbedded in paraffin and sectioned in the usual manner even after clearing, and some of the specimens were studied by both of these methods.

Fruits of the Nyssa sylvatica Complex

The mature drupe of *Nyssa sylvatica* and closely related forms is blue-black in color and about one centimeter long. It is usually ovoid, but in unusual cases — e.g., the *N. ursina* fruit — it may become quite globular. At the apical end is a wrinkled pulvinate disk one to two millimeters in diameter, a scar in a depression at its center marking the former location of the style. Surrounding the disk is the calyx rim with five indistinct teeth. At the base of the fruit there are one to three inconspicuous hairy bracts, the largest of which is about a millimeter long; these remain attached to the peduncle when the fruit falls.

Removal of the outer fleshy layers of the drupe reveals a fibrous woody stone with 9 to 12 vascular bundles situated in longitudinal grooves, the areas between the bundles standing out as rounded ridges. The dorsal (abaxial) side is flattened, the ventral side convex when only one locule is present; bilocular endocarps are a little flattened on the dorsal side of each locule, with the lateral margins somewhat convex. There is one anatropous seed ventrally attached near the apex of each locule with its extrorse micropyle directed upward. The embryo is straight, and its radicle is directed toward the micropyle. During germination the rapidly elongating radicle ruptures the thin seed-coat and pushes open a triangular germination valve at the apical end of the endocarp.

Bilocular endocarps are extremely rare in American members of the complex. Kirchheimer found one, photographs of which appear in one of his papers (1948, *fig. 4b* & *c*), in a collection of 200 fruits from plants of *Nyssa sylvatica* escaped from cultivation in Germany. In a later publication (1957, p. 571), he stated that about two per cent of the endocarps of this species are bilocular, without offering any further explanation. In the opinion of the present author, bilocular endocarps of *N. sylvatica* are far less common than Kirchheimer's estimate would indicate. During this investigation, the bilocular condition was not found in mature fruits of any American members of the complex, even though hundreds were examined. The condition would not be difficult to detect, because bilocular endocarps are thicker and have two germination valves. Herbarium sheets were examined closely in a search for flowers with two styles — in *N. sinensis* this is an indication that two locules are present — but such flowers were found only twice during the entire study. In one case the flowers are obviously abnormal: the specimen (*Fernald & Long 11599*, GH) was found flowering in the vicinity of the Dismal Swamp, Virginia, on October 12th.[12] Its incompletely developed inflorescences bear several malformed flowers as well as some apparently normal ones with two styles. Clearing one of the better flowers from this specimen revealed a bilocular ovary. In *N. sinensis,* on the other hand, two styles accompanying bilocular ovaries are present in perhaps a third of the hermaphrodite flowers. These ovaries develop into bilocular fruits with two seeds; the author has not found a fruit of *N. sinensis* in which one of two ovules has failed to develop

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[12] The author has seen cases of late-summer flowering in the Okefenokee Swamp (*Nyssa biflora*), and within the shrubby *N. ursina* thickets of the Apalachicola River delta, where such flowering is not at all uncommon. However, in every instance observed by the author, only staminate plants were flowering; at the same time, fruits were maturing on adjacent hermaphrodite plants.

or in which one locule is notably larger than the other. Kirchheimer (1948, p. 94) stated that trilocular fruits are produced occasionally by *N. sinensis*; however trilocular fruits were not found either in this species or in any modern *Nyssa* during the present investigation. It is possible that Kirchheimer erred on this point.

Examination of herbarium specimens gives the impression that fruits of *Nyssa sinensis* and *N. biflora* (exclusive of *N. ursina*) are somewhat larger than those of *N. sylvatica*. In order to test the significance of apparent size differences, a large fruit was chosen from each of 44 dried *N. sylvatica* specimens in the herbarium and its length measured with vernier calipers. Similar measurements were obtained from 44 specimens of *N. biflora* and from 41 specimens (all of the mature fruiting specimens in the Harvard collections) of *N. sinensis*. Some of the difficulty involved in separating specimens of *N. sylvatica* from those of *N. biflora* was avoided by using only those specimens of *N. sylvatica* collected outside the *N. biflora* range. Thus the measurements include a geographical bias as well as a bias in favor of larger fruits. Only length measurements were taken, because measurements of breadth or thickness of whole fruits are of little value once the outer layers of the fruit wall have been pressed flat on herbarium sheets; and experience shows that the longer fruits are usually larger in other dimensions as well. The ranges in fruit-length for the three species were: *N. sinensis,* 8.0–14.2 mm.; *N. biflora,* 8.1–12.3 mm.; *N. sylvatica,* 7.5–12.8 mm. The respective means were 10.4 mm., 10.3 mm., and 9.6 mm. Application of the "*t*-test" showed that the mean measurements for *N. sinensis* and *N. biflora* each differed significantly from the *N. sylvatica* mean (*N. sylvatica* vs. *N. biflora,* $P = .05$; *N. sylvatica* vs. *N. sinensis,* $P = .01$). If one assumes that the selection of a single large fruit from each herbarium sheet yields a sample to some extent representative of the species, it may then be inferred from the data that the fruits of *N. sinensis* and *N. biflora* are, on the average, larger than those of *N. sylvatica*.

Fruits of the putative species *Nyssa ursina* are the smallest in the complex. These are mostly the same size (7.5–10 mm. long) as the smaller fruits of *N. sylvatica* and *N. biflora*.

SIZE OF ENDOCARPS. Removal of the fleshy outer wall and apical disk from a dried fruit reduces the length by about a millimeter. The longest apparently normal endocarp encountered in the complex came from a bilocular *Nyssa sinensis* fruit 14.2 mm. long; it measured 13.1 mm. after boiling and drying, with a breadth of 6.3 mm. in the plane of symmetry between the locules and a thickness of 5.3 mm. across the locules. Broader (up to 7.4 mm.) and thicker (5.5 mm.) endocarps have been found in both *N. sylvatica* and *N. biflora*. The smallest endocarp seen during the entire investigation came from *N. sylvatica* from Martha's Vineyard (*F. MacKeever MV306,* NEBC); it is 4.4 mm. long, 4.1 mm. wide, and 3.2 mm. thick. Some abnormally long and thin specimens were obtained from *N. biflora* collected in the Okefenokee Swamp (*A. Traverse 498,* GH); the dried fruits are 15 mm. in length with endocarps up to 14.3 mm. long and only 3 mm. thick.

Variation in stones of the *Nyssa sylvatica* complex is shown in PL. I, FIGS. 3 and 5.

HISTOLOGICAL OBSERVATIONS. Cross sections of a mature fruit reveal an outer thick-walled skin of six to ten cell layers separated from the woody stone by a much wider succulent zone of large, thin-walled cells. Sclereids, solitary or in clusters, are present in the transition region between these outer tissues. The transition between fleshy tissue and endocarp[13] is marked by a few layers of small cells that are rectangular in outline and not nearly so heavily lignified or thick-walled as the fibrous elements of the endocarp. In selected sections, and in sections of younger material (PL. III, FIG. 15), it may be seen that the fused vascular bundles supplying both carpels and epigynous floral appendages are within this transition region. It may be properly called a "zone of adnation," joining the carpellary (woody) tissues with the surrounding fleshy tissues of the hypanthium. The endocarp in the species of the *Nyssa sylvatica* complex (and in other species of *Nyssa*) is made up almost exclusively of thick-walled fibers, 200–700 μ in length and 15–25 μ in diameter, with very small lumina. In the immediate vicinity of vascular bundles these are elongated in the same direction as the vascular elements; otherwise, the outermost fibers are transversely oriented, forming a sinuous pattern in conformity with the alternately ridged and grooved surface of the stone. The innermost cell layer — the inner epidermis of the carpel — is composed of longitudinally elongated fibers which become separated in places during expansion of the fruit. Locally some of the fibers adjacent to (and derived from ?) the inner epidermis may also elongate longitudinally, but this phenomenon is mostly confined to the one layer of cells. Almost everywhere, throughout the length of the endocarp, the cell layers immediately external to the inner epidermis are made up of transverse fibers, circumferentially elongated in conformity with the outline of the locule. Between this circumlocular zone of transverse fibers and the less distinct zone of transverse fibers near the periphery of the endocarp, the elements are chaotically arranged. No order is discernible in the chaotic region, except that the fibers are often parallel within aggregates of 20 to more than 50 elements. Similar aggregates are found in the stones of all *Nyssa* species. When Kirchheimer stated (1938, p. 2) that there are "nests of stone-cells" within the *Nyssa* endocarp he probably had observed some of these aggregated fibers cut transversely; the present author has found no nests of

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[13] The terms "exocarp" and "mesocarp" have been avoided here in keeping with Esau's recommendation (1953, p. 578) that they be used only in cases where the fruit wall is made up entirely of carpellary tissues. On the other hand, a loose usage of "endocarp" seems justified, since "endocarp" is universally employed in paleobotanical literature as a synonym for the woody stone of *Nyssa*. Moreover, "endocarp" is sometimes a more suitable term than "stone": the inner layers of the fruit wall may be called "endocarp" at any stage of development, but the term "stone" is applicable only at maturity, when this tissue has become sclerified.

brachysclereids, either by sectioning or by macerating the stones. There are, however, some individual strands of crystalliferous parenchyma cells visible in younger material, and these become heavily lignified along with the fibers when the fruit matures.

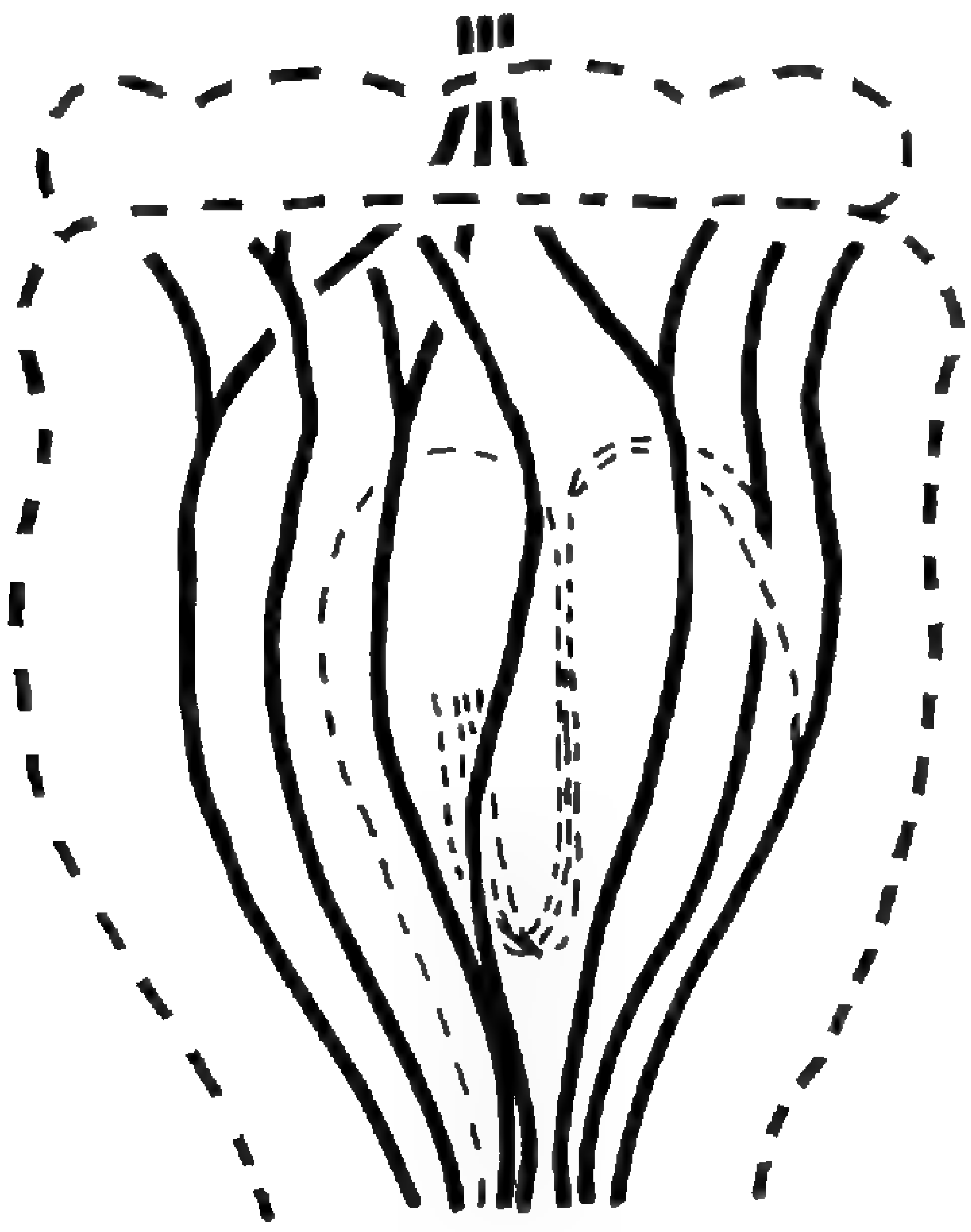
Orientation of elongating elements in a developing endocarp of *Nyssa sylvatica* may be seen in PL. IV, FIG. 20.

In transverse sections taken from the apical third of the fruit, the continuity of the fibrous tissue is interrupted by two narrow bands of smaller cells, somewhat rounded to elliptic in outline, marking the margins of the germination valve. These cells are neither as thick-walled nor as heavily lignified as the fibers, and they are very loosely united or even completely free from each other. Sections from a number of fruits show that the borders of the valve are completely free at maturity except for the cells of the adnation zone; these are easily ruptured during germination. It is possible to induce the germination valve to open in the laboratory by repeated boiling and drying. Subsequent microscopic examination of the valve margins reveals that the cells have been ruptured only in the outermost cell layers. The outer part of the margin has a ragged appearance after opening; whereas the inner part is relatively smooth. At its base the valve is continuous with the rest of the endocarp, but in this region transverse fibers are markedly predominant. The basal breaking of the valve during germination, consequently, occurs between fibers rather than across them.

The seed coat is thin and membranaceous, consisting of only a few crushed cell layers, all that remains of the thick integument to be seen in sections of flowers. In all nyssaceous species the cells in the outermost layer of the integument develop very thick, heavily lignified external walls that adhere tightly to the inner cells of the endocarp. The seed contains abundant endosperm tissue inclosing an embryo with well-developed cotyledons.

VASCULAR PATTERN. It is usually possible to identify the dorsal carpellary bundle of the endocarp with the unaided eye, for it occupies a prominent position in the center of the flattened dorsal side. Flanking this bundle, on either side, are two other bundles of similar size. The dorsal and its two flanking bundles lie closer together than most of the other bundles on the surface of the endocarp, and they are sometimes the only bundles to pass over the germination valve. This three-fold vascular pattern occurs often in Nyssaceae, making it possible to locate the dorsal side of the endocarp when other marks are not present, i.e., when the margins of the germination valve are hidden beneath the cell layers of the adnation zone and when dorsal flattening is not pronounced. Most of the details of the vascular system are no longer apparent once the endocarp has become woody. It is necessary, therefore, to examine flowers and developing fruits in order to understand the roles of the various bundles. In cleared preparations of very young specimens a ring of five vascular strands at the very base of the inferior ovary can be seen to branch at higher levels, to become the 8 to 10 bundles supplying, alternately, the petals and the calyx lobes. (Hermaphrodite flowers of the *Nyssa sylvatica* complex are pentamerous for the most part, but tetramerous specimens may be found.) Just below the distal margin of the hypanthium, a bundle supplying a sepal usually connects with a staminal bundle; however, the stamens frequently are fewer in number than the calyx lobes. The style contains three prominent strands. The median strand of these three stylar bundles is the dorsal carpellary bundle. The two lateral strands will be called ventral carpellary bundles in this paper, but it must be noted that the term "ventral" as used here does not necessarily indicate a connection with the ovular supply; it merely serves to designate the two major bundles that accompany the dorsal bundle into the style. In the present usage, "dorsal bundle" and "ventral bundle" will include both the basal part of the strand, where it is usually fused with a perianth bundle, and the apical part, where it is purely a carpellary bundle. Fusion of ventral bundles with the perianth supply is rather constant in the *N. sylvatica* complex, but the dorsal bundle occasionally is free of any connections along its entire length.

The ovular supply is visible within the ovary of a cleared flower taken at anthesis or later. A semidiagrammatic drawing of one such flower is shown in TEXT-FIG. 1. The stamens and petals have fallen away from the apical disk, and the long recurved style has broken off near its base. The ovary is viewed from its dorsal side, but it is turned a bit so that the ovular supply can be seen more clearly. The outline of the ovule is not visible and only seven of the perianth bundles are shown, the three bundles



TEXT-FIG. 1. Semidiagrammatic drawing of vascular system in cleared hermaphrodite flower of *Nyssa sylvatica*. External broken lines represent outline of hypanthium and disk; solid lines represent major vascular bundles; internal broken lines represent ovular supply. Further explained in text. See also PL. III, Figs. 14–16.

farthest from the viewer having been omitted for the sake of clarity. There is a perianth bundle on each side of the dorsal, separating it from the ventrals (in most specimens the dorsal is separated from at least one of the ventrals by *two* bundles). These are the two flanking bundles that often pass over the germination valve of the mature endocarp in close association with the dorsal bundle. The ovular vascular supply in this specimen is not connected with the stylar vascular supply. This is usually the case in unilocular flowers of the *Nyssa sylvatica* complex; in more mature ovaries the ventral bundles also will provide branches into the placenta, but instances in which the ventral carpellary bundles provide the earliest and strongest supply to the ovule are rare. Another notable point regarding the ovular supply can be seen: the strands from one side are connected with perianth bundles, but the bundle entering the ovule on the other side does not connect with any other strands. This is not due to an omission in the drawing; in most unilocular ovaries there is at least one strong ovular trace that extends from the base of the ovary to the ovule without being fused to the perianth supply. In the mature fruit, such a bundle will lie in a groove at the surface of the endocarp for most of its length, entering the endocarp wall at about the same level as the base of the germination valve (Pl. I, Fig. 4); hence, there are often more grooves and strands on the surface of the endocarp than there are perianth parts. When developing fruits are cleared just prior to thickening of the fibers, the ovular supply is even more complex; most of the perianth bundles — except the dorsal and its two flanking bundles — are connected with the placental region by one or more strands. These traces meet at the placenta and combine into one very strong strand which enters the integument and runs along the ventral side of the ovule to its base; there the strand separates into four or five anastomosing bundles that rise on the dorsal side of the ovule for more than half its length. At this advanced stage the vascular pattern of the ovary is further complicated by the appearance of additional weak bundles near the apex of the ovary; they are attached to the more ventrally situated perianth bundles and extend into the base of the style. These strands, ending blindly, could be interpreted as vestiges of the stylar supply of a second carpel.

Flowers with bilocular ovaries have two styles, each of which contains a dorsal and two ventral bundles. Each of the ventral traces has a common origin with the ventral from the other stylar branch; i.e., a pair of ventrals are fused at either side of the ovary, the two members of a pair belonging to different carpels. The fusion may be only at the base of the ovary, or it may extend for some distance, and the pairs of ventrals on opposite flanks of the ovary are usually not fused to the same degree. In addition, the carpellary bundles usually are fused to perianth bundles at the periphery of the developing endocarp. The two ovules are attached at either side of a septum — a partition in which the ventral portions of two carpels are united — that continues the length of the ovary. Two separate sets of ovular traces pass through the septum connecting the placentae with the ventral bundles and the one or two adjacent perianth bundles. The ovular traces are not connected with so many perianth bundles as in the unilocular ovary, and those peripheral bundles that do connect with the ovular supply usually connect with more than one ovular strand. It is notable that in bilocular fruits more of the ovular strands are connected with ventral carpellary bundles than is the case in unilocular fruits.

The word "usually" must be employed liberally in a description of the complex vascular system of these inferior ovaries. When a large number of cleared specimens are examined (about 50 were inspected in preparing this description) the variability is most impressive.

ORIGIN OF THE GERMINATION VALVE. This investigation did not include an exhaustive study of histological changes at various stages of development, but enough material was examined to obtain some understanding of the origin of the valve. The presence of this peculiar structure is apparently due to the interaction of two different patterns of growth in the endocarp tissue: (1) the tendency of cells in the vicinity of developing vascular bundles to elongate parallel to the bundles; (2) the transverse elongation of other cells, particularly near the inner epidermis and the adnation zone, as the ovary increases in diameter. The initial position of the valve margin is established by the first of these factors; the second factor accounts for its final form. Cross sections through young flowers show that the upper part of the endocarp already contains the entire ovular supply, at least in the form of prominent procambial strands. The strands run obliquely, sometimes almost transversely, from the ventrally and laterally situated perianth bundles into the placenta, and a great many of the developing fibers in this part of the endocarp elongate parallel to them. Since there are no ovular bundles connecting with the dorsal bundle and at least two of the bundles closest to it, the developing fibers on the dorsal side retain a predominantly transverse orientation. Between the ventral region, where obliquely oriented cells predominate, and the dorsal region, where transversely oriented cells predominate, is a narrow zone of cells that do not elongate, nor do they enlarge and become thick-walled along with the other cells of the endocarp. It is these cells that form the line of dehiscence at the edge of the germination valve. As the fruit wall increases in diameter, more growth takes place on the ventral side of the locule than on the dorsal (hence the bundles on the ventral surface of the mature unilocular endocarp are more widely spaced than the dorsally situated bundles), and the line of dehiscence comes to occupy a more dorsal position.

When developing fruits are cleared just before thickening of the fibers, which renders the endocarp opaque, the relationship between the ovular supply and the position of the germination valve is apparent. In such preparations the line of dehiscence is just visible, arising from the same level as the major ovular bundles and following a similar curved path to the apex of the endocarp. Another indication of the relationship between the ovular supply and the germination valve may be seen on the dorsal surface of the mature unilocular endocarp: on each side of the valve, the basal terminus of the line of dehiscence is usually contiguous to or closely associated with a bundle that is two bundles removed from the dorsal, i.e., a bundle that is adjacent to a flanking bundle; cross sections and cleared preparations of flowers show that this is commonly the most dorsally situated bundle with which an ovular bundle connects.

The basal terminus of the dehiscence line in bilocular endocarps is sometimes more closely associated with one of the flanking bundles. It may be that where there are fewer perianth bundles per ovule, the flanking bundles sometimes connect with ovular strands; bilocular fruits were not sectioned in sufficient number to verify this point.

Fruit of Nyssa javanica

It was not possible to examine fresh fruits of this species. Reportedly they are purple in color (Wasscher, 1948) and pleasantly acid to the taste (Koorders and Valeton, 1900). Corky spots are conspicuous on the dark-brown epidermis of dried specimens. The pulvinate disk has a pronounced stylar depression.

Cleaned endocarps are similar in shape to those of *Nyssa sylvatica*, but the apex is often more pointed, the outline of the germination valve is much more conspicuous, and above all, the surface is much smoother (Pl. II, Fig. 10). There are no vascular bundles attached to the dorsal surface, but a distinct median ridge is present at the apex of the germination valve. This ridge diminishes at the base of the valve, then reappears as a less distinct median ridge extending to the base of the endocarp. To either side of the median dorsal ridge, and separated from it by a shallow longitudinal depression, is an indistinct ridge. The three ridges occupy the same position on the surface of the endocarp as the three most dorsally situated bundles of *N. sylvatica* and other *Nyssa* species, therefore, they will be referred to as the dorsal ridge and two flanking ridges. Additional inconspicuous ridges sometimes occur on the ventral surface of the *N. javanica* stone, and occasionally a sharper ridge is present on one or both sides. A few weak vascular bundles are usually visible on the ventral surface which arise at the base of the sides and extend only part of the way to the apex. Rarely, they are heavier and divide the ventral surface at its base into a few broad rounded ribs.

The ovaries of *Nyssa javanica* are unilocular, although they bear two styles. The outline of the locule of a mature fruit (Pl. II, Fig. 11) coincides with the dorsal sculpturing of the stone: in the region below the valve there is a broad median dorsal groove flanked by two less conspicuous ridges; the ventral endocarp wall has a broad internal ridge, just opposite the dorsal groove. This is the only nyssaceous species in which internal sculpturing of the locule is evident.

The range in size of *Nyssa javanica* endocarps is very great. The smallest of 25 stones taken from 22 herbarium sheets measured 8.9 mm. in length, 6.2 mm. in breadth, and 4 mm. in the plane of symmetry; the largest was 17.8 mm. long, 10.9 mm. broad, and 6 mm. thick, the median length was

14.2 mm. These measurements do not include the remarkably large fruits collected by Parker (no. *2308*) in Burma: there are two of Parker's fruits in the herbarium of the Arnold Arboretum (and one in the paleobotanical collection of Harvard University), in the largest of which (PL. II, FIG. 10) the endocarp is 29.8 mm. long, 15.2 mm. broad, and 8.2 mm. thick.[14]

HISTOLOGICAL OBSERVATIONS. The histological composition of the fruit wall of *Nyssa javanica* differs in several respects from that of *N. sylvatica.* One difference is the greater abundance of stone cells in the outer fleshy layers of the *N. javanica* fruit, a character that can be seen very well in cleared preparations. A more important difference is the more limited extent of the fibrous tissue in the *N. javanica* fruits, i.e., the woody layers do not extend to the peripheral ring of fused vascular bundles that marks the transition between gynoecium and hypanthium. Instead, several of the outermost cell layers within this ring — layers of carpellary tissue — remain fleshy along with the noncarpellary tissues; therefore, the major bundles are surrounded by parenchyma, and they separate quite easily from the endocarp when it is cleaned. The outer zone of transversely elongated fibers forming the grooves and ridges of the *N. sylvatica* fruit is lacking in *N. javanica*; instead there are large quadrilateral thin-walled cells in the outer carpellary layers. The innermost of these, just adjacent to the stone, have somewhat thicker walls; in cross sections of herbarium specimens they do not appear so crushed and torn as the outer cells. All of the large quadrilateral cells come away from the fibrous layers when the fruit is boiled, leaving the smooth-surfaced stone that is characteristic of this species.

The innermost layers of the endocarp (PL. V, FIG. 23) are similar to the corresponding layers in *Nyssa sylvatica*; a single epidermal layer of longitudinally elongated fibers is visible in some regions, in others it is very much disrupted during circumferential growth of the fruit, and in sections taken below the germination valve a zone of tangentially elongated fibers lies just external to the inner epidermal layer. The fibers beyond this zone are not chaotic to the degree found in *N. sylvatica.* On the ventral side, longitudinal fibers predominate, and the dorsal wall is composed primarily of transverse fibers, many of them markedly radial in orientation. Corresponding fibers of the lateral walls are mostly oblique, as the transition is made from the radial trend to the longitudinal trend.

VASCULAR PATTERN. The flowers of *Nyssa javanica* are densely covered with hairs below the hypanthial margin, and it is necessary to remove this outer covering before the vascular system can be seen in cleared specimens. The arrangement of the bundles is very similar to that found in bilocular

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[14] Kirchheimer's statement (1957, p. 571) that the stones of "*Nyssa megacarpa*" are up to 40 mm. long and 20 mm. broad seems exaggerated; an illustration (p. 677, *fig. 13*) to which Kirchheimer refers is a photograph of an endocarp — supposedly shown about natural size — roughly 30 mm. long. Parker himself (1929) described these endocarps as 25 mm. long and 15 mm. broad.

flowers of *N. sinensis*, except that there is only one ovule and consequently only one set of ovular traces. Dorsal carpellary bundles for two carpels are present, the dorsal bundle of the missing carpel occurring on the placental side of the ovary. This "minor" dorsal is fused with a perianth bundle almost to the top of the hypanthium; whereas, the major dorsal — the one that will overlie the germination valve — is fused with a perianth bundle for only part of its length. The major ventrals are commonly fused for part or most of their length with the ventrals of the missing carpel, the combined ventrals in turn being fused with a perianth bundle. As in the *N. sylvatica* complex, adjacent ventrals occasionally are not united, in this case they may be fused with separate perianth bundles. They may also remain free to the base of the ovary. The ovule receives several strong strands from various bundles on the placental (missing carpel) side; these combine and then break up into a multitude of strands as they pass around the base of the ovule, rising high in the integument on the dorsal side.

The calyx lobes of *Nyssa javanica* are more developed than those of *N. sylvatica*, and they contain a broad vascular supply of short branches in contrast to a very vestigial supply in the latter species. The outermost lateral strands of one calyx lobe closely approximate those of adjacent lobes so that there is almost a complete circle of strands around the hypanthium apex.

The most interesting feature of the vascular system is its relationship with the dorsal ridges on the outer surface of the endocarp. Since the development of endocarp fibers does not extend into the outer layers of carpellary tissues, the position of the bundles at the carpel boundary does not influence the form of the stone in the same way as in *Nyssa sylvatica*. In fruits of the *N. sylvatica* complex the peripheral bundles and associated longitudinal fibers are sunken in grooves on the surface of the stone and the intervening areas stand out as ridges. On the other hand, a comparison of the *N. javanica* vascular pattern and the sculpturing of the stone shows that the external ridges in this species arise in the same radii as the dorsal bundle and its two flanking bundles.

Quite commonly there are a few bundles imbedded in grooves on the ventral or lateral surfaces of the *Nyssa javanica* stone, bundles which enter the ventral wall near the placenta (Pl. II, Fig. 10) or run along the sides to the stylar remnant. The variability in occurrence and location of such strands indicates that they are ovular and ventral bundles that have remained free of the perianth supply for all or most of their length; thus, they have been able to pass through the outer carpellary tissues and into the endocarp.

Fruit of Nyssa aquatica

The purple oblong to obovoid drupes of *Nyssa aquatica* are roughly 25–30 mm. long, about half as wide, and crowned by the flattened disk, the center of which is shallowly depressed. Frequently there is a marked constriction of the hypanthium just beneath the disk. Three to five long (5 to

10 mm.) hairy bracts subtend the hypanthium in very young specimens, but these fall away during fruit maturation.

Stones of this species are unilocular, obovate in outline, mucronate at the apex, and somewhat flattened (PL. I, FIGS. 1, 8). Each bears about 8 to 10 longitudinal ridges, which are very sharp and ragged-looking on the dorsal side, less so on the ventral. The major vascular bundles pass along the crests of these ridges; they are not so intimately connected with the endocarp as is the case in *Nyssa sylvatica*, and many of them are removed when the stone is cleaned. The region of the germination valve is depressed, and the flaring ventral margins of the valve are very much extended past the dorsal margins, indicating a much greater ventral than dorsal growth in the apical portion of the endocarp. The flaring ventral margins and a sharp apical point combine to give the valve of *N. aquatica* a distinctive appearance. When the fruit is boiled this distinctive appearance is enhanced because the dehiscence tissue frequently disintegrates leaving the stone agape. The endocarp wall, exclusive of the valve, is usually about 1200 μ thick in the depressed areas between the ridges; the valves are 700–900 μ thick.

The flesh was removed from more than a hundred fruits collected in Florida, South Carolina, and Georgia in order to estimate the variability in size of the endocarps. The largest of these was 28.3 mm. long, 11.2 mm. broad, and 6.5 mm. thick; the smallest, 14.8 mm. long, 9.4 mm. broad, and 4.9 mm. thick; median length, 21 mm. The length of the largest fruit is somewhat exaggerated, because it includes the woody apical "beak"; few stones are more than 26 mm. long when this projection is broken off.

HISTOLOGICAL OBSERVATIONS. The endocarp of *Nyssa aquatica* has a single inner epidermal layer of longitudinal fibers and an adjacent zone made up predominantly of tangential fibers, as in other *Nyssa* species (PL. V, FIG. 24). Elements external to the tangential zone are very disorderly, except where they extend radially toward the peripheral vascular bundles, thus forming the ridges on the surface of the stone. The sharp ridges on the endocarp of *N. aquatica*, like the less conspicuous dorsal ridges in *N. javanica*, arise in radial alignment with peripheral vascular bundles. *Nyssa aquatica* also resembles the Asiatic species because the outermost layers of carpellary tissue remain parenchymatous and do not take part in the formation of the woody endocarp. The latter similarity is best observed by comparing sections of young ovaries.

Transverse sections through the apical end of the fruit show the dehiscence tissue to be more plentiful here than in other species; no doubt this is related to the expansion of the ventral valve margins. It would be necessary for the dehiscence tissue to increase, to separate, or to elongate in order to accommodate the ventral expansion, and there is no indication that either separation or inordinate elongation has taken place. Sections through fruits that have been picked when full-grown but not completely ripe demonstrate the manner in which the dehiscence tissue matures: at this stage the endocarp is lignified almost throughout, except that the dehiscence tissue is still primarily parenchymatous; however, here and there isolated parenchyma cells have differentiated into very small sclereids. When the fruit is ripe, the dehiscence tissue will consist entirely of these sclereids, loosely aggregated and offering little resistance to the opening of the valve.

VASCULAR PATTERNS. In the mature fruit the positions of the dorsal and its two flanking bundles are very well marked by three prominent ridges. The flanking ridges usually connect with the basal termini of the line of dehiscence where they disappear; the dorsal ridge continues up the center of the valve. Cleared flowers show a vascular pattern similar to that of *Nyssa sylvatica* and *N. javanica*: a dorsal and two ventrals are usually fused to varying degrees with peripheral bundles that alternately supply four to seven corolla lobes and a lesser number of stamens. Corolla lobes in *N. aquatica* are the largest in the genus, and accordingly, they contain a more elaborately branched vascular supply. Occasional lobes have been found with a double vascular system, supplied by two heavy strands from the base of the ovary. There are 7 to 10 peripheral bundles arranged in a circle. In addition, when the dorsal or one of the ventral carpellaries is not fused with a peripheral bundle, it lies inside of this circle. The base of the solitary style receives, in addition to the usual three carpellary bundles, an extra strand or two from peripheral bundles on the placental side. These are, presumably, remnants of a lost carpel. Within the style the carpellary bundles ramify, forming numerous parallel strands. The ovular supply is similar to that of other *Nyssa* species in that most strands connect the placenta with peripheral bundles, but at least one independent ovular trace from the base is of common occurrence.

Fruit of Nyssa ogeche

The drupes of *Nyssa ogeche* are 20–35 mm. long, and, when not yet ripe, they somewhat resemble the fruits of *N. aquatica*. The disk, however, is usually more prominent and tends to retain the conical shape. Moreover, the fruit of *N. ogeche* is generally plumper, and corky spots are not so conspicuous. Ripe fruits are readily distinguished by their red color. The dense tomentum that covers the hypanthium is lost during development of the fruit except in the region immediately below the disk. Calyx lobes are not apparent, even in young material. The hairy, pointed basal bracts — usually three in number and much shorter than those of *N. aquatica* — abscise before maturity.

Stones of this species are very distinctive in appearance. They have about a dozen ridges, some of them very sharp, running longitudinally over the surface, with their crests extended radially as wide papery wings (PL. II, FIGS. 12, 13); 10–15 thick vascular strands lie in the grooves between these ridges. When the wings are removed the endocarp is seen to be quite narrow in comparison to that of other *Nyssa* species (PL. I, FIG. 2). Usually both ends are tapered and the apex is attenuated to a sharp point;

occasionally the upper end is broader and the stone oblanceolate in outline. A pronounced ventral convexity and dorsal concavity give the longer stones a boat-shaped appearance when viewed from the side; shorter stones are flattened on the dorsal side. The dorsal mid-line is marked by a groove — sometimes very deep and wide — instead of a ridge as in *N. aquatica*. The valve is acute, rather than acuminate, at the apex. It lacks the flaring ventral margins found in *N. aquatica*, but the most conspicuous ridges frequently occur near these margins, probably as a result of greater growth on the ventral side than on the dorsal. In some specimens there is a slight constriction at the base of the valve, and the stone then seems to bulge a bit above and below the constriction. Most endocarps inclose one locule, but one or two bilocular fruits can be found in every hundred. These are somewhat square in cross section, due to dorsal flattening on two faces. The wall is 600–1000 μ thick between the ridges, except along the center of the valve, where it may be 400 μ or less in thickness.

Endocarps of *Nyssa ogeche* vary considerably in their dimensions. (See PL. I, FIG. 2.) The longest encountered during this investigation measures 29.3 mm.; the shortest, 14.7 mm.; median length 23 mm. Specimens can be found as broad as 9.5 mm. and as narrow as 4.7 mm.; as thick as 7.5 mm. (bilocular) and as thin as 3.2 mm.

HISTOLOGICAL OBSERVATIONS. Except for its papery wings, the fruit of *Nyssa ogeche* resembles other *Nyssa* fruits, particularly those of the *N. sylvatica* complex, in histological composition. The endocarp has a distinct inner layer of epidermal fibers surrounded by a zone of tangential fibers. In the basal part of the fruit, tangential fibers predominate throughout the endocarp wall; higher up, the tangential zone is surrounded by a zone of fibers in which no order is distinguishable except for the radiation of the elements into the ridges. There seems to be some tendency for the outermost fibers to lie transversely and in conformity with the surface of the stone, but this tendency can be observed only in places where the ridges are not so sharp. The narrow transition region of slightly thickened cells resembles the adnation zone of *N. sylvatica*, except that the cells are larger (up to 200 μ long and 20 μ wide). Since the peripheral bundles are included within the transition, it follows that the succulent tissues are completely noncarpellary in *N. ogeche*, as in *N. sylvatica*. This transitional zone of adnation is histologically continuous with the somewhat longer, but otherwise similar, cells of the papery wings which extend radially from the ridges to the skin. The wings are three to eight cells in thickness. Morphologically they are not really a part of the endocarp; sections of flowers show that they are derived from cells of the succulent zone.

VASCULAR PATTERN. Since the corolla and the androecium are less reduced in *Nyssa ogeche* than in other *Nyssa* species, bundles supplying these parts are more numerous, and the vascular system is consequently the most complex in the genus. Five to ten short, rounded corolla lobes and seven to ten stamens (some of them imperfectly developed) are supplied by the peripheral ring of bundles. Within this ring there is a considerable cohesion and fusion of adjacent strands. It is notable that a few branches from each staminal bundle leave the main strand and enter the conical disk, demonstrating the androecial origin of that structure. Carpellary bundles are ordinarily fused with peripheral bundles for at least half the length of the hypanthium. The dorsal carpellary bundle is easily recognizable by its prominence and by its central position in the base of the style, but the style receives so many other strands (one from almost every peripheral bundle) that the identification of two ventrals usually is not possible. Even in bilocular flowers, the two styles each receive more than three carpellaries, and the bundles ramify into several anastomosing strands after entering. Styles of unilocular flowers are superficially simple, but the rudiment of a second style can be found on close inspection. Ovular bundles seem to be more plentiful in this species than elsewhere in the genus, in keeping with the greater number of peripheral bundles with which they connect. In some cases, branches from the ovular supply pass the placenta and end blindly above it in the apical part of the endocarp, perhaps indicating the position of a lost ovule.

A closer association of the three most dorsally situated peripheral bundles is not usually noticeable in the flower and fruit of *Nyssa ogeche*; instead, all of the bundles lie fairly close together around the periphery of the narrow endocarp.

Fruit of Camptotheca

The outer tissues of the mature *Camptotheca* fruit are not succulent, but are dry, withered, folded, and flattened; the flattening — undoubtedly related to the development of so many fruits in a single head — usually occurs parallel to the dorsal-ventral mid-plane, giving the fruit a somewhat samaroid appearance. The surface is brown and lustrous in herbarium specimens — according to Wilson (1914), this is the natural condition — and sparsely provided with corky dots. The length is from 18–25 mm.; breadth across the widest part of the flattened outer tissues, about 7 mm.; and thickness at right angles to the flattening, only 2 or 3 mm. The outline is oblong to oblanceolate. A pulvinate disk is present at the truncated apex, around which can be seen the edge of the hypanthium with a few indistinct calyx lobes. The stylar remnant is sunken in a deep pit at the center of the disk.

The narrow, thin-walled endocarp of *Camptotheca* is 15–20 mm. long and has a maximum diameter of about 2 mm. (Pl. I, Fig. 6). The apex is tapered to a sharp point, and the base gradually attenuate to an even sharper point. Dorsal flattening or concavity may be evident or may be obscured by lateral compression of the fruit during development; frequently the combined effects of dorsal and lateral flattening give the upper part of the endocarp and its single locule a triangular shape in cross section. One broadly rounded ridge is present on the ventral surface of the apical third of the endocarp, and a thick, compound vascular strand can usually be found on each side of this ridge, extending from the base of the endocarp to the placental region, and there passing into the wall. The dorsal side sometimes bears a very slight median longitudinal indentation near the apex; otherwise the endocarp is quite smooth.

Kirchheimer (1938, p. 4) erroneously reported that *Camptotheca* has no germination valve. The valve is similar in form and position to that of *Nyssa,* and it frequently opens when the fruit is boiled.

HISTOLOGICAL OBSERVATIONS. The fruit wall consists of three major zones: an outer skin of small thick-walled cells; an inner fibrous endocarp; and an intermediate zone of large thinner-walled cells, corresponding to the succulent zone of *Nyssa.* Here, however, the cells of the intermediate zone are not so thin-walled as in *Nyssa,* and they are crushed and deformed at maturity. Stone cells seem to be scattered throughout this tissue, and the peripheral bundles — quite conspicuous in *Camptotheca* fruits because of the multitude of fibers in each strand — are contained within it. The endocarp is made up of woody fibers, but these elements are much narrower (mostly under 10 μ in diameter, 400–700 μ in length) than *Nyssa* fibers. At some distance below the valve the endocarp elements are all elongated around the locule. At higher levels the outermost fibers on the ventral side are longitudinal, especially in the ventral ridge, where all of the cells are so oriented. An inner epidermis of longitudinal fibers seems to be absent. The elements are much more variable in diameter in the ridge than elsewhere; many measure 20 μ or more. The *Camptotheca* endocarp is the thinnest in the family: below the valve, it consists of about 10 fiber layers and one or two layers of transition cells, the total thickness being no more than 75 μ; through the valve, the wall is only five or six fibers (less than 50 μ) in thickness; when measured across the ventral ridge, however, the thickness may exceed 500 μ. Along the line of dehiscence, the wall is so thin and the cells so weakly lignified that a completely transparent zone surrounds the valve in cleared whole fruits. It appears that the cells of the dehiscence tissue do not develop into sclereids; during germination the wall simply tears in this very weak region. Cleared fruits also show the orientation of fibers when viewed under the dissecting microscope: elements bordering the dehiscence tissue on the ventral side are oblique, and those within the valve are tangential. Cleared preparations further reveal that the mature endocarp is separated from the ring of peripheral bundles by a zone of transparent (thin-walled) cells; thus, it is evident that the endocarp of *Camptotheca* includes only inner carpellary tissues.

VASCULAR PATTERN. There are regularly 10 peripheral bundles in the flower; these supply the rather constantly pentamerous floral appendages (5 minute calyx lobes, 5 hairy corolla lobes, and 10 stamens in two whorls). Lateral branches in adjacent calyx lobes are usually united, forming an almost uninterrupted vascular circle around the orifice of the hypanthium. The gynoecial vascular system is quite clearly that of three united carpels: a conspicuous major dorsal carpellary bundle is fused with a peripheral bundle for about half the length of the hypanthium, and two lesser dorsals (belonging to lost carpels) depart from other peripherals at a higher level. Each dorsal passes into the apex of the ovary and continues as the median strand of one of the three styles. Two or three thick ventrals, apparently consisting of several thinner strands, are more centrally situated (completely within the carpellary tissues) and are not united with peripheral bundles. These rise from the base of the ovary, provide ovular branches to the placenta, and divide again as they enter the united stylar branches, thereby providing each style with two ventral strands. Since the united proximal parts of the styles are set in an invagination of the disk, the ventrals turn downward slightly before entering.

The ovule of *Camptotheca,* like that of *Nyssa,* can receive independent traces from the base of the ovary as well as strands from the ventrals; however, the ovular traces are not so plentiful here as in *Nyssa.*

Fruit of Davidia

Ripe fruits of *Davidia* are 28–40 mm. long, 20–30 mm. in diameter, green in color, and crowned by a pointed woody remnant of the styles. The surface may be marked with an abundance of conspicuous corky spots or with a corky reticulate pattern. It has been suggested that the two types of epidermal marking might have taxonomic significance (Li, 1954); however, the present author has seen both patterns on the same herbarium specimen. Endocarps are of the same shape as the fruit (PL. I, FIG. 9). The longest encountered during this investigation was 39 mm. in length and 17 mm. in diameter; the shortest, 25 mm. in length and 11 mm. in diameter; broader stones of intermediate length, with diameters up to 26 mm., are common. Locules number six to eight in the author's material, seven being the most frequent number. Li (1954) and others have reported that nine-locular fruits also occur. Some of the ovules in every ovary fail to develop. The abortive locules become compressed and distorted during growth, but the endocarp retains its external symmetry (PL. IV, FIG. 19). The position of each interlocular septum is marked on the surface of the stone by a very thick and conspicuous longitudinal ridge, and another ridge, not quite so thick, is present along the mid-line of the long, narrow germination valve and continues to the base of the stone. This median dorsal ridge is separated from the adjacent interlocular ridges by deep grooves. Countless minor grooves, longitudinal or somewhat oblique in their orientation, occur on all of the thick ridges, marking the location of small branches departing from the major vascular bundles.

Narrow germination valves, extending about two-thirds the length of the stone, are present for all locules, both fertile and abortive. These are quite thick — up to four mm., if the median dorsal ridge is included in the measurement. The septa are 700–1000 μ in thickness.

HISTOLOGICAL OBSERVATIONS. The exceedingly hard endocarp of *Davidia* is composed of sclerified elements of very variable size and wall-thickness.

In the immediate vicinity of fertile locules they are fibrous in appearance, up to 350 μ long, and up to 40 μ in diameter. In more peripheral regions they are much shorter and some cells are isodiametric. Elements with large lumina are intermixed with others having small lumina; most lumina are much larger than those of *Nyssa* fibers. An inner epidermis of longitudinal fibers is very evident in abortive locules, where circumferential growth has not taken place to such an extent as to disrupt this layer. Around each fertile locule there is a zone of more or less fibrous elements elongated circumlocularly. The septa are made up of these circumlocular elements, except where longitudinally or obliquely oriented sclereids accompany ovular traces to the placenta. Elements in the central axis of the fruit have a jumbled appearance, but they lie mostly with their long axes in the transverse plane. The peripheral cells of the stone, including those of the germination valve, seem to have no predominant orientation. The valve is outlined by a dehiscence tissue six to eight cells thick, in which smaller, rather thin-walled elements about 70 μ long and 15 μ wide are radially oriented. The *Davidia* endocarp has no outer transition zone; the woody tissue ends abruptly at the inner margin of the zone of parenchyma and stone cells that lies just beneath the leathery skin of the fruit.

Removal of the thick valves in *Davidia* is apparently facilitated by radial growth of septa during development of the endocarp. This septal expansion is sufficient to cause a folding in of the valve region, and in places the epidermis lining the valve comes to lie against that lining the septum. The line along which this double epidermis is present is radially continuous with the dehiscence tissue, and it is probable that little resistance is encountered here when germination occurs.

VASCULAR PATTERN. The vascular system of the hermaphrodite flower of *Davidia* was investigated in detail by Horne (1909), who followed the course of the bundles by means of serial cross sections. Sections and cleared specimens examined by the present author showed the same pattern reported by Horne: a peripheral ring of bundles — about three times as many as the locules — an inner ring of carpellary bundles, and two sets of about 8 to 10 ovular traces passing through each septum to adjacent placentae (PL. III, FIG. 17). The peripheral bundles supply only stamens as the epigynous calyx and corolla apparently are absent in the *Davidia* flower. The ring of carpellary bundles contains both dorsals and ventrals, all about the same distance from the axis. Ventral bundles belonging to adjacent carpels are in pairs, each pair being radially aligned with a septum. It is because of the radial elongation of cells within the septa that these bundles come to lie in the same circle with the dorsals. In the mature fruit the paired ventrals run along the crests of the septal ridges of the endocarp, and each dorsal bundle is situated on a median dorsal ridge. Some fusion of the paired ventrals is quite common. Fusion between carpellary bundles and peripheral bundles occurs to a much less extent in *Davidia*, however, than anywhere else in the Nyssaceae; when such fusion does occur, it is limited to the basal part of the flower. A pair of flanking bundles accompanies each dorsal, but these are not to be considered homologous with the flanking bundles that appear on the dorsal side of many *Nyssa* endocarps. In *Davidia* the flanking bundles are entirely a part of the carpellary supply; whereas, in *Nyssa*, they are peripheral bundles supplying epigynous floral appendages. In the mature *Davidia* endocarp, the flanking bundles lie within the deep grooves that separate each median dorsal ridge from adjacent septal ridges. *Davidia* differs from other Nyssaceae in this respect, but a similar vascular arrangement probably prevailed in *Langtonia bisulcata*, an Eocene fruit of cornaceous affinities in which a pair of deep grooves flank the median dorsal line of each carpel (Reid and Chandler, 1933, p. 453–455). It is interesting that Horne made no mention of the flanking bundles, although he described the positions of other carpellary strands in detail; possibly the *Davidia* flowers examined by Horne were younger than those examined by the present author and some of the bundles had not yet become differentiated.

There are more traces supplying each ovule in *Davidia* than in any other member of the family. It is difficult to follow the course of these strands because they are so numerous and tend to anastomose to some extent within the septa. However, it is evident that most of the ovular traces depart from the ventral carpellary bundles in the lower part of the ovary.

Fruit of Mastixia

Only a relatively few fruiting specimens of *Mastixia* were examined during this investigation; therefore, the following description will draw heavily upon the detailed observations of Kirchheimer (1936), who had much more material at his disposal. According to Kirchheimer, the ovoid *Mastixia* fruit is from 20–37 mm. in length, the surface is sometimes spotted, and the apical disk may be prominent or indistinct. Throughout the genus the fruits are quite similar in appearance, and at present there is no sure way of identifying a particular *Mastixia* species by its fruit alone. Endocarps are smooth, finely creased, or knobby, and they are readily recognizable by the presence of a median dorsal furrow running from base to apex. All of the modern members of the genus seem to bear only unilocular fruits, with a solitary anatropous seed attached near the apex, as in *Nyssa*. The endocarp wall may be less than 1 mm. or more than 2.5 mm. thick, depending on the species. When the stone is cut open it can be seen that the external furrow is due to a deep longitudinal folding of the endocarp wall on the dorsal side (Pl. III, Fig. 18). The fold extends inward, well past the center of the fruit, causing the locule to be horseshoe-shaped in cross section. The folding undoubtedly occurs during circumferential growth of the endocarp tissue: the author has sectioned several *Mastixia* flowers and found no furrow in this younger material.

Germination in *Mastixia* differs notably from that in *Nyssa* in that the valve separates along two lines (usually visible as thickened places in the endocarp wall) running the entire length of the stone. When the stone has opened in this manner, the dorsal fold can be seen as a narrow, but very prominent, median ridge on the internal surface of the valve.

HISTOLOGICAL OBSERVATIONS. The fruit wall consists of three major tissue zones: a leathery outer skin, an inner sclerified endocarp, and an intermediate zone in which parenchyma and stone cells are intermixed. Stone cells are extremely abundant, and they seem to mature much earlier than the woody cells of the endocarp. One fruit examined by the author, *J. & M. S. Clemens 30477* (A), from Borneo, and identified by Danser as *Mastixia trichotoma* Blume (although E. D. Merrill considered it an undescribed species), had the external appearance and the hardness of a mature fruit, but inspection of transverse sections revealed that the endocarp was still thin-walled and incompletely developed and that the hardness of the fruit wall was due to the predominance of fully developed stone cells in the outer tissues. It is interesting in this connection that *Mastixia* fruits generally show no external mark of the dorsal endocarpic fold: probably it is the rigidity imparted by the stone cells that prevents outer tissues from being folded inward along with the endocarp.

Numerous secretory canals are present in the material studied by the author. These run longitudinally through the same tissue zone in which stone cells are so abundant. Usually — perhaps always — they are associated with vascular bundles, and sections of flowers show that they accompany some of the bundles into the calyx lobes. According to Kirchheimer (1936), the canals are fewer in number in some species and altogether absent in others.

Kirchheimer reported that the *Mastixia* endocarp consists of three recognizable tissue zones: one to five layers of thick-walled and more or less isodiametric cells at the periphery of the stone, a central zone of radially elongated sclereids, and a wider inner zone of fibers surrounding the locule. A sectioned endocarp of *M. arborea* Clarke (Burma, *J. H. Lace 5641*, A) shows these zones very well (PL. V, FIG. 22). The isodiametric cells are mostly confined to a single outer layer, a layer that could possibly be interpreted as the outer epidermis of the carpellary tissues. The radially elongated elements (about 120 μ long and 50 μ in diameter) are arranged in a few roughly concentric layers around the inner zone of fibers. The latter elements are longer (up to 250 μ) and more slender than the radial elements; most of them are elongated concentrically, but groups of longitudinal elements occur in places. Both transverse and longitudinal elements are present in the outer part of the dorsal fold, but the innermost extension of the fold is made up exclusively of longitudinal elements. An inner epidermal layer of longitudinal cells is apparently lacking in *Mastixia*; it is possible, however, that such a layer is formed at an earlier stage of development and is later disrupted by the very great circumferential growth of the endocarp tissue. Most cells in the endocarp have thinner walls and larger lumina than the fibers of a *Nyssa* stone. Another endocarp examined by the author, believed to belong to *M. philippinensis* Wangerin (collection data lost) is made up of cells with even thinner walls, and the zone of radially elongated cells is not well defined. Kirchheimer also observed that *M. philippinensis* lacks a distinct zone of radial elements.

Kirchheimer noted that dehiscence takes place along two lines that show up in transverse sections as thickened places in the endocarp wall and that the opening of the valve is associated with the disintegration of parenchyma cells in these thicker places. He failed to note that the thick places always occur precisely where two important vascular bundles rise from the base of the endocarp to the placenta. The bundles are surrounded by a large number of very thick-walled longitudinal fibers, and the presence of these elements probably facilitates longitudinal splitting of the valve along the path of the inclosed vascular strand (PL. V, FIG. 21).

It should be clear that the dehiscence mechanism of *Mastixia* differs substantially from that of all Nyssaceae. In the latter group the vascular bundles — especially the ovular traces — determine the position of the dehiscence tissue only indirectly, by their effect on the orientation of neighboring endocarp fibers; there are no vascular strands actually within the dehiscence tissue. In *Mastixia*, on the other hand, the endocarp splits exactly where two ovular traces pass through the endocarp from base to placenta. The line of dehiscence is independent of the ovular supply only for a very short distance between the placenta and the apex of the stone. An inspection of sections taken above the placenta suggests that orientation of the cells plays a part in the dehiscence of the valve in this limited apical region, where there are no bundles in the endocarp save the dorsal carpellary bundle.

VASCULAR PATTERN. Several flowers from two species of *Mastixia*, *M. philippinensis* (Luzon, *Ramos 23353*, GH) and *M. trichotoma* var. *maingayi* Clarke (Sumatra, *Neth. Ind. For. Serv. 98 T.3P.261*, A), were cleared, and some were subsequently sectioned, but in neither case could the vascular pattern be established very satisfactorily. The flowers are tiny and coated with lignified hairs, and the inner tissues are filled with a persistent dark substance, perhaps resulting from the presence of the secretory canals. Moreover, the bundles and associated canals are very numerous, making it difficult to follow the path of any one of them in the rather distorted tissues of flowers taken from herbarium specimens. Serial sections of the fruits proved to be more useful in this respect, but vascularization of the floral appendages and of the style is still imperfectly understood.

It is quite evident, however, that the vascular pattern of *Mastixia* flowers and fruits differs in two important respects from that found in *Nyssa*, *Camptotheca*, or *Davidia*: (1) the numerous bundles passing through the zone of parenchyma and stone cells to the calyx lobes and other epigynous parts are not in a single circle, but are spirally arranged, a pattern that can best be seen in sections taken near the base or near the apex; (2) there are only three vascular strands, the dorsal carpellary bundle and two ovular traces, within the endocarp tissue. Although it was not possible with the material at hand to trace most of the spirally arranged outer bundles into their respective appendages, it appears that each of the well developed calyx lobes receives more than one strand. Additional bundles presumably enter the four or five petals and the equal number of stamens. There are many more bundles, however, than there are floral parts, and it is likely that some of these proceed into the disk, which (at least in *M. trichotoma* var. *maingayi*) is not pulvinate, but is in the form of a thick collar around the style. Ventral carpellary bundles could not be identified in any of the specimens examined. It is possible that they no longer exist in the reduced gynoecium of *Mastixia*. The ovular traces are unconnected with any of the outer bundles from the base to the placenta: it may be that the two strands actually represent a complete phylogenetic fusion of ventral carpellary bundles with ovular traces; however, there is no continuation of these strands into the style to prove this point. The dorsal bundle is the most prominent bundle in the fruit; it is located within the outer part of the median dorsal fold, where the accompanying parenchyma frequently ruptures, leaving a conspicuous longitudinal hollow space. This bundle is also unconnected with any of the outer bundles.

MORPHOLOGICAL SUMMARY

It seems advisable at this point to summarize the major morphological features of the nyssaceous fruit so that the reader will better be able to follow the subsequent discussion of relationships between species.

(1) Only the inner part of the fruit wall is derived from carpellary tissues; the outer part is derived from the hypanthium, as is the case in most fruits that develop from flowers with inferior ovaries (Douglas, 1957; Eames, 1961). There is no epidermis between carpellary and extracarpellary tissues, but the boundary may be located by means of the vascular bundles. Tissues internal to the carpellary bundles are certainly carpellary tissues, and those tissues that are external to all bundles supplying the perianth must be considered a part of the hypanthium. In *Nyssa* and *Camptotheca*, bundles supplying the androecium are fused for most of their length with bundles supplying the perianth, and the fusion products are in turn fused with carpellary bundles, resulting in a single circle of compound vascular strands. These compound strands mark the transition between carpellary and extracarpellary tissues.

(2) In the *Nyssa sylvatica* complex and in *N. ogeche*, all of the carpellary tissues become woody. In *N. javanica*, *N. aquatica*, *Camptotheca*, and *Davidia*, the outermost layers of carpellary tissue remain parenchymatous. The stones of all species have a distinct inner zone of transverse fibers, elongated parallel with the locule. Taken alone, this inner zone of the nyssaceous endocarp is roughly comparable to some of the woody endocarps that develop in other plant groups, where the ovary is superior.

(3) Those species in which the entire carpellary portion of the fruit wall becomes woody produce endocarps marked by vascular bundles lying in longitudinal grooves, with the regions between the bundles protruding as ridges. Species in which the outer carpellary tissues remain parenchymatous produce smooth endocarps (*Camptotheca*) or ridged endocarps in

which the ridges are radially aligned with major vascular bundles (*Nyssa aquatica, Davidia*). The stone of *N. javanica* combines both of these features: it is relatively smooth, and its three inconspicuous dorsal ridges arise opposite bundles.

CONCLUSIONS

SIMILARITY OF VASCULAR PATTERNS IN NYSSA AND CORNUS. Vascular patterns in the flowers of *Nyssa* resemble very closely the vascular patterns of *Cornus* described by Wilkinson (1944). Wilkinson's generalized drawings (p. 279, figs. 1–7) representing several species of *Cornus* show a more elaborate sepallary supply than that of *Nyssa* and a somewhat different orientation of the ovule. There is a further difference in the number of peripheral bundles, for the flowers of *Cornus* are usually tetramerous and accordingly there are only eight bundles supplying the perianth. In important respects, however, the drawings are equally representative of bilocular *Nyssa* flowers; carpellary bundles are variously fused with peripheral bundles; ventrals of adjacent carpels are united for much of their length; and the ovular supply is made up of numerous traces. According to Wilkinson's descriptions, ovular traces in *Cornus* always connect with the ventrals. This is a somewhat simpler condition than that found in *Nyssa,* where ovular traces may also connect with peripheral bundles or may rise independently from the base of the ovary.

Comment is necessary regarding Wilkinson's notion that the bilocular ovary in *Cornus* has been derived from a unilocular ovary. She concluded from her study of the vascular pattern that the partition separating the two locules is not a true septum, but a pair of fused parietal placentae, citing the occurrence of an incompletely formed partition in *C. suecica* in support of her argument. Since the vascular patterns in *Cornus* and *Nyssa* are so similar, Wilkinson's conclusion, if valid, could be extended to include the nyssaceous ovary. To the present author, however, the notion that the septum in either genus is derived from fused placentae seems extreme and unjustified. Wilkinson's interpretation of the vascular system with regard to this point is not at all convincing, and her use of an unusual specimen of *C. suecica,* which she herself recognized as an advanced member of the genus, to demonstrate a supposedly primitive character is open to question. If Wilkinson's view were correct, one would expect at least some of the fossil fruits of Nyssaceae and Cornaceae to be unilocular with two or more prominent parietal placentae. Such fruits are not known. On the contrary, numerous fossil cornaceous and nyssaceous fruits dating from as long ago as the Eocene show the multilocular condition, and locules are more numerous in these ancient fruits than in their modern counterparts. Furthermore, if the septum were an advanced feature derived from the fusion of parietal placentae, one would expect unilocular fruits of modern *Cornus* to retain two placentae and two seeds. On the contrary, unilocular fruits of *Cornus* resemble those of *Nyssa* (Kirchheimer, 1948). Recently

Mittal (1960, p. 116) has also expressed disagreement with Wilkinson's concept of the septum.

AFFINITIES AMONG NYSSA SPECIES. Perhaps the most interesting result of this investigation is the discovery of a resemblance between fruits of the Asiatic *N. javanica* and the American *N. aquatica*. Since the development of the endocarp in these two species is so different from that of other *Nyssa* species, the idea that *N. javanica* and *N. aquatica* are somehow related seems very attractive. *Nyssa aquatica* is the more advanced species in several respects. The inflorescence on hermaphrodite trees has been reduced to a solitary flower, and the gynoecium, since it shows little or no evidence of the ancestral polymerous condition, is the most reduced of all *Nyssa* species. Reduction is also evident in the number of corolla lobes and in the number and fertility of the stamens present in hermaphrodite flowers. Furthermore, data from the anatomical studies of Titman (1949) may be interpreted to indicate that the wood of *N. aquatica* is more advanced than the wood of *N. javanica*. (In *N. aquatica* the vessel members are shorter and the perforation plates have fewer scalariform bars.) If the two species are indeed related, then *N. javanica* must be much closer to the ancestral form. It will be shown in a later paper that well-preserved fossil fruits of the same general morphological type as *N. javanica* fruits have been collected in early Tertiary deposits of the eastern United States. When the fossil record is considered along with the morphological similarity of the modern fruits, the affinity of *N. javanica* and *N. aquatica* can scarcely be doubted.

Affinities within the *Nyssa sylvatica* complex are sufficiently evident that little discussion is necessary. The same features that separate *N. sinensis* from its American counterparts, notably the pedicellate bisexual inflorescence and the frequent occurrence of bilocular fruits, mark the Chinese species as the most primitive member of the complex. It seems likely that the greater abundance of trichomes on young leaves and inflorescences of *N. sinensis* is also a primitive characteristic. (In this connection it may be noted that the flowers of the advanced species *N. aquatica* are glabrous; whereas those of *N. javanica* are hairy.)

Since *Nyssa biflora,* somewhat hesitantly treated in this paper as a separate species from *N. sylvatica*, has a more reduced inflorescence than the latter, it must be assumed that *N. sylvatica* is the older of these two.

The *Nyssa sylvatica* complex seems not to bear a very close relationship to *N. javanica* and *N. aquatica*. The fruits of the two latter species are histologically different from those of the *N. sylvatica* complex, and there are accompanying floral differences: staminate flowers are borne in capitate inflorescences in *N. javanica* and *N. aquatica*; in short racemes in the *N. sylvatica* complex. To the morphological differences may be added the recent report of Johnson and Fairbrothers (1961) that *N. sylvatica* and *N. aquatica* can be distinguished by serological methods. These facts indicate that the *N. sylvatica* complex has evolved independently of *N. javanica* and *N. aquatica* for quite a long time. Fossil evidence will be adduced to support this view.

The question may arise as to which of the two evolutionary lines retained more of the remote ancestral features. Actually both lines appear to have advanced as well as primitive characteristics. The short racemose inflorescences and frequent bilocular gynoecia of *Nyssa sinensis* show less evidence of reduction than the capitate inflorescences and unilocular gynoecia of *N. javanica*. On the other hand, a stone formed only from inner cell layers of the carpel is probably more primitive than a stone formed from an entire gynoecium. In this respect *N. javanica* and *N. aquatica* retain the more primitive structure.

Thus far *Nyssa ogeche* has not been mentioned in this discussion because that species shows no very close affinity with any other in the genus. Except for the dense covering of trichomes, the capitate staminate inflorescence and solitary hermaphrodite flower of *N. ogeche* resemble corresponding structures of *N. aquatica*. Moreover, Titman (1949) found that the wood of *N. ogeche*, like that of *N. aquatica*, is a bit more advanced in some ways than the wood of other *Nyssa* species.[15] On these grounds, Titman suggested that *N. ogeche* has been derived from *N. aquatica*. Titman's suggestion must now be rejected emphatically because the flowers of *N. ogeche*, with their double styles and their more numerous stamens and corolla lobes, cannot have been derived from the reduced flowers of *N. aquatica*. If there were a close relationship between these two species, it would perforce be in the other direction, with *N. ogeche* being the more primitive. However, the structure of the endocarp of *N. ogeche* is not at all like that of *N. aquatica*; rather, it resembles both externally and internally the endocarp found in the *N. sylvatica* complex. In fact, when the papery wings have been removed from some of the shorter stones of *N. ogeche*, these could be mistaken for elongated stones of *N. sylvatica* or *N. biflora* (PL. I, FIG. 7). It seems most likely that this puzzling species is not intimately related to any other modern *Nyssa* and that it has had a long evolutionary history of its own.

RELATIONSHIP OF CAMPTOTHECA AND NYSSA. The observations reported in this paper support the opinion of other workers that *Nyssa* and *Camptotheca* are closely allied. Titman (1949), noting that the vessel members in *Camptotheca* are more advanced in some respects than those of *Nyssa*, suggested that *Camptotheca* has been derived from the ancestors of *N. javanica*. Considering the structure of the fruits and the inflorescences of the two plants, this is a reasonable deduction. In *Camptotheca* the outer cell layers of the carpellary portion of the fruit wall remain parenchymatous, indicating a relationship with *N. javanica*. Moreover, *Camptotheca*

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[15] Users of Titman's data are cautioned that there are errors in the ratios of length to width employed to evaluate the degree of specialization of vessel members. For instance, the average length of vessel members in wood of *Nyssa ogeche* was reported as 802 μ, the average width as 49 μ, and the ratio as 10:1 (see both text and table on p. 254 of Titman's paper). Assuming measurements are accurate, the correct ratio is 16:1, of course.

is more specialized than the latter species with regard to dispersal of its fruits. The reduced vascular pattern, the dry outer fruit wall, the thin, light endocarp, and the great abundance of fruits in each head are correlated aspects of this specialization. Presumably the fruits of the ancestral plants resembled much more those of modern *N. javanica* than those of *Camptotheca.* The gynoecium must have been at least trimerous (but not necessarily trilocular), however, since three styles are still present in *Camptotheca.* Probably in this ancestral population, as in modern *Camptotheca,* there were not two kinds of sexually different trees.

PRIMITIVE AND ADVANCED FEATURES IN DAVIDIA. In most respects the hermaphrodite flowers of *Davidia* are much less advanced than those of other Nyssaceae. The gynoecium is usually heptamerous, and there are more than 20 stamens. Vascular bundles are very numerous, and fusion of peripheral strands with carpellaries is slight. Furthermore, woody elements of the endocarp in the mature fruit are not nearly so long, narrow, and thick-walled as in *Nyssa.* All of these features must have persisted since very remote times.

There are other characteristics of the reproductive structures of *Davidia* that are not primitive, however. The pedicels bearing the staminate flowers have been reduced so much as to be almost non-existent, and it is likely that the perianth has also been lost through reduction. Moreover, the occurrence of a single hermaphrodite flower on an otherwise staminate inflorescence can only be interpreted as a specialization.

Although *Davidia* has received much attention as an ornamental plant, it seems that little effort has been directed toward a morphological interpretation of the curious inflorescence. Actually there are two inflorescences present wherever the hermaphrodite flower appears — a capitate staminate inflorescence and a hermaphrodite inflorescence that has been reduced to a solitary flower. Serial sections of the staminate inflorescence show that the thick axis branches into two equal parts just below the insertion of the hermaphrodite flower. Evidently the compound inflorescence of *Davidia* has evolved by reduction from a panicle of inflorescences like that still found in *Camptotheca.* Hermaphrodite flowers of *Camptotheca* are located in the most distal inflorescences, and it appears that the hermaphrodite flower (inflorescence) of *Davidia* also occupies a position distal to the staminate inflorescence. The latter inference is based on the fact that the more distally situated of the two large, white subtending bracts is always attached on the same side of the main axis as the hermaphrodite flower. Li and Schramm (1954) report that two hermaphrodite flowers can occasionally occur on a single staminate head. It would be interesting to know whether both flowers in such cases belong morphologically to the same hermaphrodite inflorescence or whether there are two hermaphrodite inflorescences involved.

RELATIONSHIP OF MASTIXIA TO NYSSACEAE. The resemblance of the *Mastixia* fruit to fruits of Nyssaceae is considerably less than expected.

There are histological similarities, but differences in the vascular pattern and in the establishment of the dehiscence line are more impressive. Considering the marked resemblance of vascular patterns between *Nyssa* and *Cornus*, the dissimilarity encountered in *Mastixia* is surprising. One must infer that *Mastixia* is not so closely related to the Nyssaceae as are some other cornaceous genera.

An interesting assortment of primitive and advanced features are combined in *Mastixia*. The panicle of perfect flowers is about as primitive as any inflorescence in the Umbellales, and vessels in the secondary xylem are similarly primitive. If, as it seems, the numerous peripheral vascular bundles in the flower are spirally arranged, that may also be taken as a primitive feature. In contrast, the vascular supply of the gynoecium is very much reduced. In specimens examined for this study, only two bundles supply the ovule and no vestiges of lost carpels are present. Without additional information this gynoecium would be considered truly monomerous, but in view of the multilocular condition of fossil mastixioid fruits (Kirchheimer, 1936) and the recognizable pseudomonomerous nature of unilocular gynoecia in related genera, it must be concluded that the gynoecium in *Mastixia* is also pseudomonomerous.

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EXPLANATION OF PLATES

PLATE I

FIG. 1. Stones of *Nyssa aquatica* (*author's collection*), natural size. Specimen in upper right lateral view; others viewed from dorsal side. FIG. 2. Stones of *N. ogeche* (*author's collection*) with papery wings removed, showing variation in size and shape. Three specimens on right in bottom row are viewed from ventral (placental) side; others shown in dorsal or lateral view. FIG. 3. Variation in stones of the *N. sylvatica* complex; all specimens natural size and viewed from dorsal side. Top row, *N. sinensis*: (left to right) *Steward & Cheo 818* (A), "Yung Hsien, Ta Tseh Tsuen"; *R. C. Ching 3031* (A), Anhwei; *Y. Tsiang 5944* (A), "Yunfeushan, Tuyun"; *C. Wang 39489* (A), Kwangsi (two fruits). Center row, *N. biflora*: *A. Traverse 498* (GH), Ga.; *R. K. Godfrey 6433* (GH), N. C.; *Godfrey & Tryon 1462* (GH), S. C.; *W. W. Eggleston 4919* (GH), Va.; *A. E. Radford 6327* (GH), N.C. Bottom, *N. sylvatica*: *Svenson 10372a* (GH), Tenn.; *E. T. & S. A. Harper s. n.* (A), Charlestown, W. Va.; *F. MacKeever MV306* (NEBC), Mass. FIG. 4. *N. sylvatica* stone (*Svenson 10372*), × 2; viewed from placental side — note two pits where ovular strands, rising independently from base, enter endocarp wall en route to placenta. FIG. 5. Lateral view of stones shown in FIG. 3: (left to right) *Steward & Cheo 818, MacKeever MV306, Traverse 498, E. T. & S. A. Harper s. n., Godfrey 6433.* Natural size. FIG. 6. Fruits of *Camptotheca acuminata* (*A. Henry 13433*, A), from Yunnan, natural size — outer tissues have not been removed from fruit on left. FIG. 7. To show similarity between unusually long *N. biflora* stones and shortest stones of *N. ogeche.* First and third specimens from left are *N. biflora* (*A. Traverse 498*). FIG. 8. *N. aquatica* stone (*author's collection*), × 2; viewed from ventral side. FIG. 9. *Davidia* stone (collected *E. H. Wilson*, China), × 2 — note partially opened germination valve with prominent median dorsal ridge flanked by two deep grooves.

PLATE II

FIG. 10. Stone of *"Nyssa megacarpa"* (*Parker 2308*, A) between two smaller *N. javanica* stones from Sumatra (*Forbes 2880*, GH), all × 2.7. Smaller stones shown in ventral (above) and dorsal view. Fig. 11. Transverse section, × 7, of *N. javanica* stone, taken below the valve, showing sculpturing of locule. Dorsal side is at bottom of photo. FIG. 12. *N. ogeche* fruit, × 2.7, with skin and fleshy tissue removed carefully to show papery wings radiating from stone. FIG. 13. Transverse section, × 7, of *N. ogeche* stone, taken at base of valve — note position of peripheral bundles between ridges, abundance of ovular traces in endocarp wall. Dorsal carpellary bundle is prominent above number "13," and basal part of dehiscence tissue can be seen at lower left.

PLATE III

FIG. 14. Longitudinal section, × 23, of *Nyssa sylvatica* flower (petals and stamens no longer attached) — note nectariferous disk above rim of hypanthium and three major tissue zones that will form the fruit wall. Note also the single vascularized integument surrounding narrow nucellar peg. FIG. 15. Transverse section, × 30, of *N. sylvatica* flower (collected May 20th), showing eight

peripheral bundles at junction of carpellary and noncarpellary tissues — note presence of median dorsal bundle and two flanking bundles in lower part of photo. Ovular traces are prominent within the young endocarp tissue. FIG. 16. Transverse section, × 30, of a slightly older ovary (collected June 13th), showing more advanced differentiation of endocarp tissue. The central of the three major tissue zones will be relatively much wider in the mature fruit and will be quite succulent. Dark cells shown in this zone are probably destined to become stone cells. FIG. 17. Part of a transverse section, × 30, of *Davidia* flower — note staminal bundles near periphery of section and discrete carpellary bundles at outer boundary of young endocarp tissue. Dorsals are identifiable by their median position opposite each ovule and flanking bundles by their sunken position. Ventrals lie opposite the septa, are difficult to distinguish from minor carpellary strands in this section. FIG. 18. Transverse section, × 7, dried fruit of *Mastixia arborea* (*J. H. Lace 5641*, A) — note position of dorsal carpellary bundle in outer part of infold and thickening of endocarp wall in vicinity of ovular traces.

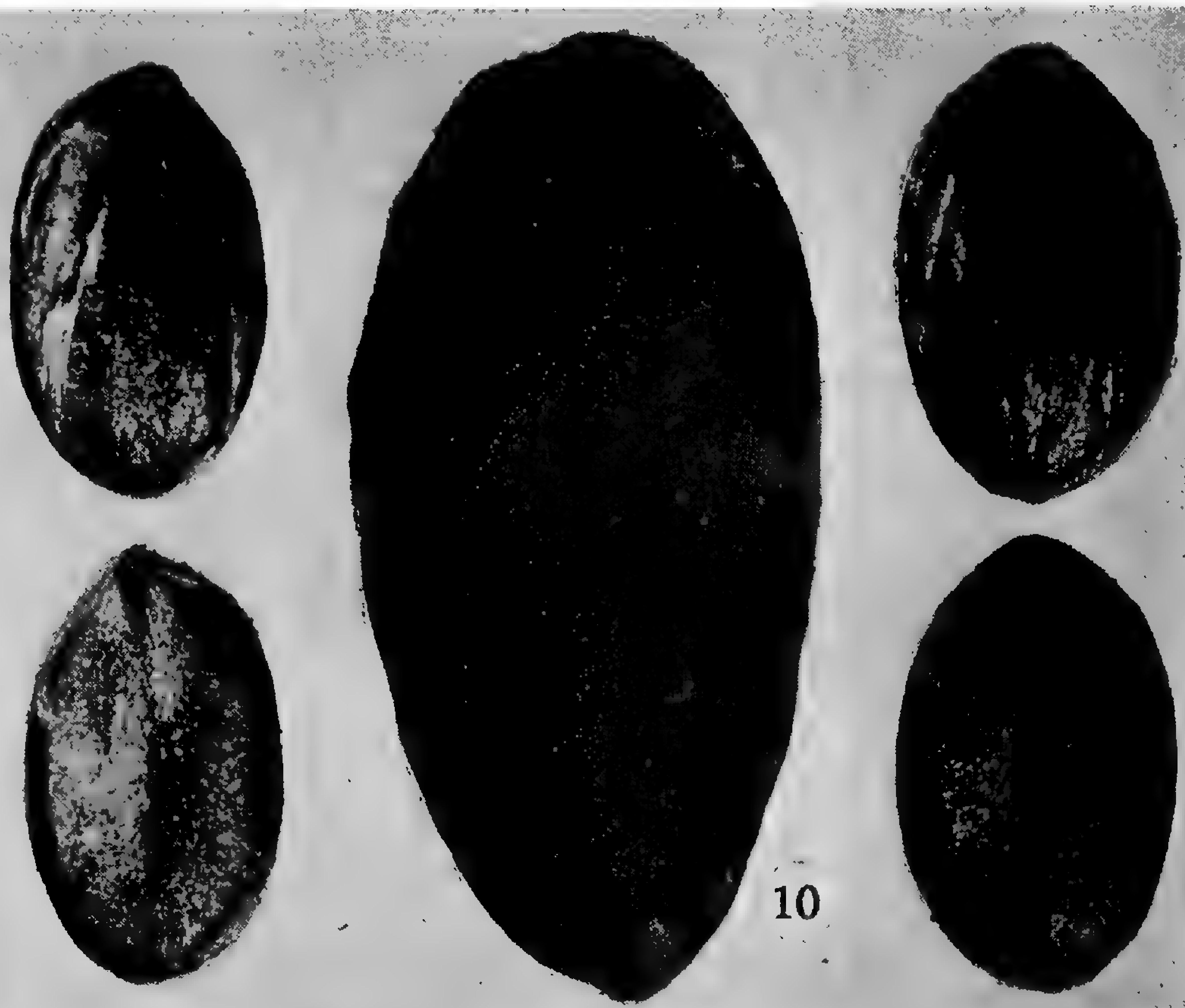
PLATE IV

FIG. 19. Transverse section, × 5, of *Davidia* stone, showing two fertile and five abortive locules, germination valves, and numerous ovular traces within the septa. FIG. 20. Transverse section, × 200, of *Nyssa sylvatica* ovary, showing early stage in development of endocarp — note single epidermal layer surrounding locule (above), transversely elongating cells near epidermis and near large peripheral bundle.

PLATE V

FIG. 21. Dehiscence region, × 50, of *Mastixia* section shown in FIG. 18 — note predominantly longitudinal orientation of fibers; hollow space forms when ovular trace deteriorates; locule is to left. FIG. 22. Ventral region of same section, × 50, showing orientation of elements; part of raphe may be seen in locule (upper left). FIG. 23. Transverse section, × 50, of dorsal portion of *Nyssa javanica* stone, showing orientation of fibers; locule below. FIG. 24. Transverse section, × 50, through ridge in *N. aquatica* stone, showing histological structure and presence of vascular bundle on crest of ridge.

EYDE, STUDIES OF NYSSACEAE, I



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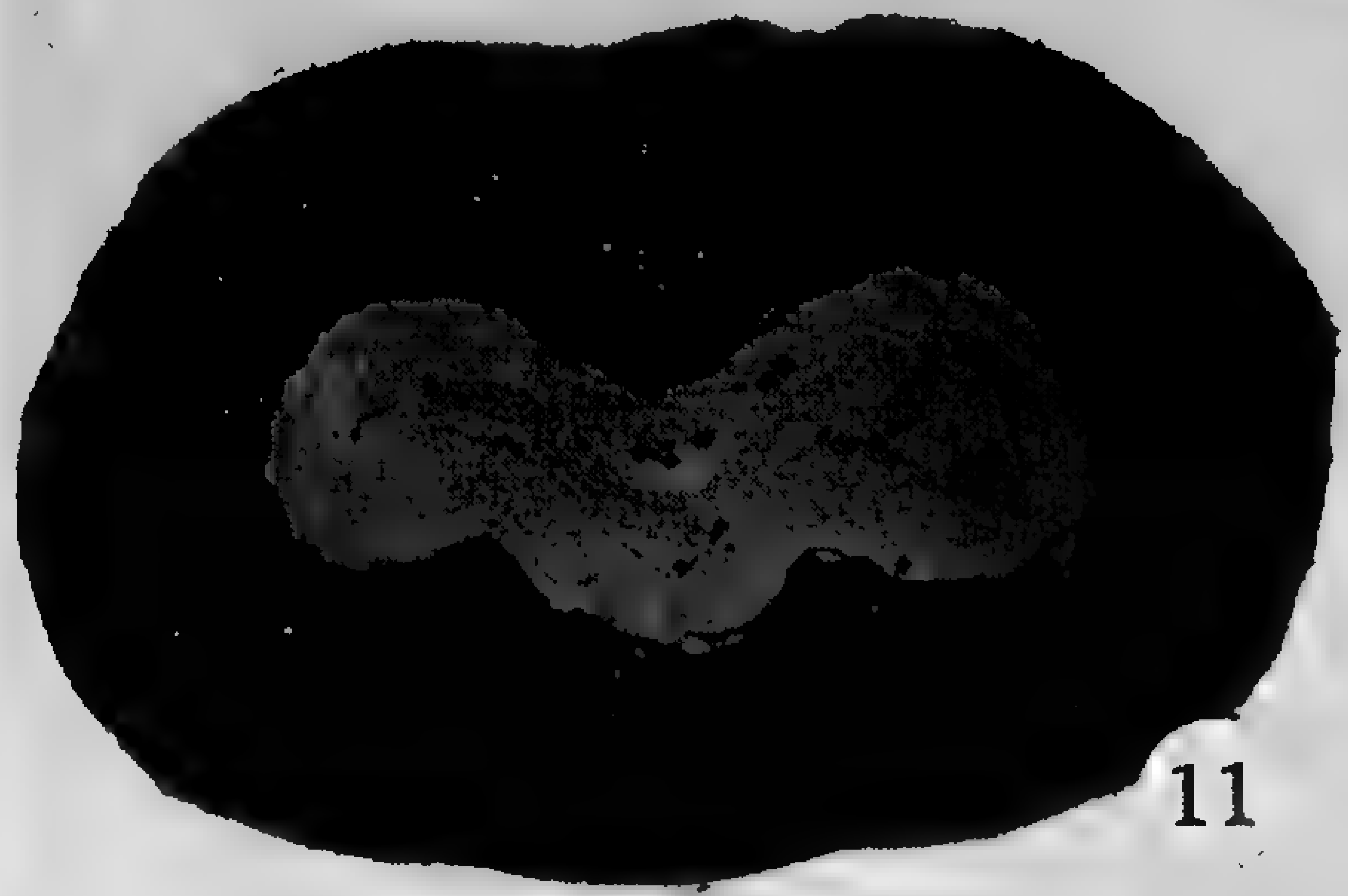

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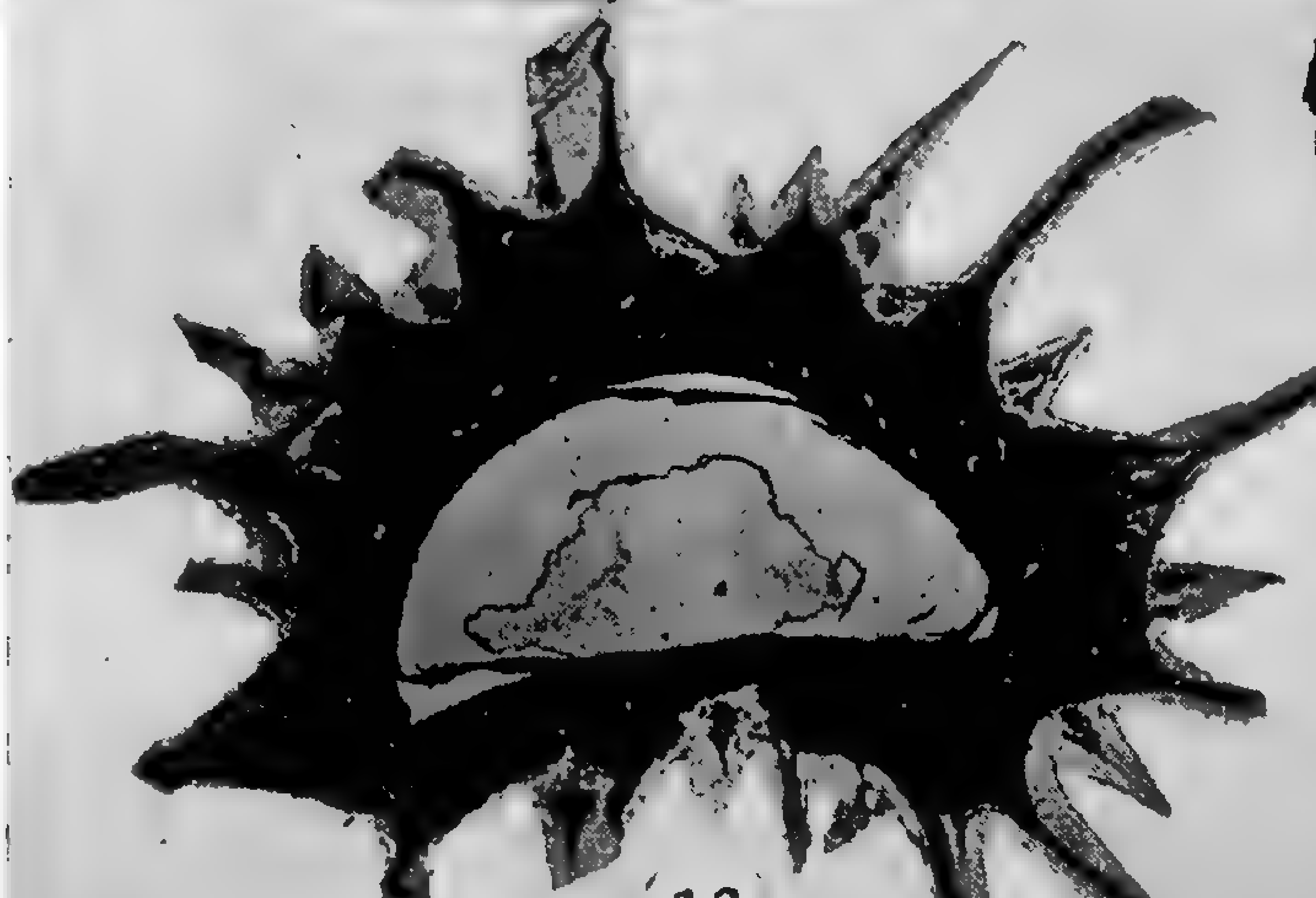

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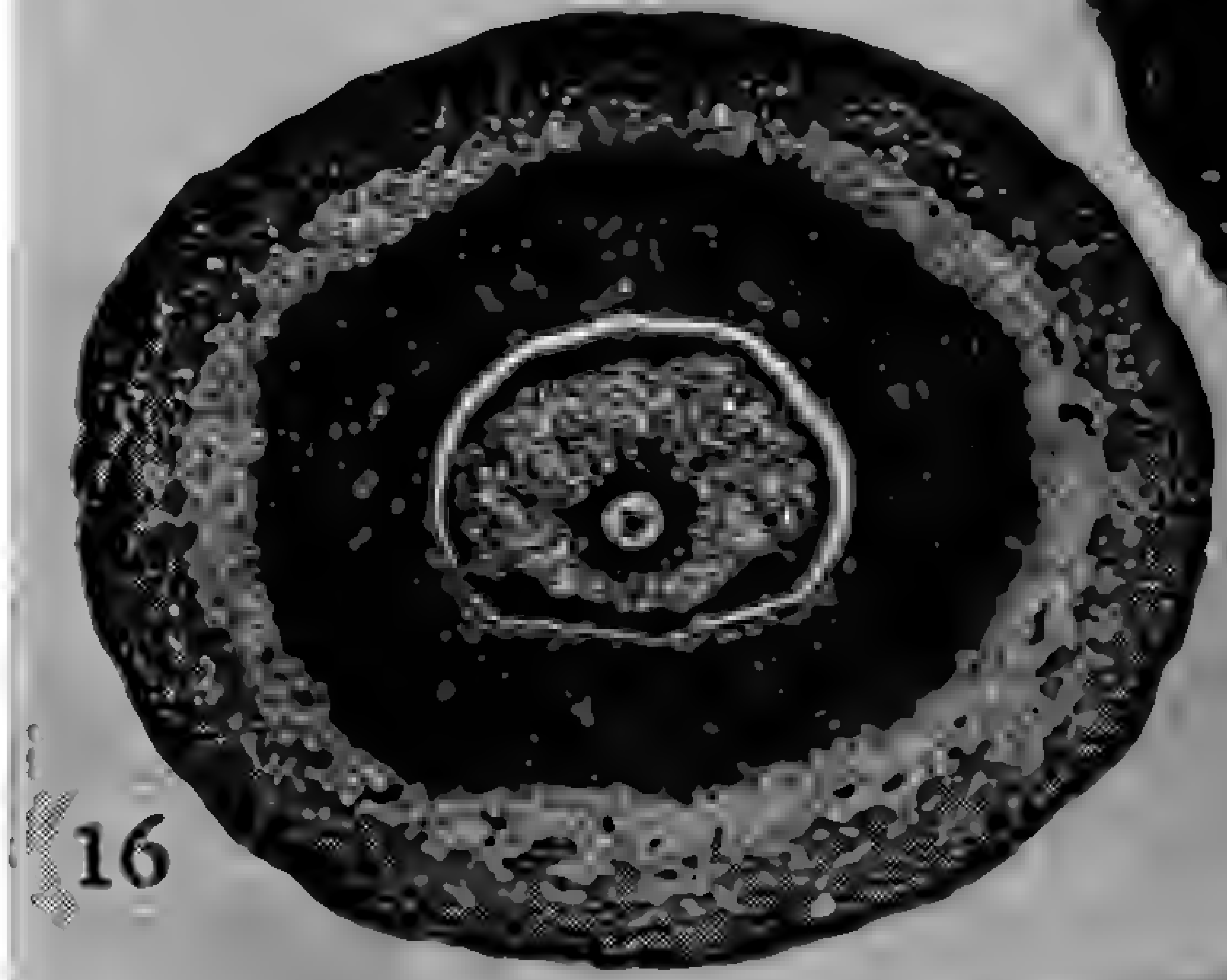

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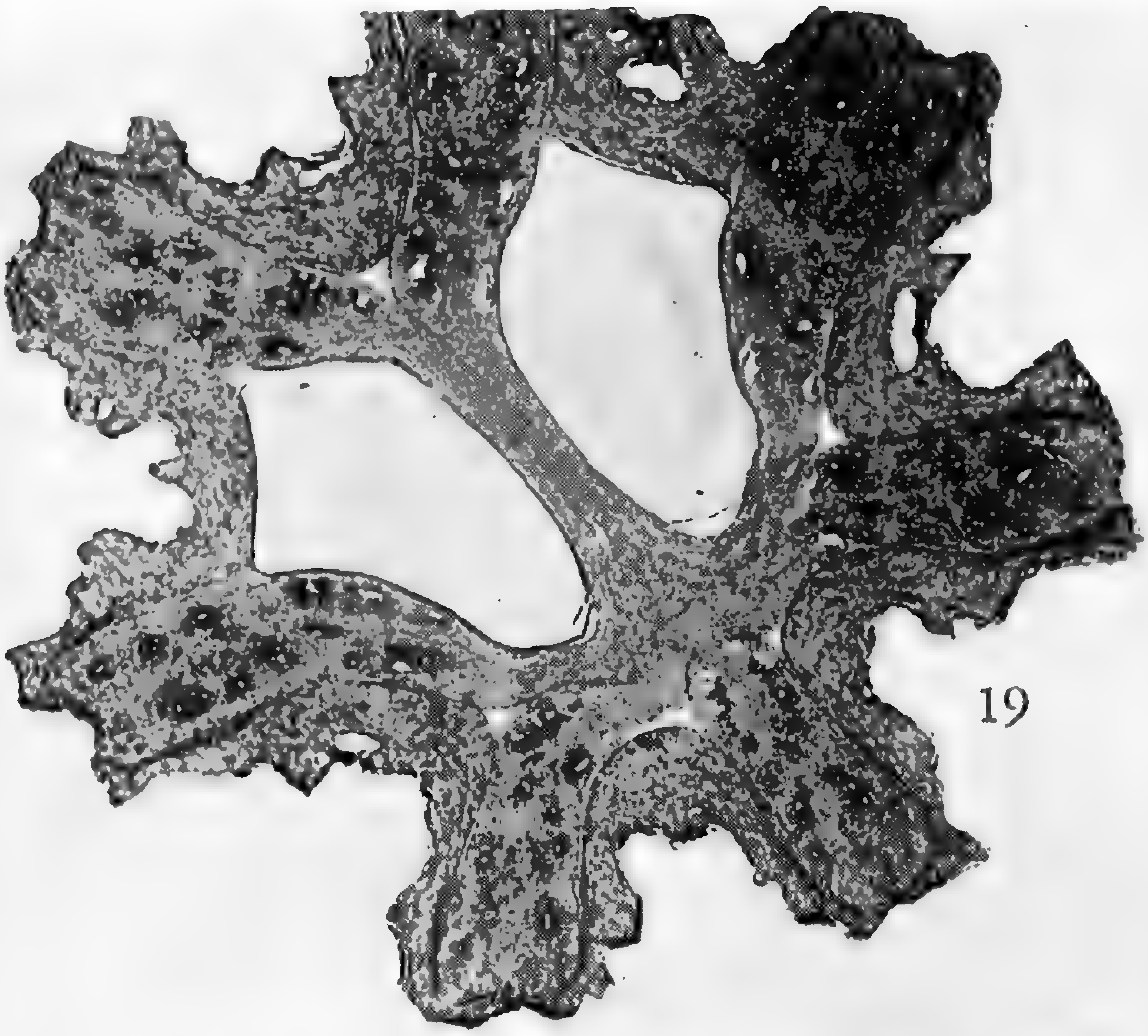

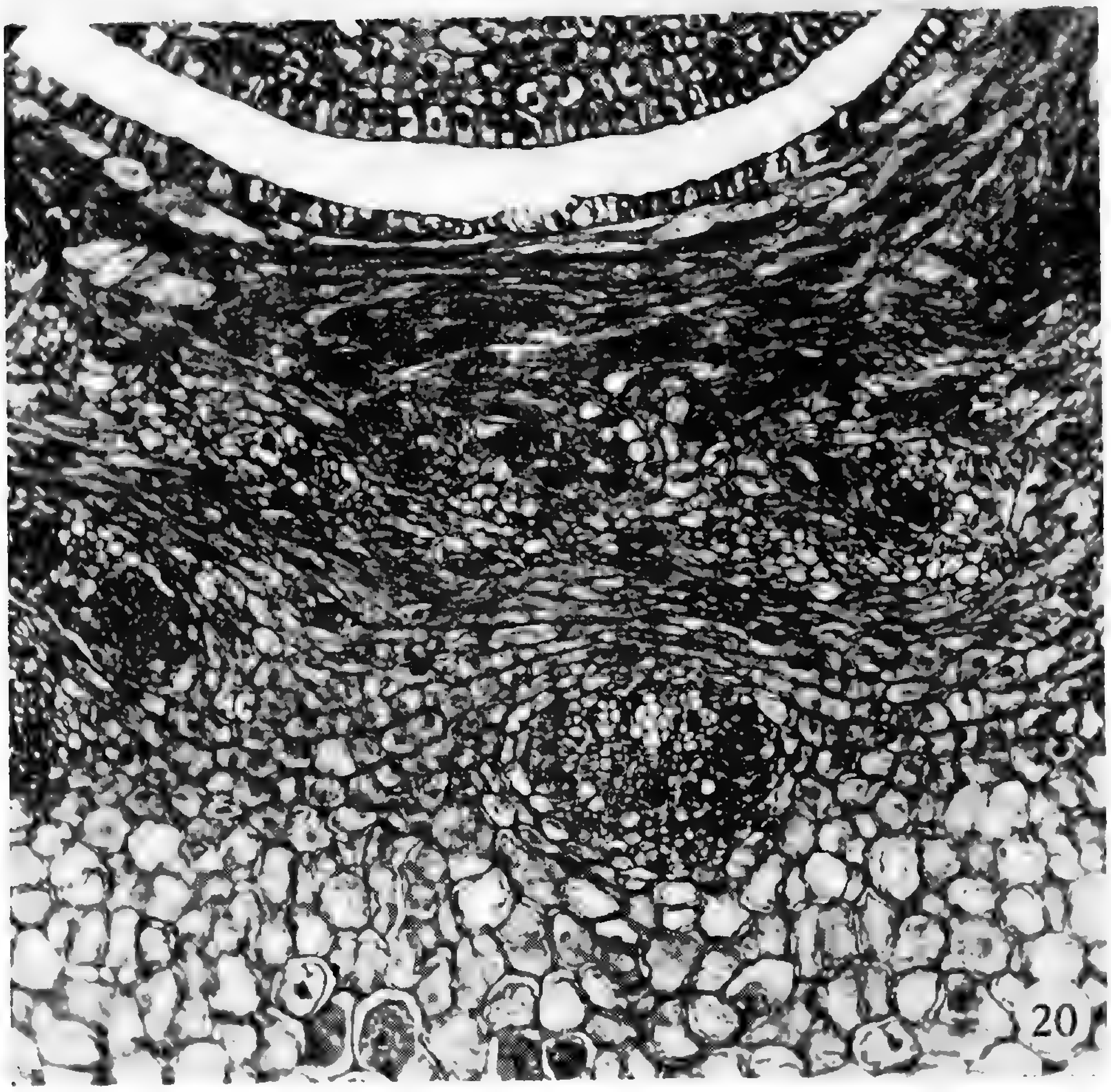

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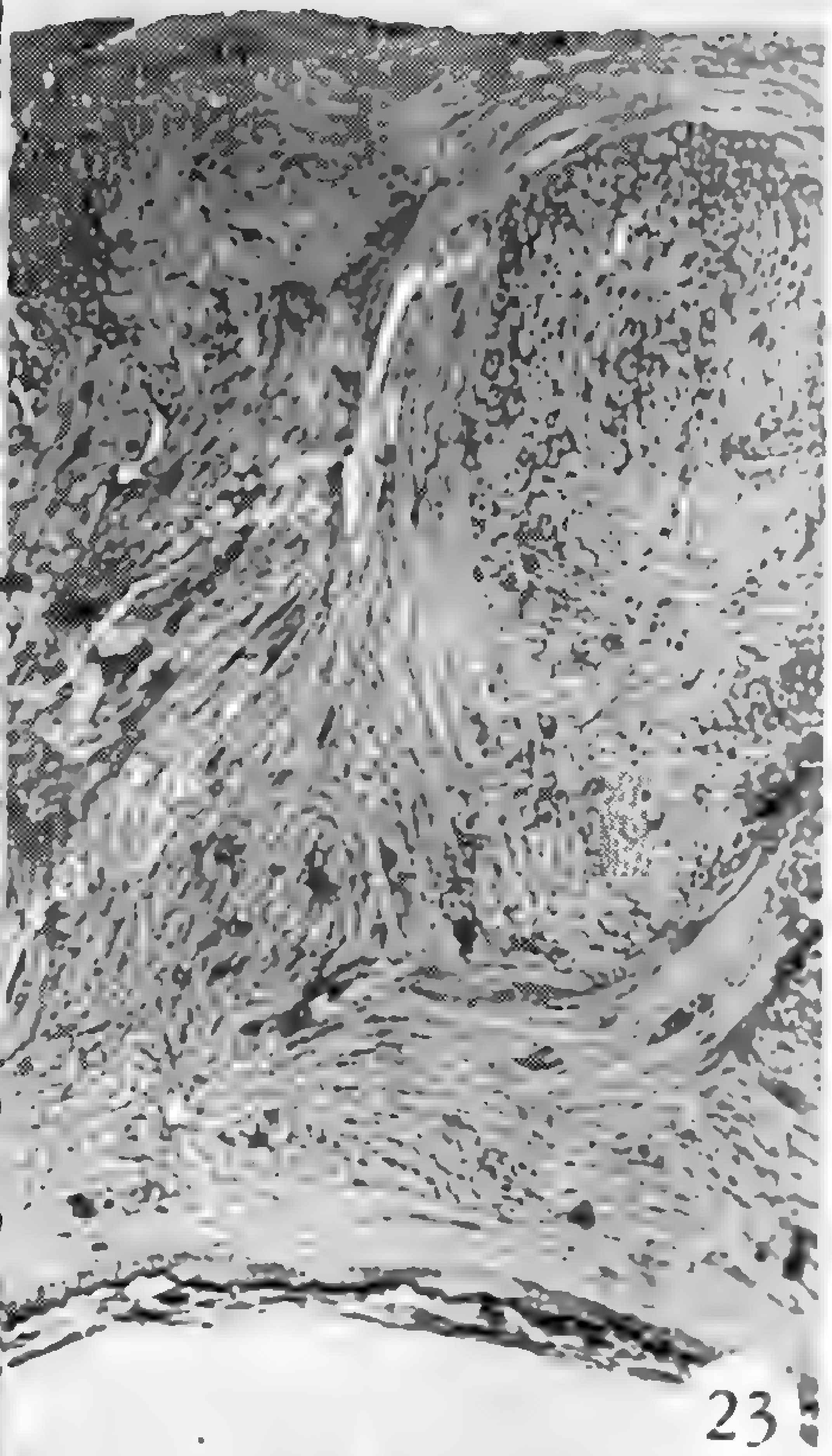
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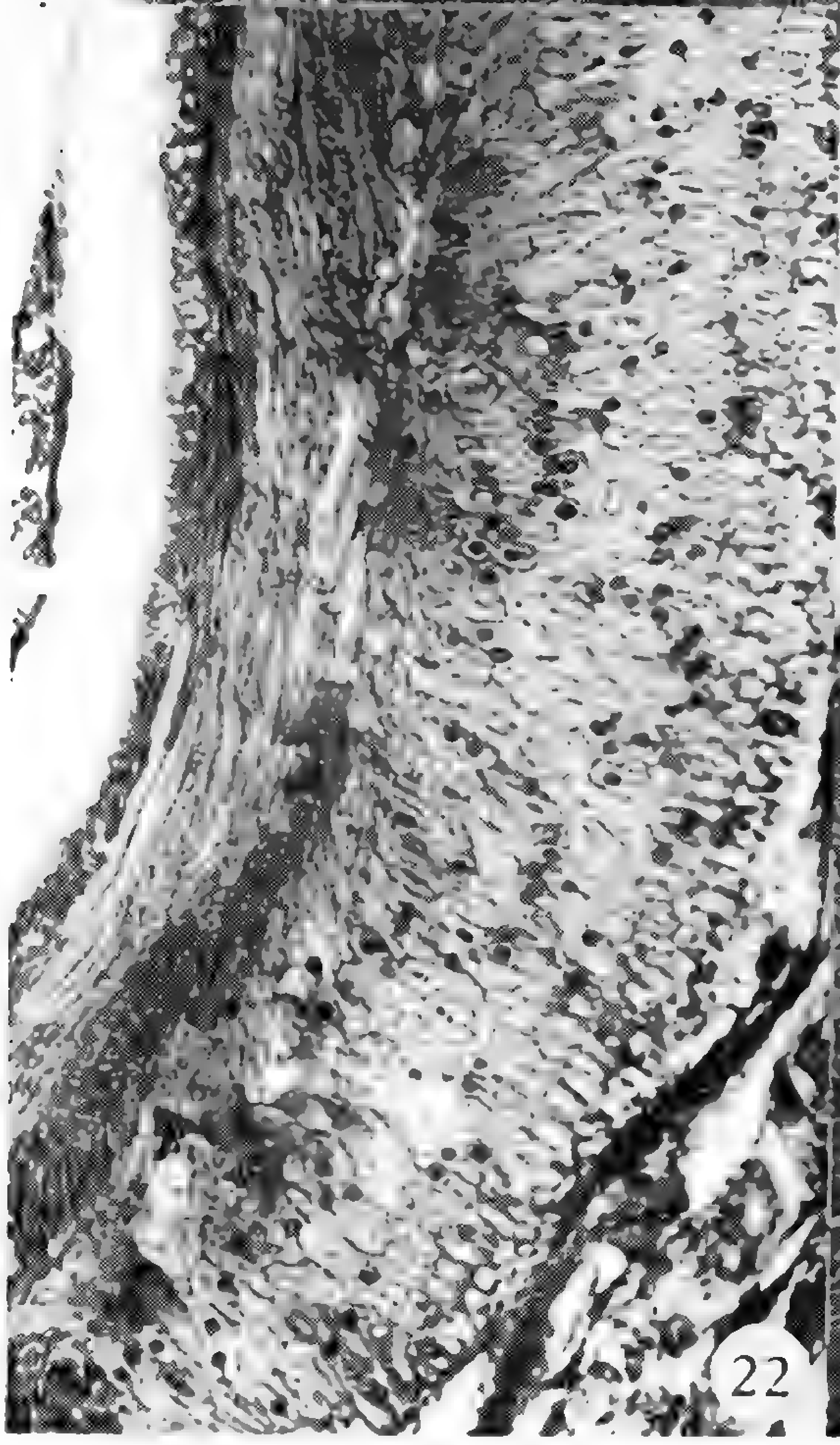
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EYDE, STUDIES OF NYSSACEAE, I

TAXONOMIC AND NOMENCLATURAL NOTES ON THE GENUS RHUS (ANACARDIACEAE) [1]

GEORGE K. BRIZICKY

THERE IS MUCH DISAGREEMENT in regard to the taxonomy of *Rhus* L. in the recent regional floras of North America. While many authors accept Engler's delimitation of the genus and recognize only *Cotinus* Mill. and *Metopium* P. Br. as segregates of *Rhus*, some taxonomists follow Barkley (1937, 1940) either completely or partly in regarding "*Schmaltzia* Desv. [ex Small] emend. Barkley & Reed" and/or *Toxicodendron* Mill. as distinct genera. The interpretation of these groups either as subdivisions of *Rhus* or as separate genera certainly is a matter of personal opinion which would hardly require any additional investigations and discussion if the differences in interpretation only pertained to different evaluations of accurately established facts (characters). However, in the course of surveying the genera of Anacardiaceae in the southeastern United States (see Jour. Arnold Arb. **43**: 359–375. 1962) and examining the herbarium material of *Rhus*, the author found that at least some of the supposed generic differences between *Rhus* and segregated genera are based on incomplete or inaccurate observations. It was therefore thought necessary to check the taxonomic values of differential characters which have been considered basic for the generic segregation of "*Schmaltzia*" and *Toxicodendron* from *Rhus* by examination of more extensive herbarium material and by consulting the literature. A discussion of the results of this effort, the delimitation of the genus *Rhus* L., comprises the first part of the present article; the second part is devoted to the correct name for the group of species segregated as "*Schmaltzia* Desv."

THE GENERIC LIMITS OF RHUS

The genus *Rhus* as established by Linnaeus in 1753 (Sp. Pl. 1: 265–267) and in 1754 (Gen. Pl. ed. 5. 129) comprised *Cotinus, Toxicodendron*, and *Rhus* of Tournefort (Inst. Rei Herb. ed. 2. 1: 610, 611; 3: *pls. 380, 381*). In 1762, Linnaeus (Sp. Pl. ed. 2. 381) also included *Metopium* P. Br. (Civ. Nat. Hist. Jamaica, 177. 1756) in the genus, as *R. Metopium*. Miller (Gard. Dict. Abridg. ed. 4. 1754) first treated the Tournefort genera as distinct, but, in 1768 (Gard. Dict. ed. 8), included *Cotinus*, as well as Browne's *Metopium*, in *Rhus*, retaining *Toxicodendron* as a distinct

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[1] Continuing a series of miscellaneous notes and papers on the flora of the southeastern United States made possible through the interest and support of George R. Cooley and a grant (G–9720) from the National Science Foundation. The author expresses his sincere gratitude to Dr. Carroll E. Wood, Jr., for his critical reading of the manuscript, valuable suggestions, and advice.

genus. Since that time *Cotinus*, *Metopium*, and *Toxicodendron* have been treated by different authors either as subdivisions (sections or subgenera) of *Rhus* or as distinct genera.

Besides these taxa, smaller groups of species of *Rhus* also have been segregated. Thus, in 1819, Rafinesque (p. 357) established the genus *Lobadium*, based on *Rhus aromatica* Ait., distinguishing it from *Rhus* on the basis of its precocious, spikelike inflorescences and a supposed difference in the floral structure, the conspicuous lobes of the nectariferous disc in this species being interpreted by him as "glandular bilobed appendages to the petals." Rafinesque's genus was afterwards recognized as distinct from *Rhus* by several authors (e.g., Greene, 1905; Britton & Brown, 1913; Small, 1933) under its earlier provisional name *Schmaltzia* Desv. In 1838, Torrey and Gray (p. 220) published a new genus attributed to Nuttall, *Styphonia*, based on *S. integrifolia* Nutt. (= *Rhus integrifolia* (Nutt.) Benth. & Hook. f.). This species had "fruit similar in most respects to that of *Rhus* § *Sumac*; inflorescence somewhat approaching that of *Lobadium*; differing from both, particularly in the gradual transition from bracts to petals." Finally, in 1917, Abrams (p. 220) validated Nuttall's *Malosma* (published by Torrey and Gray as a subgenus of *Rhus* in 1838) and segregated it from *Rhus*; later, however, he (1951, p. 51) included *Malosma* in the latter.

In the most important recent work on the American species of *Rhus* and its immediate allies, Barkley (1937) treated *Cotinus*, *Metopium*, *Rhus*, *Toxicodendron*, *Malosma*, and the earlier segregated *Actinocheita* Barkley as distinct genera. The group known as "*Schmaltzia* Desv." was emended by Barkley to include *Lobadium* Raf., *Styphonia* Nutt., *Rhoeidium* Greene, and other closely related species and was treated as a subgenus of *Rhus*. In 1940, however, apparently under the influence of Heimsch's work (1940) on wood anatomy and pollen morphology of *Rhus* and allied genera, Barkley and Reed segregated "*Schmaltzia* Desv. emend. Barkley & Reed" from *Rhus*, as a distinct genus. In contrast with the tendency toward splitting the genus, Perrier de la Bathie (1946, p. 31) included the Madagascan genus *Baronia* Baker (three species) in *Rhus* as a section.

The recognition of the generic status of *Cotinus* and *Metopium* seems to be reasonable (at least at present) and is in agreement with the view of Engler (1881), who certainly was a prominent specialist in the *Rhus* complex, as well as in Anacardiaceae in general. The segregation, however, of "*Schmaltzia*" and *Toxicodendron* as distinct genera appears questionable with regard to the characters on which this segregation has been based. These supposedly generic differences are surveyed and discussed below.

Since the extra-American subdivisions of *Rhus*, sects. *Gerontogeae* Engl. and *Melanocarpae* Engl., are also involved in the discussion, it is expedient for purposes of comparison to regard them as units at the subgeneric level, rather than to compare subgenera with sections. Consequently, the nomenclatural and taxonomic classification of this complex genus as adopted in the present article is given below.

Rhus Linnaeus, Sp. Pl. 1: 265. 1753; Gen. Pl. ed. 5. 129. 1754.

Rhus subgen. **Rhus.** (LECTOTYPE SPECIES: *R. Coriaria* L.; see E. L. Greene, Leafl. Bot. Obs. Crit. 1: 114. 1905.)

Rhus sect. *Sumac* DC. Prodr. **2:** 67. 1825, in part. (LECTOTYPE SPECIES: *R. Coriaria* L.[2])
Rhus subgen. *Sumac* (DC.) Torr. & Gray, Fl. N. Am. **1:** 217. 1838[3]; emend. Schneider, Illus. Handb. Laubholzk. **2:** 153. 1907.
Rhus sect. *Trichocarpae* Engl. Bot. Jahrb. **1:** 379. 1881, in part. (LECTOTYPE SPECIES: *R. Coriaria* L.[2])
Schmaltzia Desv. ex Small, Fl. Southeast. U.S. 727. 1903, in part.

Rhus subgen. **Lobadium** (Raf.) Torr. & Gray, Fl. N. Am. 1: 219. 1838.[3]

Lobadium Raf. Am. Monthly Mag. Crit. Rev. **4:** 357. 1819. (TYPE SPECIES: *Rhus suaveolens* Ait. [*L. amentaceum* Raf. = *R. aromatica* Ait.].)
Rhus sect. *Lobadium* (Raf.) DC. Prodr. **2:** 72. 1825.
Turpinia Raf. Med. Repos. New York II. **5:** 352. 1808, *nomen provisorium.*
Schmaltzia Desv. Jour. Bot. Appl. **1:** 229. 1813, *nomen provisorium.*
Schmaltzia Desv. ex Small, Fl. Southeast. U.S. 727. 1903, in part. (LECTOTYPE SPECIES: *Rhus aromatica* Ait. [*Schmaltzia aromatica* (Ait.) Desv. ex Small] see E. L. Greene, Leafl. Bot. Obs. Crit. **1:** 129. 1905.)
Schmaltzia Desv. [ex Small] emend. Barkley & Reed, Am. Midl. Nat. **24:** 647, 672. 1940.
Rhus subgen. *Schmaltzia* Schneider, Illus. Handb. Laubholzk. **2:** 148. 1907; emend. Barkley, Ann. Missouri Bot. Gard. **24:** 341. 1937. (LECTOTYPE SPECIES: *R. aromatica* Ait.; see Barkley, *loc. cit.*)
Rhus sect. *Trichocarpae* Engl. Bot. Jahrb. **1:** 379. 1881, in part.

Rhus subgen. **Toxicodendron** (Mill.) K. Koch, Hort. Dendr. 197. 1853; emend. Schneider, Illus. Handb. Laubholzk. 2: 149. 1907.

Toxicodendron Mill. Gard. Dict. Abridg. ed. 4. 1754, in part. (LECTOTYPE SPECIES: *Rhus Toxicodendron* L.; see O. Kuntze, Rev. Gen. Pl. **1:** 153. 1891.)
Rhus L. sensu Small, Fl. Southeast. U.S. 726. 1903.
Rhus sect. *Sumac* DC. Prodr. **2:** 67. 1825, in part.
Rhus sect. *Trichocarpae* Engl. Bot. Jahrb. **1:** 379. 1881, as to *R. trichocarpa* Miq.

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[2] In order to fix the application of all of the names involved, lectotype species have been chosen in instances in which the author of a name did not indicate the type species or in those apparent instances in which no lectotype has been designated previously.

[3] When applying the Torrey and Gray (1838–1843) and Gray (Manual, eds. 1–5, 1848–1869) names for the subdivisions of the genera, one should bear in mind that these authors consistently employed the sectional mark (§) followed by a Latin name (noun) for indication of the "Divisions of the highest rank or *Subgenera*" (Gray, 1869, p. 17). The sectional mark without an accompanying name was used to mark a lesser, informal category. It is notable, and somewhat confusing, that in the English text Torrey and Gray used the word "section" both for the indication of a *subgenus* and in an informal sense, in contrast to contemporary French botanists who sometimes translated the Latin *sectio* as "sous-genre."

Rhus sect. *Venenatae* Engl. *loc. cit.* (LECTOTYPE SPECIES: *R. Toxicodendron* L.[2])

Rhus subgen. **Malosma** Nutt. ex Torr. & Gray, Fl. N. Am. 1: 219. 1838.[3] (TYPE SPECIES: *R. laurina* Nutt. ex Torr. & Gray.)

Malosma Nutt. ex Abrams, Fl. Los Angeles [ed. 3.] 220. 1917.

Rhus subgen. **Thezera** (DC.) K. Koch, Hort. Dendr. 197. 1853.

Rhus sect. *Thezera* DC. Prodr. **2:** 72. 1825. (LECTOTYPE SPECIES: *R. pentaphylla* (Jacq.) Desf. [*R. Thezera* Pers.].[2])

Rhus sect. *Sumac* DC. *loc. cit.* 67, in part.

Rhus sect. *Gerontogeae* Engl. Bot. Jahrb. **1:** 379. 1881. (LECTOTYPE SPECIES: *R. pentaphylla* (Jacq.) Desf.[2])

Searsia Barkley, Am. Midl. Nat. **28:** 472. 1942. (Based on *Rhus* sect. *Gerontogeae* Engl.)

Rhus subgen. **Melanococca** (Blume) Brizicky, stat. nov.

Melanococca Blume, Mus. Bot. Lugd.-Bat. **1:** 236. 1850 (fide Engler, Bot. Jahrb. **1:** 380. 1881, et in DC. Monogr. Phaner. **4:** 450. 1883). (TYPE SPECIES: *M. tomentosa* Blume = *Rhus retusa* [var.] β, *Blumei* Engl. = *R. taitensis* Guill.)

Rhus sect. *Melanocarpae* Engl. Bot. Jahrb. **1:** 380. 1881. (LECTOTYPE SPECIES: *R. taitensis* Guill.[2])

Duckera Barkley, Am. Midl. Nat. **28:** 472. 1942. (Based on *Rhus* sect. *Melanocarpae* Engl.)

Rhus and "Schmaltzia"

Barkley (1940) mentioned the following characters as basic for separation of the two genera.

RHUS	"SCHMALTZIA"
1. Inflorescence a compact, many-flowered thyrse, appearing after the leaves; each flower subtended by a lanceolate, caducous bract; bractlets wanting.	1. Inflorescence a group of spikes or less commonly a group of racemes; each flower subtended by a persistent bract and two similar bractlets.
2. Shrubs and small trees, erect; branches usually few, and rather thick.	2. Shrubs and small trees, several subscandent; branches many, slender.
3. Resin canals absent in the wood rays, the latter from two to four cells wide.	3. Resin canals present in the wood rays in two species studied by Heimsch (1940), the rays one to two cells wide.
4. Surface of pollen grains reticulate or striate.	4. Surface of pollen grains generally smooth, striations when occurring faint and widely spaced.
5. Pubescence on fruits of red glandular hairs intermixed with deeply red-stained nonglandular hairs.	5. Pubescence on fruits of red glandular hairs intermixed with hyaline nonglandular hairs.

INFLORESCENCE. The type of inflorescence, thyrsoid in *Rhus* and usually indeterminate in *Schmaltzia*, seems to be the most conspicuous and perhaps the most important character distinguishing these groups. The latter type of inflorescence is, however, easily derivable from the former by reduction and contraction. The occurrence of "a terminal open thyrse" (and caducous bracts and bractlets) in *S. Lentii* (Kellogg) Barkley (= *Rhus Lentii* Kellogg), a species supposed to be a "primitive type" in the segregate genus, confirms the preceding statement and shows a possible connecting line between *Rhus* and *Schmaltzia*. It is notable also that minute and caducous bractlets are usually present in *Rhus*, too, although they are not easily detectable because of their small size and the complexity of the inflorescence. Even in regard to the time of flowering there is no sharp line between the two taxa, since many species of *Schmaltzia* (§§ *Pseudosumac*, *Styphonia*, and *Pseudoschmaltzia* of Barkley) possess at least coetaneous inflorescences.

The somewhat different habit, although of diagnostic value, can hardly be of generic significance.

ANATOMY. The significance of the presence or absence of resin ducts in the wood rays (if a constant character) in the taxa involved can only be determined from an extensive study of *Rhus*, *sensu lato*. The presence of resin ducts in wood rays in three of four investigated species of the Indo-African-New Guinean subgen. *Thezera* (*Rhus* § *Gerontogeae* Engl.) has been recorded by Heimsch (1940). Thus this character does not seem to be constant even in that very natural group. The width of wood rays (two to four cells in *Rhus* against one to two cells in *Schmaltzia*) can hardly be considered a reliable character in *Rhus*, since in this genus it seems to be liable to variation even within a species. Thus, Kanehira (1921a, b) describes wood rays in *R. javanica* L. (*R. chinensis* Mill.) as "1–5 cells wide, 10–30 cells high" in wood from Formosa, and "1 or 2 sometimes 3 cells wide, up to 55 cells high" in specimens from Japan. Gammerman *et al.* (p. 46) characterize wood rays of *R. typhina* L. as being one or two cells wide and up to 20, more rarely 30–40, cells high. In addition, Heimsch (1942, p. 141) wrote of the anatomical evidence for the generic segregation of *Schmaltzia* that "*Schmaltzia* is too poorly represented in available wood collections to test properly the validity of this proposal from the standpoint of xylem structure."

POLLEN. Heimsch (*loc. cit.*) was, however, of the opinion that "evidence from pollen morphology supports such a change [segregation of *Schmaltzia*] [for,] pollen grains of species of *Rhus* possess a sculptured exine [reticulate or striate] in contrast to the usual smooth, unsculptured [rarely faintly striate] pollen grains of *Schmaltzia*." This statement may be objected to on at least two bases, however. First, the taxonomic value of the surface character of pollen grains in general (like the value of many other endo- and exomorphic characters) may not be assumed *a priori* but must be accurately determined in each individual case since it may vary in different groups of affinity. This problem can hardly be solved at present since it requires not only additional and more extensive palynological data, but also data from other branches of botany, especially from floral ontogeny and biology, and ecology of the species. Second, neither Heimsch (1940, 1942) nor Barkley (1940), who applied Heimsch's data for the generic segregation of "*Schmaltzia*," has shown that reticulate, striate, faintly striate, and smooth pollen grains cannot occur within the limits of a genus. Indeed, the data compiled from Wodehouse (1935), Erdtman (1952), and Ikuse (1956) demonstrate that a situation in regard to the sculpturing of pollen grains similar to that in *Rhus* can be found in at least several very natural genera, e.g., *Rosa*, *Acer*, and *Viola*. Thus, seven species and one variety of *Rosa* listed by Ikuse (p. 91) have "fine reticulate" pollen; however, the texture of exine is striate "vaguely suggesting the markings of a fingerprint" in *R. rugosa* Thunb., *R. bracteata* Wendl., *R. centifolia* L., and *R. rubiginosa* L. (= *R. Eglanteria* L. fide Fernald), and is variously granular in *R. setigera* Michx., *R. multiflora* Thunb., and *R. Noisettiana* Thory (*R. chinensis* × *moschata*) (Wodehouse, 1935, p. 428). Pollen grains in 17 Japanese species of *Acer* listed by Ikuse (*loc. cit.*, pp. 101, 102) are "striato-fine reticulate" (in 12 species) or striate (in four species and two varieties) or spinulose (in *A. carpinifolium* Sieb. & Zucc.). According to Wodehouse's data on pollen of the same genus, the exine is distinctly striate in *A. Pseudo-Platanus* L. and *A. platanoides* L., less distinctly striate in *A. rubrum* L., extremely faintly striate, sometimes only granular, in *A. saccharum* Marsh., and smooth with a granular texture in *A. Negundo* L. (Wodehouse, *loc. cit.*, pp. 439–442). Finally, in the genus *Viola*, 30 species listed by Ikuse (pp. 106, 107) have "fine reticulate" pollen grains, but seven species mentioned by Wodehouse (*loc. cit.*, p. 443, e.g., *V. palmata* L., *V. cucullata* Ait., *V. conspersa* Reichenb.) and several Hawaiian species of *Viola* (Selling, pp. 117–120) possess a smooth, granular exine.

From the above-mentioned examples, the conclusion may be drawn that pollen grains with a reticulate, striate, faintly striate, and smooth surface may occur within the limits of a natural genus (e.g., *Rosa*, *Acer*, *Viola*) and the smoothness of pollen surface in most species of "*Schmaltzia*" may hardly be regarded as a character of generic significance. As in the genus *Acer* where the extremely faintly striate, sometimes only granular, pollen grains of *A. saccharum* are intermediate between the striate pollen of some species of *Acer* (e.g., *A. Pseudo-Platanus*, *A. rubrum*) and the smooth pollen of *A. Negundo*, the faintly striate pollen grains of some species of *Schmaltzia* § *Styphonia* (including *R. Lentii* with its thyrsoid inflorescences with caducous bracts and bractlets) may be regarded as transitional between the (finely) reticulate or striate pollen grains of *Rhus* and the usually smooth pollen of "*Schmaltzia*."

FRUIT. In fruit structure *Rhus* and "*Schmaltzia*" agree to a great extent, the exo- and mesocarp usually being permanently united and easily detachable from the bony endocarp. In a few species of "*Schmaltzia*," however, the inner layers of mesocarp, striate with conspicuous resin ducts, remain attached to the stone thus simulating (always?) fruits of species of *Toxicodendron*. Even the pubescence on fruits of *Rhus* and *Schmaltzia* is of the same kind, consisting of amber-colored to reddish-brown glandular hairs with a short unicellular stalk and a multicellular, usually ellipsoidal, obovate to club-shaped head and often also of red to colorless nonglandular hairs. So, for example, the nonglandular hairs on the fruit coat are deeply red stained in *R. typhina*, *R. glabra* L. and *R. Michauxii* Sarg., but are colorless in *R. copallina* L.; on the other hand, the nonglandular pubescence on fruits of *Rhus* (*Schmaltzia*) *aromatica* consisting largely of colorless hairs always includes at least a small number of red-stained hairs.

Since the characters distinguishing *Schmaltzia* from *Rhus* do not appear to be of generic significance, and apparent transitions between these groups in inflorescence type (*S. Lentii*) and sculpture of pollen grains (*Schmaltzia* § *Styphonia*) do occur, a close relationship between these groups so clearly displayed in the similar flower and fruit structures can be best expressed by considering *Schmaltzia*, under its correct name *Lobadium* Raf., a subgenus of *Rhus*.

Rhus and Toxicodendron

The following characters are usually considered to be of importance for separation of these groups as distinct genera.

RHUS	TOXICODENDRON
1. Inflorescences terminal thyrses.	1. Inflorescences axillary panicles.
2. Fruits reddish or red, always glandular-pubescent; exocarp and nonwaxy mesocarp permanently united and separating from the smooth stone.	2. Fruits greenish or yellowish white to dun colored, never glandular-pubescent; exocarp fragile, breaking and exposing waxy mesocarp remaining attached to the usually ± ribbed stone.
3. Resin nonpoisonous.	3. Resin consistently poisonous.
4. High content of tannins.	4. Low content of tannins.
5. Vessels clustered in late wood; resin ducts present in the wood rays of some species; septate wood fibers absent.	5. Vessels not clustered in late wood; resin ducts absent in the wood rays; septate wood fibers present.
6. Pollen grains ellipsoidal, the longer axis 31–43 μ long.	6. Pollen grains spherical, about 29 μ in diameter.
7. Root hairs tawny pink or lighter (Gillis, 1961).	7. Roots hairs dark brown in American species (Gillis, 1961).

INFLORESCENCE. There is no basic difference in the type of inflorescence between the two groups. The "panicles" of *Toxicodendron* are thyrses (although sometimes considerably reduced and appearing almost racemose) as has already been stated by Copeland and Doyel (p. 933) for *Rhus* (*Toxicodendron*) *diversiloba* T. & G. The taxonomic significance of the terminal or axillary position of these inflorescences is obscure and seems to decrease in value when the distribution of this character within *Rhus* as a whole is taken into consideration. Thus, although terminal inflorescences seem to be the rule in subgen. *Rhus*, in *R. Coriaria* additional inflorescences sometimes develop in the axils of the upper two to six leaves (e.g., in a few specimens seen from Iraq, Palestine, and the USSR [A, GH]). The occurrence of terminal and/or axillary inflorescences in subgen. *Lobadium* has already been mentioned (see Jour. Arnold Arb. **43**: 371. 1962). In South African species of the very extensive subgen. *Thezera*, mostly both terminal and axillary inflorescences occur within a species. However, in some (e.g., *R. tomentosa* L., *R. incisa* L. f., *R. Keetii* Schonl.) terminal inflorescences, in others (e.g., *R. horrida* Eckl. & Zeyh., *R. natalensis* Bernh., *R. albomarginata* Sond.) axillary inflorescences seem to be constant. In *R. Legatii* Schonl., staminate and carpellate plants differ in this respect, the former usually bearing terminal, the latter mostly axillary inflorescences (Schonland, p. 51).

In *Rhus taitensis*, of the southwestern Pacific subgen. *Melanococca* (*Rhus* § *Melanocarpae*), terminal inflorescences, sometimes accompanied by a few additional axillary inflorescences in the axils of the upper leaves, are most usual. However, in some specimens from Fiji (e.g., *A. C. Smith 6792* [A], *Gillespie 4167* [GH]) only axillary inflorescences have been seen. Also, the original description of *R. simarubifolia* A. Gray (usually included in *R. taitensis*) notes, "Panicles axillary, rather shorter than the leaf, loosely flowered" (Gray, 1854, p. 368). Gibbs (p. 144), too, characterized the latter species as "A very handsome tree, 17 m. high, with white trunk and flat crown. The erect, axillary racemes of white flowers are very freely produced, and stand well above the pinnate leaves." It is possible that in *R. taitensis* terminal or axillary inflorescences can occur on different branches of the same plant, since *Gillespie 4162* (GH) from Fiji is represented by two branchlets, one with a single axillary inflorescence, the other with a terminal infructescence.

Although in *Toxicodendron* the axillary inflorescences seem to be fixed (the occurrence of axillary and terminal inflorescences in *R. perakensis* Scortechini ex King, mentioned by King (p. 500), should, however, be checked), this good diagnostic character alone can only be regarded as of questionably generic significance in view of the distribution of axillary inflorescences within the genus *Rhus* as a whole.

FRUITS. The fruits of *Toxicodendron* are said to differ essentially from those of *Rhus* in their color; in the lack of glandular pubescence on the fruit coat; in the exocarp separating from the mesocarp; and in the waxy mesocarp adherent to the usually ± ribbed stone. The color of fruits varies in *Toxicodendron* from greenish- or yellowish-white to tan. However, in *Rhus, sensu stricto,* the color of the fruit coat is not always red or reddish as could be assumed from descriptions which indicate a visual effect of the red or reddish nonglandular pubescence covering the fruit, rather than the color of exocarp. The exocarp varies in the species of subgen. *Rhus* (and subgen. *Lobadium*) from red or orange (e.g., *R. glabra*, *R. Michauxii*) to different shades of brown (e.g., *R. Coriaria*, *R. copallina*, *R. javanica*, *R. punjabensis* Brandis, thus overlapping some species of *Toxicodendron* with brown fruits (e.g., *R. Griffithii* Hook. f.). It is also notable that the field data accompanying the specimen *Purseglove 4440* (A) of *Rhus* (*Toxicodendron*) *perakensis* from Borneo indicate "fruits red drying glossy buff." Although color of the fruit may be regarded as a good diagnostic character on the specific level, it can hardly be useful for distinguishing larger groups because of its variation within the subdivisions and the degree of overlap.

The glandular pubescence on the fruit coat, consisting of amber-colored to reddish-brown hairs with a short unicellular stalk and multi-cellular head, is quite characteristic of the subgenera *Rhus* and *Lobadium* (in which it also occurs on the other parts of the plant body), and does not occur on fruits in *Toxicodendron* or in the subgenera *Thezera* and *Melanococca*. It is notable, however, that morphologically similar, but minute, hairs have been recorded by McNair (1921, p. 137, *pl. 2, F*) in *R.* (*Toxicodendron*) *diversiloba* where "they are found mostly on the young rapidly growing organs of the plant, especially on the floral region and the leaves, less on the green stems and hardly at all on the woody portions." Copeland and Doyel (p. 934) observed such hairs also on the ovaries of the same species. Möbius (p. 213, *fig. 7, III*) described and illustrated a similar glandular hair from the leaf of *R.* (*Toxicodendron*) *verniciflua* Stokes ("*R. vernicifera* DC."). In South African species of subgen. *Thezera*, where the glandular pubescence of the vegetative organs reaches the maximum of its morphological diversity and complexity within *Rhus*, species with transitory or persistent glandular pubescence are known. However, glandular-pubescent ovaries (but glabrous fruits) have been recorded only in *R. Steingroeveri* Engl. (Diels, p. 592). From this brief and superficial survey one may conclude that, although the taxonomic significance of glandular pubescence on fruits of species of the subgenera *Rhus* and *Lobadium* cannot be evaluated at present, this character appears to be of a certain diagnostic value.[4]

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[4] The diagnostic value at the specific level seems to be evident from the following examples based on the author's observations and some data from the literature on the morphology of nonglandular, uniseriate, "acid" hairs which cover fruits in *Rhus glabra*, *R. Michauxii*, *R. typhina*, and *R.* × *pulvinata* Greene (including *R. glabra* var. *borealis* Britt.). These hairs are of the same morphological structure in *R. glabra* and *R. Michauxii*, being 3–several-celled, about 0.3 mm. long, stout, usually club shaped or elliptical, rounded at the top (cf. Barkley, 1938, p. 600, *fig. 2a*; Gleason, p. 497, *fig.* ref. to *R. glabra*). The homologous hairs in *R. typhina* are several-celled, about 2–3 mm. long, fine, gradually tapering to a usually sharp point (cf. Barkley, 1938, p. 600, *fig. 2d*; Gleason, p. 497, *fig.* ref. to *R. typhina*). In his treatment of *Rhus*, Barkley (1937, p. 326) stated concerning its relationships, "*Rhus Michauxii* is a very distinct species whose closest affinities seem to be with *R. javanica* L. and *R. Coriaria* L. of Asia and Europe." However, the occurrence of morphologically similar hairs in both *R. Michauxii* and *R. glabra* seems to speak for a closer relationship of the former with

Fruit histology seems to be basically the same in all the subdivisions of *Rhus*. The exocarp is always formed by a single cell layer. The mesocarp is predominantly parenchymatous or parenchymatous throughout and is traversed by vascular bundles usually accompanied with resin ducts. The endocarp is usually hard, composed of four cell layers: an outermost parenchymatous, crystal-bearing layer, followed by the three layers of radially oriented columnar sclereids the innermost layer of which consists of the longest and the middle layer of the shortest cells (Möbius, pp. 239–242, *fig. 29*, for *R. verniciflua*; Copeland & Doyel, pp. 936, 937, *figs. 38, 39*, for *R. diversiloba*).

While the histological structure of the endocarp seems to be almost invariably the same in all the subdivisions of *Rhus*, that of the mesocarp appears to be somewhat different, not only in the representatives of different subdivisions, but also in the species belonging to the same group. Thus, the mesocarp in *R. Coriaria* has been described (Reboul, pp. 39, 40) as parenchymatous throughout and only slightly heterogeneous, its layers adjacent to the endocarp being composed of cells differing only in the brightness of their walls ("à parois mince et très claires") from those forming the bulk of mesocarp and having the cell walls very refringent ("à parois minces et très refringentes"). In *R. glabra*, however, the two zones of the mesocarp are sharply defined; the inner zone (adjacent to the endocarp) differs from the outer in its yellowish color, greater fragility, and presence of "small stone cells" (Youngken, p. 530). This difference between the two zones of mesocarp is so well marked that Youngken (*loc. cit.*) apparently mistook the inner zone of the latter for the endocarp, regarding the true endocarp as a "very hard" seed coat. In some species of *Toxicodendron* (e.g., *R. diversiloba*, *R. radicans* L., *R. Vernix* L.) the parenchymatous mesocarp seems to be homogeneous, consisting of cells filled with "wax," while in other species (e.g., *R. Griffithii*, *R. insignis* Hook. f.) the outer layers of parenchyma differ from the inner in the absence of "wax" in their cells. In *R. verniciflua* (Möbius, p. 240), and probably in all the other species of *Toxicodendron*, the two or three innermost layers of mesocarp are formed by small, roundish sclereids (cf. *R. glabra*, above). Apparently the histological peculiarities of the fruits in *Rhus*, *sensu lato*, are responsible for the fruit characters on which Engler based his sections of *Rhus*. Thus, the fruits of sect. *Trichocarpae* Engl.

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the latter, rather than with the species "of Asia and Europe," which have hairs morphologically different from those of both American species. The occurrence of a fertile, putative hybrid between *R. Michauxii* and *R. glabra* (cf. Ashe, p. 581, "× *Schmaltzia Ashei*") seems to confirm the evidence from the morphology of hairs. Rollins (1944) showed in the case of hybrids between *Parthenium argentatum* A. Gray and *P. incanum* A. Gray that evidence from the morphology of trichomes can present "the primary basis for determination of the hybrids" (p. 98). This seems to be applicable also to the hybrids between *Rhus glabra* and *R. typhina*, "cigar-shaped" hairs on the fruit coats of which appear to be intermediate in their shape and size between those of the supposed parents (cf. Barkley, 1938, pp. 598, 600 *figs. 2b, 2c*). The examples mentioned above demonstrate the probable taxonomic importance of the hair covering in *Rhus* and suggest a careful study of the morphology of hairs in the genus.

(i.e., subgenera *Rhus* and *Lobadium*) have been described as having "Exocarp und Mesocarp bei der Reife im Zusammenhang bleibend und sich vom Endocarp loslösend," while in the sect. *Venenatae*, i.e., *Toxicodendron*, "Das Exocarp bei der Reife sich ablösend . . . Mesocarp dem dicken Endocarp anhängend" (Engler, 1881, p. 379). These characters, however, do not have a general validity either in Engler's *Trichocarpae* or in *Venenatae*. Although in most species of the subgenera *Rhus* and *Lobadium* the exocarp and mesocarp are permanently united and easily separable as a whole from the endocarp, in *R. glabra* only the outer reddish-green zone of mesocarp remains permanently united with the exocarp and separates from the inner yellowish zone which, in turn, detaches easily from the endocarp. Also, in some species of *Lobadium* (e.g., *R. aromatica, R. trilobata* Nutt.) and *Toxicodendron* (e.g., *R. Griffithii, R. insignis*) the outermost layers of mesocarp are permanently united with exocarp and separate themselves from the bulk of the mesocarp (filled with "wax" in the latter group) which remains attached to the stone. In other species of *Toxicodendron* (e.g., *R. diversiloba, R. radicans, R. Vernix*), the exocarp alone separates from the uniformly "waxy" parenchymatous mesocarp. Probably the situation in respect to the fruit characters, similar to that of most species of subgen. *Rhus* (e.g., *R. Coriaria, R. typhina*) exists in subgen. *Melanococca* (*Rhus* § *Melanocarpae*), that of *Toxicodendron* in the species of the subgen. *Thezera* (*Rhus* § *Gerontogeae*).

The character of the stone surface, smooth in subgenera *Rhus* and *Lobadium* and ± ribbed or bumpy in *Toxicodendron*, may be applied as a diagnostic feature only to a limited degree, since the stones in some Asiatic species of the latter (e.g., *R. verniciflua*) are smooth.

This brief survey of the fruit characters shows that the mode of connection and/or separation of the fleshy parts of the pericarp from each other and from the endocarp can hardly be regarded as a reliable differential feature of the subdivisions of *Rhus*; however, knowledge of fruit histology, very fragmentary and inadequate at present, may perhaps be of primary importance for distinguishing the subdivisions and for solution of the problem of their relationships.

CHEMISTRY. The "wax" which occurs within the cells of the mesocarp in *Toxicodendron* and *Rhus* (*Malosma*) *laurina* is a solid fat (tallow) composed of glycerides of fatty acids, mainly of palmitin (in larger amounts) and olein (in smaller amounts); also a small percentage of one or two free, dibasic, high-molecular fatty acids has been found in fat of all the species investigated, except *R. trichocarpa* Miq. (Wehmer, 1911, 450–453; 1935, p. 175; Merck Index, p. 550). The iodine value of this fat varies from 4 to 17 (Long, King & Sperry, p. 988). In contrast to the mesocarp, the seeds contain a semiliquid oil (Wehmer, 1935, p. 175, for *R. succedanea* L.). Unfortunately, only a few incomplete data on the fruit chemistry of the species of subgen. *Rhus* (and none for those of subgenera *Lobadium, Thezera*, and *Melanococca*) have been available. Thus Reboul (p. 50) says about the oil which in the form of droplets fills the cells of the mesocarp and of the seed in *R. Coriaria*, "L'huile de *Rhus coriaria* est composée surtout par 75% d'acide oleique et par 25% d'acides gras solides, appelés industriellement stéarines, formée surtout par l'acide palmitique." The iodine value of this oil (unfortunately a mixture of oils of both the seeds and the mesocarp) is given by Reboul (*loc. cit.*, p. 52) as 83.06. Millspaugh (p. 36-4) mentions the "oil of *Rhus*" saying, "This waxy oil may be extracted from the seeds [fruits?] of this [*Rhus glabra*] and other species of the genus. It will aquire a tallow-like consistence on standing, and can be made into candles, which burn brilliantly, but emit a very annoying pungent smoke." Wiesner (p. 715) in his brief description of the same oil points out a difference between the oil of seeds and mesocarp (?) of fruits saying, "Rhusöl wurde aus den enthülsten Samen von *R. glabra* in einer Ausbeute von 9% erhalten. Es war ein angenehm schmeckendes, eigenartig riechendes, hellgelbes Öl. Auch aus den Samenschalen [mesocarp?] wurde etwas die gleiche Menge Öl gewonnen, das bei gewöhnlicher Temperatur halbfest war." Finally, McNair (1930, p. 49) gives some data on chemical and physical properties of the oil from "kernels" [seeds] of *R. glabra*. This oil belongs to the group of semidrying oils, having an iodine value of 126.9. The big difference between the iodine value of the oil of fruits in *R. Coriaria* (given by Reboul) and that of the oil of seeds in *R. glabra* is notable, but this difference apparently is due to the fact that the iodine value of the oil in the former pertains to the mixture of oils from seeds and mesocarp.

It is known, however, that the fats and/or oils from seeds and mesocarp may be quite different (McNair, 1930, pp. 48, 49; Steele, p. 38), e.g., *Oenocarpus* (Palmae) and *Sapium* (Euphorbiaceae) with oil in seeds, but a solid fat in mesocarp. McNair's survey (1930, pp. 64–68) of the distribution of fats and oils in seeds of the families of the Angiosperms shows that, although in some cases one kind of oil (classified as drying, semidrying, or nondrying) or fat can be characteristic for a subfamily, tribe, or genus, there also are genera in which the species differ in this respect: e.g., seeds with nondrying oil or with a solid fat occur in species of *Coula* (Olacaceae), *Canarium* (Burseraceae), *Polygala* (Polygalaceae), while seeds with semidrying oil or with a solid fat can be found in species of *Laurus* (Lauraceae) and *Luffa* (Cucurbitaceae). Apparently, similar or perhaps more variable conditions can be expected in regard to the distribution of oils and fats in the mesocarp of fruits in the Angiosperms. Although the chemical nature of fats and oils occurring in seeds and mesocarp of the species of the *Rhus* complex may certainly be of taxonomic importance as are many other biochemical characters, the taxonomic significance of this feature cannot be evaluated at present because of lack of adequate and comparable data. We even may hardly assert that solid fat is completely absent from subgenera *Rhus* and *Lobadium*, as well as *Thezera* and *Melanococca*.

A resin constantly poisonous because of the presence of toxic catechols (Gillis, 1961, p. 30) has been assumed to be one of the most distinguishing features of *Toxicodendron* in contrast to the nonpoisonous resin of all the other groups of *Rhus*. Four poisonous substances identified "as variations in saturation of the alkyl side chain in 3-*n*-pentadecylcatechol" have been found in *Rhus* (*Toxicodendron*) *radicans* L. "The Japanese lac tree (*T. vernicifera*) differs in poison chemistry in only one of the four poisons. . . . There is some evidence that the chemistry of the poisons in poison sumac is different from that of poison ivy" (Gillis, *loc. cit.*). While the resin of the species of *Toxicodendron* has been the subject of frequent and thorough investigations for at least several decades, there are no data available concerning the chemical nature of the resin in any of the other groups of *Rhus*. Therefore, no conclusions can be drawn on the degree of chemical relationship of the resins in the groups involved or on the taxonomic significance of this character. It is notable, however, that *R. punjabensis* Steward ex Brandis (subgen. *Rhus*) is still regarded as very poisonous. "The juice of this tree is corrosive and vesicant. For this reason it is not cut or hacked wantonly" (Chopra, Badhwar & Ghosh, 1949, p. 322).

The difference between *Rhus* and *Toxicodendron* in tannin content, high in the former and low in the latter, is hardly of any taxonomic significance, being of a quantitative nature only. Moreover, the leaves in *R.* (*Toxicodendron*) *succedanea* contain about 20 per cent of tannin (Chopra, Badhwar & Ghosh, p. 323).

WOOD ANATOMY. The wood anatomical evidence often quoted in support of the generic segregation of *Toxicodendron* from *Rhus* does not seem to be unequivocal. There is no comprehensive comparative anatomical monograph of the *Rhus* complex, and the two excellent, but brief and rather general, wood anatomical surveys of Heimsch (1940, 1942) do not include some important characters (e.g., nodal anatomy[5]) nor provide data on possible variations and correlations of the anatomical characters within the genera of Rhoëae (Rhoideae). Therefore, the evaluation of these characters is difficult, and the significance can easily be overestimated.

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[5] Since the above was written, Dr. Richard A. Howard, to whom I am most grateful, has given the use of his data on six species of *Rhus* which have been investigated by him in the course of a survey of petiolar anatomy. All of these species have a trilacunar node. *Rhus* (*Lobadium*) *ovata*, a simple-leaved species, has a vascular pattern which is found in many types of simple leaves and differs from that found in dissected or compound leaves of the other species. No secondary tissue was developed from the cambium in this species. In two trifoliolate species, *R.* (*Lobadium*) *aromatica* and *R.* (*Toxicodendron*) *Toxicodendron*, the median trace contributes to the vascular supply of the terminal and lateral portions of the blade. In three pinnately multifoliolate species of subgenus *Rhus* (*R. copallina, R. glabra,* and *R. typhina*) the median trace does not contribute to the vascular supply of the leaflets of the lower third of the blade, these being supplied only by the two lateral traces. Both the lateral and median traces contribute to the supply of the upper leaflets, the median alone seeming to vascularize the terminal segment. The amount of secondary tissue in species with trifoliolate or pinnate leaves varied with the size of the leaf. Two characteristics distinguish these species of *Rhus* from other anacardiaceous genera studied: the median and the two lateral traces all quickly divide into three parts, and resin canals (present in the stem cortex) are missing from the lower pulvinus and redevelop in the petiole.

Thus, the presence or absence of vessel clusters in wood of the taxa involved can hardly be regarded as an indisputable generic character.

This is quite evident from a summary of pertinent anatomical features of the genera of Lauraceae, given by Stern (pp. 18, 19). Although most of the genera of this family have some percentage of clustered vessels which is liable to considerable variation within a genus (e.g., *Aniba Kappleri*, 6 per cent; *A. ovalifolia*, 1 per cent; *Sassafras albidum*, 1 per cent; *S. Tsumu*, 7 per cent), there are also genera in which species with clustered or with nonclustered vessels do occur (e.g., *Lindera communis*, 1 per cent of clustered vessels; *L. Benzoin*, no clustered vessels; *Eusideroxylon Melangangai*, 20 per cent of clustered vessels; *E. Zwageri*, no clusters). Perhaps the pattern of vessel arrangement has a different value in Anacardiaceae, but there are no detailed data available to test this.

It is notable, however, that at least in *Rhus* (*Malosma*) *laurina* the pattern of vessel arrangement seems to be liable to variation. Thus, although the vessels in the diffuse-porous wood of this species are usually solitary or in short multiples, "one specimen, however, showed longer radial multiples with frequent clusters" (Heimsch, 1940, p. 280). Although the absence of vessel clusters in wood of *Toxicodendron* and the presence of such in the species of the subgenera *Rhus* and *Lobadium* appears to be a good diagnostic feature, especially in the limits of a regional flora, there are no reasons at present to generalize this character, ascribing to it a generic significance.

The occurrence of resin ducts in the wood rays of some species of subgenera *Lobadium* and *Thezera* and the absence of these in the species of *Toxicodendron* may hardly be quoted in support of segregation of the latter from *Rhus*, since all the species of subgen. *Rhus* also lack such resin ducts.

The occurrence of septate wood fibers in the secondary wood of Angiosperms is generally considered to be a good diagnostic feature, but the significance of this character apparently varies in different families and genera. Thus, septate wood fibers have been found by Heimsch (1942, pp. 122, 123) in all the material of Burseraceae investigated by him (40 species in 19 genera), except two apparently misidentified specimens of two species of *Canarium*. However, septate fibers have not been found in wood of *Commiphora Holziana* (Metcalf & Chalk, p. 458) of this family. In Simaroubaceae septate wood fibers are common only in *Alvaradoa* and *Kirkia*, occurring sporadically in *Ailanthus malabarica*, two species of *Soulamea*, in *Suriana*, *Guilfoylia*, and in *Picramnia*.

In the tribe Anacardieae ("Mangifereae") of Anacardiaceae septate wood fibers have been recorded by Heimsch (1942) only in *Buchanania*; however, such fibers have been found "äusserst spärlich, zwischen den einfachen [Libriformfasern] zerstreut" by Janssonius (Moll & Janssonius, pp. 440, 462) in *Mangifera indica* L. and a few other species of *Mangifera* from Java. In the tribe Spondieae septate fibers have been recorded in all the genera; in Rhoëae ("Rhoideae") in about 60 species in 20 genera (of the total 93 species in 30 genera) of this tribe investigated by Heimsch

(1942, pp. 139, 140). The occurrence of varying numbers of septate wood fibers in the wood of *Metopium* and *Toxicodendron* has been mentioned by Record (1939, pp. 29 & 45 respectively) and Heimsch (1940, p. 282); the latter also found such fibers in three of four species of *Rhus* subgen. *Thezera* (*Rhus* § *Gerontogeae*) investigated. Since the species of the latter group apparently can differ in regard to the occurrence of septate wood fibers, the question arises whether it cannot be the same in the species of *Toxicodendron.* Thus, Kanehira (1921a, p. 86; 1961b, pp. 20, 21) did not mention the occurrence of septate wood fibers either in *R.* (*Toxicodendron*) *succedanea* or in *R.* (*Toxicodendron*) *verniciflua* and did not include *Rhus* (*Toxicodendron*) in his list of the genera in which such fibers occur (1921a, p. 288). Since only a relatively small number of species of *Rhus, sensu lato,* have been investigated in regard to their wood anatomy and the constancy of the occurrence of septate wood fibers in *Toxicodendron* and *Rhus* (*Thezera*) is not unquestionable, the taxonomic significance of this character remains obscure at present.

This discussion of the wood anatomical evidence for a generic segregation of *Toxicodendron* from *Rhus* shows that the differential wood anatomical characters constituting the evidence, although they may have a certain diagnostic value, at present appear inconclusive for the solution of the problem.

POLLEN. The difference between *Rhus* and *Toxicodendron* in shape and size of the pollen grains is sometimes quoted in support of the generic segregation of the latter. Thus, the pollen in *Toxicodendron* is mentioned as spherical, in contrast to ellipsoidal grains in *Rhus.* This antithesis, however, hardly has a real basis. According to Heimsch (1940, pp. 284, 285), the pollen grains of four Asiatic species and all but one of the American species investigated by him were spherical. The only exception was the largely Central and South American *R. striata* Ruiz & Pavon on which Heimsch comments, "*Toxicodendron striata,* the tropical species of the genus, possesses pollen which is from 4 to 8 μ larger than pollen of the other species. Grains are also elliptical, whereas the grains of the other species are spherical." However, some other data speak against such a general statement regarding the spherical shape of pollen grains in *Toxicodendron.* Concerning the pollen grains of *Rhus* (*Toxicodendron*) *diversiloba,* McNair (1921b, p. 189) says, "The fresh pollen grains of *Rhus diversiloba* are ellipsoidal with a width $1/3$ to $1/2$ the length . . . When the pollen grains are immersed in $N/_4KOH$ they assume a spherical form." Also the data supplied by Ikuse (p. 100) for three species of *Toxicodendron* indicate that, although the pollen grains in *R. verniciflua* are spherical, those in *R. ambigua* Lavallée ex Dippel (*R. orientalis* (Greene) Schneider) and *R. sylvestris* Sieb. & Zucc. are at least subspheroidal (prolate-spheroidal). On the other hand, the shapes of pollen grains in subgen. *Rhus* varies from ellipsoidal (Heimsch, 1940, p. 284 "elliptical"; Wodehouse, p. 332, for *R. glabra*) to subspheroidal or spheroidal (Wodehouse, *loc. cit.,* p. 333, for *R. typhina*). The size of pollen grains varies from 26 μ to 43 (53) μ in subgen. *Rhus* (the grains averaging 26 μ are cited by Oszast, p. 28, for *R. Coriaria*), and from 27 μ to 35 (37) μ in *Toxicodendron*. The size apparently varies to some degree also within the limits of a species, since the pollen grains in *Rhus* (*Toxicodendron*) *verniciflua* are cited as being 27–28 μ × 27–28 μ by Ikuse (p. 100), and 33 μ (average) by Oszast (p. 128), those in *R. typhina* have been recorded as 37.5–39 μ by Wodehouse (1932, p. 333), and 53 μ × 35 μ by Erdtman (1943, p. 66). Overlaps in the shape and size of pollen grains in *Rhus* and *Toxicodendron* make these characters taxonomically insignificant.

ROOT HAIRS. The different colors of root hairs, "generally tawny pink or lighter" in *Rhus* in contrast to the "dark brown root hairs" in North American species of *Toxicodendron* (Gillis, 1960, p. 28) perhaps is a good diagnostic character (if proved constant). Its taxonomic significance, however, remains obscure.

Since *Rhus* and *Toxicodendron* essentially agree in the type of inflorescence and the structure of flowers and fruits, the differential characters of the latter (axillary position of the thyrses, absence of glandular hairs on fruits with "waxy" mesocarp, lack [constant?] of vessel clustering in the late wood and presence [constant?] of varying amounts of septate fibers, and, finally, poisonous properties of resin) being of at least obscure taxonomic significance, it seems preferable at present to treat *Toxicodendron* as a subgenus of *Rhus*.

LOBADIUM RAFINESQUE VERSUS SCHMALTZIA DESVAUX

In 1808, an article by Rafinesque appeared in which he made known his intention to publish his "Nova Genera and Species Plantarum Boreali-Americanorum." According to him this work would contain "accurate descriptions and histories of all the new genuses and species of plants discovered in the United States of America, and published since Linnaeus, as well as those which though mentioned by that great author, were by him badly described . . . Besides a variety of others, I shall re-establish in this work about thirty new genuses, from plants already mentioned in authors; but which I have, by observation, found to disagree sufficiently from the genuses where they were placed, to oblige me to separate them for the advantage of the science." Among thirty genera to be segregated, Rafinesque mentioned (p. 352) "*Turpinia* (*pubescens* and *glabra*), *Rhus aromaticum* and *suaveolens* Wild. and Mich. [sic]." A genus published in this way may not be considered validly published, and the name is to be regarded as a *nomen provisorium*. In 1813, Desvaux (p. 229) proposed *Schmaltzia* as a new name for *Turpinia* of Rafinesque, the name being preoccupied, saying, "Si M. Rafinesque Schmaltz a réellement observé dans le *Rhus aromaticus* et *suaveolens* des caractères suffisant pour en constituer un genre, et qu'il a nommé *Turpinia* dans le *Medical Repertory* de

New-Yorck, et dont j'ai donné un aperçu il y a long-temps; alors il faudra changer ce nom, et je propose celui de *Schmaltzia.*" Thus *Schmaltzia*, a new name for an invalidly published genus, is a *nomen provisorium.*

In 1819, Rafinesque described the genus *Lobadium*, based on *Rhus aromatica* and *R. suaveolens*, and this genus was validly published. Torrey and Gray (1838) and Gray (1848–1868) apparently did not accept the name *Schmaltzia* Desv. since they established the subgenus *Lobadium* (Raf.) of *Rhus.* Somewhat later, however, some botanists, especially the American, used the invalid name *Schmaltzia* Desv. instead of the correct *Lobadium.* Small (1903) apparently was the first to validate *Schmaltzia* Desv., providing it with a formal description, but including in this genus not only the species of *Lodadium* Raf., but also all the American species of *Rhus* proper (sumacs), leaving in *Rhus* only the species of subgen. *Toxicodendron.* However, even the validated *Schmaltzia* Desv. ex Small remains illegitimate, being a superfluous name for the earlier *Lobadium*, and presumably (from Small's taxonomic circumscription) including the type species of *Rhus* (*R. Coriaria*). Greene (1905) and Small in his later publications (1913, 1933) applied *Schmaltzia* in a limited sense to the species of *Lobadium* Raf. Finally, in 1940, Barkley and Reed reestablished the genus *Schmaltzia* Desv. [ex Small] and emended it to include the species of *Styphonia* Nutt. and *Rhoeidium* Greene, as well as several species previously included in *Rhus.* All the new combinations made by Barkley (1940) under *Schmaltzia* are illegitimate, and the species have to be transferred either to *Rhus* or to *Lobadium* (for those botanists who interpret it as a separate genus).

CONCLUSIONS

Having reviewed the situation concerning the delimitation of *Rhus*, the author has reached the following conclusions:

1) Our knowledge of the genus *Rhus* as a whole in regard to the internal and some external characters (e.g., pubescence) is very incomplete. The wood-anatomical and palynological data, although more numerous than those from other fields, still are inadequate and cannot be evaluated taxonomically at present. Only a few, often fragmentary, data on fruit histology, biochemistry, embryology, and cytology and none on floral anatomy, populations, and genetics have been available. More or less careful attention to the morphology of nonglandular and glandular hairs which occur on the vegetative, and sometimes on the reproductive, organs of *Rhus* apparently has been given only by Diels (pp. 592–594, 596, *pl. 14*) in his study on the adaptive evolution of the vegetative organs in the South African species of the subgen. *Thezera* (*Rhus* § *Gerontogeae*). The data on hair morphology for the species of the other subdivisions of *Rhus* are scanty and have not been applied to the taxonomy of the genus. However, the morphology of hairs may apparently be of considerable taxonomic importance, at least in subgen. *Rhus*, serving not only for

distinguishing the species but also as a criterion of interspecific relationships and an evidence for natural hybridity.

2) Of the countries where at least two or three subdivisions of *Rhus* occur and which, therefore, seem to be of importance for the study of intrageneric relationships, only North America seems to have been adequately explored, the species occurring here having been revised more or less recently. No recent revision of the species of Asia, Malaysia, and New Guinea has been available. New Guinea, a very insufficiently explored island, seems to be of special interest, since here the subdivisions *Toxicodendron* (*R. lamprocarpa* Merr. & Perry), *Melanococca* (*R. taitensis* Guill.), and *Thezera* (*R. lenticellosa* Lauterb., *R. caudata* Lauterb., and *R. linguata* Slis) meet. Not only is the very disjunct extension of *Thezera* from its continental Indo-African range remarkable, but equallv so is the circumstance that the New Guinean species of this section differ from the continental species in some perhaps essential characters. (Unfortunately, no herbarium material of the New Guinean species has been available, and the citations are taken from the specific descriptions and notes of Lauterbach (1910, 1920) and Slis (1924). While the continental species of *Thezera* possess almost exclusively 3-foliolate, rarely palmately 5–7-foliolate (never pinnate) leaves and non- or indistinctly fibrous mesocarp and are nonscandent shrubs or trees, *R. lenticellosa* has been described as a scandent shrub with trifoliolate, unifoliolate or pinnately 5-foliolate leaves and "fibrous" mesocarp; and *R. caudata* is characterized as a small tree or perhaps sometimes an "armdicke Liane" (Lauterbach, 1920, p. 362, note to *Ledermann 12132*) with pinnate, 5–7-foliolate leaves. These differential characters of the New Guinean species seem to suggest a greater similarity in morphology and biology between the subgenera *Thezera* and *Toxicodendron* than that exhibited by the continental species of the former section. Hence, study of the full diversity of the species of the genus might prove to be very helpful for the determination of the intrageneric (as well as intergeneric) relationships and should precede any decisions on generic segregation, especially in the cases where the taxonomic significance of many differential characters appears to be uncertain.

3) Although the interpretation of *Toxicodendron, Lobadium,* etc., as subgenera of *Rhus* or as separate genera is a matter of personal evaluation and opinion, the former interpretation seems to be preferable as a provisional classification (until the accumulation of more adequate data on the species of the groups involved makes possible a solution of the problem of the taxonomic status of these subdivisions) for the following reasons:

a) Both close relationships and a considerable individuality are stressed by granting subgeneric rank to these groups.

b) A subgeneric status does not require creation of new combinations (except a few transfers from *"Schmaltzia,"* which have to be made in any case) and a consequent overflow of synonyms in the event that some rearrangement of the groups or a change in their subgeneric rank (e.g., *Lobadium* to a section of subgen. *Rhus*, or *Thezera* to a section of subgen. *Toxicodendron*) may be found necessary by some taxonomists.

4) In the application of the older generic names to the new or reestablished generic segregates, the International Code should be followed strictly, and generic names must first be checked in regard to their validity. Failure to do this has resulted in a profusion of invalid generic names and binomials in the American botanical literature (e.g., "*Schmaltzia* Desv.," "*Malosma* (Nutt.) Engl.").

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THE GENERA OF CAPPARACEAE AND MORINGACEAE IN THE SOUTHEASTERN UNITED STATES[1]

WALLACE R. ERNST

CAPPARACEAE A. L. de Jussieu, Gen. Pl. 242. 1789, "Capparides," nom. cons.

(CAPER FAMILY)

Annual herbs or shrubs to trees, often with strongly scented or glutinous herbage. Leaves alternate [sometimes ± lacking], simple or palmately compound, usually petiolate; stipules absent (or inconspicuous) or thornlike. Hairs 1 to many celled, simple or branched, sometimes peltate, thornlike or glandular. Inflorescences few to many flowered, usually bracteate, terminal and racemose, or flowers solitary and axillary. Flowers ± irregular, hypogynous, with open or closed aestivation, bisexual (or polygamous) [to unisexual, the plants dioecious]; perianth usually 4-merous [sometimes tubular or ± perigynous basally, or very rarely undifferentiated]. Sepals usually 4 [rarely 3–8], 1(or ± 2)-seriate, ± free or calyx lobed [or synsepalous]. Petals usually 4, free, and alternisepalous [rarely 2, ± sympetalous, or apetalous]. Receptacle usually glandular and often prolonged into an androgynophore. Stamens few [4 and alternipetalous] to many [sometimes sterile]; filaments filiform [or clavate]; anthers ± basifixed [to versatile], introrse, 2-locular at anthesis, dehiscent longitudinally; pollen usually 3-colporate and ± prolate. Gynoecium syncarpous, 2[-8]-carpellate, usually on a gynophore; stigma ± capitate; style obsolete to long-filiform; ovary 1-(2-)[or more]-locular with 2 [or more] parietal [or rarely central] placentae; ovules few [1] to many, campylotropous, 2-integumented [sometimes with an inner layer of tracheary elements]. Fruits siliquiform [to siliculiform], dehiscent by 2 valves to indehiscent [sometimes ± baccate or inflated]. Seeds usually many [or 1], folded or ± coiled, sometimes ± arillate; endosperm scanty; embryo curved [to variously convoluted]. (Capparidaceae of authors.) TYPE GENUS: *Capparis* L.

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[1] Prepared for a generic flora of the southeastern United States, a joint project of the Gray Herbarium and the Arnold Arboretum made possible through the support of the National Science Foundation and of George R. Cooley and under the direction of Reed C. Rollins and Carroll E. Wood, Jr. This treatment follows the style established in the first paper of the series, Jour. Arnold Arb. **39**: 296–346. 1958, and that of similar papers appearing through Volume **43**. The area covered is bounded by and includes North Carolina, Tennessee, Arkansas, and Louisiana. The descriptions apply primarily to the plants of this area, with supplementary information in brackets. References not verified by the author are marked with an asterisk. In the presentation of this synopsis, the author has benefited from the technical assistance and advice of Dr. Caroline K. Allen, Dr. George K. Brizicky, Dr. Robert C. Foster, Dr. Richard A. Howard, Dr. Hugh H. Iltis, Dr. Lily M. Perry, Mrs. Lazella Schwarten, and Dr. Carroll E. Wood, Jr. Mrs. Gordon W. Dillon has helped materially in the preparation of the manuscript.

Perhaps 45 genera and 450–1000 species, mostly of open, drier, tropical to temperate regions, well developed in America and Africa to altitudes of about 2000 m. About 20 genera may be monotypic; eight to twelve genera are indigenous to North America; two genera, including about ten species, occur in our area.

Eight subfamilies, four monogeneric and three of these monotypic, were recognized by Pax & Hoffman, with the bulk of the species seeming to fall into two worldwide groups. About two-thirds of the species (comprising subfam. Capparoideae, with four tribes and 25 genera) tend to be ± woody with simple leaves and ± indehiscent fruits. Nearly a third of the species (constituting subfam. Cleomoideae Pax in Engler & Prantl, largely American with perhaps 12 genera) tend to be herbaceous with palmate leaves and dehiscent fruits. The remaining six subfamilies include only eight genera and nine species, primarily of the Old World.

The alternisepalous petals, the nature of the receptacle (often variously glandular and frequently prolonged into an androgynophore and/or gynophore), and the folded or ± coiled seeds are important characteristics of the family; in many species the herbage is ill scented. Branched sclereids occur in the leaves of some taxa (Vesque), while a layer of tracheary elements is found in the seeds of some others (Orr). Idioblastic cells containing the enzyme myrosin have been identified in Capparaceae, Cruciferae, Resedaceae, Moringaceae, and Tropaeolaceae. More or less similar valvular fruits with persistent, parietal placentae are found in Papaveraceae, Fumariaceae, and Cruciferae. While perhaps closest to those of Cruciferae, the flowers of Capparaceae, sometimes with septate or plurilocular ovaries, are usually bracteate, and the stamens are not tetradynamous. The pollen of Capparaceae is commonly tricolporate and ± prolate (verified in about 18 genera), but variable in size; pollen of *Capparis cynophallophora*, about 46 μ in length, is three times that of *Cleome erosa*. The pollen of Moringaceae, Tovariaceae, and Resedaceae is ± similar, that of Papaveraceae and Cruciferae less so (Erdtman).

The nature of floral aestivation (whether open or closed) and the complete or periodic sterility of either stamens or gynoecia (perhaps more widespread than generally realized, functionally unisexual flowers having been observed in ten genera) are of interest; dioecism occurs in two or three genera. Periodicity of anthesis, whether diurnal or nocturnal, may be important in some groups. Birds (including hummingbirds) and possibly bats, in addition to many kinds of insects, are suspected pollinators.

The family is morphologically and taxonomically complex with little agreement concerning relationships, especially in regard to the sections of *Capparis* and the segregates from *Cleome*. Moringaceae Dumortier, Koeberliniaceae Engler in Engler & Prantl, and Tovariaceae Pax in Engler & Prantl, monogeneric taxa of uncertain affinities, are sometimes placed with Capparaceae. *Oceanopapaver* Guillaumin, of New Caledonia, described in Papaveraceae, probably is better included among Capparaceae.

Capparaceae are poorly known cytologically. Chromosome numbers of $2n = 16, 18, 20, 22, 24, 26, 28, 30, 32, 34, 38, 40, 70$, ca. 84, ca. 85, and

140 are reported. The unusual view of Billings that *Isomeris arborea* Nutt. ex Torr. & Gray is haplodiplont has not been substantiated (see Snow).

Capers commonly are the pickled flower buds of *Capparis spinosa*, although apparently portions of other taxa also are pickled. A few species, including *Cleome gynandra*, are eaten as potherbs and some are claimed to be medicinal or sometimes poisonous, occasionally with references to anthelmintic or insecticidal properties; a number of insect galls are known (Pax & Hoffman), however, and specimens are frequently riddled. Many species have attractive flowers, but only a few, especially of *Cleome*, are cultivated.

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KEY TO THE GENERA OF CAPPARACEAE

General characters: *herbs, shrubs, or small trees; leaves alternate, simple or palmately compound, often ill scented; flowers bisexual (or polygamous), ± hypogynous; sepals 4, 1(or 2)-seriate; petals 4, alternisepalous; receptacle often glandular; stamens few to many, often inserted on an androgynophore; ovary 1(or 2)-locular with 2 parietal placentae, often inserted on a gynophore; fruits siliquiform, dehiscent by 2 valves or ± indehiscent; seeds usually folded or coiled.*

A. Leaves simple, coriaceous; fruits ± indehiscent; shrubs or small trees of coastal Florida. .... 1. *Capparis.*

A. Leaves compound, 3(or more)-foliolate; fruits 2-valved and dehiscent; usually annual herbs. .... 2. *Cleome.*

Subfam. CAPPAROIDEAE

1. **Capparis** Linnaeus, Sp. Pl. 1: 503. 1753; Gen. Pl. ed. 5. 222. 1754.

Shrubs or small trees [sprawling or climbing], glabrous or with simple or lepidote [or stellate] hairs. Leaves simple [very rarely also 3-parted, or plants ± leafless]. Flowers few [axillary or extra-axillary; sometimes resupinate] to many, pedicellate, usually bracteate, in terminal, ± racemose [or various] inflorescences. Sepals ± free, appearing 2-seriate [rarely the outer pair connate, or calyx 4-lobed]. Petals broad [the upper pair sometimes with adjacent glandular regions]. Receptacle gland ± disclike [or membranaceous], sometimes ± lobed opposite the sepals. Stamens few to many, radiating; androgynophore very short or absent. Gynoecium on a long gynophore; stigma ± sessile; ovary 1(or 2)-locular with 2 parietal placentae [to several locular]. Fruit narrowly elongate, siliquiform [to baccate], ±indehiscent; seeds few to many, ± coiled (or irregular). LECTOTYPE SPECIES: *C. spinosa* L.; see Britton, N. Am. Trees 405. 1908. (The classical Latin name of the caper, from Greek, *kapparis*, perhaps derived from Persian, *kabar*, the caper.) — CAPER.

About 150–350 species, usually of coastal vegetation but to altitudes of 1700 m., through tropical and subtropical America, Africa, and southeastern Asia; two species occur in coastal Florida.

De Candolle divided *Capparis* into six sections (five native to the New

World), placing our two species in different sections. Pax and Hoffmann recognized fourteen sections (nine New World) and included both of our species in sect. CYNOPHALLA (with about 15–20 species distributed from Florida to South America). *Capparis cynophallophora* L., 1753 (*C. jamaicensis* Jacq.) (§ *Quadrella* DC., subg. *Quadrella* (DC.) Eichl.), Jamaica caper tree, $2n = 18$, occurring from subtropical peninsular Florida to South America, is lepidote (the scales probably equivalent to stellate hairs) on the pedicels, sepals, petals, gynoecia, and the lower surface of the leaves. The buds are quadrangular, ± acute, and the seeds are ± coiled with the hypocotyl free of the cotyledons. *Capparis flexuosa* L., 1762 (*C. cynophallophora* L., 1759) (§ *Cynophalla* DC., subg. *Cynophalla* (DC.) Eichl.), bay-leaved caper tree, occurring from Palm Beach County, Florida, southward through the Florida Keys to South America, is glabrous and with globose buds. The seeds (possibly exceptional in the family) are ± ellipsoid with the embryo ± straight, but the oblique, imbricate cotyledons enfold (and conceal) the hypocotyl. Both species (with distinctive inflorescences, buds, sepals, receptacle glands, fruits, and seeds) have conspicuously elongate fruits and were described at different times by Linnaeus as *C. cynophallophora* (see Fawcett & Rendle); later authors sometimes have mistakenly reversed the names. The sections to which our species should be referred cannot be determined without a revisionary study of the genus.

The fruits of *Capparis* are either globular, with two to several placentae (sometimes plurilocular), or elongate and siliquiform, with only two placentae (and one- or two-locular). A conspicuous septum is formed in the two-locular ovaries of *C. flexuosa*, but in *C. cynophallophora* the septum is absent, inconspicuous, or possibly discontinuous. In "*C. horrida*," the fruits are unilocular when young but four-locular when older; in "*C. galeata*," the eight septa are free or united centrally (Rao). The initially one-locular fruits of *Crateva* L., a related genus, are divided by a double-layered proliferation from the placentae until the time of fertilization, but as the ovules mature and the ovary increases in size, this septum is ruptured (Raghavan & Venkatasubban, 1940a, b). The median carpellary bundles of the multilocular fruits of *C. spinosa* are absent (Eggers), suggesting that multiplacental fruits of *Capparis*, as in some Papaveraceae, are possibly more specialized than two-placental fruits which have well-developed median carpellary veins.

On the basis of wood anatomy, Cristiani placed *Capparis* at the end of the series *Cleome*, *Crateva*, *Atamisquea*. De Wolf, in agreement with a brief comment by White, makes the interesting suggestion that American species of *Capparis* are not congeneric with the lectotype species, *C. spinosa*, $2n = 38$, ca. 84, a straggling shrub of the Old World with resupinate flowers. Little is recorded concerning floral biology, but in Israel, flowers of *C. spinosa* open in the early evening and wither by the next afternoon; many flowers have rudimentary ovaries; when ripe, the fruits burst open.

Juvenile leaves and sterile twigs are sometimes different from flowering branches and should be noted by collectors.

Chromosome numbers have been reported for only a few species: $2n = 18, 30, 32, 38, 40$, ca. 84, ca. 85. Chromosome counts of our two species, determined from our area, would be desirable.

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Subfam. CLEOMOIDEAE Pax in Engler & Prantl

2. **Cleome** Linnaeus, Sp. Pl. 2: 671. 1753; Gen. Pl. ed. 5. 302. 1754.

Annual [to perennial] herbs, often pubescent, glandular, and ill scented, sometimes thorny. Leaves palmately compound [or simple]. Flowers in terminal inflorescences (or axillary); aestivation closed or open. Sepals ± free, 1-seriate, sometimes imbricate in the buds. Petals usually clawed, sometimes dissected. Stamens 6 [or 4] to many, often inserted on an androgynophore. Receptacle gland various. Style distinct or indistinct; ovary 1-locular with 2 placentae, usually on a gynophore; flowers bisexual, sometimes ♀-sterile or polygamous. Fruit usually siliquiform [to siliculiform], 2-valved, sometimes ± sessile; dehiscence ± acropetal and usually complete or basipetal (or lateral) and often incomplete.

Seeds few to many, ± folded and orbicular to ± coiled, sometimes ± arillate. (*Gynandropsis* DC., *Neocleome* Small, *Peritoma* DC., *Physostemon* Mart. & Zucc., *Atalanta* Nutt., *Polanisia* Raf., *Aldenella* Greene, *Cristatella* Nutt.); LECTOTYPE SPECIES:[2] *C. ornithopodioides* L.; see Hitchcock & Greene, *in* Int. Bot. Congr. Cambridge 1930. Nomencl. Propos. Brit. Bot. 172. 1929. (Latin name of some mustard-like plant; applied by Linnaeus to this genus, which Tournefort called *Sinapistrum*; perhaps derived from Greek, *kleio*, to shut up or inclose.)

Perhaps 200 species, mostly of open or disturbed habitats through the tropics and subtropics, a few of cooler areas, concentrated in America and Africa. About three to five species are indigenous to our area and about six are introduced.

Section GYNANDROPSIS (DC.) R. Br. (including § *Gymnogonia* R. Br.; subg. *Gynandropsis* (DC.) Schultes & Schultes), tending to have the receptacle prolonged into an androgynophore, the style often short and thick, the valves of the fruits inconspicuously veined and without prominent median vein, and the dehiscence of the valves ± acropetal and usually complete, is represented with us by at least three species. *Cleome gynandra* L. (*Gynandropsis gynandra* (L.) Briq.), $2n = 30, 32, 34$, with prominent androgynophore, a pantropic weed probably of Old World origin, is reported in the Coastal Plain of our area and in Bermuda; *C. spinosa* Jacq. (*Neocleome spinosa* (Jacq.) Small) (§ *Pedicellaria* DC., § *Herbaceae* Pax in Engler & Prantl, § *Eucleome* O. Kuntze in Post & Kuntze), spiderflower, $2n = 20, 24, 38, 70, 140$, pubescent and with thornlike stipules and epidermal outgrowths, neotropical in origin, has been collected in each state of our area with the apparent exception of Alabama; *C. speciosa* HBK.[3] (*Gynandropsis speciosa* (HBK.) DC., *G. Tracyi* Briq.), closely resembling *C. spinosa* but glabrate and without thorns, may occur as an escape from cultivation. *Cleome serrata* Jacq. (*Neocleome serrata* (Jacq.) Small), native to the West Indies but reported from Georgia by Small, may belong to this section. The flowers of *C. gynandra*, *C. speciosa*, and *C.*

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[2] Robert Brown (1826, p. 222), critical of the generic status of *Gynandropsis* segregated by De Candolle from Linnaean species of *Cleome*, remarked that *C. pentaphylla* L. [= *C. gynandra* L., *Gynandropsis gynandra* (L.) Briq.] was the earliest known species of *Cleome* and the one on which the genus was chiefly constituted; this could be looked upon as designation by Brown of the lectotype species of *Cleome*. The same taxon was chosen as lectotype by Britton & Brown (Illus. Fl. No. U. S. ed. 2. **2**: 196. 1913). Hitchcock & Green agreed that *C. gynandra* is undoubtedly the type species of *Cleome* but selected *C. ornithopodioides* as a new lectotype because *C. gynandra* is regarded as the type of the genus *Gynandropsis*, now conserved; previously, however, the lectotype species of *Gynandropsis* had not been designated. In this instance, the complications of the taxonomic framework of *Cleome* were compounded by the selection of a substitute generic lectotype.

[3] The correct name for this taxon, which may be only a smooth form of *Cleome spinosa*, is uncertain. The description of *C. speciosa* Raf., 1817, based on a plant, possibly of Mexican origin, in cultivation in Louisiana, is inadequate and was doubtless based upon a different holotype than *C. speciosa* HBK., 1821, described from Colombian material.

spinosa open in the evening. All of the above species are more frequent south of our area.

Section POLANISIA (Raf.) Baill. (*Polanisia* Raf., *Polanisia* § *Eupolanisia* Endl., *Cleome* subg. *Polanisia* (Raf.) Schultes & Schultes; including *Cristatella* Nutt., *Aldenella* Greene), without prominent androgynophore, with the gland of the receptacle usually adaxial and ± columnar, the style narrow and elongate, the ovary often broad, the valves of the fruits coarsely veined and usually with a distinct but incomplete median vein, and the dehiscence of the valves basipetal and usually incomplete, is represented with us by at least four species. The styles often are filiform, fragile in fruit, and frequently missing from herbarium specimens, but are neither articulated nor deciduous. *Cleome graveolens* (Raf.) Schultes & Schultes (*Polanisia* [§ *Brachystyla* DC.] *graveolens* Raf.; *P. dodecandra* (L.) DC. sensu Iltis, not *Cleome dodecandra* L.), clammyweed, with relatively broad leaflets, occurs from Mexico to Canada but is collected infrequently in our area. Iltis (1958) included in this species both *C. trachysperma* (Torr. & Gray) Pax & Hoffmann (*Polanisia trachysperma* Torr. & Gray, *P. dodecandra* subsp. *dodecandra* var. *trachysperma* (Torr. & Gray) Iltis), and *C. uniglandulosa* Cav. (*P. dodecandra* subsp. *uniglandulosa* (Cav.) Iltis) (*Polanisia* § *Stylaria* DC.), the latter with styles to 4 cm. long, occurring to the west and south of our area.[4] This complex of taxa is seen by Iltis as a morphological continuum which tends to diminish in flower size from south to north. *Cleome Aldenella* W. R. Ernst[5] (*Polanisia* § *Aldenella* (Greene) Iltis), with linear leaflets and fruits, occurs in the coastal plain of Georgia, Florida, and Mississippi. *Cleome erosa* (Nutt.) Eaton (*Cristatella erosa* Nutt., *Polanisia erosa* (Nutt.) Iltis subsp. *erosa*) (*Cleome* § *Cristatella* (Nutt.) Baill., *Polanisia* § *Cristatella* (Nutt.) Iltis), with linear leaflets and distinctive, broad, laciniate petals, primarily of Texas, is reported from central Louisiana. The closely related taxa treated as *Polanisia erosa* (Nutt.) Iltis subsp. *breviglandulosa* Iltis and *P. Jamesii* (Torr. & Gray) Iltis (*Cristatella Jamesii* Torr. & Gray) occur west of our area; combinations in *Cleome* are not available for these two taxa. *Cleome viscosa* L. (*Polanisia viscosa* (L.) DC.) (*Polanisia* § *Brachystyla* DC., § *Ranmanissa* Endl.), $2n = 20$, a pantropic weed of Old World origin, with broad leaflets, eight to many stamens (sometimes with clavate filaments), androgynophore and gynophore essentially absent, is introduced in Pinellas County, Florida, in Bermuda, and south of our area. *Cleome rutidosperma* DC. (*C. ciliata* Schum. & Thonn. [see Iltis, 1960]) (*Cleome* § *Siliquaria* (Forsk.) DC., § *Herbaceae* Pax in Engler & Prantl, § *Rutidosperma* Iltis), with ± indeterminate growth, axillary flowers, and dehiscence of the valves ± lateral and incomplete, is an Old World species introduced in Orange and Palm

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[4] Nomenclatural combinations have not been made for *Cleome trachysperma* and *C. uniglandulosa* as infraspecific taxa of *C. graveolens*.

[5] **Cleome Aldenella**, nom. nov., based on *Polanisia tenuifolia* Torr. & Gray, Fl. N. Am. **1**: 123. 1833 (*Aldenella tenuifolia* (Torr. & Gray) Greene, Pittonia **4**: 212. 1900); not *Cleome tenuifolia* (Mart. & Zucc.) Iltis, Brittonia **11**: 161. 1959.

Beach counties, Florida, and south of our area; it is somewhat similar to *C. aculeata* L. (also introduced into the New World) and in some respects resembles members of sect. POLANISIA. *Cleome diffusa* Banks ex DC. (*C. aculeata* var. *diffusa* (DC.) O. Ktze.), of tropical America, was collected by Mohr on ballast at Mobile, Alabama, in 1893 (Iltis).

The taxonomy of *Cleome* is unsettled, with radical disagreement as to the composition of sections and of segregate genera. Of particular concern in our area is the status of sect. POLANISIA. De Candolle separated the Old World taxa of *Cleome* with more than six stamens as the genus POLANISIA, thus including among them *C. viscosa*; *C. gynandra*, having six stamens but with a conspicuous androgynophore and gynophore, was placed in the genus *Gynandropsis*. While taking a broad view of the *Cleome* complex, Pax & Hoffmann reduced *Polanisia* to *Cleome* but separated *Isomeris*, *Gynandropsis*, *Cristatella*, and *Physostemon* (see also Pax, 1891). In contrast, Iltis would reduce *Isomeris*, *Gynandropsis*, and *Physostemon* to *Cleome* but would separate *Polanisia*, restricting the last to North American species and including *Cristatella*. (See Iltis, 1957, for presumed relationships of *Cleome*, *Cleomella*, *Wislizenia*, and *Oxystylis*).

Iltis emphasizes that the indigenous North American species of sect. POLANISIA are highly specialized and that their closest affinities are with Old World species of *Cleome*, rather than with other New World species. Our species of sect. POLANISIA recall in some respects, however, *Cleome* § PHYSOSTEMON (Mart. & Zucc.) Benth. & Hook., of the New World, as well as *C. arabica* L. and *C. ornithopodioides* L., both of sect. CLEOME (§ *Herbaceae* Pax in Engler & Prantl, § *Eucleome* O. Kuntze in Post & Kuntze), of the Old World. A logical means of separating at the sectional level the indigenous North American species of sect. POLANISIA from *Cleome viscosa*, on the one hand, and from *C. ornithopodioides*, on the other hand, is not readily apparent. Recognition of *Polanisia* as a genus and its restriction to indigenous North American species rests heavily on the nature of the petal margins, the nature of the apex of the receptacular gland, and, in large measure, on the identity of the lectotype species.[6]

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[6] In presenting *Polanisia* as a new genus, Rafinesque (Am. Jour. Sci. 1: 378. 1819) described *P. graveolens* but stated that the "type" of his genus was *Cleome dodecandra* L.; he also stated that his species was the same one that Michaux and Pursh called *C. dodecandra*. The meaning of the word "type" is debatable. I am assuming, in this instance, that "type" was not used in the strict, modern, nomenclatural sense, but to indicate an abstract, morphological relationship; therefore, I am taking *P. graveolens* as the type species of *Polanisia*.

Iltis (1954, *et seq.*) concluded that *Cleome dodecandra* L. was the same taxon as our indigenous *Polanisia graveolens*, and he adopted for our plant the combination *P. dodecandra* (L.) DC., which De Candolle, however, maintained as distinct from *P. graveolens*. By way of a poor photograph, Iltis selected as lectotype for *C. dodecandra* L., an immature specimen in the Linnaean herbarium bearing a tag on the plant with "HU. 12andr." [*Hortus Upsaliensis, dodecandra*] but with Linnaeus' annotation "viscosa" on the sheet. Iltis' interpretation that this plant was grown at Upsala from seeds gathered in North America and that this specimen represents the same taxon described by Rafinesque as *P. graveolens* may be correct; however, the lectotype for *C. dodecandra* should be selected from the Hermann herbarium, not from the Linnaean.

For insight into the confusion surrounding the interpretation of *Polanisia* Raf., see Britton, Greene, House, and Iltis.

Polygamous or ♀-sterile flowers and the consequent intermittent production of fruits are conspicuous in the inflorescences of several species, among them *Cleome spinosa* and *C. gynandra*; as many as 50 per cent of the flowers on some plants of *C. rutidosperma* are ♀-sterile (Johnson & Seng). Woodson recommends retaining *C. gynandra*, which he considers hermaphrodite, in *Cleome* and transferring the monoecious species of *Gynandropsis* to *Podandrogyne* Ducke, of South and Central America. Sexuality in the Cleomoideae appears variable and requires further investigation. The tendency for an androgynophore and/or gynophore is characteristic of the family, but these structures seem to be unreliably variable in length, becoming conspicuous, in many instances, only with the maturation of the fruits.

The cytological information is fragmentary and usually poorly documented. Chromosome numbers of $2n = 18, 20, 22, 24, 30, 32, 34, 38, 70,$ and 140 are reported. Documented chromosome counts for the species in our area would be welcome.

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Linnaeus did not indicate clearly in *Species Plantarum* (p. 672. 1753) which taxon he intended to name *Cleome dodecandra*, for which he gave the habitat as "*in* Indiis." The primary reference, to his original description in *Flora Zeylanica* (p. 109, species 242. 1742), is marked by an asterisk, indicating it as a good description. The other references include a plate ("*Burm. zeyl.* 212. *t.* 11. *f.* 1") possibly referable to *C. rutidosperma* DC., and a plate ("*Sloan. jam.* 80. *hist.* 1. *p.* 194. *t.* 124. *f.* 1") probably of *C. serrata* Jacq. As shown by Iltis (1954), the name *Cleome dodecandra* L. ultimately must rest upon Linnaeus' own description in *Flora Zeylanica*. The name, however, should be typified in Hermann's Ceylon herbarium, the basis of the descriptions in *Flora Zeylanica*, and not in the Linnaean herbarium. According to Trimen (Jour. Linn. Soc. **24**: 129–155. 1888), the Hermann herbarium, now in the British Museum (Natural History), consists of four volumes of plants and one volume of drawings, collected or drawn in Ceylon but including also some American plants cultivated in Ceylon and some plants collected in Africa. In Trimen's list equating the species of *Flora Zeylanica* with the Hermann materials (p. 146), the item corresponding to species 242 (the polynomial and description upon which *Cleome dodecandra* is based) is a drawing which Trimen identified as "*C. viscosa* L., var." This drawing should be taken as the type of *C. dodecandra* L. The equation of the American *Polanisia graveolens* Raf. with the Asiatic *Cleome dodecandra* L. appears erroneous.

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MORINGACEAE Dumortier, Anal. Fam. 43, 48. 1829, nom. cons.
(HORSE-RADISH TREE FAMILY)

A family of a single genus characterized by alternate, pinnatifid, deciduous leaves; clustered, weakly perigynous flowers with 10 perianth segments and 10 stamens; 3-carpellate gynoecia; and elongate, woody, 3-valved fruits with the seeds (usually winged) attached medially to the valves.

1. **Moringa** Adanson, Fam. Pl. 2: 318. 1763.

Trees to about 10 m. tall with spreading branches, usually with thick trunk and gummy bark. Hairs 1-celled. Leaves deciduous, alternate, exstipulate (or stipules small and stipitate, at the base of the petioles and petiolules), 2(or 3)-odd-pinnate with many opposite leaflets. Flowers many, in axillary panicles or panicles of cymes, irregular, bisexual, weakly perigynous. Perianth 5-merous, 2-seriate; sepals and petals ± similar, spreading to reflexed, white, pink [or red]. Stamens 10, ± unequal, the antisepalous ones ± staminodial; filaments swollen toward the base, sometimes variously connivent; anthers dorsifixed, 1-locular at anthesis, longitudinally dehiscent; pollen 3(4)-colporate. Gynoecium 3(rarely 2 or 4)-

carpellate, on a short gynophore; stigma inconspicuous; style slender; ovary 1-locular with 3 parietal placentae; ovules numerous, in 2 vertical series on the placentae, anatropous, 2-integumented, the micropyle directed upward with the funiculus beneath (i.e., apotropous). Fruits pendent, linear, 3-valved and ± 3-sided; dehiscence explosive, basipetal and complete; seeds many, usually conspicuously 3-winged [or wings absent], attached medially to the woody valves; embryo straight; endosperm lacking. Seedling cotyledons hypogeous, retained within the seed coat [or epigeous]. TYPE SPECIES: *Guilandina Moringa* L. = *Moringa oleifera* Lam. (Name derived from the native Malabar name.)

Perhaps ten species distributed in drier regions from Africa and Madagascar to the East Indies. Two sections have been recognized on the basis of the shape of the receptacle: tubular in the monotypic sect. DYSMORINGA Engler and cup shaped in sect. MORINGA (§ *Eumoringa* Engler), represented with us by *Moringa oleifera* (*M. pterygosperma* Gaertn., *M. Moringa* (L.) Millsp.), horse-radish tree or drumstick tree, $2n = 28$, planted throughout the warmer portions of the world, including the Bahama Islands and subtropical Florida where it is possibly naturalized. Modern distribution records in our area are needed.

Described by Linnaeus as a legume, *Moringa* has been placed with various groups, among them Capparaceae, with which it shares the gynophore and uniseriate, alternisepalous corolla. Cells containing myrosin have been identified in Moringaceae, Cruciferae, Capparaceae, Resedaceae, and Tropaeolaceae. *Moringa* probably has no very close allies.

The distinctive fruits, unique in the Rhoeadales, are completely dehiscent but lack the persistent replum characteristic of the dehiscent fruits of Papaveraceae, Fumariaceae, Cruciferae, and Capparaceae; instead, the seeds are attached medially to the valves. Puri advanced the opinion, somewhat paralleling the account by Eames & Wilson of the cruciferous gynoecium, that the placentation was extracarpellary, the result of solidification of the carpels with the coincidental extrusion of the ovules into a central loculus. It is not certain how the Gonophyll Theory (Melville) would explain this situation. Under the simpler, classical view, the valves of *Moringa* separate at the carpellary midrib.

Up to 20 per cent of the seeds of *Moringa oleifera* in India are without an embryo, and some embryos have an extra cotyledon (Puri, 1941).

The leaves, young fruits, and roots of *Moringa oleifera*, said to have the flavor of horse-radish, are eaten in India. Various medicinal properties are claimed, and oil from the seeds, ben (or bene) oil, is sometimes used as a mechanical lubricant and in cosmetics.

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NOTES ON BUXUS IN THE LESSER ANTILLES AND ON MATHOU'S OVERLOOKED PUBLICATION

RICHARD A. HOWARD [1]

CRANTZIA SW., TRICERA SW., AND BUXUS L.

THE FIRST NEW WORLD species now assigned to the genus *Buxus* was described by Swartz as *Crantzia laevigata* (Prodr. 38. 1788), based on material collected in Jamaica. In 1797 Swartz (Fl. Ind. Occ. **1**: 333. 1797) renamed the genus *Crantzia* as *Tricera* calling attention to the use of the former name by Schreber (Gen. Pl. ed. 8, **1**: 143. 1789). Swartz's refusal to continue the use of one of his own generic names, seemingly having priority, occurred in other instances as Rendle has pointed out (Jour. Bot. **35**: 20. 1897). In this case, however, *Crantzia* Scopoli (Intr. 173. 1777), not known to Swartz, makes *Crantzia* Swartz illegitimate. Willdenow (Sp. Pl. **4**: 338. 1805) described additional species under the name *Tricera,* and Sprengel (Syst. Veg. **3**: 847. 1826) transferred all species known until then to the genus *Buxus*. Jussieu (Euphorb. Tentam. 14. 1824) had suggested the close relationship of the two genera. Later, Baillon (Monogr. Bux. 66. 1859) treated *Tricera* as a section of the genus *Buxus*. Britton and his coworkers in a series of local floras and special treatments between 1906 and 1925 re-established the genus *Tricera* as distinct from the genus *Buxus*, but there seems to be no discussion of this action nor any foundation for it. Urban and all other workers on the West Indian vegetation have considered the species as members of the genus *Buxus*.

In a monograph overlooked by subsequent workers, Miss Th. Mathou (Recherches sur la famille des Buxacées; Étude anatomique, microchimique et systématique, Thèse, 1–448. 1939, Toulouse) has re-examined the Buxaceae. She has described new taxa and made new combinations, some legitimate and some illegitimate, but none of them listed correctly, if at all, in Index Kewensis or the Gray Herbarium Index.

Miss Mathou maintained, with emendation, the "section Tricera Baillon ex Swartz." She pointed out that the stems of the American species of *Buxus* comprising the section *Tricera* lack cortical bundles and meristeles; have a different petiole structure, and possess several distinctive characteristics in the inflorescence. In a discussion of the sectional status of *Tricera*, Miss Mathou concluded that the combinations of anatomical and external morphological characteristics permitted the recognition of the American

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[1] These notes represent part of a continuing study of the flora of the Lesser Antilles. The financial support of a grant from the National Science Foundation is gratefully acknowledged. I also appreciate the courtesies and the cooperation offered by the directors and curators of the herbaria cited in the paper.

species as a section but not as a distinct genus. My own investigations of the petiole vascular structure support her work. The distinctive feature of the American species is the origin of the lateral vascular bundles of the petiole from the same stelar gap as the median bundle. In their path through the length of the petiole, these lateral bundles remain distinct. In contrast the Asiatic and African species of *Buxus* may have cortical or medullary vascular bundles in the stem which contribute to the vascular supply of the leaf at the node; and within the petioles the lateral bundles may remain distinct or may become involved with the median in a complicated stelar arrangement. I have found no other character or group of characters which prove satisfactory for recognizing the New World species as a distinct genus. It appears desirable to consider *Crantzia* Sw. and *Tricera* Sw. as synonyms of *Buxus* L.

BUXUS SPECIES IN THE LESSER ANTILLES

A Bredemeyer collection from Caracas, Venezuela is the basis of *Tricera citrifolia* Willd. (Sp. Pl. **4**: 338. 1805). In transferring this species to *Buxus* Sprengel (Syst. Veg. **3**: 847. 1826) gave the distribution as "*Martinica, Caracas*" but cited no specimens. Baillon (*loc. cit.* 70) cited under this species a Wydler collection from Puerto Rico in the Jussieu and Lessert herbaria. Mueller Arg. (DC. Prodr. **16**(1): 15. 1869) described three varieties for *B. citrifolia* with the range Venezuela, Puerto Rico, and Cuba. Variety *genuina* contained the Bredemeyer type. Variety *fuscescens* contained the Wydler specimen from Puerto Rico. Variety *brevipes* was based on *Wright 1919 p. p.* from Cuba. In the same work Mueller described *Buxus subcolumnaris* and cited *Sieber 208* from Martinique and *Wright 1920* from Cuba. Pax (Nat. Pflanzenfam. III, **5**: 133. 1896) recognized *Buxus citrifolia* as occurring in Cuba and Puerto Rico and *Buxus subcolumnaris* in Martinique and Cuba. Urban (Symb. Antill. **5**: 400. 1908) partially clarified the situation by describing *Buxus muelleriana* based on *Wright 1920* from Cuba, and *Buxus brevipes* based on *Wright 1919*, also from Cuba. Urban recognized *Buxus subcolumnaris* from Martinique but commented about *B. citrifolia* that he could not distinguish between Mueller's variety *genuina* and variety *fuscescens* and was persuaded that the Bredemeyer collection like the Wydler collection came from Puerto Rico. Britton and Wilson (Sci. Surv. Puerto Rico & V.I. **5**: 507. 1924) cited Mueller's variety *fuscescens* in the synonymy of *Tricera citrifolia* and stated "Eastern Porto Rico, collected only by Wydler, or perhaps also by Bredemeyer: — Venezuela. A rare plant, known to us from Porto Rico only as recorded by Mueller and by Urban." More recently Mathou (*loc. cit.* 195) has returned to the original confused state regarding the distribution of *B. citrifolia* and cited its range as "Venezuela, Porto-Rico and Martinique."

I have had the opportunity of studying these collections and others in various American and European herbaria. I suggest the correct treatment of these old collections is the following:

Buxus citrifolia (Willd.) Sprengel, Syst. Veg. 3: 847. 1826.

Tricera citrifolia Willd., Sp. Pl. **4**: 338. 1805.
Buxus citrifolia var. *genuina* Muell. Arg., DC. Prodr. **16**(1): 15. 1869.

This species is endemic to Venezuela. In addition to the Bredemeyer type (*Herb. Willd. 17384*) it is represented by *Fendler 1296* (GH) from Tovar, *Pittier 11016* (GH) from El Carenero, Miranda, and *Pittier 8696* (GH) from El Zigzag on the road from Guaira to Caracas, all in Venezuela. No additional material from Venezuela has been seen in other herbaria.

Buxus subcolumnaris Muell. Arg., DC. Prodr. **16**(1): 14. 1869, *p.p.*

Tricera subcolumnaris (Muell. Arg.) Britton, Bull. Torrey Club **42**: 498. 1915.
Buxus aquartiana Rich. ex Baillon, Monogr. Bux. 69. 1859.

This species was based on two collections, *Sieber 208* from Martinique and *Wright 1920* from Cuba. Urban has selected the latter collection as the type of *Buxus muelleriana*. *Sieber 208* should, therefore, be considered the type of *B. subcolumnaris*. This species is known only from Martinique and is distinguished from *B. citrifolia* by the fused, narrowed apices of the carpels as well as the longer petioles of the leaves. *Buxus subcolumnaris* and *B. muelleriana* are readily distinguished by their leaf shape and venation.

The manuscript name *Buxus aquartiana* attributed to L. C. Richard and used by Baillon appears on several specimens in the Jussieu and the general herbaria in Paris. The specimens are to be referred to *B. subcolumnaris*. In addition to several specimens of *Sieber 208* I have seen *Duss 578* (NY, P), *4630* (NY), *Hahn 321* (K, P), *969* (GH, K), *1506* (BM, K) and *Richard s.n.* (P), all from Martinique.

Buxus muelleriana Urb., Symb. Antill. **5**: 400. 1908.

Buxus subcolumnaris Muell. Arg., DC. Prodr. **16**(1): 14. 1869 *p.p.* as to plant of Cuba.

The type of this species is *Wright 1920* from Cuba.

Buxus brevipes Urb., Symb. Antill. **5**: 401. 1908.

Buxus citrifolia var. *brevipes* Muell. Arg., DC. Prodr. **16**(1): 15. 1869.

The type of this species is *Wright 1919* from Cuba. *Wright 1919*, however, is a mixed collection, another portion being the type of *Buxus acuminata* (Griseb.) Muell. Arg.

Buxus laevigata (Sw.) Sprengel, Syst. Veg. **3**: 847. 1826.

Crantzia laevigata Sw., Prodr. 38. 1788.
Tricera laevigata (Sw.) Sw., Fl. Ind. Occ. **1**: 333. 1797.
Buxus citrifolia var. *fuscescens* Muell. Arg., DC. Prodr. **16**(1): 15. 1869.
Tricera citrifolia sensu Britton & Wilson, Sci. Surv. Puerto Rico & V.I. **5**: 507. 1924, not Willd.

A fragment of the collection *Wydler 406* from Puerto Rico was examined in the herbarium at Paris. The specimen is referable to *B. laevigata* (Sw.) Spreng., known from Jamaica and matching well such collections as *Harris 9492* or *Howard & Proctor 15042*. Urban (Symb. Antill. **4**: 358. 1910) had suggested that perhaps the Bredemeyer collection was also from Puerto Rico and not Venezuela. It seems more likely that the Wydler collection carries an erroneous label since *B. citrifolia* is represented by more recent collections from Venezuela and neither *B. laevigata* nor *B. citrifolia* has been recollected in Puerto Rico.

The Wydler specimen in Paris bears an annotation of a new specific name attributed to Mueller Arg. The epithet has never been published by Mueller, to my knowledge, but has been used since as *Tricera* (?) *crassifolia* Britton and *Buxus crassifolia* (Britton) Urban, for an entirely different plant from Cuba typified by the collection *Shafer 4163*.

Buxus olivacea Urb., Symb. Antill. **9**: 172. 1924.

Mathou's reference to this species as occurring in Martinique (*loc. cit.* 139) is clearly an error and is not supported in the remainder of her study. Urban based the species on *Ekman 4992* from Cuba and Mathou studied only material of *Ekman 9783* also from Cuba, and cited by Urban.

MATHOU'S MONOGRAPH

Miss Mathou's monograph of the Buxaceae, stated in the title to be anatomical, microchemical and systematic studies, has been overlooked by recent workers. Perhaps its obscure publication as a thesis (Faculté des sciences de Toulouse, Toulouse, 1939) and its limited distribution account for the fact that its several new combinations have not been seen either by compilers of the Index Kewensis or of the Gray Herbarium Index. On the basis of her studies, Miss Mathou recognizes one new section of the genus *Buxus*, maintains two sections in a "sensu novo," and emends a fourth section. In addition two subsections are cited as new and two genera reduced to subsections. No Latin descriptions are given and the names of all subgeneric categories must be regarded as illegitimate. The subgeneric taxa are distinguished by evidence obtained from study of the inflorescences and from the anatomy of the stem and the petiole.

The systematic treatment used by Miss Mathou is subject to criticism. Several new combinations are made correctly but several others are incorrectly made or cited erroneously. Miss Mathou retains or re-establishes taxa previously considered synonyms by earlier workers, without comment or without evidence. The following taxonomic decisions in her paper are worthy of notice:

"**Buxus microphylla** var. **japonica** Rehd. et Wils. comb. nov." (Mathou *loc. cit.* 43). This combination was made by Rehder and Wilson in Sargent, Plantae Wilsonianae **2**: 168. 1914.

Buxus longifolia Boissier var. **latifolia** Mathou, *loc. cit.* 84. 1939. TYPE: *Pr. Lys s.n.*, collected April 1932 near Antioche, Syria.

Buxus flaviramea (Britton) Mathou, *loc. cit.* 140. 1939. This combination antedates my own, published in the Journal of the Arnold Arboretum **28**: 126. 1947.

Buxus purdieana Baillon. Mathou recognizes this species although Fawcett and Rendle (Fl. Jam. **5**: 2. 1926) had placed it in the synonomy of *B. laevigata.* Mathou compares *B. purdieana* with *B. macrophylla* but not with *B. laevigata.*

"**Buxus citrifolia** (Sprengel) Urban." A combination manufactured by Miss Mathou (*loc. cit.* 195) presumably intended for *Buxus citrifolia* (Willd.) Sprengel.

Buxus brevipes (Mueller) Urban (Mathou *loc. cit.* 199). An incorrect citation for *Buxus brevipes* Urban.

Buxus subcolumnaris (Mueller) Urban (Mathou *loc. cit.* 214). An incorrect combination for *Buxus subcolumnaris* Muell. Arg.

Buxus rotundifolia (Britton) Mathou, *loc. cit.* 229. 1939. This combination antedates that made by Brother Alain (Contr. Ocas. Mus. Hist. Nat. Col. "De La Salle," Havana, No. 12, 2. 1953).

Buxus pulchella Baillon. Mathou (*loc. cit.* 242) re-establishes this species. Mueller Arg. had reduced the Baillon species to synonomy under *B. vahlii* Baillon, but Mathou found no support for this decision. Miss Mathou did not compare *B. pulchella* with *B. laevigata* where Fawcett and Rendle (*op. cit.*) had placed Baillon's species.

Buxus revoluta (Britton) Mathou, *loc. cit.* 268. 1939. This combination antedates that made by Brother Alain (*loc. cit.* 2. 1953).

Buxus leoni (Britton) Mathou, *loc. cit.* 268. 1939. This new combination has not been recorded in international indices. Mathou concluded that in anatomical characteristics *B. leoni* was very similar to *B. aneura*, but that specimens of the latter species could be distinguished on the basis of the pubescent fruit. Miss Mathou also noted the anatomical similarity of *B. leoni* with *B. wrightii.* More recently Alain (Contr. Ocas. Mus. Hist. Nat. Col. "De La Salle," Havana, No. 13, 144. 1953) has placed *Tricera leoni* in the synonomy of *Buxus wrightii.*

Buxus macowani var. **benguellensis** (Gilg) Mathou, *loc. cit.* 303. 1939. Miss Mathou has reduced Gilg's species to varietal status and has made the combination.

Buxus hirta (Hutchinson) Mathou, *loc. cit.* 306. 1939. The basionym of this new combination is *Buxus benguellensis* Gilg var. *hirta* Hutchinson, Kew Bull. **1912**: 55. 1912. The combination is cited in Index Kewensis as *Mathou in Trav. Lab. For. Toulouse*, Tome I. iii. Art. II, 25. (1940).

POLLEN MORPHOLOGY IN THE JUGLANDACEAE, I: POLLEN SIZE AND PORE NUMBER VARIATION

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ALTHOUGH IDENTIFICATION OF fossil pollen and spores to the family or generic level provides valuable paleoecological data, it is obvious that specific identifications are to be desired. Unfortunately in many taxa there are no distinctive morphological features which can be used to effect such identifications, although in some difficult groups measurable characters such as pollen size or pore number have been utilized. Examples of this are the use of pollen size in *Pinus* (Cain 1940, 1944, Cain and Cain 1944, 1948a, 1948b, Buell 1946a, 1946b, Hansen 1947) and *Betula* (Leopold 1956) and the use of pore number in *Alnus* (Leopold 1955). It has been emphasized repeatedly (e.g., Christensen 1946, Faegri and Iversen 1950, and Whitehead 1962) that the use of such criteria is beset with many difficulties. First of all, one must have adequate knowledge of the range of variation displayed by the character selected. This can be obtained only by accumulating data from a large number of collections selected to cover the geographic range of the species and the spectrum of ecological conditions in which it occurs. For pollen size frequency studies one must also assess with care the effect of chemical treatment, mounting medium, and environment of preservation.

As yet the statistical approach has not been applied to members of the Juglandaceae, even though studies of Pleistocene and Tertiary sediments have suggested the possibility of separating species of *Carya* on the basis of pollen size and species of *Juglans* on the basis of pore number. For example, it is readily apparent from studying any sample which contains much *Carya* pollen that there is a considerable size range for the grains. This suggests that there might be distinct size differences among the various species. Similarly, work with Pleistocene material in the east has indicated the possibility of separating grains of *Juglans cinerea* L. from those of *J. nigra* L. on the basis of pore number. Grains of the former appear to have fewer pores. However, adequate data on pollen size in the extant species of *Carya* and pore number variation in the aforementioned species of *Juglans* have not been available.

In the present paper the results of a study of the pollen size-frequency characteristics of *Carya tomentosa* Nutt. and *C. cordiformis* (Wang.) K. Koch will be described. These two species were selected so that extensive data would be available for at least one species from each section of the genus (*C. tomentosa* from section CARYA (sect. *Eucarya* C. DC.) and *C. cordiformis* from section APOCARYA C. DC.). In addition, preliminary size frequency data for several other species of *Carya* will be discussed.

Lastly, the results of a detailed study of pore number variation in *Juglans cinerea* and *J. nigra* will be presented and the reliability of this criterion for specific identifications discussed.

The author wishes to express his appreciation to Dr. Elso S. Barghoorn, under whose thoughtful direction the variational study was initiated, and to the Jersey Production Research Company, Tulsa, Oklahoma, for permission to publish the results of the size study which was carried out as part of a general survey of pollen morphology in the Juglandaceae while the writer was a consultant during the summer of 1960. Grant G-17277 from the National Science Foundation has provided support for the final phase of the project.

1. POLLEN SIZE VARIATION IN CARYA TOMENTOSA AND C. CORDIFORMIS

Eleven collections each of *Carya tomentosa* and *C. cordiformis* were used for the size variation study. Between 1 and 3 collections have been used for study of the other species of *Carya* examined. The specimens studied are cited at the end of this paper.

Pollen of *Carya* was prepared according to the following technique:

1. Boil in KOH for 3 minutes.
2. Wash twice with distilled water.
3. Wash once with glacial acetic acid.
4. Acetolyze for 1 minute (10:1, acetic anhydride: concentrated sulfuric acid).
5. Wash twice with distilled water.
6. Wash once with 95% alcohol.
7. Wash twice with absolute alcohol.
8. Wash once with benzene (U.S.P., thiophene free).
9. Mount in silicone oil (Dow Corning 200 Fluid, viscosity 12,500 centistokes).

Use of the above preparation and of silicone oil for the size study was predicated by the considerations outlined by Christensen (1946, 1954), Andersen (1960), and Whitehead (1961, 1962).

Size measurements were carried out under high dry magnification utilizing an ocular interval of 2.04 micra. One hundred grains were measured for each collection of *Carya tomentosa* and *C. cordiformis*, and 50 grains for the collections of the other species. The linear dimension selected for measurement is illustrated in FIGURE 4.

The results of the pollen size study are presented in FIGURE 1, and in TABLES 1, 2, and 3. It is clear that there is considerable variation in pollen size in *Carya*.

Grains of *Carya cordiformis* range in size from 26.52 μ to 46. 92 μ, with a mean of 40.36 ± 2.89 μ. The modal class for the entire population is 40.80 μ. For the individual collections the modal class varies from 34.68 μ to 42.84 μ. The pollen grains of *C. tomentosa* vary in size from 40.80 μ to 63.24 μ, with a mean of 50.65 ± 3.41 μ. The modal class is

51.00 μ. Modes for the individual collections range from 46.92 μ to 53.04 μ.

Size data on the other species of *Carya* studied are as follows:

Section APOCARYA: *Carya aquatica*, 2 collections, range 36.72–46.92 μ. mean 41.80 μ; *C. illinoensis*, 2 collections, range 38.76–55.08 μ, mean

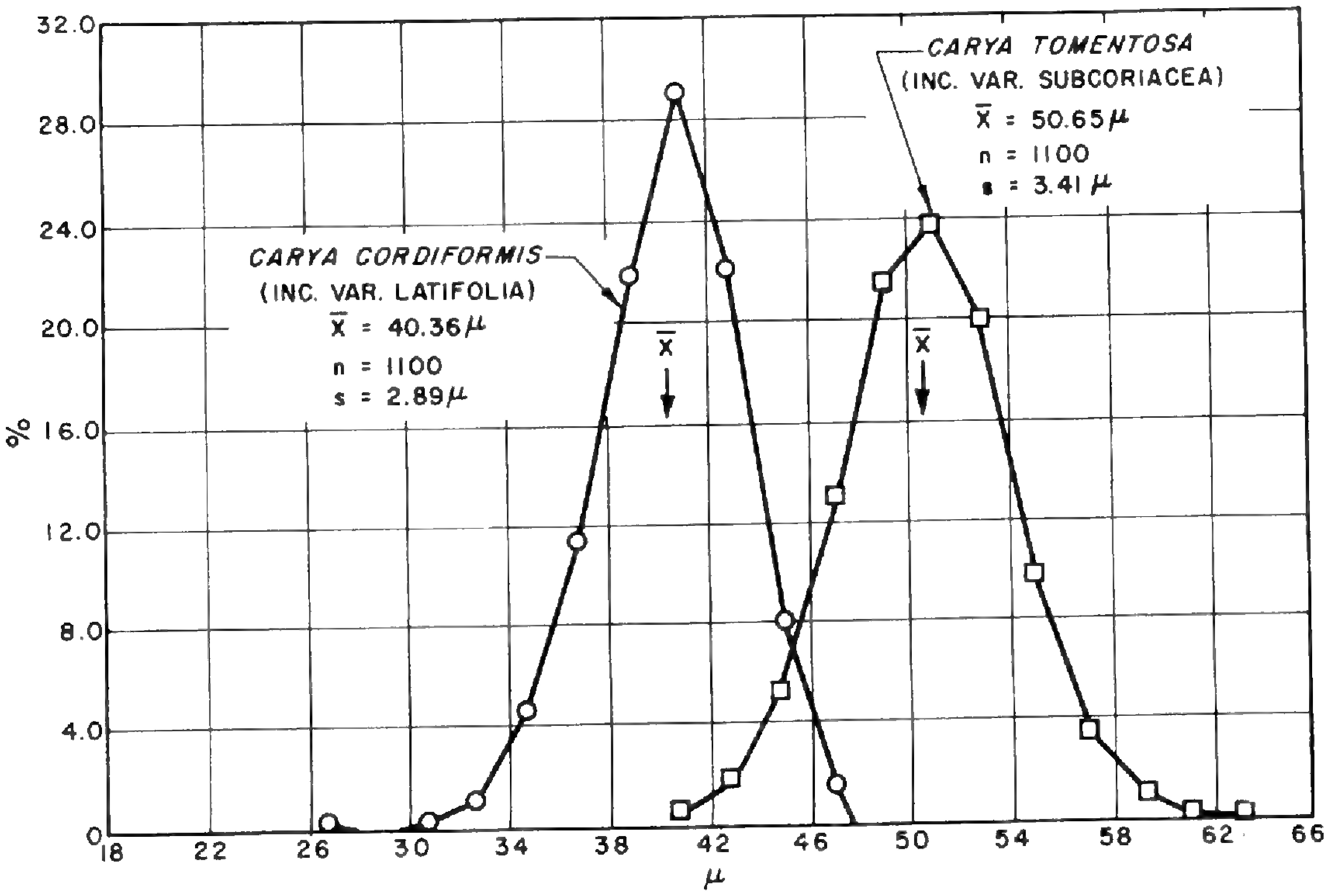


FIG. 1. Pollen size variation in *Carya tomentosa* Nutt. and *Carya cordiformis* (Wang.) K. Koch.

TABLE 1. **Pollen Size Variation in Carya cordiformis**

	SAMPLE NUMBER											
MICRA	1	2	3	4	5	6	7	8	9	10	11	TOTALS
26.52				1								1
28.56				0								0
30.60				2								2
32.64				10		1				1		12
34.68	1	1		42		3	2			3		52
36.72	10	5	4	36	5	17	20	2	2	9	15	125
38.76	38	11	15	7	17	34	38	11	2	24	43	240
40.80	34	38	32	2	32	33	28	34	18	36	32	319
42.84	15	29	31		37	9	11	38	40	23	9	242
44.88	1	13	14		9	3	1	15	28	4	1	89
46.92	1	3	4						10			18
												1100

$\overline{X} = 40.36$

$s = \pm 2.89$

1, Minnesota; 2, Kentucky; 3, Missouri; 4, South Carolina; 5, Washington, D.C.; 6, New York; 7, Missouri (var. *latifolia*); 8, Oklahoma (var. *latifolia*); 9, Texas; 10, Mississippi; 11, Tennessee.

46.10 μ; *C. myristiciformis,* 2 collections, range 32.64–44.88 μ, mean 39.64 μ.

Section CARYA (sect. *Eucarya* C. DC.) *C. laciniosa,* 2 collections, range 38.76–51.00 μ, mean 45.00 μ; *C. ovata,* 3 collections, range 36.72–51.00 μ, mean 44.93 μ; *C. pallida,* 1 collection, range 42.84–55.08 μ, mean 49.82 μ; *C. glabra,* 2 collections, range 40.80–53.04 μ, mean 46.88 μ; *C. leiodermis,* 1 collection, range 40.80–53.04 μ, mean 47.49 μ; *C. texana,* 2 collections, range 40.80–53.04 μ, mean 46.27 μ; *C. ovalis,* 2 collections, range 36.72–53.04 μ, mean 47.65 μ.

Since only a few measurements are as yet available for most species of *Carya,* it is premature to suggest the possibility of differentiating species on the basis of pollen size. However, the considerable difference in mean pollen size for *C. tomentosa* and *C. cordiformis* (10 micra) and the interspecific differences indicated by the preliminary data on TABLE 2, do suggest that the preparation of a size-frequency curve for fossil material might be instructive. A bimodal curve could then be taken as an indication of the presence of at least 2 species. Further work on pollen size for the other species of *Carya* might then allow one to make tentative suggestions as to the species represented, provided that one has evaluated the variables mentioned previously. Similarly, size frequency analyses of this sort could be utilized for the delimitation of "form species" in pre-Pleistocene sediments.

It is interesting to note that *Carya tomentosa,* like several other species of section CARYA, is a tetraploid, and that *C. cordiformis,* like other species

TABLE 2. **Pollen Size Variation in Carya tomentosa**

	SAMPLE NUMBER											
MICRA	1	2	3	4	5	6	7	8	9	10	11	TOTALS
40.80				3	1		1					5
42.84	1		1	7	5		2		2			18
44.88	5	1	1	28	11	1	7		1		3	58
46.92	20	4	3	38	25	7	21	4	2	2	17	143
48.96	29	20	7	15	40	24	34	10	20	6	32	237
51.00	26	32	18	7	14	31	22	31	30	26	24	261
53.04	13	28	26	2	4	22	10	32	28	41	13	219
55.08	5	12	22			10	3	18	12	17	9	108
57.12	1	3	13			4		4	4	7	2	38
59.16			7			1		1	1	1		11
61.20			1									1
63.24			1									1
												1100

$\overline{X} = 50.648$

$s = \pm 3.41$

1, Texas (var. *subcoriacea*); 2, Indiana (var. *subcoriacea*); 3, Missouri; 4, Pennsylvania; 5, Virginia; 6, Mississippi; 7, Indiana; 8, Georgia; 9, Massachusetts; 10, Oklahoma; 11, Tennessee.

of section APOCARYA, is a diploid (Woodworth 1930, Stone 1961). Since grains of *C. tomentosa* are 10 micra larger on the average than those of *C. cordiformis,* it is possible that pollen size in *Carya* may be correlated with ploidal level. This is true in a number of other taxa (e.g., *Andropogon* (Gould 1957)). Stomatal size shows a similar correlation in *Carya* (Stone 1961). The preliminary size data for the other known tetraploids indicate that mean pollen size (for grains treated with KOH, acetolysis, and mounted in silicone oil) for this ploidal level in *Carya* is above 46 μ (*C. glabra,* 46.88 μ; *C. texana,* 46.27 μ; *C. ovalis,* 47.65 μ), while data for the known diploids suggest that the mean pollen size for that ploidal level is less than 46 μ (*C. aquatica,* 41.80 μ; *C. illinoensis,* 46.10 μ; *C. laciniosa,* 45.00 μ; *C. ovata,* 44.93 μ).

The preliminary data on pollen size for *Carya myristiciformis* (39.64 μ) supports Stone's information on stomatal size, and suggests that this species is a diploid. Similarly, the pollen size data for *C. pallida* (49.82 μ) and *C. leiodermis* (47.49 μ) and Stone's stomatal measurements indicate that these two species are probably tetraploids.

TABLE 3. **Pollen Size Variation in Several Species of Carya**

MICRA	C. AQUATICA	C. GLABRA	C. ILLINOENSIS	C. LACINIOSA	C. LEIODERMIS	C. MYRISTICIFORMIS	C. OVALIS	C. OVATA	C. PALLIDA	C. TEXANA
26.52										
28.56										
30.60										
32.64						2				
34.68						7				
36.72	4					12	1	2		
38.76	12		1	1		28	1	4		
40.80	30	1	4	12	2	31	1	22		4
42.84	40	5	21	18	3	16	5	22	2	21
44.88	13	26	29	31	9	4	16	36	1	20
46.92	1	40	17	27	12		25	40	6	25
48.96		20	14	9	15		32	22	17	19
51.00		7	10	2	7		15	2	15	10
53.04		1	3		2		4		7	1
55.08			1						2	
57.12										
59.16										
61.20										
63.24										
TOTALS	100	100	100	100	50	100	100	150	50	100
MEAN	41.80 μ	46.88 μ	46.10 μ	45.00 μ	47.49 μ	39.64 μ	47.65 μ	44.93 μ	49.82 μ	46.27 μ

2. PORE NUMBER VARIATION IN JUGLANS CINEREA AND J. NIGRA

Forty-four collections of *Juglans cinerea* and 42 of *J. nigra* have been utilized for the pore number investigation. Pollen of *Juglans* was prepared by acetolysis and mounted in glycerine jelly. The pore number study of *Juglans* was carried out by counting the pores in 100 grains for each collection. Counts were made under high dry magnification by focusing carefully up and down through the individual grains. The problems inherent in making such counts will be apparent in FIGURES 5–10. The results of this study are presented in FIGURE 2.

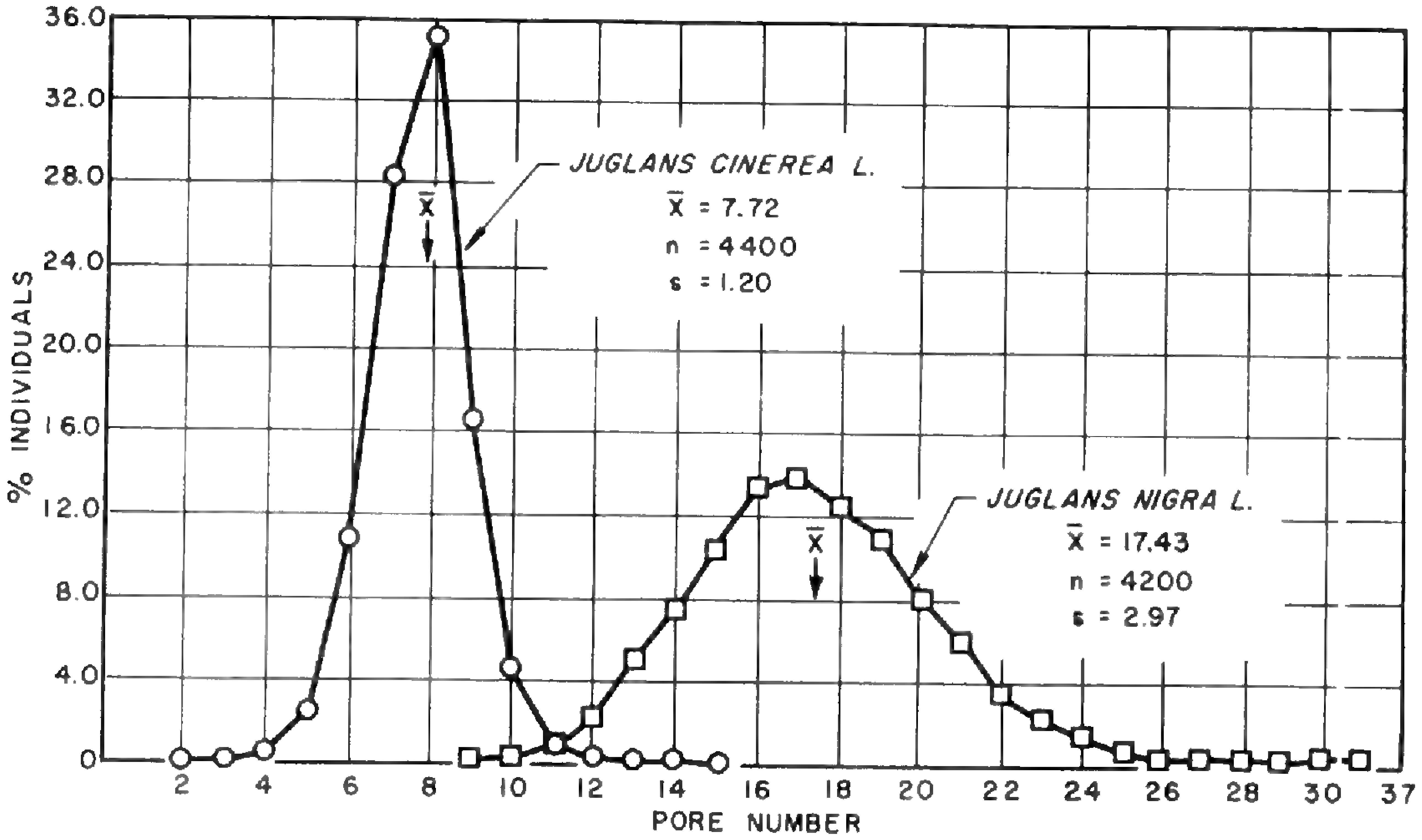
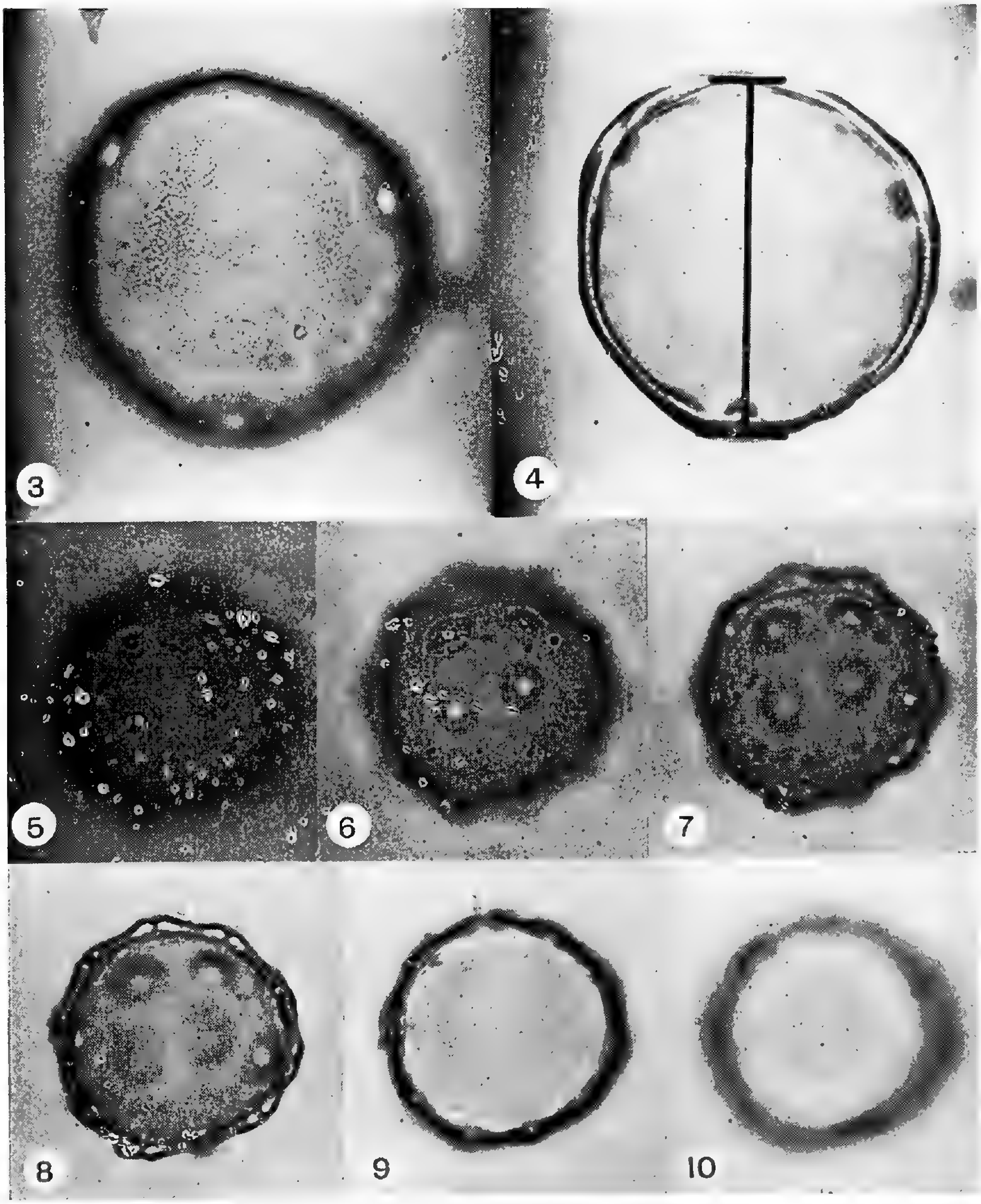


FIG. 2. Pore number variation in *Juglans cinerea* L. and *Juglans nigra* L.

Pore number in *Juglans cinerea* varies from 2 to 15 with a mean of 7.72 ± 1.20. The modal class for the total population is 8 pores. Pore number in *J. nigra* varies from 9 to 37 with a mean of 17.43 ± 2.97. The modal class for the total population is 17. In the individual collections of *J. cinerea* the modal class varies from 6 to 9 pores and in *J. nigra* from 12 to 22.

It is evident that the majority of grains of *Juglans cinerea* can be separated from those of *J. nigra* with reasonable certainty. There is overlap only between 9 and 15 pores, hence grains with less than 9 pores would most certainly be those of *J. cinerea,* and grains with more than 15, *J. nigra.* Grains having 9 and 10 pores are more likely to be those of *J. cinerea,* and grains with from 12 to 15 are more likely to be those of *J. nigra.* Pollen with 11 pores could be assigned with equal probability to either species.

However, one must approach these assumptions with some caution, remembering that the modal class in one collection of *Juglans cinerea*



FIGURES 3–10. Photomicrographs of *Carya* and *Juglans* pollen. FIGURES 3 and 4, *Carya tomentosa* pollen, polar view, two levels of focus. Dimension measured is marked in FIGURE 4. FIGURES 5–10, consecutive levels of focus through a grain of *Juglans nigra*, polar view. Note the heteropolar characteristic of the grain, with the pores being located equatorially and globally, but with one hemisphere pore-free. Magnification 725×.

was as high as 9 and in one collection of *J. nigra* as low as 12. If an entire local population of *J. cinerea* possessed grains with a mean pore number close to 9, then the chances of encountering white walnut grains with from 10 to 15 pores would, of course, be greater. Similarly, if a local population of black walnut possessed grains with a mean pore number close to 12, then the chances of encountering *J. nigra* grains with from 9 to 11 pores would also be greater. In this respect, information on pore number variation within several local populations of each species would be instructive.

Obviously, the preparation of a pore number frequency curve for fossil material would aid in determining whether only one or both of the species were represented. Unfortunately, one almost never encounters a sufficient number of *Juglans* grains to allow for this. However, noting the number of pores in any other walnut grains encountered in a sample will help suggest which species were present.

SPECIMENS EXAMINED[1]

1. **Carya cordiformis** (Wang.) K. Koch. UNITED STATES. Rhode Island: *Palmer 44337* (A). New York: *Thomas 2152* (A). Minnesota: *Mearns 814* (GH). District of Columbia: *Ward*, 1879 (GH). Kentucky: *Horsey 2321* (A). South Carolina: *Griscom 16503* (GH). Missouri: *Palmer 3943* (A). Mississippi: *Harbison 10* (GH). Texas: *Bush 5588* (A).
2. **Carya cordiformis** (Wang.) K. Koch var. **latifolia** Sarg. UNITED STATES. Missouri: *Palmer 5499* (A). Oklahoma: *Bush 1139* (GH).
3. **Carya tomentosa** Nutt. UNITED STATES. Massachusetts: *Manning*, 1942 (A). Pennsylvania: *Byhouwser & Kobuski 216* (A). Indiana: *Deam 27014* (GH). Virginia: *Allard 2621* (GH). Tennessee: *Ruth 426* (GH). Georgia: *Small*, 1895 (GH). Mississippi: *Harbison 17* (GH). Missouri: *Palmer 5761* (A). Oklahoma: *Palmer 21647* (GH).
4. **Carya tomentosa** Nutt. var. **subcoriacea** Sarg. UNITED STATES. Indiana: *Deam 10182* (A). Texas: *Palmer 7269* (A).
5. **Carya aquatica** Nutt. UNITED STATES. Georgia: *Gillespie 5045* (A). Mississippi: *Harbison 191* (A).
6. **Carya glabra** (Mill.) Sweet. UNITED STATES. Massachusetts: *Faxon*, no date (GH). Georgia: *Harbison 1026* (A).
7. **Carya illinoensis** (Wang.) K. Koch. UNITED STATES. Tennessee: *Gattinger 2565* (GH). Missouri: *Bush 5759* (A).
8. **Carya laciniosa** (Michx. f.) Loud. UNITED STATES. Massachusetts: *Manning*, 1941 (GH). Missouri: *Palmer 39144* (A).
9. **Carya leiodermis** Sarg. UNITED STATES. Arkansas: *Palmer 39298* (A).
10. **Carya myristiciformis** (Michx. f.) Nutt. UNITED STATES. Arkansas: *Letterman*, 1881 (GH). Texas: *Palmer 22438* (A).
11. **Carya ovalis** (Wang.) Sarg. UNITED STATES. Massachusetts: *Manning*, 1935 (GH). Ohio: *Horsey 479* (GH).
12. **Carya ovata** (Mill.) K. Koch. CANADA. Quebec: *Marie-Victorin 28234* (GH). UNITED STATES. North Carolina: *Biltmore Herbarium 1838a* (A). Arkansas: *Palmer 22461* (A).
13. **Carya pallida** (Ashe) Engl. & Graebn. UNITED STATES. North Carolina: *Biltmore Herbarium 5551a* (GH).
14. **Carya texana** Buckl. UNITED STATES. Texas: *Bush 197* (A).
15. **Carya texana** Buckl. var. **arkansana** Sarg. UNITED STATES. Missouri: *Palmer 3928* (GH).

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[1] Material of all collections cited was obtained from the herbarium of the Arnold Arboretum (A) or from the Gray Herbarium (GH), Harvard University.

16. **Juglans cinerea L.** CANADA. Quebec: Massawippi, *Jack*, 1914 (A); Ile Perrot, *Marie-Victorin 28230* (GH); Phillipsburg, *Knowlton*, 1925 (GH). Ontario: *Shields*, 1948 (GH). UNITED STATES. Maine: *Narlin*, 1896 (GH). New Hampshire: Jaffrey, *Williams*, 1898 (GH); Lebanon, *Kennedy*, 1894 (GH). Vermont: Charlotte, *Pringle*, 1879 (A); Wallingford, *Williams*, 1908 (GH); Brandon, *Williams*, 1908 (GH). Massachusetts: Waltham, *Williams*, 1897 (GH); Walpole, *Rich*, 1897 (GH); Boxford, *Robinson*, 19?? (A); South Egremont, *C. B. (surname illegible)*, 1919 (A). Connecticut: *Harger*, 1902 (GH). New York: Vaughns, *Burnham*, 1891 (GH); Fall Creek, *Muenscher & Bechtel 665* (A). Ohio: Oberlin, *Kofoid*, 1890 (GH); Friendship, *Demaree 10639* (GH); Columbus, *Horsey*, 1914 (A). Michigan: *W. J. B.*, 1899 (A). Minnesota: *Moore & Thatcher 13015* (A). Wisconsin: *J. H. V.*, 1896 (GH). Iowa: *Pammel 102* (GH). Indiana. *Hill*, 1894 (A). Pennsylvania: Martin's Creek, *Bartram*, 1907 (A); Bradford County, *Byhouwser & Kobuski 212* (A); Bethlehem, *No collector or date listed* (GH); Conestoga River, *Heller*, 1900 (GH). Delaware: *Canby*, 1897 (A). Virginia: Natural Bridge, *Deane*, 1886 (GH); Hot Springs, *Hunnewell 4000* (GH); Marion, *Britton et al.*, 1892 (A). West Virginia: *Harbison 7108* (A). Tennesee: *Palmer 17310* (A). Kentucky: Middleborough, *Horsey 1927* (A); Beattyville, *Horsey 1156* (A). Missouri: Hazelgreen, *Palmer 39201* (A); Booneville, *Palmer 29972* (A); Arcadia, *Palmer 22703* (A); Pontiac, *Bush 13374* (A); Allenton, *Letterman*, 1882 (A); Ralls County, *Davis 1360* (A); Patton, *Kellogg 25860* (A). Arkansas: *Bush 13402* (A).

17. **Juglans nigra L.** UNITED STATES. Rhode Island: *Rehder*, 1927 (A). New York: Tompkins County, *Thomas 2148a* (GH); Queensbury, *Burnham*, 1893 (GH); Hempstead, *Churchill*, 1910 (GH). Pennsylvania: Whitehorse, *Travis 31* (A); Stewartstown, *Adams 4431* (A). Ohio: Gallipolis, *Horsey 2108* (A); Roosevelt Game Preserve, *Demaree 10678* (GH). Michigan: Monroe Lake, *Ehlers 369* (A; GH); Herb. Agricultural College, Michigan, *Beal*, 1899 (A). Illinois: Stark County, *Chase*, 1896 (GH); Havana, *Jones 11231* (GH); Cairo, *Palmer 14920* (A). Indiana: Ingalls, *Smith 5602* (GH); Long Swamp, *Ek*, 1942 (GH). New Jersey: *Long 34600* (GH). Delaware: *Canby*, 1899 (GH). Virginia: Prince George County, *Fernald & Long 11814* (GH); Walker Creek, *Small*, 1892 (A); Gertie, *Fernald & Griscom 4381* (GH). Kentucky: Battlesburg, *Horsey 893* (A); Richmond, *Horsey 1065* (A), Olympia, *Horsey 1714* (A); Mt. Sterling, *Horsey 2307* (A). Tennessee: *Palmer 17541* (A). North Carolina: Granville County, *Faxon*, no date (GH); Biltmore, *Biltmore Herbarium 1314* (GH). Georgia: *Small*, 1895 (A). Missouri: Allenton, *Letterman*, 1882 (A); Joplin, *Palmer 22743* (A); Galena, *Palmer 22793* (A). Kansas: Riley County, *Norton 502* (GH); Neodesha, *Palmer 20823* (A); Ellsworth, *Palmer 21281* (A). Oklahoma: Ft. Sill, *Clemens 11541* (GH); Norman, *Bruner*, 1924 (A); Oklahoma City, *Slavin 421* (A); Purcell, *Stevens 137* (GH); Sulphur, *Merrill*, 1935 (A). Texas: Travis County, *Warnock 46090* (GH); Dallas, *Reverchon*, 1874 (GH).

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THE RUBIACEOUS GENUS MUSSAENDA: THE MORPHOLOGY OF THE ASIATIC SPECIES

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The rubiaceous genus *Mussaenda* comprises some 190 species distributed in a broad band extending through the Old World tropics from Africa and Madagascar to India and Ceylon, China, Malaysia, the Philippines, Polynesia, New Guinea, and Australia. The group includes several valuable ornamental shrubs and is of considerable biological interest, both because of the unusual development of one or more of the calyx lobes into large, colorful, petaloid structures and because of the presence of heterostyly (associated with differences in pollen size) in every species of the genus. Although a number of hybrids have been produced in the Philippine Islands using a "double" form in which all of the sepals are petaloid, nothing seems to be known of the breeding mechanisms, other biological features, or chromosome numbers within the genus.

Various taxonomic and floristic studies have treated parts of the genus, but *Mussaenda* has not been monographed since 1830 when only 27 species were known to A. P. de Candolle. At the present time, the large number of species involved, the paucity of herbarium materials, the difficulty of establishing specific characters, and the lack of opportunity for field studies of live plants make an approach on a regional basis most feasible. Accordingly, the present paper is a general survey of morphological variation in the genus, especially as represented in Asia. This will be followed by taxonomic treatments of the species of various areas, the two papers to follow immediately dealing with those of India and Ceylon and of the Philippine Islands.

A number of morphological characteristics have been used in the classification of species of *Mussaenda*. De Candolle (1830) distinguished three sections (no longer tenable) on the basis of the presence or absence of the expanded petaloid calyx segments, the number of leaves at each node, and the persistence or deciduousness of the calyx segments on the fruit. In connection with Asiatic species, J. D. Hooker (1880), Gamble (1921), Ridley (1923), Kurz (1877), and Pitard (1923) based their classifications on a combination of characters of the inflorescence, calyx lobes, corolla tube, and the pubescence and venation of the leaves. Wernham (1913) suggested a character of the stipule to be important in treating *Mussaenda* in Africa. Valeton (1925) used leaf characteristics in classifying the species of New Guinea. Bremekamp (1940) has stressed the extent of hairiness inside the corolla tube, the nature of the stipules, the presence or absence of floral dimorphism, the insertion of the stamens, and the nature of the pubescence in determining relationships between the Rubiaceae in general, but such a study has not been made for *Mussaenda*, *sensu lato*.

Since 1916 a number of segregate genera, none of which is included in the present consideration of *Mussaenda*, have been proposed. Wernham (1916) established *Pseudomussaenda*, basing it on the African *M. luteola* Del. and including *M. monteiroi* Wernh., *M. capsulifera* Balf. f., and a new species *P. gossweileri*, and stated that "the character of the fruit of this plant certainly suffices to remove it not only from the genus *Mussaenda*, but also from the tribe Mussaendeae in spite of its resemblance in habit to other species of that genus." In 1939, Ridley raised *Mussaenda* sect. *Asemanthia* to generic rank, stating that this name was first "proposed by Stapf for a number of plants originally described as belonging to the genus *Mussaenda* but differing in the large size of the corolla and in the absence of the white phyllomorphic calyx lobes so conspicuous in that genus." Assigning the Malayan and Bornean *M. mutabilis* Hemsl., *M. spectabilis* Ridley, and *M. coccinea* Stapf, and a new species *A. lobbii* Ridley to the group, he suggested that species from tropical Africa possessing these same characters should be transferred here.

In 1937, Bremekamp proposed that the genus *Aphaenandra* Miquel, based on a Sumatran plant, be recognized to include two species, *A. uniflora* (*Acranthera uniflora* Kurz, *Aphaenandra sumatrana* Miq., *Mussaenda uniflora* Wall. ex G. Don, *M. theifera* Pierre) and *A. parva* (*M. parva* Wall. ex G. Don, *M. sootepensis* Craib, *M. neosootepensis* Craib). These species are herbaceous, (10–20 cm. tall), spread by runners, and have a terminal dichasium with stout monochasial branches reduced to two or three flowers, with parts resembling those of *Mussaenda* except for the dehiscence of the fruit.

Finally, in 1948, Li proposed the genus *Schizomussaenda* to include *Mussaenda dehiscens* Craib (*Greenea hoaensis* Pierre ex Pitard, *Schizophragma macrosepalum* Hu, *Emmenopteris rehderi* Metcalf). Li did not discuss the relationship of his new genus with the earlier *Pseudomussaenda*, and the differences between them do not seem to be sufficient to warrant a distinction.

The validity of these generic segregates is beyond the scope of the present paper and will be considered at a later time. Hence, generic synonymy has been omitted here, and the generic description and notes on morphology given here are based on the Asiatic species of *Mussaenda*, *sensu stricto*.

Herbarium specimens were obtained on loan from the following institutions for which the standard abbreviations cited are used in the text.

A	Arnold Arboretum of Harvard University, Cambridge, Massachusetts.
BSI	Herbarium, Botanical Survey of India, Poona.
C	Botanical Museum and Herbarium, Copenhagen.
GH	Gray Herbarium of Harvard University, Cambridge, Massachusetts.
K	Herbarium, Royal Botanic Gardens, Kew.
LWG	Herbarium, National Botanic Gardens, Lucknow.
NY	Herbarium, New York Botanical Garden.

PNH Philippine National Herbarium, Manila.
US U. S. National Herbarium, Washington.

I wish to take this opportunity to thank the directors and curators of the institutions named above for allowing me to examine the specimens under their care. I wish also to thank in particular Dr. Richard A. Howard, under whose supervision and guidance this investigation was conducted, and Dr. Lily M. Perry, for her unfailing interest and encouragement. Mrs. Lazella Schwarten, librarian of the Arnold Arboretum and Gray Herbarium, was of immense help to me in tracing pertinent literature, and Drs. Bernice G. Schubert and C. E. Wood, Jr., have contributed materially in their editorial capacities. Further, I wish to express my appreciation and deep gratitude to the Rockefeller Foundation, for grant of scholarship funds during this period, and to the Arnold Arboretum, for a Mercer Fellowship.

Mussaenda Linnaeus, Sp. Pl. 1: 177. 1753; Gen. Pl. ed. 5. 82. 1754.[1]

Erect or scandent shrubs or undershrubs, rarely herbs; stems branching, glabrous or pubescent; bark thin, gray or brown, lenticellate and firm or papery, peeling off in flakes. Leaves opposite or ternately whorled, petiolate, unequal, membranous, large or small, lanceolate to ovate or obovate, entire, glabrous or hairy, the upper surface less hairy, more hairy on the usually prominent veins below, apex acute or obtuse, long or short acuminate, base long or short cuneate, equilateral or inequilateral, acute, obtuse, rounded or sometimes subcordate; petioles varying in length, thin or stout, pubescent or glabrous. Stipules interpetiolar, caducous or persistent, large or small, membranous or thick, ovate to lanceolate or oblong, opposite pairs sometimes fusing at their bases forming a ring round the node, pubescent outside, glabrous or pubescent and with glands inside, with 2 or more pairs of branching vascular strands, the apex acuminate, acute and entire or bifurcate, the base expanded laterally within the petiolar bases. Inflorescences terminal and from the axils of the terminal pair of leaves, large or small, spreading or compact, few to many flowered, dichotomous or trichotomous cymose corymbs. Flowers small to large, heterostylous, bisexual, and radially symmetrical, sessile or pedicellate. Bracts and bracteoles deciduous, linear to ovate, glabrous or pubescent, bracteoles usually trifid or trilaciniate. Calyx tube oblong to turbinate, lobes 5, small or large, triangular, linear, subulate, lanceolate to obovate or foliar, deciduous or persistent, glabrous or pubescent inside and/or outside with one or more pairs of glands at the base of each lobe, vascular strands usually 3, the 2 laterals sometimes branching at their bases; one lobe in some flowers often transformed to a large, petaloid, white to yellowish appendage or sometimes all five petaloid.

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[1] The first collection of the genus was made by Paul Hermann, chief medical officer in the Dutch East India Company, in Ceylon, between 1672 and 1677, and he gave it the vernacular name "Mussaenda." Hermann's plant was described by Burmann in his *Thesaurus Zeylanicus* (1737), and the name was then adopted by Linnaeus, the plant becoming *Mussaenda frondosa* L., the type species of the genus.

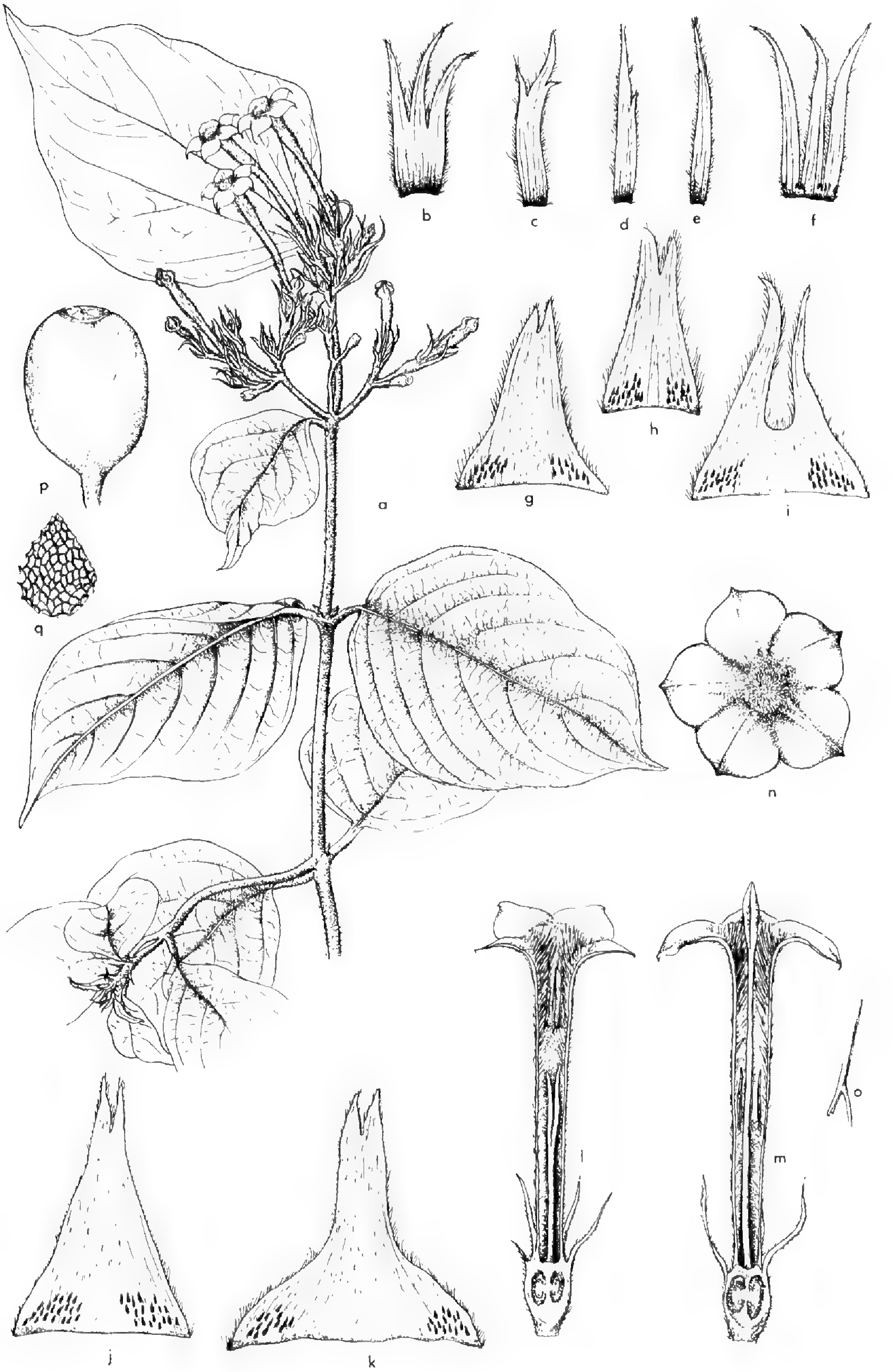

FIG. 1. *Mussaenda frondosa*: (sketches from a series of collections by the author) *a*, branch with inflorescence and petaloid sepal; *b–d*, bracteoles; *e*, bract; *f*, calyx lobes viewed from within to show glands at their bases; *g–k*, stipules spread out and viewed from the adaxial surface showing degree of bifurcation at apex and glands at base; *l*, longitudinal section of short-styled

Corolla salverform, the tube white to greenish yellow, cylindrical, or infundibuliform, broader at the top, short or long, glabrous or hairy outside and inside, hairiness varying according to the length of the style and stigma, in short-styled forms with longer hairs at the throat and between stamens and in long-styled forms with short hairs, hairiness extending as far as the bases of anthers or shortly and scantily beyond, sometimes as far as the base of the tube; hairs usually strap shaped, but if globular becoming linear and longer below the stamens; corolla lobes 5, yellow to orange-red, small or large, thick or thin, linear to lanceolate to orbicular, acute, obtuse or rounded, apiculate or caudate, glabrous or hairy outside and inside, hairs papillate by extensions of gradually shortening mouth hairs along the midline. Stamens 5, sessile or with short filaments, epipetalous towards the middle or top of the tube, never protruding beyond; anthers linear, dorsifixed, introrse, acute or obtuse at the apex, sterile and bilobed at the base, the lobes diverging, protandrous, pollen sacs dehiscing longitudinally; pollen grains usually of two sizes, those from short-styled flowers larger than those from long-styled forms. Ovary inferior, hairy or glabrous, obconical, fusiform, or cylindrical, 2-loculed with numerous ovules on fleshy, peltate, axile placentae; style long or short (heterostylous), filiform or stout, arising from the middle of a fleshy, circular, nectariferous disc, sometimes grooved on opposite sides, very rarely pubescent; stigma bilobed, long or short, the lobes diverging or firmly appressed on their papillate, receptive surfaces. Fruit a berry, short, ellipsoid, globular or long-cylindrical, glabrous or pubescent, sometimes lenticellate, with or without a crown of persistent calyx segments; seeds numerous, minute, smooth or spiny, reticulate, black or brown, triangular, oblong or ovate, embedded in a fleshy pulp; testa areolate with a varying number of foveae in the minute areoles; endosperm present; germination epigeal.

HABIT. Species of *Mussaenda* grow in a variety of climatic and environmental conditions from sea level up to an elevation of about 2000 m., along river banks, sandy river beds, in sloping ravines, and at the edge of the tropical jungles which merge into grassy, savanna slopes. They seem to prefer a well-drained, clayey or gravelly, humic soil. Most are low or medium-sized shrubs which assume a climbing or scandent habit at the edge of the jungle, so that various collectors have referred to climbing shrubs, scandent shrubs, semiwoody climbers or lianas. A few species which are vines or small trees also occur, so that the habit is not a very reliable character taxonomically.

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flower with tufted hairs at mouth and stamens in throat of the corolla tube; *m*, longitudinal section of long-styled flower with tufted hairs at mouth and stamens about halfway on the corolla tube; *n*, corolla from above; *o*, dorsifixed anther with short filament and bilobed base; *p*, berry showing nectariferous gland on top and scars left by the deciduous calyx segments; *q*, seed, showing reticulations, foveae within reticulations omitted. *a* × ½, *b–f*, *l–n*, *p*, × 1½; *g–k*, × 4–6; *o*, × 3; *q* × 15.

Some species prefer the shade of the thick jungle, but the majority flourish in the semishade with opportunity for extending their branches over the neighboring shrubs and at the same time flanking the open side of the jungle, displaying their colorful "bracts."

The stem is woody, lenticellate, often brittle with considerable pith in the center. Young stems are glabrous or covered with whitish or reddish-brown pubescence.

LEAVES. The leaves are very variable in their form as well as in their pubescence. The two leaves at a node are usually unequal in size and in the length of petioles. Younger leaves are smaller and more pubescent than older ones. Even on the glabrate leaves scattered hairs may be found along the veins but are more frequent on the lower surface. The pubescence on the leaves and the stem is also variable in the length of the hairs, their placement, density, and location. In some species (*Mussaenda wrayi* King, *M. hirsutissima* Hutch. ex Gamble) the hairs are long and more or less at right angles to the surface of the leaf and stem, but in others, though long, they are appressed to the surface, becoming a felt-like mixture with other shorter hairs. In still other species, the hairs are very short and appressed to the surface (*M. laxa* Hutch. ex Gamble, *M. calycina* Wall.). Even the "glabrous" species are hairy in some part or other, especially in the mouth of the corolla tube or on the stipules. Variations in the shape of the apex and base of the leaf even in the same species are very considerable, while the number of pairs of lateral veins in smaller leaves is less than in the larger ones in the same plant. The petiole is short (*M. sanderiana* Ridley, *M. incana* Wall.) or long (*M. scratchleyi* Wernh., *M. benguetensis* Elmer), characteristically thick (*M. lanata* C. B. Robins., *M. whitei* S. Moore) or thin (*M. ridleyana* Wernh., *M. aestuarii* K. Schum.). Usually the base of the lamina is cuneate (*M. laxa*, *M. scratchleyi*) or acuminate-decurrent (*M. attenuifolia* Elmer, *M. treutleri* Stapf), rarely distinct from the petiole.

STIPULES. The stipules are somewhat characteristic in many species of the genus. Bases of the stipules at a node extend laterally into and are overlapped by the bases of petioles. They may extend farther and fuse so as to form a ring round the node, as in *Mussaenda keenanii* Hook. f. They are rarely completely glabrous on both surfaces, and the pubescence varies in the length of the hairs, intensity, and location. Stipules nearing complete glabrousness but with a band of hairs along the midline outside (*M. ridleyana*) and also the margin (*M. aestuarii*) are encountered in some species, while in others they may be completely glabrous inside but hairy outside (*M. glabra* Vahl, *M. incana*, *M. macrophylla* Wall. [Philippine variety], *M. keenanii*, etc.). Stipules are completely hairy on both surfaces (*M. treutleri*, *M. lanata*, *M. whitei*) or hairy outside and inside at the base only (*M. glabrata* Hutch. ex Gamble, *M. hirsutissima*, *M. vidalii* Elmer, *M. setosa* Merr., *M. scratchleyi*, *M. pilosissima* Valeton, *M. aestuarii*). In a few species (*M. benguetensis*, *M. multibracteata* Merr.)

they are completely hairy outside, and inside at the apex and base only.

The size, shape and bifurcation at the apex of stipules vary. The stipules are large (*Mussaenda keenanii, M. corymbosa* Roxb.) or small (*M. glabra, M. frondosa* L., *M. parryorum* Fischer), acute or acuminate, mostly bifurcate at the apex while in a few the apex is entire or faintly bifid (*M. magallanensis* Elmer, *M. chlorantha* Merr., *M. ridleyana*). The bifurcation of the stipule may extend up to ¼ – ⅓ of the way (*M. albiflora* Merr., *M. lanata*), ⅓–½ of the way (*M. setosa, M. philippica* A. Rich., *M. vidalii, M. laxa*), more than halfway or almost to the base (*M. palawanensis* Merr., *M. scandens* Elmer, *M. hirsutissima*, etc.). The lobes of these divisions are usually subulate, straight on the stem or diverging, a character used by Gamble in the classification of some of the Indian mussaendas.

The distribution of glands on the stipule is a character which has not been exploited previously. The number of glands varies from few to many, usually in paired groups, or may be continuous at the base. *Mussaenda glabra, M. palawanensis, M. cylindrocarpa* Burck, *M. variolosa* Wall., etc., have few glands at the bases of stipules, while in others they are numerous. The two groups of glands run into each other and form a continuous band in certain species (*M. roxburghii* Hook. f., *M. keenanii, M. corymbosa, M. anisophylla* Vidal, *M. erosa* Champ., *M. pilosissima*).

The ontogeny and structure of the comparable glands have been worked out by Mitra (1948) for *Paederia foetida* L. and *Ixora parviflora* Vahl. The glands are periclinal divisions in the subepidermal layer, appearing as protuberances. Each gland has a central core consisting of several rows of elongated cells and a peripheral layer of palisade-like cells at right angles to it. These glands contain mucilaginous and resinous secretions.

The stipules are traversed by two to eleven pairs of vascular strands. The smaller stipules possess two or three pairs of veins (*Mussaenda philippica, M. scandens*), while the larger ones (*M. corymbosa, M. keenanii, M. anisophylla*) bear about five to nine pairs which are branched.

Inflorescences. The type of inflorescence can easily be used to distinguish certain species, such as *Mussaenda uniflora* Hutch. & Dalz., with one to three large flowers, and *M. roxburghii, M. corymbosa*, and several others with the flowers condensed into heads or contracted cymes. In other species the inflorescences are spread out or diffuse (*M. philippica, M. laxiflora* Hutch., etc.). The presence or absence of hairs in the inflorescences and the hair-color are also striking characters. The hairs may be short and closely appressed (*M. glabra*) or long and spreading, giving a grizzled appearance as in *M. hirsutissima, M. wrayi, M. multibracteata*, and *M. pilosissima*. They are grayish white, brown, or reddish brown in color.

The form and nature of bracts and bracteoles are not discussed here as it is felt that their contribution is not significant owing to their variability. However, they range from large to small, lanceolate to ovate, and glabrous to pubescent, and are normally caducous. Bracteoles are usually trifid or trilaciniate.

CALYX. The calyx consists of a tube which is fused with the ovary, only the terminal segments emerging above the junction, though a portion of the tube may still be visible joining the segments together at the top of the ovary. These calyx segments are of considerable importance in the classification of the species. They vary from minute, triangular stubs less than 0.5 mm. in length (*Mussaenda bammleri* Valeton) to large, expanded white petaloid segments resembling so-called "bracts" (*M. pentasemia* Fischer, *M. anomala* Li, *M. philippica* var. *aurorae* Sulit). The sepals vary in length, shape, thickness, and pubescence, and each sepal carries at the base one or more pairs of glands. The number of pairs of glands seems to be characteristic of certain species. Several species (such as *M. frondosa*, *M. glabra*, *M. incana*, *M. lanata*, *M. multibracteata*, *M. scandens*, *M. chlorantha*, *M. grandifolia* Elmer, *M. acuminatissima* Merr.) bear one pair of glands at the base of each sepal, while others (such as *M. macrophylla*, *M. treutleri*, *M. roxburghii*, *M. albiflora*, *M. vidalii*, *M. nervosa* Elmer, *M. anisophylla*) bear two pairs of glands. Still others (such as *M. keenanii*, *M. corymbosa*, *M. benguetensis*) carry three pairs, and four or more pairs are borne by species such as *M. philippica* and *M. oreadum* Wernh. The number of glands does not seem to be a very reliable character to be used alone, for the number varies even on individual sepals of the same flower. Hairiness of the sepals, too, does not seem to be constant. Sepals of *M. frondosa*, for instance, are always hairy outside but glabrous inside or occasionally hairy inside as well.

Each sepal is usually supplied by three vascular strands, the middle strand arising as an extension of five alternating vascular bundles in the wall of the ovary, which is supplied by ten strands. Branches from the middle strands unite with branches of adjacent vascular bundles to form the lateral strands of the sepal, and these may branch further in certain species (FIG. 2). In broader-sepaled species transverse or arched intervascular connections unite these vascular strands (*Mussaenda macrophylla*, *M. multibracteata*).

COROLLA. The corolla tube is narrow and tapering or sometimes infundibuliform, usually broadening above the point of attachment of the stamens and varying in length from 1.1 cm. (*Mussaenda lanata*) to over 6 cm. (*M. pluviatilis* S. Moore). In most species the corolla tube is pubescent outside, the hairs extending onto the outside of the petals but towards the base becoming shorter and scantier, so that in some species the tubes are almost glabrous at the base. The corolla tubes are entirely glabrous in a few species, such as *M. corymbosa*, *M. cylindrocarpa*, and *M. scratchleyi*. In some species the hairs are short and appressed, while in others they are long and directed forwards or horizontally (*M. macrophylla*, *M. multibracteata*, and *M. vidalii*).

Hairiness inside the tube appears to be associated with heterostyly in

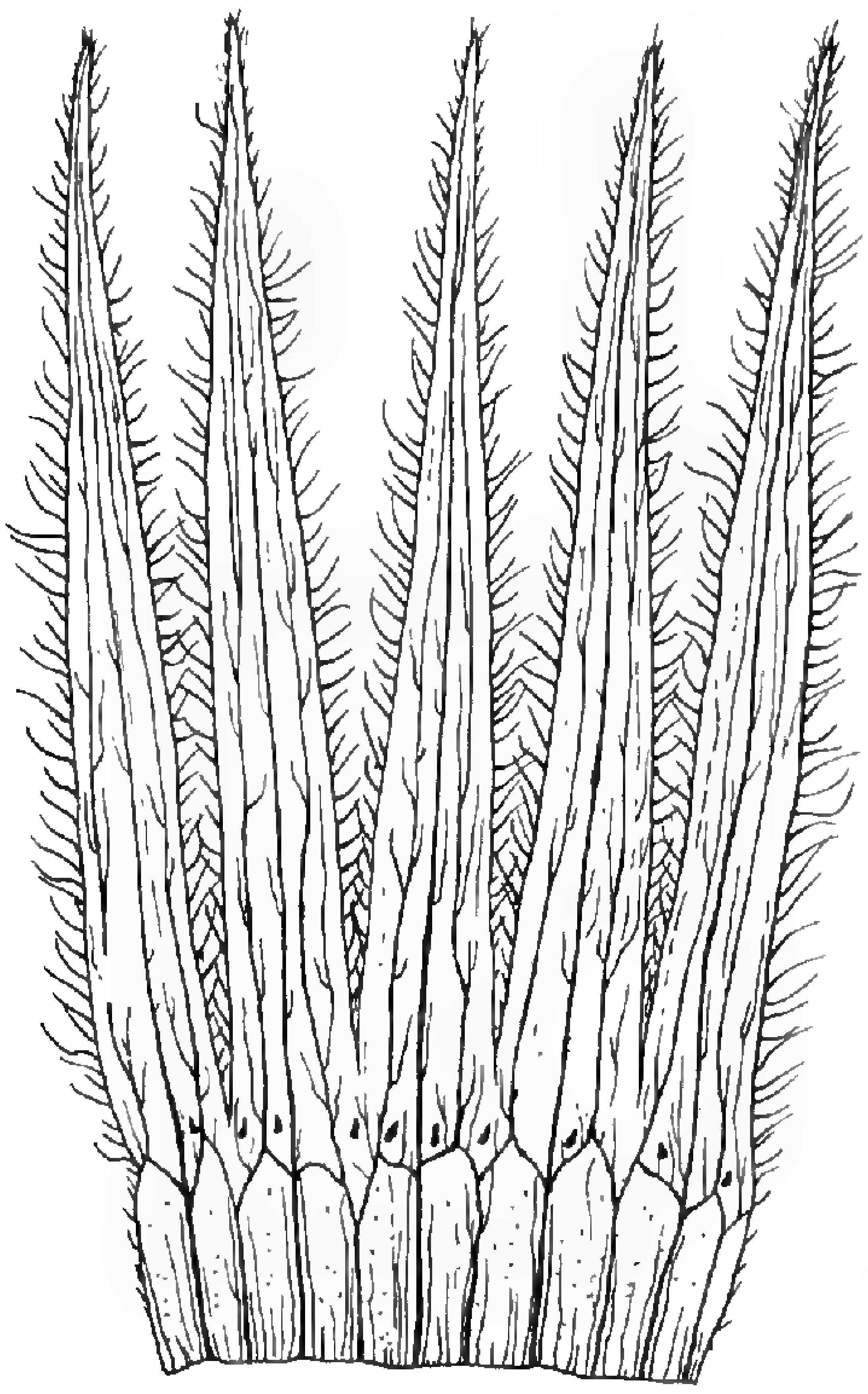

FIG. 2. Calyx lobes of *Mussaenda frondosa* together with a portion of ovary wall spread out to show vascular distribution and glands, × 5.

this genus and offers characteristics of morphological and taxonomic interest. Long-styled forms usually bear shorter hairs (0.16–0.5 mm. long) than in short-styled forms (hairs inside 1.2–2 mm. long), except in the *Mussaenda frondosa* group. In all Indian mussaendas they are tufted at the mouth of the tube, a feature not observed in the Philippine and New Guinea species. Hairs are absent from inside the tube in the long-styled forms of *M. grandifolia,* except for a few short ones at the base of the corolla lobes. Elmer (1906) in describing this species says, "Corolla yellow, 3 cm. long, tubular, broadest across the top, exterior pubescent, lanose on the interior." However, the type collection was examined by me and found to be glabrous inside. In *M. ridleyana* the hairs are long, stiffish, and tapering. Hairs in the long-styled forms of species such as *M. aestuarii* and *M. oreadum* are globular (0.16 mm. long) extending as far as the base of anthers, becoming longer (0.26 mm. long), linear, and strap shaped lower down in the tube, which is glabrous at the base. Hairiness inside the tube generally extends as far as the base of the anthers or a little lower, but in certain species it extends to $\frac{1}{2}$, $\frac{3}{4}$, $\frac{4}{5}$, $\frac{9}{10}$, or the entire length of the tube. Species such as *M. roxburghii* are not only completely hairy inside but also possess a tufted ring of hairs at the base, a very useful specific character.

The corolla lobes vary in size, shape, and color (yellow to orange-red). They are lanceolate to ovate or suborbicular (broader than long) in the Indian and Philippine species, except in *Mussaenda albiflora*, the lobes of which are linear. The species of New Guinea, on the other hand, show a larger range of variations. In these the corolla lobes may be oval (*M.*

oreadum), obovate (*M. aestuarii*), oblong-lanceolate (*M. ridleyana*), or oblong (*M. ferruginea* K. Schum., etc.). They are hairy outside, and glabrous or covered with papillate hairs inside.

ANDROECIUM. The stamens are epipetalous, all attached at the same level in a ring, the position of which varies from below the middle to the top portion of the tube. They are inclosed in the tube and never protrude beyond the mouth. Hairs in the throat extend between anthers. The free portions of the filaments are very short (1–3 mm. long) (or are absent in exceptional cases, such as *Mussaenda oreadum* and *M. aestuarii*), adhere to the tube through their entire length, but exceptions in which they become free for a short distance have been observed in *M. macrophylla* (Philippine material) and several others. The dorsifixed anther is linear, short or long, acute or obtuse at the apex; the base is bilobed, with the sterile lobes rounded and appressed or diverging. The anthers are generally longer in short-styled forms than in long-styled forms. In some specimens of the long-styled forms examined the anthers do not appear to shed their pollen (*M. glabra, Parkinson 1692; M. scratchleyi, Clemens 523*), possibly an evolutionary tendency towards functional dioecism.

GYNOECIUM. The ovary is obconical, oblong or cylindrical, hairy or glabrous, and somewhat smaller in the short-styled forms. The wall is supplied by ten vascular bundles which branch at the bases of the sepals, supplying them with vascular strands but at the same time forming a continuous ring at the top. The style arises from the center of a nectariferous disc located at the top of the ovary. The style usually disappears in the fruit, but in a few it persists as a pointed structure (a distinguishing feature of *Mussaenda attenuifolia*). In all species the styles and stigmas of long-styled forms extend as far as the mouth of the corolla tube and lie surrounded by long, linear, strap-shaped hairs, while those of short-styled forms are much reduced and do not grow beyond the anthers. Extreme reduction is shown in some of the Javanese forms of *M. glabra*. The proportion of stigma to style varies from species to species. Stigmas over 1 cm. in length were observed in *M. grandifolia* (*Edano 77424*), *M. benguetensis* (*Loher 1523*), *M. cylindrocarpa* (*Sigafoos 97*), and *M. aestuarii* (*Brass 3896*), while the stigma in *M. pluviatilis* (*Brass 24306*) was very small, though its style was over 6 cm. long. A style pubescent at the top was observed for the first time in the genus in *M. oreadum* from New Guinea (*Brass 32073*).

FRUIT AND SEED. The fruit is a fleshy berry which varies in size, shape, and pubescence. In *Mussaenda parryorum* it is less than 1 cm. long, while in *M. pluviatilis* it is over 3 cm. in length. It may be oval, ellipsoid, clavate, cylindrical, or fusiform, pubescent or glabrous, smooth or rugose, with or without lenticels. The calyx may be persistent on the fruit or deciduous leaving conspicuous scars behind. The seeds, too, vary in size and shape. They are usually very small, numerous, varying in length from about 0.5 mm. to over 1 mm., attached to cushion-shaped, fleshy placentae.

The only instance where they are embedded in the placental cushion is in *M. parryorum*, a fruit of which may contain about 80 seeds, while the normal number of seeds in a fruit of *Mussaenda* exceeds several hundred. The seeds of species such as *M. keenanii*, *M. roxburghii*, and *M. laxa* are small (0.36–0.76 mm. long), while in others (*M. incana*, *M. treutleri*, *M. hirsutissima*) they are comparatively larger (0.9–1.16 mm. long). They are minute, somewhat plump, reticulate, oval, oblong, broadly ovate, pyriform or triangular in shape. The testa is made up of an irregular network of minute ridged areas or areoles which are foveolate. This foveolate character of the areoles of the testa was used by Bremekamp (1952) to group some genera of the Rubiaceae together into closely related tribes. The number of foveae in the areoles of the testa in some species is less than in others. There is a range of overlapping limited by a fixed maximum for each species. The seeds of *M. grandifolia* bear 1–4 foveae in the testa areoles, while those of *M. lanata*, *M. anisophylla*, *M. griffithii* Wight, etc., bear 3–6 foveae. A greater number of foveae (4–12) are borne in seeds of *M. chlorantha*, *M. magallanensis*, *M. nervosa*, etc., while the largest number (5–18) occurs in *M. parryorum*. *Mussaenda glabra*, however, bears seeds with two distinct numbers of foveae (2–7 and 3–14) in the areoles of the testa. The significance of this is not yet clear. The points at which the areolar ridges meet in the seed are usually raised, but in some species, such as *M. glabrata* and *M. scandens*, these points develop into conspicuous spines. The hilum is located at the narrow end of the seed or at the back. The characters of the fruit and seed discussed above are of diagnostic value.

HETEROSTYLY. In the preceding discussion mention has been made of long-styled and short-styled flower types. Burck (1883) appears to have been the first botanist to report a heterostylous condition for *Mussaenda* when he discussed some species cultivated at Buitenzorg (Bogor). More recently, Baker (1958) noted the occurrence of this condition in some species in Ghana. The many taxonomists who have described species of *Mussaenda* have usually given detailed measurements on the length of the style, the position of the anthers, and the nature of the hairs in the throat of the corolla, but apparently not one has been aware of the heterostyly in this genus. It was apparent in the Asiatic specimens available for this study that some "species" differed only in their style-anther relationships. In the random collections assembled only a few species were not represented by both long-styled and short-styled forms. In extreme examples the long-styled forms had styles exceeding those of short-styled flowers on a ratio of 12 to 1. The average ratio appeared to be between 3 and 5 to 1. A few species showed no major difference in style length, but the length of the stigmas was in contrast between the two types.

The following tabulation (TABLE I) reports the length in millimeters of the style, stigma, ovary, and anther respectively for long-styled (L. S.) and short-styled (S. S.) flowers for species from India and Ceylon, the Philippines, and New Guinea.

TABLE I. **Comparative Floral Dimensions of Long-styled and Short-styled Forms of Some Asiatic Species of Mussaenda**

	STYLE	STIGMA	OVARY	ANTHER
India and Ceylon				
M. CORYMBOSA				
L. S. (*Bot. Gard. Calcutta*)	20	3.5	4.5	5
S. S. (*Kamphovener 954*, Galathea Exped.)	12.5	3	2.5	4.5
M. FRONDOSA				
L. S. (*Jayaweera*, Ceylon)	18–21	2.5–4	3–4	4.5–5.5
S. S. "	13–15	3	3–3.7	5–5.5
L. S. (*Anglade*, Kodaikanal)	23	3	3.5	5.6
S. S. (*Bot. Gard.* Calcutta)	13.5	5	3.3	5.6
M. GLABRA				
L. S. (*Masters*, Assam)	14	5.5	3	5
S. S. (*Voigt*, Calcutta)	7	3	2.5	5.5
M. HIRSUTISSIMA				
L. S. (*Gamble 11393*, Madras)	23.5	1.8	3	4.2
S. S. (*Barnes 120*, Travancore)	11	2.5	4.5	6.5
M. INCANA				
L. S. (*Voigt 136*, Calcutta)	20	2.5	3.2	4.2
S. S. (*Hook. f.*, Assam)	13	2	3	4
M. LAXA				
L. S. (*Barnes 403*, Madras)	29	3.5	4	6
S. S. (*Gamble 20541*, Madras)	16.5	4.5	4.5	6
M. MACROPHYLLA				
L. S. (*Parry 274*, Assam)	23	3.5	3.5	5
S. S. (*Belcher 145*, Assam)	14	3.5	4	5.7
M. ROXBURGHII				
L. S. (*Jenkins 496*, Assam)	20	3	3	5
S. S. (*Juan 178*, Assam)	13.5	2.5	3	5
M. TREUTLERI				
L. S. (*Gamble 9565*, Sikkim)	27	4	2.5	5
S. S. (*Hook. f. & Thomson 20*, Assam)	14	4.5	4	5.5
Philippine Islands				
M. ACUMINATISSIMA				
L. S. (*Ramos 33133*, Luzon)	20	7	5	4.5
M. ALBIFLORA				
L. S. (*Dias 29885*, Negros)	20	6.5	3	3.5
S. S. (*Ramos & Edano 31107*, Panay)	3	3	4	4
M. ANISOPHYLLA				
L. S. (*Elmer 17481*, Luzon)	22	9	4.5	5.5
S. S. (*Merrill 2508*, Luzon)	4	2	4.5	6.5
M. BENGUETENSIS				
L. S. (*Loher 1523*, Cult. Trinidad)	22	12	5	5

TABLE I (*Continued*)

	STYLE	STIGMA	OVARY	ANTHER
S. S. (*Santos 5497*, Mountain Prov.)	2.5	1.5	5	7
M. GRANDIFOLIA				
L. S. (*Edano 77424*, Palawan)	22	10	4.5	4–4.2
M. LANATA				
L. S. (*Merrill 1768*, Luzon)	7	5	3.5	3
S. S. (*Elmer 6195*, Luzon)	1.6	1.8	4	4
M. MAGALLANENSIS				
L. S. (*Merrill 986*, Mindoro)	16	6.5	3.5	3.7
S. S. (*Elmer 124551*, Sibuyan)	1.5	1.5	3.2	3
M. MULTIBRACTEATA				
L. S. (*Convocar 2820*, Luzon)	17	9	5	4.5
S. S. (*Ramos & Edano 28783* Luzon)	3	2.5	4.5	5
M. NERVOSA				
L. S. (*Elmer 10510*, Mindanao)	17	8.5	4.5	6.5
S. S. (*Ramos & Edano 26422*, Luzon)	14.5	2	4	7.5
M. PALAWANENSIS				
S. S. (*Ebalo & Conklin*, Palawan)	4	2.5	4.7	6
M. PHILIPPICA				
L. S. (*Ramos 30452*, Catanduanes)	20	6	3.5	5
S. S. (*Sulit & Conklin 16840*, Mindoro)	2.5	2.5	4.5	6.5
M. PHILIPPINENSIS				
L. S. (*Sulit & Conklin 17652*, Mindoro)	19	6.5	3.5	4
S. S. (*Sulit 18877*, Luzon)	4	3.5	4.5	5.7
M. SCANDENS				
L. S. (*Elmer 11291*, Mindanao)	13	6	3.5	3.5
S. S. (*Wenzel 3354*, Surigao)	4	2.5	3	4.5
M. VIDALII				
L. S. (*Elmer 11309*, Mindanao)	17	6	4	5.6
S. S. (*Ramos & Edano 39035*, Mindanao)	2.5	2	3.5	5
New Guinea				
M. AESTUARII				
L. S. (*Brass 3896*, Dieni)	23	17	13	6.7
S. S. (*Brass 3947*, Dieni)	6	5	1.5	7
M. CYLINDROCARPA				
L. S. (*Hort. Bogor 416*, cult.)	9	6.5	8.5	3.2
S. S. (*Brass 7346*, Papua)	9	3.5	9	3.5
M. CYLINDROCARPA var. TOMENTOSA				
L. S. (*Sigafoos 97*, Sentani Lake)	11	9	5	4
S. S. "	4.5	3	5	5.8

TABLE I (*Continued*)

	STYLE	STIGMA	OVARY	ANTHER
M. OREADUM				
L. S. (*Carr 14801*, Boridi)	25	8.5	7	5.5–7.5
S. S. (*Brass 5040*, Mt. Tafa)	9	4.5	7.5	9
M. PILOSISSIMA				
L. S. (*Womersley & Millar 7880*, Morobe Dist.)	21	7	6.5	7.5
S. S. (*Brass 32492*, Morobe Dist.)	4	2.5	4.5	4.5
M. PLUVIATILIS				
L. S. (*Brass 1401*, New Guinea)	54.5	1.5	8	7.5
L. S. (*Brass 24306*, Peria Creek)	60	2	13.5	6.5
M. PROCERA				
L. S. (*Brass 3276*, Nakeo Dist.)	19	7	5.5	5
S. S. (*Carr 11037*, New Guinea)	4	2	4	5.5
M. RIDLEYANA				
S. S. (*Brass 13065*, New Guinea)	6.2	2	4–4.5	6–7
M. SCRATCHLEYI				
L. S. (*Brass 5333*, Mafulu)	16	5	4.5	5.5
S. S. (*Clemens 523*, Morobe Dist.)	7.5	2.7	3	6
M. WHITEI				
L. S. (*Brass 11682*, Balim River)	21–23	6.5–7	5	6.5–7

In the flowering plants heterostyly represents a functionally dioecious condition. In *Mussaenda* this is apparently true of all the species examined. There is also some indication that, given time, a heterostylous condition will lead to actual dioecism or unisexual flowers. In *Mussaenda* the reduction in the length of the style from long-styled forms to short-styled forms has brought about a small but corresponding reduction in the length of the stigma and the ovary. Short-styled flower types tend to have slightly longer anthers than do long-styled flower types. A few long-styled flower forms examined do not appear either to shed or to form pollen. In short-styled flower forms there appears to be a reduction in the number of ovules developed and a tendency for the stigmatic lobes to remain appressed by their receptive surfaces in fully mature condition. A comprehensive field study of living plants is necessary to determine whether there is a tendency in either long-styled or short-styled flowers toward a greater sepal development into petaloid structures. Likewise, no information can be obtained from herbarium specimens whether one flower or the other tends to produce more fruit or a greater number of seeds.

The type of pubescence inside the corolla tube appears to be correlated with the style length. With the exception of a group of species related to *Mussaenda frondosa*, the short-styled forms tend to have longer throat hairs than do the long-styled ones. As Baker has already suggested, the throat hairs of the short-styled forms may well cause visiting insects to struggle for entrance to the nectar-bearing area and thereby cause them to collect more pollen. In long-styled forms the insects would leave accumulated pollen on the diverging stigma lobes before approaching the area of throat hairs. Tentatively, there appear to be five types of hairs and pubescence in the corolla tubes of *Mussaenda* species. As listed below, these may well serve as a means of grouping species for further study.

The hairs in the corolla throats of the different species of *Mussaenda* can be divided into the following categories:

(1) Long, linear, strap-shaped hairs in the throat of both long-styled and short-styled forms, e.g., the *M. frondosa* group, *M. pluviatilis,* etc.

(2) Long, linear, strap-shaped hairs in the short-styled forms and short, strap-shaped hairs in the long-styled forms, e.g., *M. glabra, M. philippinensis* Merr., *M. philippica,* etc.

(3) Long, linear, strap-shaped hairs in the short-styled forms and short, globular hairs in the long-styled forms, e.g., *M. aestuarii.*

(4) Long, stiffish, tapering hairs in the throat of short-styled forms (long-styled forms not seen), e.g., *M. ridleyana.*

(5) Hairs absent in the throat of long-styled forms (short-styled forms not seen), e.g., *M. grandifolia.*

SUMMARY

The present study has attempted to show the range of variation to be expected in the parts normally used in taxonomic descriptions of *Mussaenda* and the relative value of each. Heterostyly is recognized as general in the genus, hence the exserted stigmas or length of the style prove of little value in limiting species. Homostylous forms have not been encountered in the specimens studied. A great many observations need to be made on living plants to aid in a future monograph.

Several groups of characteristics not used by previous students of the group are suggested as of potential value. These include the nature of the glands inside the stipules, the types of hairs found in the throat of the corolla, and the sculpturing of the seeds. The morphological characteristics which appear to be of greatest taxonomic usefulness are:

Habit (herb, shrub, or tree).
Type of inflorescence and number and distribution of flowers.
Presence or absence of petaloid sepals.
Type of fruit (dry capsule, berry, or fleshy capsule).
Number and distribution of glands inside the stipules.
Type of hairs inside the corolla tube.
Presence or absence of hairs on the style.
Size, number, and ornamentation of the seeds.

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ROYAL BOTANIC GARDENS,
PERADENIYA, CEYLON

COMPARATIVE ANATOMY OF THE LEAF-BEARING CACTACEAE, VII
THE XYLEM OF PERESKIAS FROM PERU AND BOLIVIA

I. W. BAILEY [1]

THE PUTATIVE SPECIES OF *Pereskia*, viz. *P. humboldtii* Britt. & Rose, *P. vargasii* H. Johnson, *P. weberiana* K. Schum., and *P. diaz-romeroana* Cárd., which occur east of the higher elevations of the Andes in Peru and Bolivia have been described as shrubs or trees varying in height from one to six meters, and having numerous slender terminal branches a few millimeters in diameter. These plants are characterized by the small size of their flowers, fruits and leaves.

The largest stems of which I have succeeded in obtaining anatomical material are six centimeters in diameter in the case of *P. diaz-romeroana*, five centimeters in that of *P. humboldtii*, and three centimeters in that of *P. weberiana*.

The secondary xylem in stems of these representatives of *Pereskia* is of a dense form (FIGS. 1, 2), resembling that which occurs in shoots of comparable diameter in the case of *P. sacharosa* Griseb. described in the preceding paper of this series (Bailey, 1962). As in *P. sacharosa*, the vessels which occur singly and in small clusters are distributed either diffusely (FIG. 2), particularly in the earlier formed secondary xylem, or in more or less zonate patterns (FIG. 1), in subsequently formed wood of large stems. The libriform fibers which commonly are septate and starch containing are abundant and thick walled. The wood parenchyma tends to be scanty paratracheal, but arcs or zones of more abundant parenchyma occur at times, especially where the vessels exhibit zonation in their distributional pattern (FIG. 1). In such arcs of wood parenchyma some cells having very thin unlignified walls occur at times. Furthermore, where multiseriate rays pass through patches of unlignified wood parenchyma their cells also may have unlignified walls as occurs in some stems of *P. aculeata* Mill. (Bailey, 1962). Occasionally in large stems close to the level of the ground, broad zones of unlignified wood parenchyma and ray parenchyma are formed. Such zones may contain isolated clusters of lignified vessels with scanty lignified paratracheal parenchyma.

As in stems of *Pereskia sacharosa*, the multiseriate rays vary in height, breadth and form and in the intervals between them as seen in transverse sections of the xylem (compare FIGS. 1 and 2). When first formed, those which extend outward from parenchymatous gaps in the eustele, tend to

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be vertically extensive and subsequently to be dissected into lower derivatives (FIG. 3). In the outer xylem of large stems their derivative parts tend to be more or less laterally displaced (FIG. 4), during increasing girth of the cambium. In addition, there is some tendency for the rays to become broader, as well as lower, during their radial extension outward (compare FIGS. 3 and 4). The cells of the innermost part of the first formed multiseriate rays are of "erect" form and subsequently are succeeded by more or less isodiametric and even slightly "procumbent" ones. Such changes in the form and orientation of the ray cells vary in magnitude and may be precocious or considerably delayed. At times erect cells are retained on the sides and upper and lower margins of the rays (FIG. 4) as in some stems of *P. sacharosa.*

In the third paper of this series (Bailey, 1961b), I noted that where the multiseriate rays of the leaf-bearing cacti are composed throughout of cells with thick, heavily lignified walls deposition of crystals of calcium oxalate when it occurs does so in the form of single crystals or several independent ones, aggregation into druses being absent or of rare occurrence. On the contrary, where the rays or parts of them are composed of cells with thin, unlignified walls such rays or parts contain numerous druses. Although patches of unlignified ray tissue are of limited and sporadic occurrence in stems of the Andean pereskias, the lignified parts of the rays, as well as the unlignified areas, contain druses. This suggests, as does the occurrence of some druses of rotund form in the outermost layer of the cortex and the character of the foliar vasculature (Bailey, 1960), that in these species there may be tendencies towards trends of phylogenetic modifications such as become exaggerated in *Quiabentia* and *Pereskiopsis.*

In the Peruvian and Bolivian pereskias, as in *Pereskia aculeata,* the primary vascular cylinder and pith vary from one or two millimeters to as much as a centimeter in diameter. Furthermore, as in *P. aculeata,* the number of fascicular strands is fewer than in stems of comparable diameters of *P. sacharosa.* This appears to be correlated with the fact that *P. aculeata* and the Andean pereskias tend to have less modified 2-trace unilacunar nodes than in the case of *P. sacharosa.*

In stems of the Peruvian and Bolivian pereskias, as in stouter young stems of *Pereskia sacharosa,* broadening of the parenchymatous gaps in the eustele allows for an increase in circumference of the primary vascular cylinder and enlargement of the pith after cambial activity is initiated in the fascicular parts. However, there is less broadening of the first formed part of the multiseriate rays than in comparable stems of *P. sacharosa,* two or three rays rather than a single very broad one extending outward from the parenchymatous gaps of the eustele. It should be emphasized in this connection that the tendency for increase in circumference of the eustele and concomitant enlargement of the pith after cambial activity is initiated in the fascicular strands of the primary vascular cylinder becomes increasingly exaggerated and of fundamental significance in more succulent forms of cacti.

The underground parts of *Pereskia humboldtii* of Peru and *P. diazromeroana* and *P. weberiana* of Bolivia are characterized by having more or less numerous, spindle-shaped and globular, tuberous appearing enlargements which may attain diameters of four centimeters. Some unswollen parts of the underground ramifications fourteen millimeters in diameter, when sectioned and examined with a hand lens, superficially resemble rhizomes in internal structure. As shown in FIG. 6, there is a cylinder of dense secondary xylem enclosing a pith-like core of soft tissue. However, in thin transverse sections (treated with phloroglucin-hydrochloric acid as a test for lignification and examined under higher magnification) one finds that there are no strands of primary xylem subtending the cylinder of lignified secondary xylem, the only remnants of such strands occurring near the center of the axis. Furthermore, the form and radial arrangement of thin-walled unlignified cells in the central core indicate that most of the tissue was formed by cambial activity and contains isolated strands of lignified vessels (FIG. 6).

That such a root structure is due to drastic modification of the derivatives of cambial activity is demonstrated by variations in the internal structure of different roots from the same plant. In some roots, e.g. inner part of FIG. 5, the multiseriate rays are unlignified as in roots of *Pereskia aculeata* (Bailey, 1962). In their extensions outward such rays may exhibit alternations of lignified and unlignified cells. Other roots, while retaining vestiges of a primary body typical of roots, have early cambial activity which forms a larger proportion of unlignified parenchyma. In such roots (FIG. 7) the cambium may subsequently form a cylinder of lignified secondary xylem which at times contains relatively few vessels. This cylinder, as in FIG. 7, may be succeeded in certain cases by an outer zone having a markedly reduced proportion of lignified cells. In larger roots having broad cylinders of normal appearing secondary xylem (FIG. 6) the derivatives of both fusiform and ray initials may have thick lignified walls throughout the cylinder. The vessels which occur singly and in small clusters may be more or less diffusely distributed. In other cases, the vessels exhibit conspicuous zonation in their distribution and patches or arcs of unlignified cells may be present.

Transverse sections cut adjacent to fully matured tuberous enlargements of the roots as shown in FIG. 8 resemble those shown in FIG. 6 in having a cylinder of lignified secondary xylem surrounding a core of unlignified tissue. However, the transition between unlignified and lignified secondary xylem may be less abrupt and uniform, with narrow wedges of lignified tissue extending inward toward the center of the root. Furthermore, the first unlignified cells formed by the cambium exhibit conspicuous enlargement and changes in form and orientation. Particularly between the slender, radially oriented wedges of lignified tissue the enlarged cells have a tangential, rather than a radial, orientation, indicating additional enlargement of the central core of unlignified tissue during early ontogenetic stages of the formation of the root.

The fully matured tuberous swellings of the root system are composed largely of a greatly enlarged core of unlignified tissue, formed by the cambium and subsequently much expanded by enlargement of its constituent cells. The formation of a tenuous cylinder of lignified secondary xylem is deferred to the final stages of cambial activity (FIGS. 9, 10). In the central core of soft tissue the radial seriation of recently formed derivatives of the cambium becomes displaced and more or less rapidly modified by subsequent enlargement of the unlignified cells (FIGS. 9, 10). Relatively few strands of lignified vessels are formed in the soft tissue. Those that are, become more or less extensively disrupted and displaced during enlargement of the unlignified derivatives of the cambium (FIG. 10). In the few tuberous swellings available to me, the immature ones contain abundant starch, whereas in the case of fully matured ones the central core of unlignified cells contains comparatively little starch. This raises an important question regarding the physiological function of the tuberous enlargements.

In both unswollen and swollen roots examined by me all unlignified parts of the secondary xylem — whether formed by fusiform or ray initials of the cambium — contain some cells with inclusions of druses. However, as in the case of stems, druses also occur in lignified parts of the rays. Furthermore, in all roots there tends to be a precocious and abundant development in the secondary phloem of huge fiber sclereids (FIGS. 7, 9, 10) of a characteristic form discussed in the second paper of this series (Bailey, 1961a).

It is evident that *Pereskia humboldtii* of Peru and *P. diaz-romeroana* and *P. weberiana* of Bolivia are characterized by the potentiality of forming tuberous swellings on their roots. No material of the white-flowered variant of *P. humboldtii*, viz. *P. vargasii*, is available at present. Cárdenas states (personal communication) "the presence of the swellings on the roots of *Pereskia diaz-romeroana* and *P. weberiana*, of variable size (0.5–10 cm.) and either globose or spindle shaped seems to be related to the dry environment in which these plants grow in the wild . . . I have seen in many places those chains of swellings hanging out of the soil where soil was disintegrated by erosion. . . . I have seen *P. sacharosa* in the wild at North Argentina in flat soils with normal roots, that is without swellings. . . . In the low land of Bolivia they used to grow this latter *Pereskia* as fences in flat soils and then too there are no swellings."

These comments of Dr. Cárdenas raise morphological, physiological and taxonomic questions of considerable significance. Is the occurrence of tuberous swellings on the roots of Andean pereskias an "obligate" or "facultative" phenomenon? In other words, do these pereskias form such tuberous enlargements when grown in richer moist soils in level environments? Conversely do other pereskias, e.g. *P. aculeata*, *P. sacharosa*, *P. conzattii* Britt. & Rose, etc., do so when grown in excessively dry habits?

That *P. diaz-romeroana* and *P. humboldtii* form tuberous enlargements in richer moister soils is revealed by plants under cultivation in Norman, Oklahoma, and Berkeley, California. Dr. Boke states (personal communication) "my specimens of *P. diaz-romeroana* (1 year old) have the tuberous growths of which you speak. They are growing in rather rich soil and they get plenty of water during the summer months." Mr. P. C. Hutchinson writes "I have examined only *P. humboldtii* in the wild, and we have two seedlings of it here, both of which form tubers early in the seedling stages. *P. diaz-romeroana* cultivated outside here from seed, and now mature has formed them also on all plants." Therefore, it appears probable that the formation of tuberous enlargements is a genetically "obligate," rather than a "facultative," phenomenon in the case of *P. humboldtii* and allied taxa. Thus it appears to be a significant diagnostic characteristic of these pereskias.

My material of roots of other pereskias does not have tuberous enlargements. The swollen roots of pot-bound plants are not homologous anatomical structures. Mr. Hutchinson states (personal communication) "As to whether other species than these three form such structures, so far as we know, they do not." Therefore, whether other pereskias ever form tuberous enlargements when growing under unusual environmental influences must remain for the present an inconclusively answered question.

DISCUSSION

Although the secondary xylem in stems of the Andean pereskias in general resembles that in shoots of comparable sizes of *Pereskia sacharosa*, it differs in the sporadic occurrence of small patches of unlignified tissue and in the common occurrence of druses of calcium oxalate in its lignified multiseriate rays. It is in their roots that the Andean pereskias differ most drastically from *P. sacharosa* and exhibit possible relationships to *P. aculeata*.

Many roots of *Pereskia sacharosa* are of normal dicotyledonous structure, the multiseriate rays throughout their radial extension being composed of cells having relatively thick, lignified secondary walls. However, in some roots of this species the inner parts of the first-formed multiseriate rays close to the primary xylem are unlignified. Such unlignified parts do not contain druses of calcium oxalate and little if any starch, their cells being packed with granular contents of at least semi-proteinaceous composition.

This tendency for the elimination of secondary walls and lignification in derivatives of the cambium, although detectable at times in stems of the Andean pereskias, obviously becomes much exaggerated in their root system, culminating in the formation of tuberous enlargements. The unlignified tissue of these plants, as that formed in both stems and roots of *Pereskia aculeata*, differs from *P. sacharosa* in containing numerous druses of calcium oxalate and more or less abundant starch. One may suspect from a physiological point of view that the much exaggerated tendency toward the formation of druses of calcium oxalate in roots of the Andean pereskias is extended into the lignified rays of the stem.

As demonstrated in the second paper of this series (Bailey 1961a), there are three distinct categories of pereskias which can be differentiated by consistent differences in the form and distribution of sclereids in their secondary phloem. *Pereskia aculeata*, the Andean pereskias, and species from southern Mexico and Central America occur in one of these categories, whereas *P. sacharosa* together with *P. grandifolia*, *P. bleo*, *P. corrugata* and *P. tampicana* occur in a second category.

In the preceding paper of this series (Bailey, 1962), it was shown that the vinelike habit of growth and the secondary xylem of *Pereskia aculeata*, in contrast to those of *P. sacharosa*, tend to negate any possibility of considering this species to be one of the most, if not the most, primitive living representative of the Cactaceae. Similarly the highly modified structure in roots of the Andean pereskias negates the conclusion that these species have retained primitive structures in all of their organs and parts. Indeed, available evidence indicates that in the Cactaceae, as in many other families of angiosperms, trends of phylogenetic specialization in reproductive and vegetative parts are not always closely synchronized. Reliable clues regarding the form and internal structure of ancestral Cactaceae, in the absence of fossils in the geological record, can be obtained at present only by synthesizing evidence from all organs and parts of surviving genera and species. Of pereskias thus far dealt with in this series of papers, *P. sacharosa* is significant in having less advanced specializations in both its flowers and its secondary xylem. Therefore, it will be of interest from both phylogenetic and taxonomic points of view to compare the form and internal structure of this species with those of pereskias from southern Mexico and Central America, from eastern and northern South America and from the West Indies.

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EXPLANATION OF PLATES

PLATE I

FIGS. 1–4. Transverse and tangential longitudinal sections of the secondary xylem of stems. 1, Transverse section of the outer secondary xylem of a large stem of *Pereskia diaz-romeroana* [*Cárdenas*], × 11. 2, Transverse section of the inner secondary xylem of *P.* aff. *humboldtii* [*Ferreyra 14200*], × 11. 3, Tangential section of the outer secondary xylem of *P. weberiana* [*Cárdenas*], × 43. 4, Tangential section of the outer secondary xylem of larger stem of *P. diaz-romeroana* [*Cárdenas*], × 43.

PLATE II

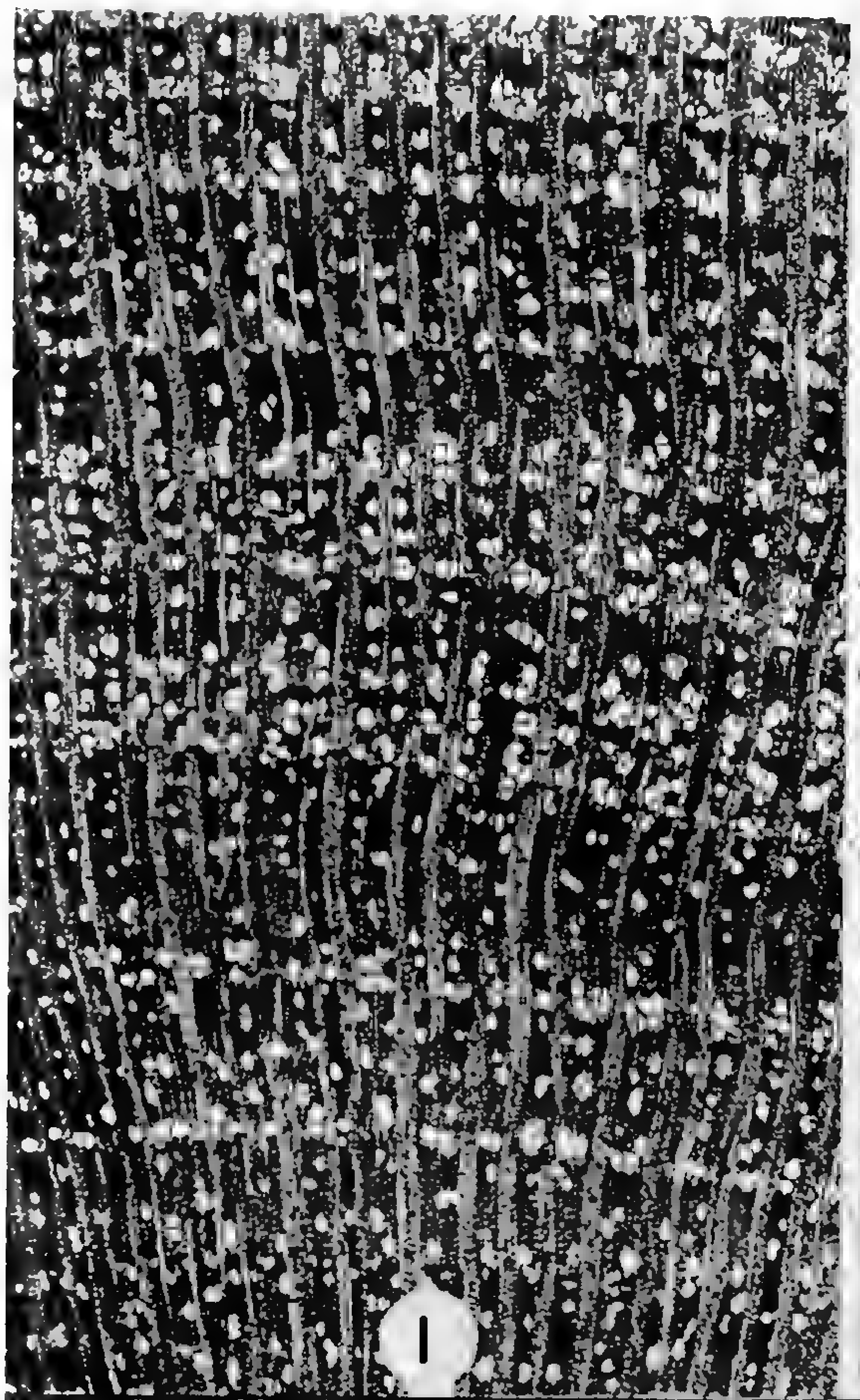
FIGS. 5–6. Transverse sections of roots treated with phloroglucin-hydrochloric acid. 5, Xylem of *Pereskia weberiana* [*Cárdenas*] showing unlignified parts (white) of multiseriate rays, × 34. 6, Xylem of *P.* aff. *humboldtii* [*Ferreyra 14204*] showing central core of unlignified tissue (white) which contains scattered strands of lignified vessels and abundant druses of calcium oxalate in its central part, × 11.

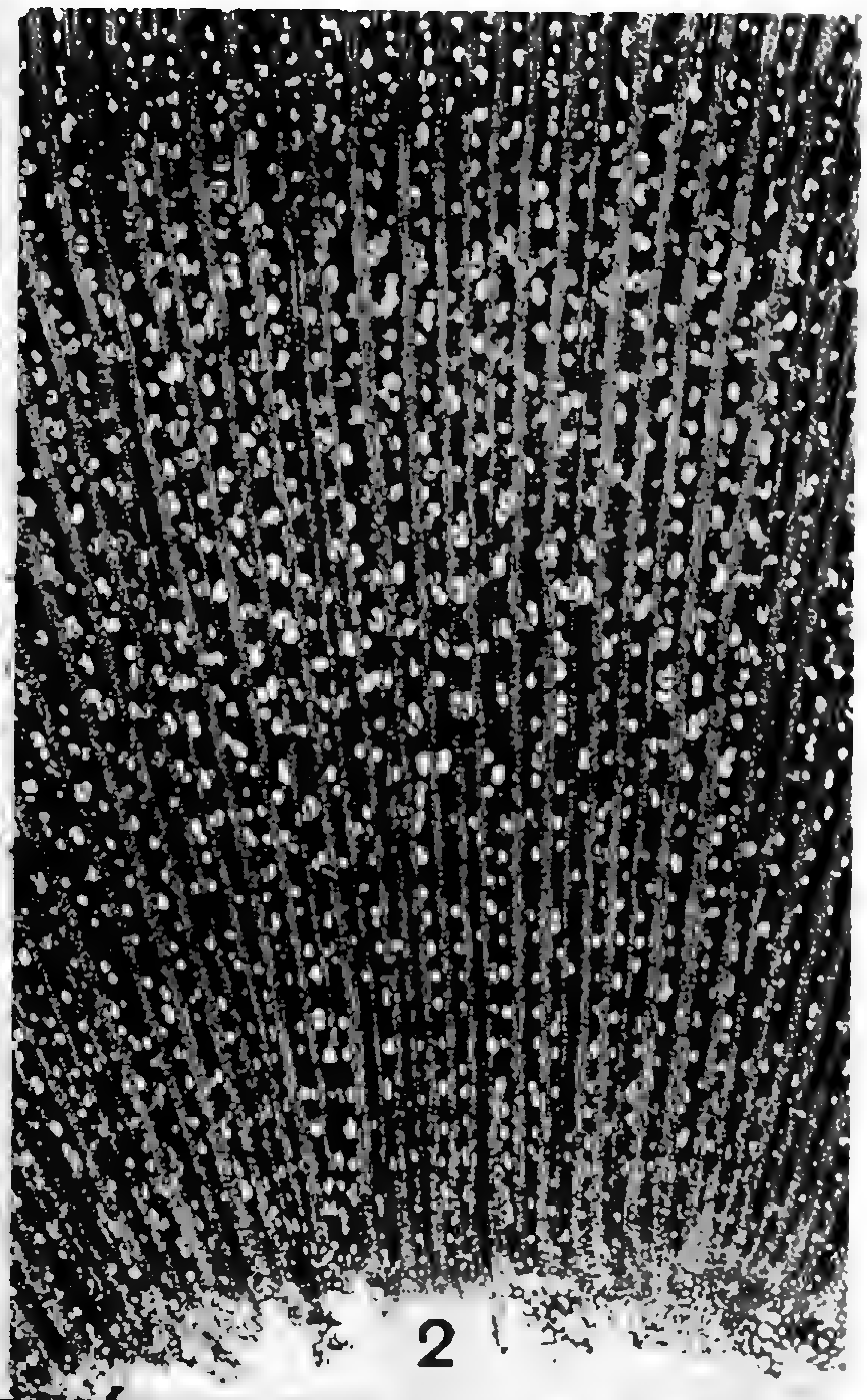
PLATE III

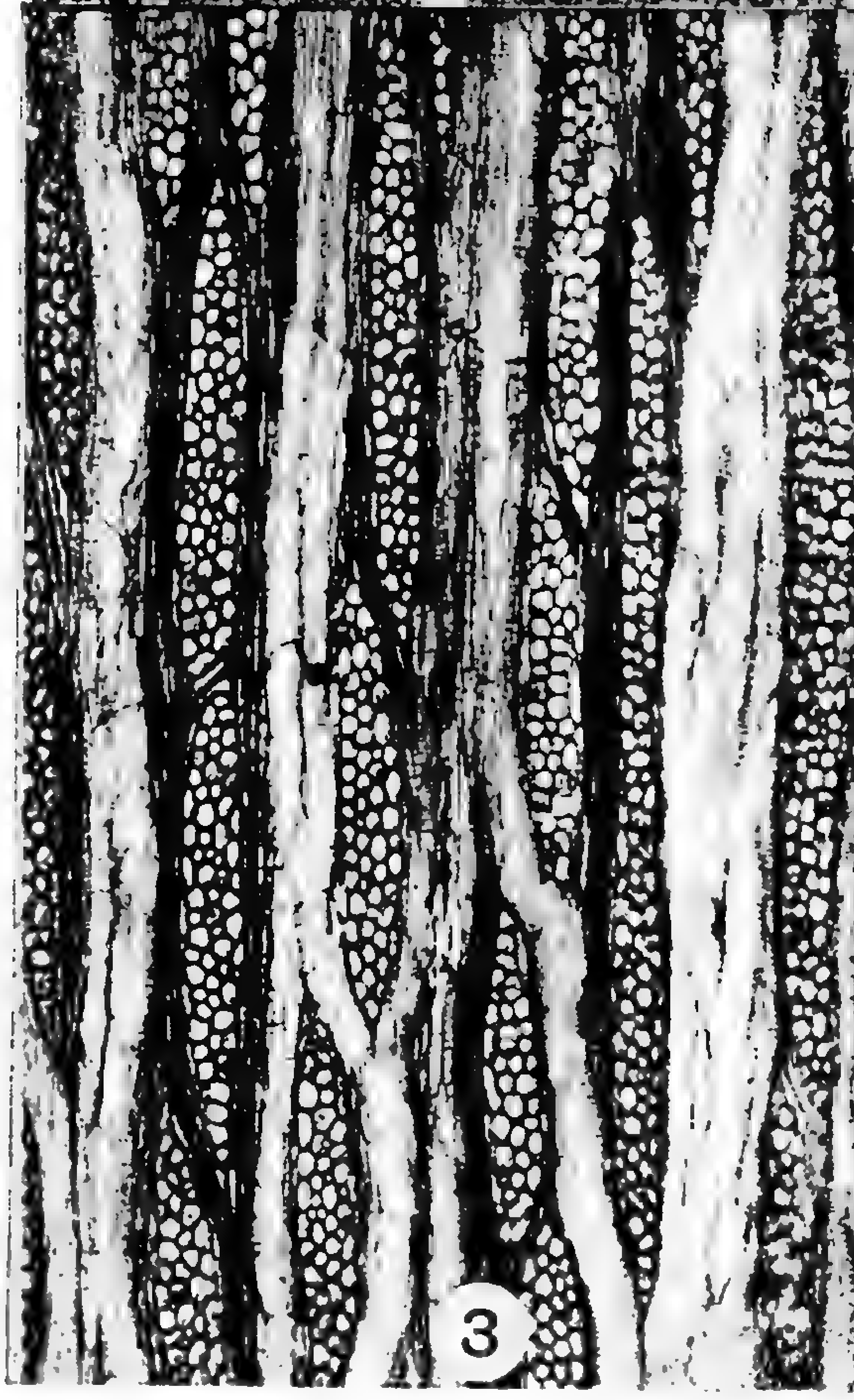
FIGS. 7–8. Transverse sections of roots treated with phloroglucin-hydrochloric acid. 7, Slender root of *P.* aff. *humboldtii* [*Ferreyra 14204*] showing unlignified parts of xylem (white), also the occurrence of fiber-sclereids in the outer secondary phloem and cortex, × 22. 8, Section of root adjacent to spindle-shaped tuberous swelling of *P.* aff. *humboldtii* [*Ferreyra 14204*], × 11.

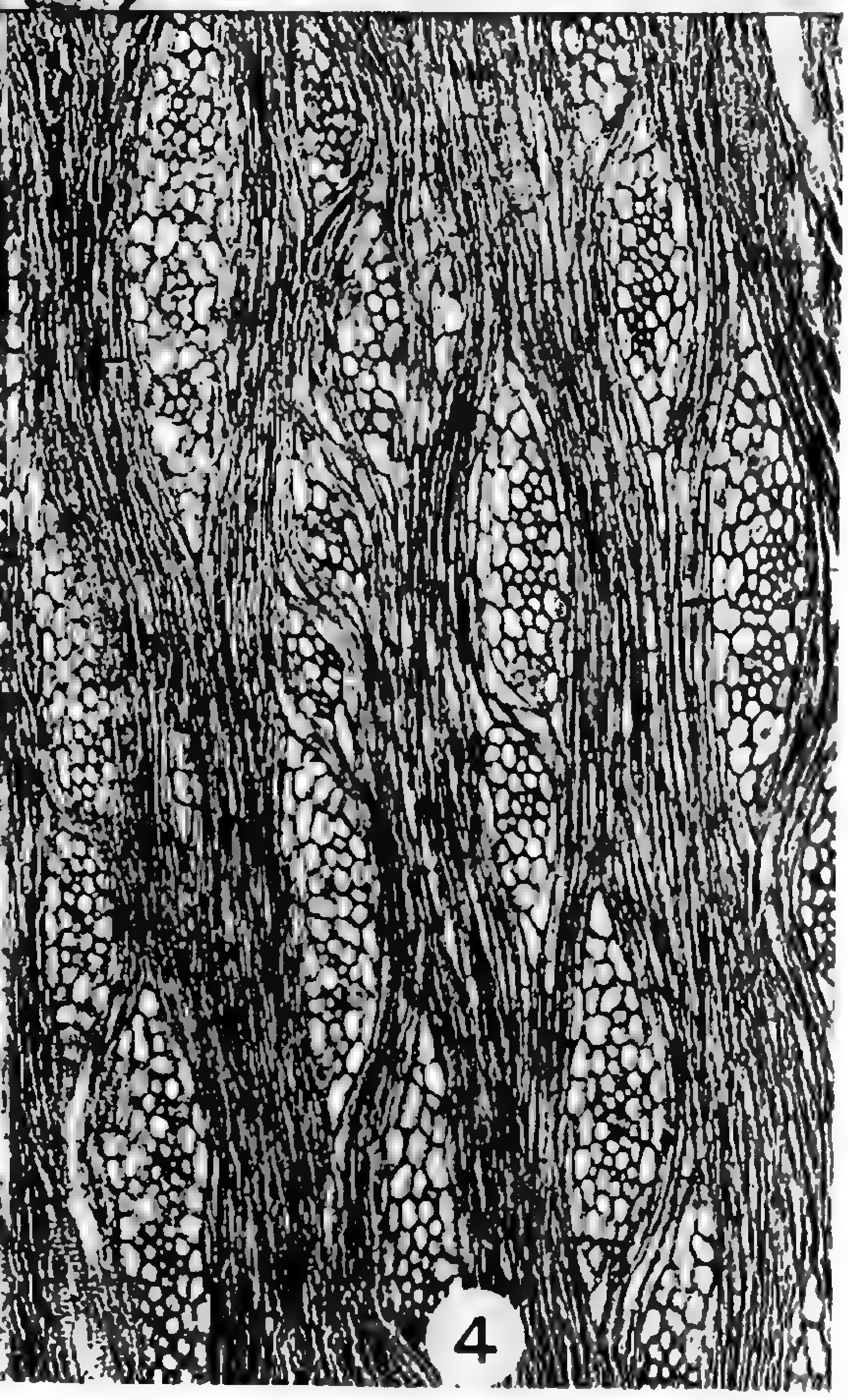
PLATE IV

FIGS. 9–10. Transverse and radial longitudinal sections of fully matured tuberous enlargement of *P.* aff. *humboldtii* [*Ferreyra 14204*], treated with phloroglucin-hydrochloric acid, × 11. 9, Transverse section showing part of the huge core of unlignified tissue (light), narrow outer zone of lignified secondary xylem (dark), abundant fiber-sclereids in the outer secondary phloem, and the occurrence of druses in many cells of the unlignified core. 10, Radial section showing the same structural features, also disruption of isolated strands of lignified vessels during enlargement of derivatives of the cambium in the central part of the unlignified core. In this section most of the druses were dissolved during prolonged treatment in phloroglucin-hydrochloric acid.

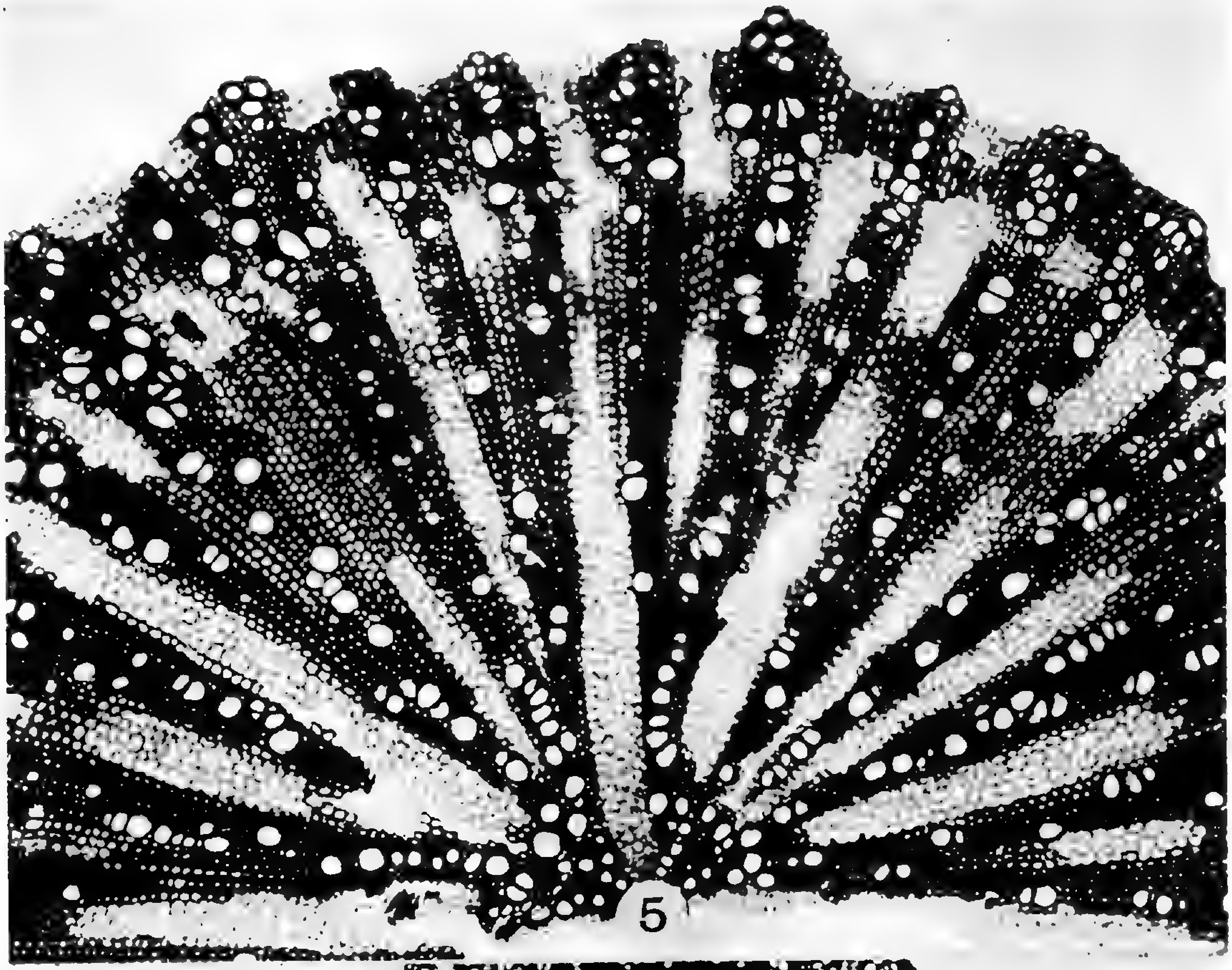








Bailey, Leaf-bearing Cactaceae, VII



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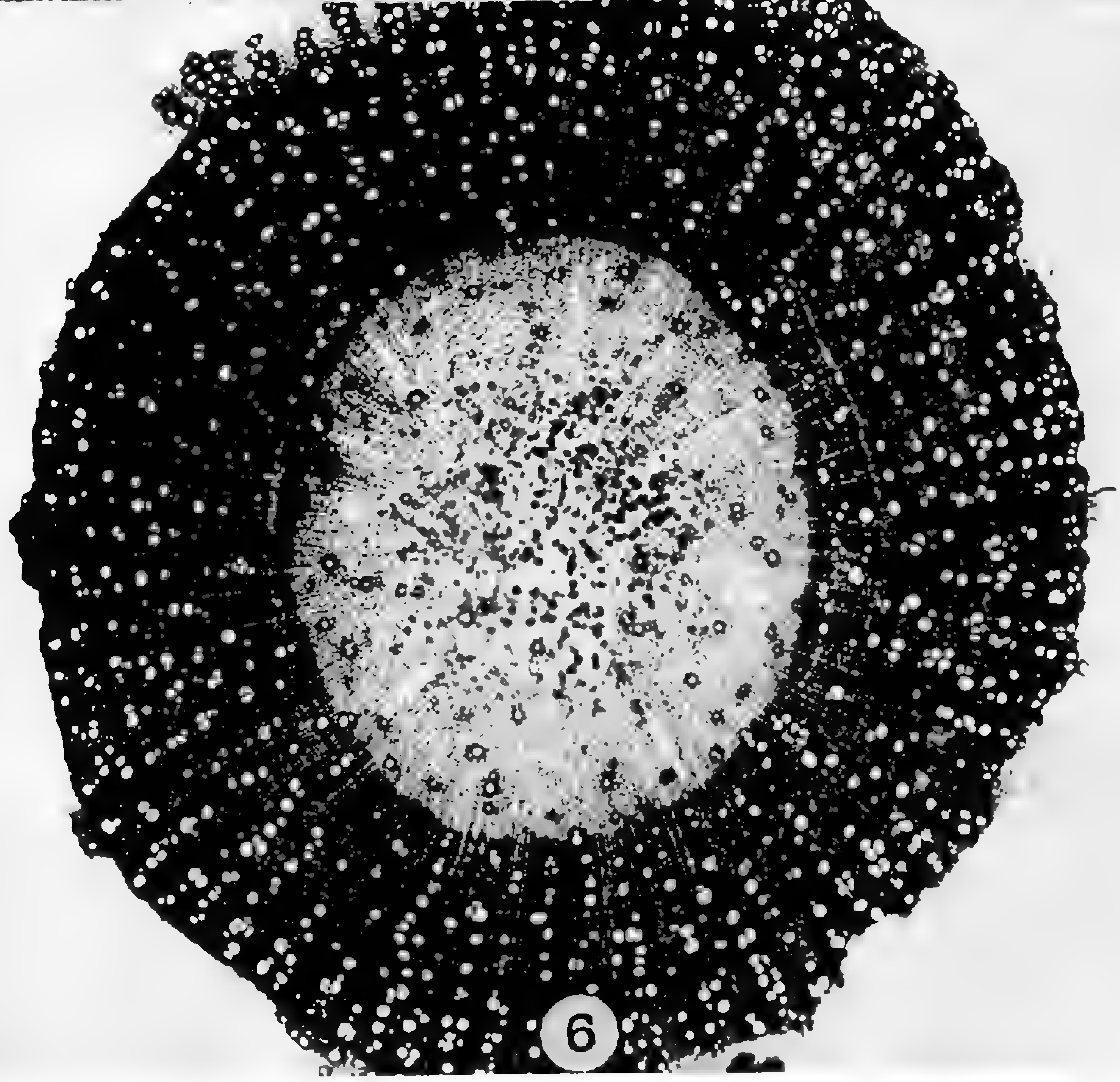

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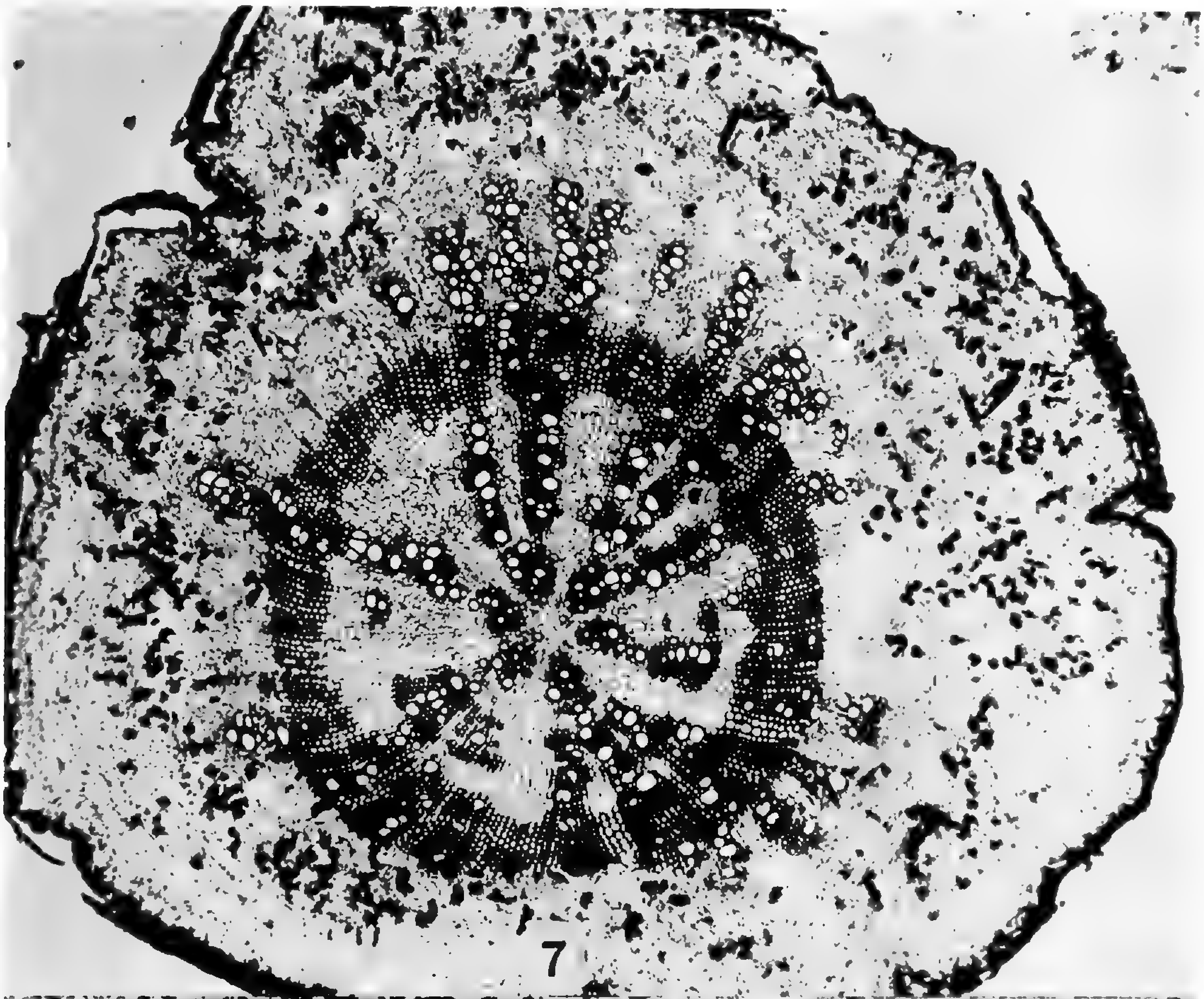

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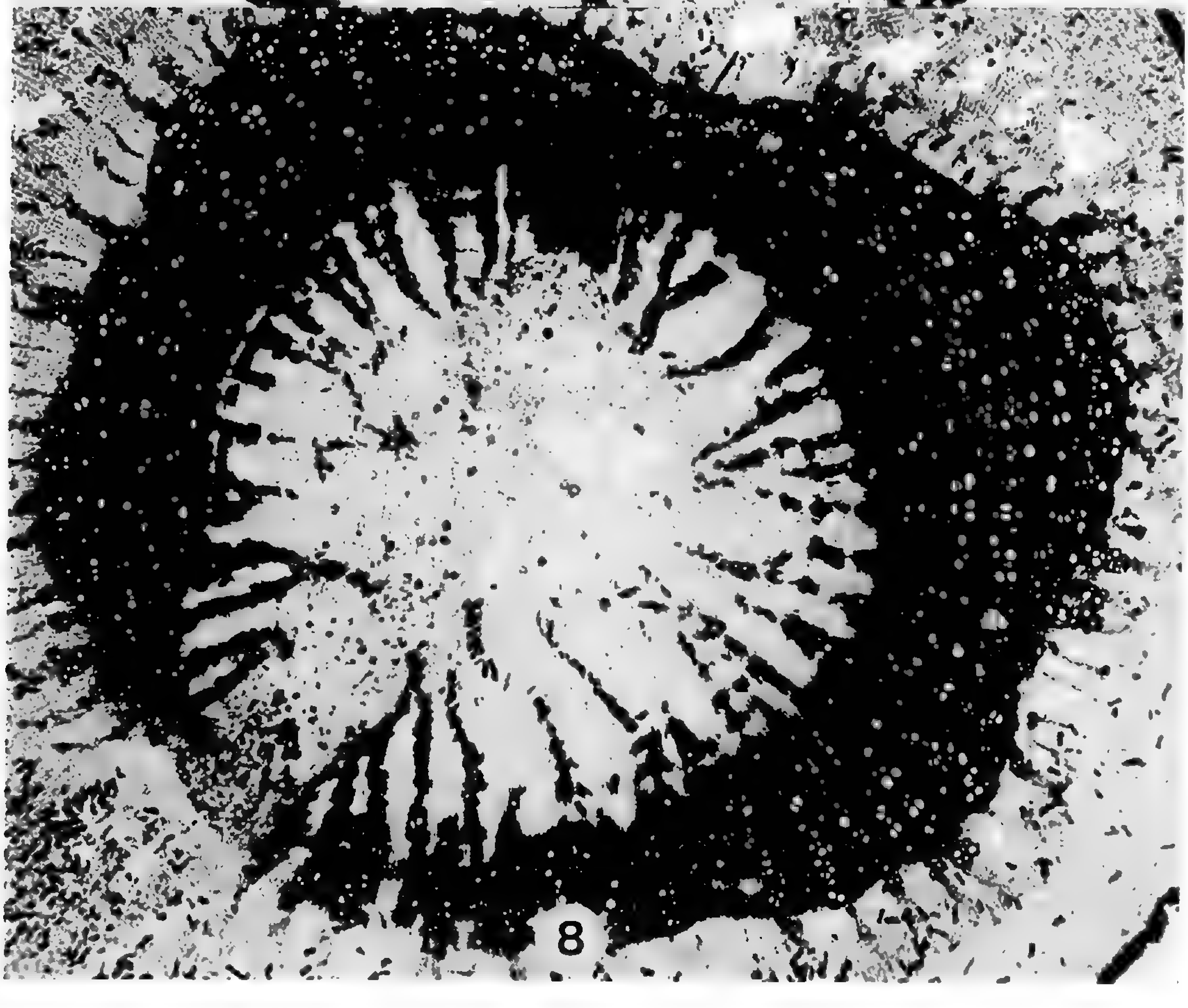

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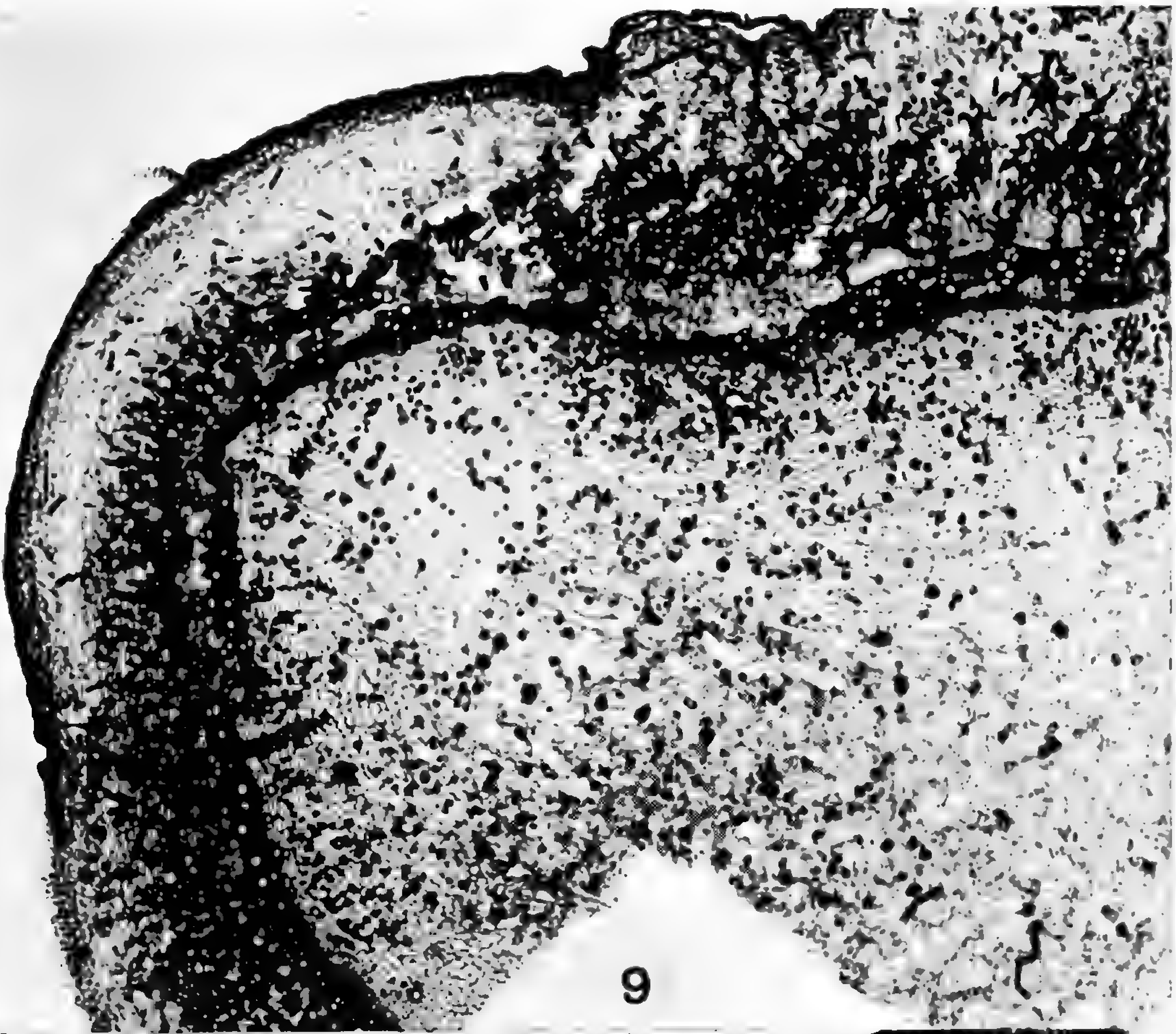

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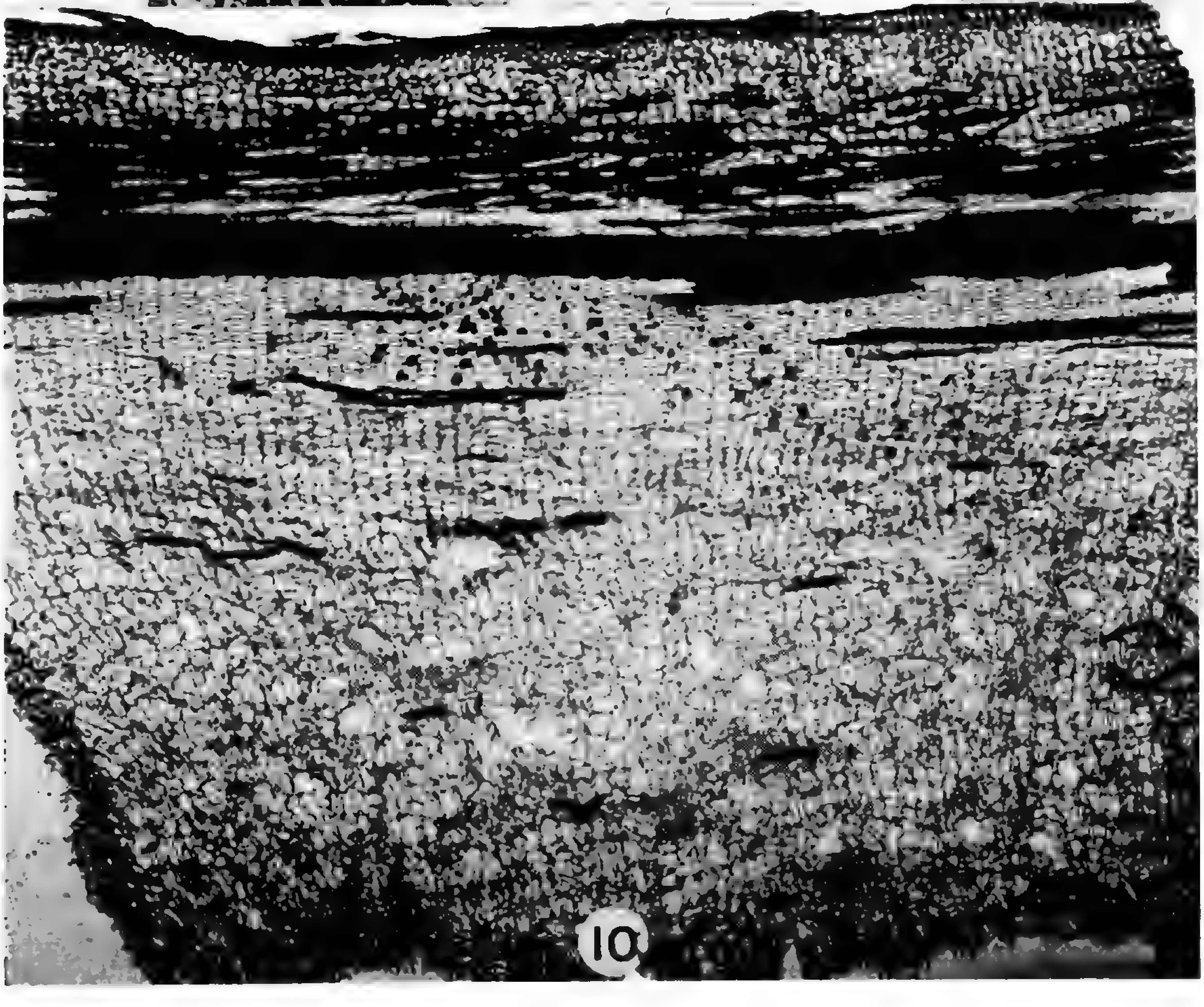

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Bailey, Leaf-bearing Cactaceae, VII

THE LOASACEAE IN THE SOUTHEASTERN UNITED STATES[1]

WALLACE R. ERNST AND HENRY J. THOMPSON

LOASACEAE Dumortier, Comment. 58. 1822, "Loaseae," nom. cons.
(STICK-LEAF FAMILY)

Perennial herbs [to woody or annual], usually scabrous with barbed hairs. Flowers bisexual, regular, epigynous. Perianth cyclic, usually 5[4–7]-merous and 2-seriate. Sepals persistent. Corolla apopetalous [to sympetalous, sometimes with petaloid staminodia alternate with the petals]. Stamens usually many [sometimes fascicled, petaloid, or 5 and alternate with the petals]; anthers basifixed, laterally dehiscent by longitudinal slits, usually 2-locular at anthesis [or seldom 1-locular, subsessile, and epipetalous]; pollen 3-colporate. Gynoecium syncarpous; stigmas usually connate; style often persistent; ovary inferior, usually 1-locular, with 3 [1, 4–6] parietal placentae; ovules few [or 1 and pendent, to numerous], anatropous, 1-integumented. Fruits dry, ± dehiscent [to indehiscent and 1-seeded]. Seeds various; embryo straight or somewhat hooked. TYPE GENUS: *Loasa* Adanson.

About 14 genera and perhaps 200 species of temperate and tropical America to altitudes above 4,000 m. Only *Fissenia* R. Br. ex Endl. [*Kissenia* of authors], exceptional in several respects, occurs in the Old World with one species in South-West Africa and another near the mouth of the Red Sea. About four genera, all with ranges extending southward at least into Mexico, occur in the United States; two species of *Mentzelia* occur in our area.

Loasaceae have been divided into three subfamilies: Gronovioideae Gilg have five stamens and indehiscent, one-seeded fruits presumed to be formed of a single carpel; Loasoideae [including the aberrant *Fissenia*] have many centrifugal stamens in fascicles opposite the petals and elaborate, petaloid staminodia alternate with the petals; and Mentzelioideae Gilg usually have many centripetal stamens, sometimes a few of them petaloid.

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[1] Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium made possible through the support of George R. Cooley and the National Science Foundation and under the direction of Reed C. Rollins and Carroll E. Wood, Jr. This treatment follows the style established in the first paper of the series, Jour. Arnold Arb. **39**: 296–346. 1958, and continued through volume **43**. The area covered in this, as in earlier treatments, is bounded by and includes North Carolina, Tennessee, Arkansas, and Louisiana. The descriptions apply primarily to the plants of this area, with supplementary information in brackets. The manuscript was prepared by Mrs. Gordon W. Dillon. Material for cytological study was provided by Dr. P. H. Raven and by Dr. K. L. Chambers.

Loasaceae are well marked, particularly in the Northern Hemisphere, by the characteristic barbed, rigid hairs lending a scabrous or adhesive quality to the herbage and giving rise to the names "stick-leaf" and "sandpaper plant." The hairs, seldom important taxonomically, are exceedingly variable, often with several forms on one plant, in some instances smooth, glassy, needle-sharp, and swollen at the base. They appear to be primarily one-celled, often from multicellular platforms, and sometimes with a cystolith-like body; multicellular as well as glandular hairs are also reported.

The elaborate development of the staminodia in the Loasoideae, the timing of anthesis of some Mentzelioideae, the tendency for a tubular corolla in some taxa (probably all favoring certain pollinators), and the nature of the seeds are significant taxonomically. An inconsistency in floral symmetry is evident when there are as many placentae as sepals; in some instances the placentae are opposite the sepals and in others alternate with them.

Although relationships with other families have been supposed by several authors (see Gilg, p. 529), Loasaceae are without close morphological allies.

A few showy-flowered species are grown for ornament or novelty.

Chromosome numbers of $2n = 16, 18, 20, 22, 24, 26, 28, 30, 36, 40, 42, 46, 54, 67$, and 72 have been reported.

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Subfam. MENTZELIOIDEAE Gilg

1. **Mentzelia** Linnaeus, Sp. Pl. 1: 516. 1753; Gen. Pl. ed. 5. 233. 1754.

Adhesive, usually brittle, intricately branched perennials [simple annuals, or rarely arborescent], pubescent throughout with unicellular, usually variously reflexly barbed to smooth hairs. Leaves alternate [to opposite], pinnately veined and lobed, ± petiolate, reduced upward. Flowers solitary and axillary, or in terminal, ± cymose, bracteate inflorescences, sessile to ± pedicellate, often with a short hypanthium. Perianth 5-merous, usually 2-seriate. Petals 5 [or rarely apparently 8 or 10, sometimes grading into staminodia], ± free, yellow [or whitish to reddish-orange]. Stamens few [to many]; filaments elongate, filiform [sometimes expanded or bicuspidate apically], usually unequal, ± fused basally and adnate to the petals. Stigmas represented by 3 furrows or a tuft of hairs; style filiform; ovary with 3 [rarely 5] placentae; ovules few [to many] in 2 vertical rows on each placenta. Fruit ± sessile, apically truncate and somewhat discoid, ± indehiscent [or forming 3 or 5 valves]. Seeds few [to many], pendent [to horizontal], narrowly oblong or flattened pyriform [wrinkled to irregularly angled or orbicular and sometimes winged]. TYPE SPECIES: *M. aspera* L. (Named for Christian Mentzel, 1622–1701, physician and botanical author of Brandenburg.) — STICK-LEAF, BLAZING-STAR.

About 60 species of temperate and tropical America, concentrated in the southwestern United States and Mexico, divided on characteristics of the stamens, placentae, and seeds (the last probably the most significant) into six sections by Gilg, seven sections by Urban & Gilg, and four sections by Darlington. *Mentzelia arborescens* Urb. & Gilg in Gilg, the only species of § DENDROMENTZELIA Urb. & Gilg in Gilg, is arborescent, has flat, winged seeds, and ± opposite leaves. Section MENTZELIA (§ *Eument-*

zelia Torr. & Gray), largely of Mexico and South America, is represented in our area by two species.

Mentzelia floridana Nutt. ex Torr. & Gray, poor-man's patches, $2n = 20$,[2] with enlarged roots, reported from hammocks, sand dunes, and shell mounds, may be restricted to Florida and the Bahama Islands. The seeds, about six per fruit, are flattened pyriform and eventually ± loose in the broad, brittle fruits. The closest affinities are with *M. aspera*, of Texas, with *M. adhaerens* Benth., $2n = 20$,[2] of Baja California, and with *M. hispida* Willd., of Mexico.

Mentzelia oligosperma Nutt. ex Sims, $2n = 22$,[2] also with enlarged roots, is known in our area from northern Arkansas and westward from Texas, Missouri, and South Dakota to Colorado. The seeds, about three per fruit, are oblong, ± 3-sided and are held tightly within the narrow, hard fruits. The seeds resemble those of the monotypic § MICROMENTZELIA Urb. & Gilg of the western United States.

The stamens in *Mentzelia*, often unequal, are shorter toward the center; maturation of the microsporocytes proceeds centripetally. The filaments are ± connate basally and ± adnate to the base of the corolla, thus tending to hold the petals together when they fall off. In some species, the outermost filaments are expanded, apically bicuspidate, or petaloid.

The ovules are usually in two vertical series on each of the three placentae, a feature not clearly evident in a single transverse section of the ovary, especially when there are only a few ovules or seeds. The shapes of the seeds, spectacularly diverse, and the time of anthesis of the flowers, which may open in bright daylight or at dusk, provide important biological and taxonomic criteria.

The affinities of *Mentzelia* are with *Eucnide* Zucc. (primarily of Mexico), which is clearly distinct in its tendency toward somewhat more tubular corollas and in its five placentae bearing numerous, minute, furrowed or ribbed seeds. The genus *Schismocarpus* Blake, of Oaxaca and Chiapas, Mexico, placed with the tribe Mentzelieae by Blake, is discordant in the Mentzelioideae.

Chromosome numbers of $2n = 18, 20, 22, 28, 36, 54,$ and 72 have been reported.

A few of the species are cultivated for their showy flowers.

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[2] The chromosome numbers given above are new reports, determined from squash preparations of microsporocytes, with the following vouchers: ten pairs of chromosomes were observed in *Mentzelia floridana* (*Chambers 1280* [LA], Lower Matecumbe Key, Monroe County, Florida), and in *M. adhaerens* (*Raven 14771, 14800* [LA], Baja California); and eleven pairs of chromosomes were observed in *M. oligosperma* (*Thompson & Ernst 3113* [LA], Payne County, Oklahoma).

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A REVISION OF THE GENUS LOPHOSTOMA (THYMELAEACEAE)

LORIN I. NEVLING, JR.

THIS STUDY OF LOPHOSTOMA is the last of three revisions treating the three genera which are currently recognized as comprising the subtribe Linostomatinae. Although a revision, as such, of *Lophostoma* has not previously appeared, Ducke (1915) in conjunction with the description of a new species of the genus, included a key which delimited the species as they were known at that time. His paper did not, however, include a full descriptive account or distribution of each species.

This genus of the Thymelaeaceae was chosen for study because it appeared to have what is considered the largest aggregation of primitive features found in the New World genera of the family. Some authors have included the species of this genus incorrectly with the Asiatic genus *Linostoma* Wall. ex Endl., even as recently as 1954 (Lemée). To be able to judge this relationship accurately, the two Asian members of the subtribe Linostomatinae were revised in preparation for the present study. As a result, I am convinced that while *Lophostoma* may be described as primitive it is at the same time unquestionably one of the most specialized of the eleven American genera. All three genera of the subtribe Linostomatinae occupy a rather specialized ecological niche, in that they tend to be scrambling shrubs which eventually become large lianas; while the other members of the family are generally trees or shrubs.

SPECIAL MORPHOLOGY

A few of the interesting morphological and anatomical features found within the genus *Lophostoma* are presented in this section. No attempt to include a complete anatomical survey of plant parts has been made; the emphasis being placed on paralleling information already published for the genera *Linostoma* and *Enkleia* Griff. (Nevling, 1961a, b). Although studies containing considerable anatomical information concerning members of the family have been published, the finest contribution most recently by Hamaya (1959), relatively little information is available concerning the New World genera. Additional gross morphological information can be found in the descriptions and discussion dealing with the individual species. In all instances, the materials examined were from herbarium specimens.

Mature stem and inflorescence axes were studied by means of free-hand sections which were stained with either safranin or phloroglucin and hydrochloric acid. This technique was employed also with young shoots.

Gross and microscopic structure of leaf blade and petiole was studied by clearing and staining gross specimens and thin sections. Staining was with safranin or with ferric chloride and tannic acid, in the case of cleared material, or with safranin and fast green, in the case of thin sections. Leaf material was tested also with phloroglucin and hydrochloric acid, as well as with potassium iodide and sulphuric acid, to estimate chemically the lignification or lack of it in certain tissues. As a supplementary test, leaf sections were stained with 0.5% Sudan IV in a solution of 80% ethyl alcohol to determine the presence or absence of cutin or fatty substances in epidermal walls. All specimens were examined with normal and polarized light.

Flower structure, including vascular pattern, was studied from cleared and stained whole mounts. The details of these techniques can be found in the first paper of this series (Nevling, 1961a).

Vegetative Morphology. The vegetative axis is monopodial with the leaves oppositely to alternately arranged upon it. The opposite leaf position is superficial and is the result of drastic condensation of the internode between two adjacent nodes. Alternate internodes seem to be affected in this manner. The degree of condensation is rather variable, accounting for the variation in leaf position from opposite to subopposite or alternate. Free-hand sections of the stem clearly show the initiation of the leaf traces to be on two separate levels, i.e., one usually departing from the stele of the stem prior to or simultaneously with the initiation of the second. The alternate leaf position appears to be restricted to shoots which are extremely vigorous, particularly those immediately subtending the floriferous region. This position is due to nondifferential elongation of all internodes. In every case, a single leaf trace per node is formed and the resultant gap is unilacunar.

Bifurcate and trifurcate branching of the vegetative shoots is found regularly in all species. In some instances, branching is induced by damage to the apical bud but generally it is spontaneous. The branches, which may be equal or unequal, are the result of the coordinate development of one or more axillary buds with the apical bud. The apical bud usually retains its dominance. On one sheet, *Huber 8103* (*Lophostoma calophylloides*), the opposite axillary buds of the "nodal pair" have developed coordinately with the apical bud at five separate "nodes." Each branch is gracefully curved and bears inflorescences at its terminus. In the same collection, one specimen (BM) also has axillary branch development in which the buds do not occur in "pairs" but in an alternate position. The resulting branches, therefore, are alternately arranged. In *L.*

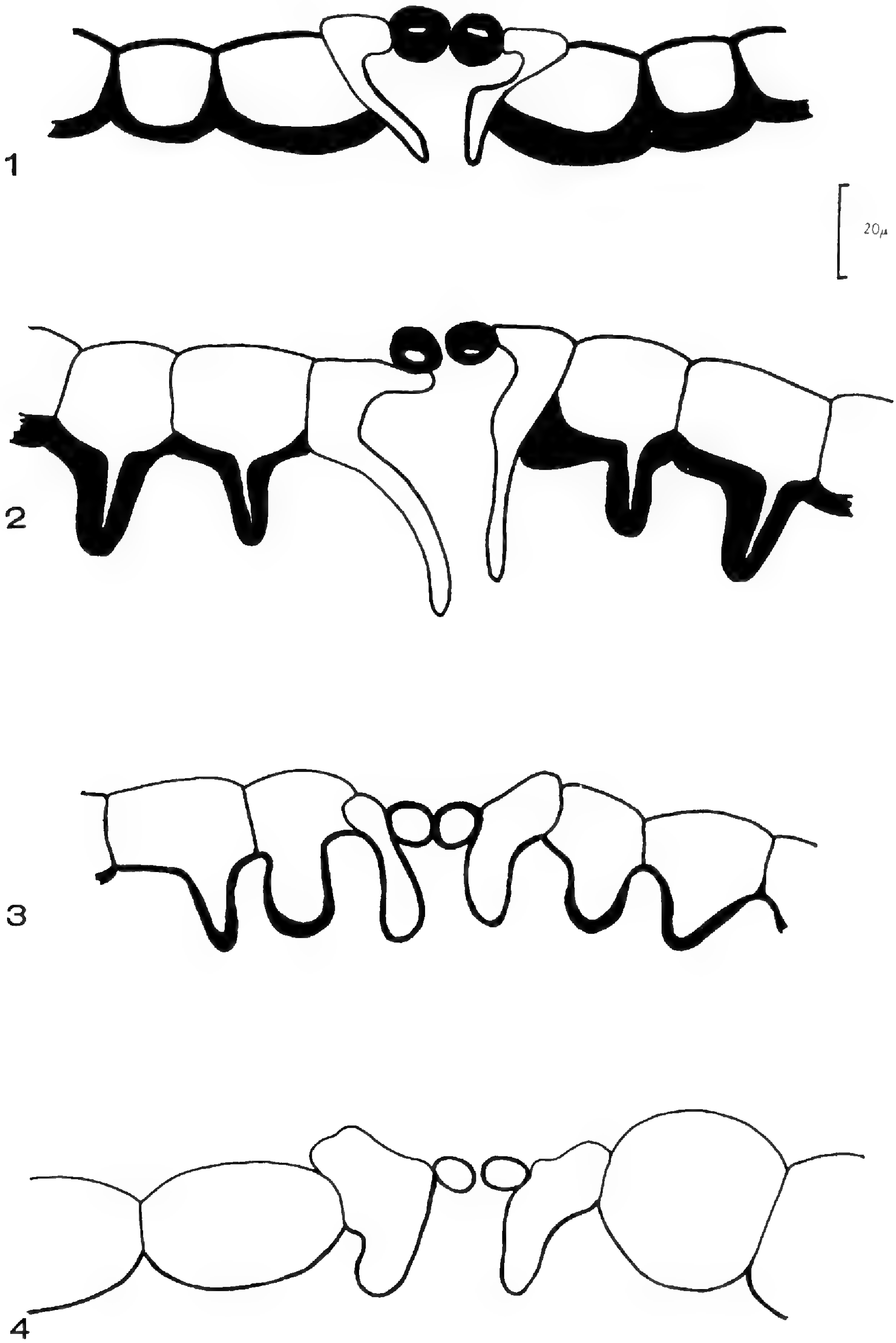
dinizii Huber ex Ducke, the leaves subtending the developing axillary branches are found in the normal position, i.e., on the main axis immediately below the developing branch. In *L. calophylloides* (Meissn.) Meissn., *L. amoenum* Nevl., and *L. ovatum* Meissn., however, this leaf usually, but not always, is displaced and is borne upon the developing branch which it actually subtends. This type of displacement, which may be as much as three centimeters in *Huber 8103*, has been discussed previously in other papers (Nevling, 1961a, b).

Supernumerary axillary buds can be demonstrated for all species but appear to be most common in *Lophostoma calophylloides*. The result of the development of supernumerary buds can be seen in *Ducke 413* in which three branches have developed from a single leaf axil. The occurrence of such extra buds is important when interpreting the inflorescence forms found within the family.

All four species of the genus are known to be climbers or scramblers. Unciform branches are quite conspicuous in *Lophostoma ovatum* (see *Spruce 1461* and *Ule 8953*) where they are well developed, tapering very rapidly from the much enlarged base to the slender apex. Several reduced leaves are borne at the apex. Modified axillary branches, to facilitate climbing, are rarely encountered in *L. calophylloides* and *L. dinizii*. The single specimen of *L. amoenum* has several hooked branches. It is possible that, in these latter three species, the modified branches are formed regularly only on more mature shoots which are poorly represented in the herbarium material.

The extraxylary fiber sheath surrounding the stele, by which the family often is identified in the field, is well developed. These fibers, as determined by chemical means, are lignified. In addition, other lignified fibers are found within the pith where they appear to compose the bulk of the tissue internal to the stele. In contrast to the situation in *Enkleia* where the fibers are scattered throughout the pith, the fibers in *Lophostoma* are compactly organized as a solid central core surrounded by parenchyma. The xylary elements of the stem are lignified to a greater extent than the corresponding elements in either *Linostoma* or *Enkleia*.

The leaves are dorsiventral. The upper epidermis is uniseriate, composed of tabular cells (except in *Lophostoma ovatum* and *L. amoenum* in which they are vertically elongate), and is uninterrupted by stomata. The upper epidermal cells are thin-walled in *L. calophylloides* but the outer periclinal wall is conspicuously thickened in *L. dinizii*, *L. ovatum*, and *L. amoenum*. The thickened walls of the latter three species when treated with Sudan IV give the characteristic staining for cutin or other waxy substances. The palisade tissue is composed of very compact columnar cells which occupy, together with the upper epidermis, one-third (*L. calophylloides* and *L. dinizii*) to one-half (*L. ovatum* and *L. amoenum*) the depth of the leaf. The spongy parenchyma is quite loosely organized except in *L. ovatum* in which this tissue is the most compact of any species of the subtribe. The individual parenchyma cells are irregularly shaped. The xylary tissue of the midrib in *L. ovatum* is arc-shaped with the phloem



FIGS. 1–4. Cross section of lower leaf epidermis of species of *Lophostoma* including the stomatal apparatus. Guard cells are shown in cross section, accessory cells (immediately adjacent to guard cells) are shown in longitudinal section. Mesophyll and other leaf tissues not illustrated. Note differences in shape of

restricted to the lower surface; in *L. amoenum* it may encircle the midrib. In both *L. calophylloides* and *L. dinizii* the margins of the xylary arc have folded back on the arc itself with the phloem being carried partially around (*L. calophylloides*), or completely around (*L. dinizii*), the midrib. The xylary elements are poorly lignified as determined by chemical tests. The phloem elements are of the largest size in the latter species. The lower epidermis is uniseriate and is interrupted often by stomata. In all species the outer periclinal walls are thickened and stain with Sudan IV. Some thickening of anticlinal cell walls occurs in *L. calophylloides*. In some instances, the inner periclinal walls also may be thickened, particularly when they overlie air chambers. The outer periclinal cell walls of the lower epidermis, in *L. dinizii* and *L. ovatum*, in addition to being thickened each bear a conspicuous papilla.

The stomata of all species of this genus are of the pit-type previously described for *Linostoma decandrum* (Roxb.) Wall. ex Endl. and for all species of *Enkleia*. A rosette of awl-shaped accessory cells surrounds each stoma, the number of accessory cells being variable (generally seven, eight, or nine, but as few as five and as many as eleven). Each accessory cell extends beyond the guard cells forming an urceolate (*Lophostoma calophylloides*) or campanulate (*L. dinizii, L. ovatum* and *L. amoenum*) structure. Occasionally an accessory cell may be found being shared by two adjoining stomata. The guard cells are borne at the base of the accessory-cell rosette and therefore are not truly sunken. Some differences in stomatal structure, as well as epidermal structure may be found among the species (Figs. 1–4), but the amount of variation has not been determined, so their taxonomic worth cannot be evaluated at this time.

The pinnate venation is similar throughout the genus. The primary lateral veins generally are quite numerous, although the number appears to be variable. They are straight or slightly arcuate and end in a variously developed submarginal vein. The orientation of veins forms a pattern which is indistinguishable from that found in the Asiatic genus *Linostoma*. A fiber sheath is associated with all veins. The submarginal vein is better developed in *Lophostoma amoenum* than in the three other species, and in all instances it very nearly corresponds with the leaf margin.

The secondary veins after departing from the primary veins appear, for the most part, to reverse direction, i.e., toward the midrib. In addition, they are oriented parallel to the primary veins. Direct cross connections between primary veins are not formed. Extraxylary fibers are associated also with the veinlets.

Extraxylary fibers are not restricted to close proximity to vascular tissue in *Lophostoma calophylloides* and *L. dinizii* but wander aimlessly about the leaf. They are vermiform and reminiscent of those found in *Enkleia malaccensis* (Nevling, *Fig. 9*, 1961b) and *Passerina filiformis* L. (Thoday,

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epidermal cells and differential thickening of cell walls. 1, *L. calophylloides* (*Spruce s.n.*); 2, *L. dinizii* (*Ducke 9050*); 3, *L. ovatum* (*Fróes 2057*); 4, *L. amoenum* (*Wurdack & Adderley 43208*).

1921). The situation in *L. ovatum* and *L. amoenum* is quite different, the fibers being associated only with the veins and veinlets. These fibers are replaced at the extremities of the veinlets by irregularly shaped sclereids similar to those found in the leaf of *Linostoma pauciflorum* (Nevling, *Text Fig. II, 5,* 1961a). I found it impossible to stain the fiber walls with either phloroglucin and hydrochloric acid or potassium iodide and sulphuric acid.

In all species of the genus, the xylem, at mid-petiole, is arc shaped but the precise configuration depends entirely on the position of the section, as a sequence of forms is found when progressing from the proximal (i.e., attached to the stem) to the distal end. As the trace leaves the stem and enters the petiole it is arc shaped, the edge of the arc begins to involute in a very short distance, and the lateral edges become adjacent and form a complete ring of xylem (except in *Lophostoma dinizii* in which the ring is not quite continuous). The center of the ring is occupied by parenchyma cells. Serial sections of the petiole of *L. amoenum* show that the circle of xylary tissue, formed by the involution of its lateral margins, reopens into an arc prior to entering the leaf blade. The leaf traces have their origin from the lateral margins of this arc. External to the xylem "ring" is a continuous band of phloem. The phloem is always external to the last formed xylary elements regardless of the position of the xylem. Individual xylary elements have very thickened walls similar to those previously reported for *Enkleia*. These cells stain with phloroglucin and hydrochloric acid indicating lignification.

Extraxylary fibers are found in the petioles of *Lophostoma calophylloides, L. dinizii,* and *L. amoenum* but are lacking in *L. ovatum*. They do not stain either with phloroglucin and hydrochloric acid or with potassium iodide and sulphuric acid. A considerable cortex of parenchyma cells is found in all species. Irregular crystals can be found in a few cortical cells in *L. calophylloides, L. dinizii,* and *L. amoenum* (birefringent in polarized light) but have not been found in *L. ovatum*. This character probably is of no taxonomic significance as indicated by work in other genera of this family (Gilg, 1894; Hamaya, 1959; Nevling, 1961).

Reproductive Morphology. The same terminology which I applied in previous papers concerning the Thymelaeaceae is used here. The inflorescence is composed of a primary peduncle, a rachis, secondary peduncles, and flowers with their pedicels. In striking contrast to the other members of the Linostomatinae, the species of *Lophostoma* lack the conspicuous pair of bracts associated with the primary peduncle. In addition, the bracteole may or may not be present.

The floriferous branches of *Lophostoma* are composed of one to several inflorescences which collectively appear to form a single terminal "inflorescence." The flowering branches generally are young shoots, either terminal or ascending branchlets. In *L. ovatum* and *L. amoenum* the "inflorescence" is simple, di- or trichotomously divided and consists of a terminal inflorescence, which is sometimes reduced to a single flower, and one or two lateral inflorescences. In *L. calophylloides* the "inflorescence" is composed of three to five individual inflorescences which are pinnately arranged. The individual inflorescences are relatively closely spaced. In *L. dinizii* the "inflorescence" appears dichotomously paniculate. As there is nondifferential elongation of the internodes, the inflorescences appear to alternate on a flexuose main axis. In actuality, the inflorescences terminate the shoot, but their formation is accompanied by the coordinate development of an axillary branch which assumes the role of a main axis until the succeeding node where the pattern is repeated. In all species, each individual inflorescence is simple with the flowers racemosely arranged.

The bract-like reduced leaves which are found at the base (in *Lophostoma calophylloides, L. ovatum*, and *L. amoenum*) or the summit (*L. dinizii*) of the primary peduncle are analogous to the paired bracts found in *Linostoma* and *Enkleia*. Their bract-like appearance is due to reduced size, thinner texture, and striking color. Their lack of homology to bracts is shown by their deciduous nature and the source of their vascular supply. The trace which supplies vascularization to this "reduced" leaf departs from the stele prior to inflorescence branching. The leaf is displaced onto the axillary branch which it subtends anatomically. This developmental pattern precisely repeats that found in the reduced and displaced leaves of both *Linostoma* and *Enkleia*. In addition to these features, in *L. amoenum*, several pairs of leaves subtending the inflorescence may also be colored and bract-like. It is entirely possible that if the paired bracts in *Linostoma* serve as insect attracting devices that the bract-like leaves in *Lophostoma* have assumed the same function regardless of their position. Indeed, the inflorescence structure and floral morphology indicate adaptations for insect pollination.

The bracteole, usually situated at the summit of the primary peduncle, has been seen regularly only in *Lophostoma ovatum* and *L. amoenum*. In both species it is small and somewhat ephemeral which leads me to believe that this structure may also be found in living material of the other species.

The flowers, as in all members of the Linostomatinae, are bisexual, regular, pentamerous, perigynous and pedicellate. The terminology applied to floral parts is the same as I have used in previous papers (Nevling, 1959, 1961a, b). Additional information concerning the gross morphology of the flower, beyond that presented in the following discussion, may be found in the specific descriptions.

The calyx tube, which is composed of the fused bases of calyx, corolla, and androecial members, is cylindric in all species. The size of the tube is rather constant throughout the genus, varying from 10–16 mm. in length. The exterior is glabrous (*Lophostoma dinizii*), puberulent (*L. calophylloides* and *L. amoenum*), or puberulent to tomentulose (*L. ovatum*). All species bear trichomes in the tube interior which are exclusively unicellular and unbranched with a somewhat crinkled appearance due to an undulate cell wall. This undulate wall distinguishes them immediately from the trichomes of *Linostoma* and *Enkleia* in which the wall is straight. The interior is villous in the lower one-half or two-thirds, the density of trichomes varying somewhat among the species. In the upper one-half or one-third the tube is glabrous or nearly so. The trichome distribution is assumed to be associated with pollinators to encourage outcrossing. Spruce has noted that the flowers of *L. calophylloides* are perfumed, strengthening the probability that the plants are oriented toward insect pollination. The pollinating agent is unknown up to the present time but Burrows has shown in his recent work (1960) on New Zealand *Pimelea* that the pollinators tend to be nonspecific.

The calyx tube is vascularized by ten distinct veins (the anatomical observations are based on *Lophostoma calophylloides*, *L. ovatum* and *L. amoenum* only, due to lack of sufficient material). Five of the traces are in the antisepalous position (median traces) and five are in the alternisepalous position (commissural traces). The traces to the alternisepalous staminal whorl depart from the commissural traces only slightly below the insertion of the stamens. Shortly thereafter, the traces to the antisepalous staminal whorl depart from the median traces. Immediately after the departure of the androecial traces, both median and commissural traces undergo repeated divisions to form a complex network of vasculature which innervates the calyx lobes. A fiber sheath is associated with each vein, being more highly developed in *L. ovatum* than in *L. calophylloides*.

The shape of the calyx lobes varies among the species, and in *Lophostoma ovatum* within the species, but not significantly so. The inner surface is glabrous in all species. The lobes are vascularized by approximately a dozen veins which branch and anastomose freely. This large number of veins contrasts with the three or five trace condition in *Linostoma* and *Enkleia*. The aestivation is quincuncial.

The petals are inserted at the orifice of the calyx tube in an alternisepalous position but the median clefting of the petals is complete resulting in the formation of five petal-pairs (appearing to be 10 distinct petals). The lobes are squamelliform, erect, subexserted to exserted, and at most 1 mm. long. They are variously comose except in a few specimens of *Lophostoma calophylloides* in which they are glabrous. The trichomes are distributed on both surfaces of the petals in *L. calophylloides* (when trichomes are present) and *L. dinizii*, on the outer surface only in *L. ovatum* and, in *L. amoenum* either on the outer surface or on both surfaces. The trichomes appear nearly moniliform due to the strongly undulate cell walls. There is no vascularization of the petals in any of the specimens which I have examined.

The androecium consists of ten stamens inserted on the calyx tube. They are in two whorls, the upper whorl in the antisepalous, the lower whorl in the alternisepalous position. The traces which vascularize the stamens reflect the two-whorl pattern. The traces to the alternisepalous whorl depart from the commissural calyx traces lower in the tube than those from the median calyx traces depart to vascularize the antisepalous whorl.

The filaments are relatively short (to 3 mm. long) and filiform, with those of the antisepalous whorl longer than those of the alternisepalous whorl. They are glabrous exclusively. Vascularization is by a single bundle which ends blindly at the middle of the connective in *Lophostoma calophylloides* or at the apex of the connective in *L. ovatum.*

The anthers are exserted except in *Lophostoma amoenum* where the alternisepalous are sometimes included. They are 4-lobed and 4-locular in cross section. Dehiscence is longitudinal.

The pollen grains of all species are uniform and indistinguishable from those of *Linostoma* and *Enkleia.* As in the latter two genera, they are polyporate and highly sculptured.

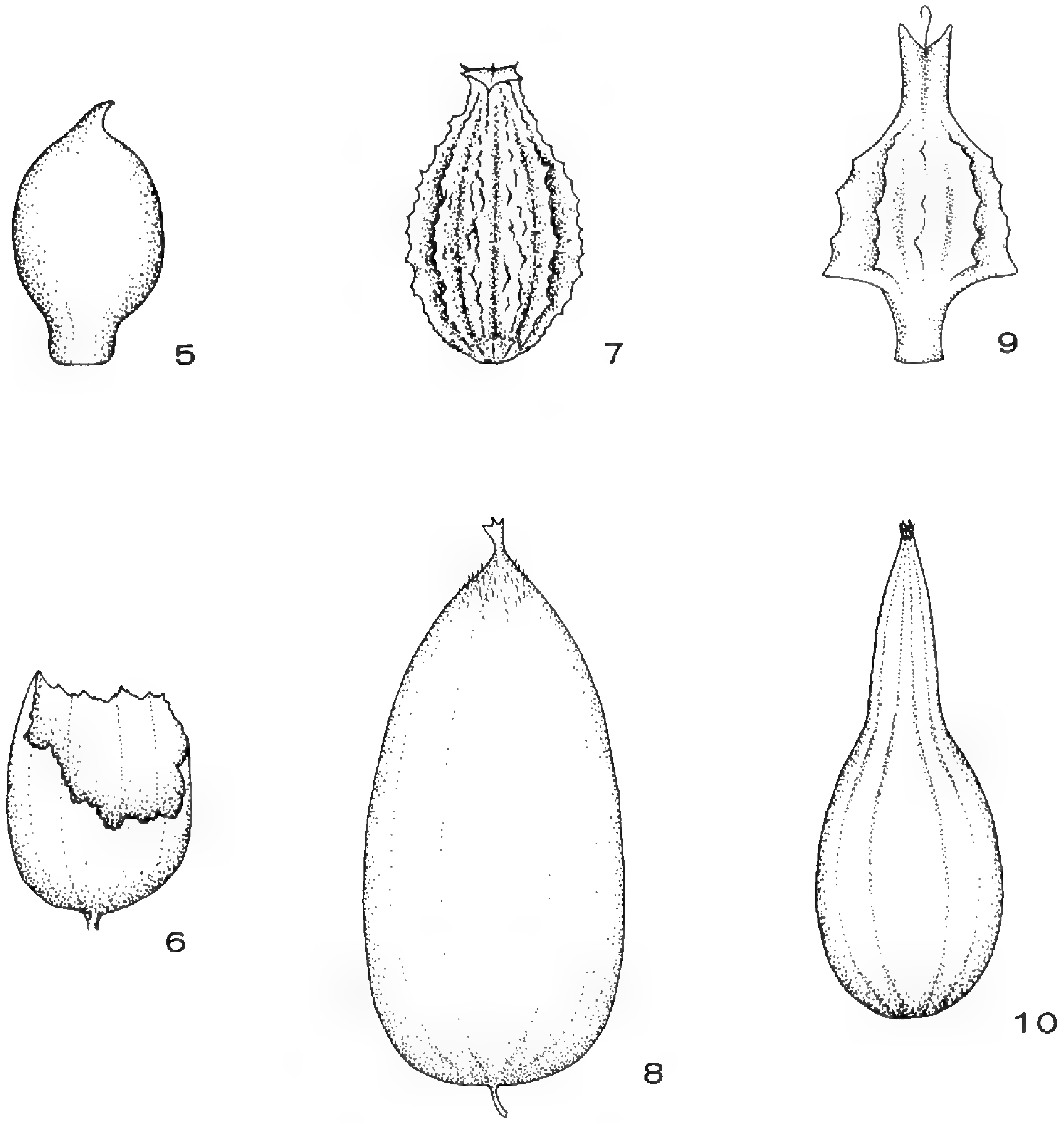
The presence of a disc, contrary to many previous reports, is confirmed in *Lophostoma calophylloides* and *L. ovatum* but appears to be absent in *L. amoenum,* and is questionable in *L. dinizii* due to insufficient material. It is borne at the base of the calyx tube and surrounds the base of the gynoecium. It is insignificant in size, annular, minutely lobed and glabrous. The vascularization, if any, could not be determined.

The gynoecium is composed of a single more or less sessile pistil, presumably of the pseudomonomeric type. Vascular patterns could not be established, except in *Lophostoma ovatum* and *L. amoenum,* because of overwhelming difficulties in clearing this organ. The gynoecium was treated with a variety of clearing agents for greatly extended periods of time without satisfactory results.

The ovary is superior, ellipsoid and unilocular. It is densely sericeous. The trichomes are unicellular and erect. The trichome walls are undulate (except in *Lophostoma amoenum* in which the walls are nearly smooth) and quite similar to the walls of the trichomes borne on the petal lobes. The pattern of vascular supply in *L. ovatum* is quite similar to that illustrated for *Linostoma decandrum* (Nevling, *Text Fig. III. 1,* 1961a). There are two main veins, one of which remains unbranched into the style and the other gives rise to four or five small branches, which vascularize the ovary wall, before passing into the style. A third accessory trace ends slightly above the middle of the ovary and is unbranched. No ovular trace was observed. In *Lophostoma amoenum* the vascular supply is similar to that illustrated for *Linostoma pauciflorum* (Nevling, *Text Fig. III. 3,* 1961a). Two main veins are continuous from the ovary base to the base of the stigma. One of these traces gives off a few small branched traces in the upper part of the ovary wall; the other gives rise to a well-developed, hook-shaped, ovular trace.

The style is borne terminally (or somewhat eccentrically in *Lophostoma amoenum* only) and seems to be intercalated about one-quarter from the base. This trace has no connection at either end and has no cross connections with any other trace. Near the summit of the style in *L. ovatum* one of the main traces dichotomizes so that a total of four veins is found just below the stigma, whereas in *L. ovatum* the traces remain unbranched. The stigma is capitate and its position within the calyx tube is variable and dependent on the time of pollination (see Burrows, 1960). Stylar elongation must be rather rapid as the protoxylem elements are straight and quite elongate in comparison to the much shorter and sinuous elements vascularizing the ovary wall.

Unlike *Linostoma* and *Enkleia*, the fruit preservation in *Lophostoma* is good. In three species of the latter genus a single fruit per inflorescence develops. The drupe is enclosed by the accrescent, papery, urceolate calyx tube. The tremendous development of the tube following anthesis is quite extraordinary. The shape and armature of the drupe varies among the species (FIGS. 5–10). The simplest drupe is found in *L. calophylloides* in which the eccentric apex is abruptly acuminate and somewhat hooked. The wall is smooth (although subject to considerable wrinkling on drying). In *L. dinizii* the drupe apex is flat with a horizontal corona of irregularly shaped spines. The drupe wall, in this species, is marked by ten



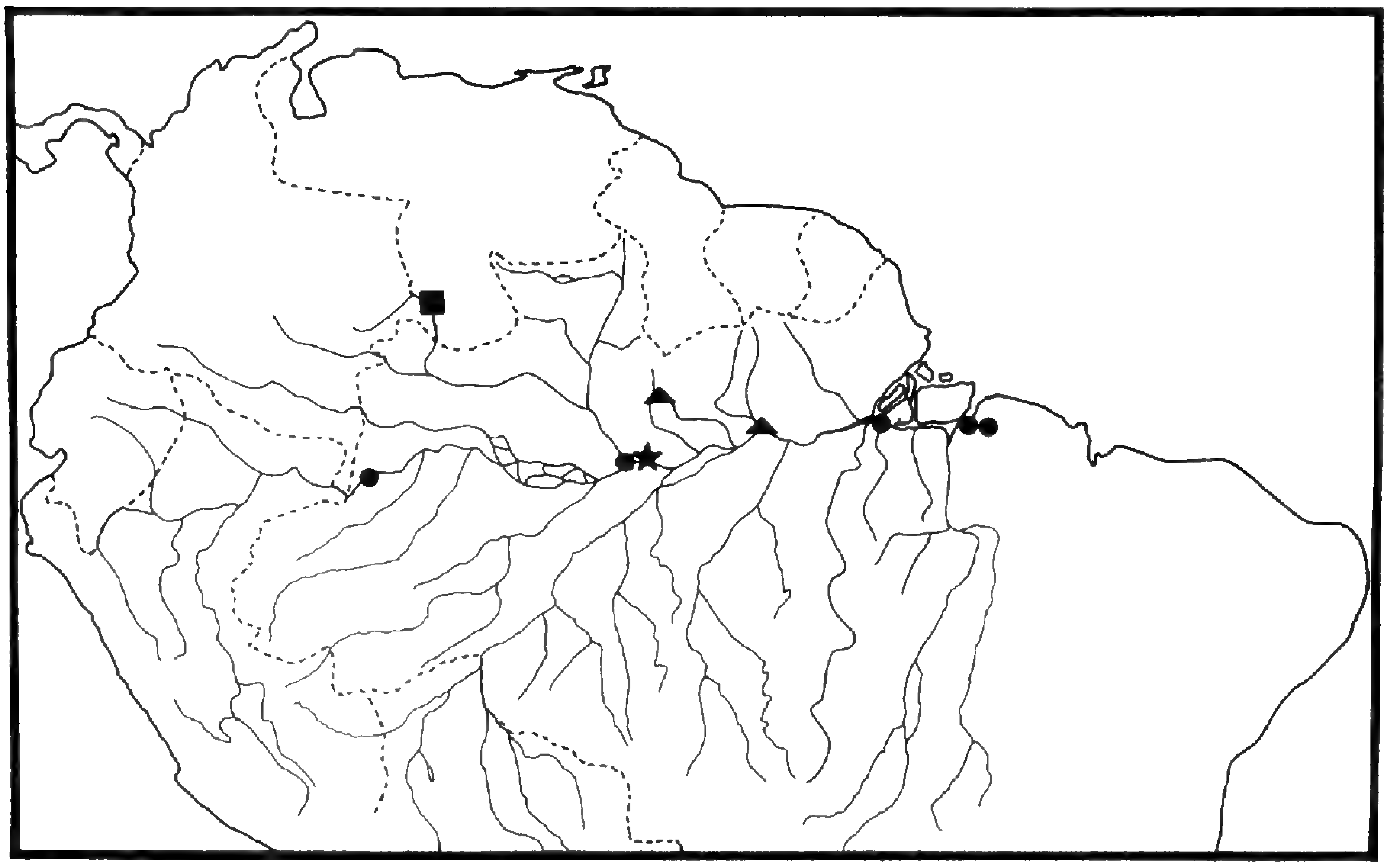
FIGS. 5–10. Illustrations of the drupes and accrescent calyces of species of *Lophostoma*, × 1. FIGS. 5, 6. *L. calophylloides* (*Spruce 1305*); 5, drupe; 6, accrescent calyx (broken at apex). FIGS. 7, 8. *L. dinizii* (*Ducke 9050*); 7, drupe; 8, accrescent calyx. FIGS. 9, 10. *L. ovatum* (*Ducke 704*); 9, drupe; 10, accrescent calyx.

heavy ribs which bear mammillate projections. The ribs run from apex to base. In addition, an inconspicuous groove is found on one side which may interrupt the corona. The most complex drupe is found in *L. ovatum* in which the apex is bicornate and the middle third of the wall is marked by ten vertical, strongly serrate wings. The wings are abruptly truncate one-third the distance from the base of the drupe, the lower third of the drupe being nearly cylindrical. What function, if any, these fancy elaborations of the drupe apex and wall serve, or may have served, is beyond my imagination.

GEOGRAPHY

As in the other genera of the Linostomatinae, the geographic distribution of species and of the genus *Lophostoma* presents no problems which could not be anticipated. The genus as presently known is restricted to the Amazon drainage system (see map for distribution of the species). *Lophostoma calophylloides* has the most extensive range but it is almost certain, even in this case, that the full range is not yet known. The disjunctions shown on the map probably will prove to be of no significance and to be due only to insufficient collection. Some 50 years hence it may be possible to delimit more precisely the range of this species.

The geographic range of the genus presents only three notable differences from that presented by Domke (*Karte 3*, 1934). The first involves the elimination of two disjunct localities: specimens marked, "Rio Janeiro" (*Glaziou 14080*) are either in error or the specimen was collected from horticulture; Spruce's "Barra" collections which are from present day



Map 1. Distribution of the species of *Lophostoma*: dots, *L. calophylloides*; triangles, *L. dinizii*; star, *L. ovatum*; square, *L. amoenum*.

Manaus (see Spruce p. 200. 1908) were apparently thought to be from Barra, State of Bahia on the Rio São Francisco. The second change is due to the collection of *Lophostoma calophylloides* by Ricardo de Lemos Fróes at São Paulo de Olivença which extends the range of this species, and the genus, almost 700 miles to the west. The third and most significant change is the result of the discovery of *L. amoenum* in Venezuela by Wurdack and Adderley. Collection of this new species, the result of exploration by the New York Botanical Garden, suggests the possibility of the discovery of additional species as exploration continues.

Specimens of *Lophostoma calophylloides* bear notations indicating the presence of the species in ecological situations called "igapó," "restinga" and "terra firme. The igapó is defined (Ducke & Black, p. 11. 1943) as "swamp forest where the soil never dries out completely even in summer. . ." The restinga are (Ducke & Black, *ibid.*) "narrow bands of higher alluvions rarely or never flooded. . ." *Lophostoma ovatum* is known from "igapo" and "campina." The campina is defined (Ducke & Black, p. 10) as "small spots of open land, surrounded on all sides by the great virgin forest." Unfortunately, comparable information for *L. dinizii* and *L. amoenum* is lacking.

MATERIALS

This revision is based on specimens from the following herbaria, the abbreviations for which are taken from Lanjouw & Stafleu's *Index Herbariorum, Part I.* Ed. 4 (Regnum Vegetabile, **15.** 1959).

A	Arnold Arboretum of Harvard University, Cambridge
BM	British Museum (Natural History), London
C	Botanical Museum and Herbarium, Copenhagen
F	Chicago Natural History Museum, Chicago
G	Conservatoire et Jardin botaniques, Genève
GH	Gray Herbarium of Harvard University, Cambridge
IPA	Instituto de Pesquisas Agronômicas, Dois Irmaõs
K	Herbarium, Royal Botanic Gardens, Kew
L	Rijksherbarium, Leiden
LE	Herbarium of the Department of Systematics and Plant geography of the Botanical Institute of the Academy of Sciences of the U.S.S.R., Leningrad
MO	Missouri Botanical Garden, Saint Louis
NY	New York Botanical Garden, New York
P	Muséum National d'Histoire Naturelle, Paris
RB	Jardim Botânico, Rio de Janeiro
S	Naturhistoriska Riksmuseum, Stockholm
U	Botanical Museum and Herbarium, Utrecht
US	U. S. National Museum, Smithsonian Institution, Washington
W	Naturhistorisches Museum, Wien.

I wish to take this opportunity to thank the directors and curators of the above institutions for allowing me to examine the specimens in their care.

The illustrations of the new species and of the fruits of *Lophostoma* are the work of Miss Judith A. Kroll to whom I am most grateful.

TAXONOMY

Lophostoma (Meissn.) Meissn. in DC. Prodr. **14**: 600. 1857.

> *Linostoma* sect. *Lophostoma* Meissn. in Mart. Fl. Bras. **5**(1): *72, t. 30.* 1855 (TYPE SPECIES: *Linostoma calophylloides Meissn.*).

Scandent shrubs or lianas, the axillary branches sometimes modified for climbing, the bark containing many fibers. Leaves opposite (or approximate) to alternate, simple, pinnately veined, entire, petiolate, estipulate, the primary lateral veins numerous, more or less straight and parallel. Inflorescences borne from the terminal portions of young shoots, racemiform, the primary peduncle bearing a colored bract-like reduced leaf, true paired bracts absent. Flowers bisexual, pentamerous, perigynous; calyx tube cylindric, nonarticulated, inconspicuously ribbed, glabrous or variously pubescent; calyx lobes 5, quincuncial, subequal; petals 5, medially cleft to the base, alternisepalous, inserted at the calyx tube orifice, the lobes variously squamelliform, erect, glabrous to densely comose; stamens 10, inserted in 2 whorls, the upper whorl antisepalous, the lower alternisepalous, the anthers basifixed, longitudinally dehiscent; disc (when known) minute, annular, lobed, glabrous; gynoecium single, pseudomonomeric, superior, sessile or nearly so, unilocular with a single anatropous ovule, the style terminal or eccentric, the stigma (when known) capitate. Fruit drupaceous and enclosed by the persistent and accrescent calyx.

KEY TO THE SPECIES

a. Bract-like leaves associated with the inflorescence glabrous, white, reddish or reddish purple; leaves 6–14 cm. long, 3–6.5 cm. broad, the apex short to long acuminate; calyx tube glabrous to sparsely puberulent without; drupe apex abruptly acuminate or flat with a horizontal corona of irregular spines, the wall smooth or with 10 heavy, mammillate, vertical ribs from apex to base.

  b. Primary lateral veins slightly arcuate; primary peduncle 1–6 mm. long, the secondary peduncles obsolete or nearly so; bract-like leaf borne near the base or very rarely at the summit of the primary peduncle, white; calyx tube sparsely puberulent and glabrescent without; drupe apex eccentric, abruptly acuminate and somewhat hooked, the wall smooth. . . . . 1. *L. calophylloides.*

  b. Primary lateral veins more or less straight; primary peduncle 10–35 mm. long, the secondary peduncles 2–5 mm. long; bract-like leaf borne near the summit of the primary peduncle, reddish or reddish purple; calyx tube glabrous without; drupe apex flat with a horizontal corona of irregular spines, the wall with 10 heavy vertical ribs with mammillate projections from apex to base. . . . . 2. *L. dinizii.*

a. Bract-like leaves associated with the inflorescence minutely woolly or puberulent, white or rose; leaves 2–5.5 cm. long, 1–3 cm. broad, the apex acute to obtuse, sometimes mucronulate; calyx tube puberulent to tomentose without; drupe (unknown in *L. amoenum*) with 2 horns at the apex, the middle one-third of the drupe wall with 10 strongly serrate vertical wings.

c. Bract-like leaves associated with the inflorescence white; leaf apex acute and sometimes mucronulate; calyx tube white; disc minute, annular; style terminal. .... 3. *L. ovatum.*

c. Bract-like leaves associated with the inflorescence rose; leaf apex acute to obtuse; calyx tube pink to rose; disc absent; style somewhat eccentric. .... 4. *L. amoenum.*

1. **Lophostoma calophylloides** (Meissn.) Meissn. in DC. Prodr. **14**: 600. 1857.

Linostoma calophylloides Meissn. in Mart. Fl. Bras. **5**(1): 72, *t. 30.* 1855 (TYPE: *Spruce 967*!).

Shrubs, becoming large lianas; young stems sparsely puberulent and glabrescent, reddish brown, minutely lenticellate; axillary branches normal or gently curved, rarely recurved. Leaves opposite or subopposite to rarely alternate, the blade ovate to elliptic or oblong, 6–12 (–14) cm. long, 3–5 cm. broad, short to long acuminate at the apex, obtuse at the base, coriaceous, glabrous, varnished above and darker than below, the costa immersed above, elevated beneath, the primary lateral nerves very inconspicuous, parallel and slightly arcuate; petiole canaliculate, rugose, glabrous, 5–7 mm. long. Inflorescences borne terminally on young shoots, often compound, generally composed of one terminal and two or rarely four lateral inflorescences; each inflorescence 3–8 (–12)-flowered, racemiform, puberulent, the primary peduncle 1–6 mm. long, the rachis 3–12 mm. long, the secondary peduncles obsolete or nearly so; bracts and bracteole absent or the bracteole rarely present and caducous, the displaced leaf of the subtending node borne near the base of the primary peduncle or very rarely near the summit, white or cream, usually bract-like and deciduous. Calyx tube cylindric, 13–15 mm. long, about 2 mm. in diameter at the orifice, sparsely puberulent and soon glabrescent without, minutely villous within; calyx lobes obovate, glabrous within; petals cleft to the base, the lobes squamelliform, with irregular margin, usually 0.5 mm. long but rarely to 1 mm., 0.5 mm. broad, erect, exserted, glabrous to densely and irregularly comose; filaments filiform, glabrous, the antisepalous filaments ca. 3 mm. long, the alternisepalous filaments ca. 1.5 mm. long, the anthers oblong, 0.5 mm. long, 0.25 mm. broad, exserted, the connective at most minutely produced beyond the pollen sacs, the antisepalous whorl inserted just below the petals, the alternisepalous whorl inserted about an anther's length below the antisepalous one; disc minute, annular, lobed, glabrous; ovary broadly ellipsoid, ca. 1 mm. long, short-sericeous, sessile, the style terminal, filiform, 1–1.5 cm. long, glabrous, the stigma capitate, included to exserted; pedicel ca. 4 mm. long. In fruit the calyx accrescent, subampullaceous, apex generally broken prior to drupe maturation, 3 cm. long, 2 cm. in diameter, glabrescent; drupe ellipsoid, ca. 2.5 cm. long, 1 cm. in diameter, smooth, abruptly and eccentrically acuminate at the apex, the acumen usually slightly hooked.

ILLUSTRATIONS: Mart. Fl. Bras. **5**(1): *t. 30.* 1855; Gilg in Engl. Nat. Pflanzenfam. III. **6a**: *232, fig. 82f, g.* 1894; Correa, Diccion. Pl. Uteis Brasil **2**: 470. 1931.

DISTRIBUTION: Brazil, known only from five localities in the Amazon basin. This species has been collected in flower from August through February (May at São Paulo de Olivença) and in fruit from December through March. Ducke (1915) cites the plant as "frequent" around Belem. Spruce says that the plants are found in the forest where "the flowers are scented like the lilac, and being accompanied by young and perfectly white leaves, have a very pretty appearance." He further indicates that the perianth tube is "greenish tinged with purple; limb white." According to Ducke and Correa the plant is known locally as "cumacahy."

Brazil. AMAZONAS: Barra [Manaus] *Spruce 967* (NY — lectotype), "1850–51" (C, G, GH, W; photo. F, GH), *1305* (K, P), *Fróes 20491* (F, US), *Ducke 413* (A, F, MO, NY, S, US), *41311*[a] (US), *35690* (U); São Paulo de Olivença, *Fróes 20898* (NY); without precise locality, *Ducke 323* (NY). PARÁ: Rio Guamá, São Miguel do Guamá, beira do rio, *Dardano & Black 48–3094* (IPA, U); Belém, *Ducke 15516* (BM, G, US), *Pires 2652* (NY), *3180* (US), *51807* (NY); Belém (Hort. Bot.) *Huber 8103* (BM, P, U, US); Gurupá, *Ducke 15942* (BM, G, US).

This genus was founded by Meissner, in 1857, in De Candolle's *Prodromus.* It is obvious from his writing (particularly in Mart. Fl. Bras. **5**(1): 72. 1855) that the establishment of the genus had been on his mind for some time. In the latter publication he established a new section of *Linostoma* which he called sect. LOPHOSTOMA. This section, as he recognized it, was composed of a single species, *Linostoma calophylloides.* He listed as a synonym "*Lophostoma Nov. Gen. Meisn. Mss. in Herb. Reg. Monac.*" and "*Lophostoma calophylloides Meisn. Mss.*" Obviously at some time previous to the publication of the Flora Brasiliensis he seriously considered the publication of a new genus (*Lophostoma*) but changed his mind and described it as a new section instead. What facts or events led him in 1857 finally to establish the new genus are not known. Possibly the acquisition of new material which permitted him to describe the second species of the genus (*Lophostoma ovatum*) made him more certain of the position of the South American plant.

The typification of this species, the type species of the genus, is somewhat problematic. The basis for Meissner's *Linostoma calophylloides* (1855) is a specimen or specimens which were collected "c. Barra, oppidum prov. Rio Negro, floret m. Dec.-Mart. 1850–51 legit: R. Spruce." Elsewhere in the same publication, Meissner intimates the name is based on his manuscript name in "Herb. Acad. Monac." The question of whether or not this Spruce collection actually bore a collector's number is posed in the subsequent treatment, by Meissner (1857), of the Thymelaeaceae for De Candolle's *Prodromus.* In this publication, *Lophostoma* is given generic rank and the combination *Lophostoma calophylloides* is made. Meissner cited two specimens: *Spruce 967* and *Spruce 1305*; the citation of the former is followed by an exclamation point and the latter by a question mark. At the end of the description he said that the specimens were seen in the herbaria of "Monac. et DC." At present there are no specimens referable to the genus deposited at Munich and the photograph of the presumed type of *L. calophylloides*, deposited in the De Candolle herbarium is a Spruce specimen lacking a collector's number. Meissner's personal herbarium was purchased by the New York Botanical Garden and is on deposit there. In this collection are many sheets upon which one to several packets are attached which often contain fragments of classic material and are usually annotated fully by Meissner. On one such sheet I found a packet containing a number of detached leaves, a short stem and several flowers, bearing the following notation, "Barra, prov. Rio Negro, Spruce 967! Lophostoma calophylloides Dec.-Mart. 1850–51. legit R. Spruce Meisn. (26. III. 54.) in Hb. Ac. Monac." This information coincides perfectly with the citation both in the 1855 and 1857 publications and it seems clear that the New York fragment is a portion of the holotype and should therefore be designated as the lectotype until the holotype is relocated. On the same sheet is a packet containing a single fruit with the notation, "R. Spruce 1305, DC. Lophostoma calophylloides?" This specimen and information checks with Meissner's second citation of 1857.

2. **Lophostoma dinizii** Huber ex Ducke, Arch. Jard. Bot. Rio de Janeiro 1: 51. 1915 (TYPE: *Ducke 9050!*).

Linostoma dinizii (Huber ex Ducke) Lemée, Fl. Guyan. Fr. 3: 108. 1954, lacking full basionym citation; Nevl. Jour. Arnold Arb. **42**: 320. 1961, *pro syn.*

Shrubs becoming scandent with age; young stems terete, sparsely reddish-puberulent and glabrescent, reddish brown becoming grayish, the lenticels few, horizontally elongate, whitish; axillary branches not observed. Leaves opposite or subopposite except where the shoots are extremely vigorous as in subtending the inflorescences, the blade oblong-elliptic or rarely broadly elliptic, 8.5–11 cm. long, 3–4.5 (–6.5) cm. broad, long-acuminate at the apex, obtuse to truncate at the base, thick-coriaceous, glabrous, darker above than beneath, the costa plane to immersed above, elevated beneath, the primary lateral veins usually inconspicuous, parallel and more or less straight; petiole shallowly canaliculate, rugose, glabrous, ca. 5 mm. long. Inflorescences borne terminally on the young shoots, appearing dichotomously paniculiform, sparsely reddish puberulent; each inflorescence 5–12-flowered, racemiform, the primary peduncle 1–3.5 cm. long, the rachis 5–13 mm. long, the secondary peduncles 2–5 mm. long, dilated at the summit, the true bracts and bracteoles absent but the reduced leaf of the subtending node borne near the summit of the primary peduncle, bract-like, broadly ovate, 2–7 cm. long, 1.5–4(–6) cm. broad, chartaceous, glabrous, reddish or reddish-purple, not persistent.

Flower description based on a single flower: calyx tube cylindric, ca. 11.5 mm. long, 1 mm. in diameter at the orifice, glabrous on the outer surface, sparsely villous within except for the glabrous upper third; calyx lobes lanceolate, ca. 3 mm. long, 0.75 mm. broad, glabrous within; petals cleft to the base, the lobes squamelliform, ca. 0.5 mm. long and broad, completely comose; stamens exserted, the filaments filiform, ca. 1.5 mm. long, glabrous, the anthers oblong, ca. 1 mm. long, 0.5 mm. broad, the antisepalous whorl inserted about an anther's length below the petals, the alternisepalous whorl inserted about an anther's length below the antisepalous whorl; disc (?); ovary ellipsoid, ca. 2 mm. long, densely sericeous, the style terminal, filiform, glabrous, the stigma not seen. In fruit the calyx accrescent, ampulliform, ca. 5 cm. long, 1.7 cm. in diameter, glabrous, the drupe ellipsoid, ca. 3 cm. long, 1.5 cm. in diameter, sparsely villous, with 10 heavy vertical ribs with irregularly-shaped, short-mammillate projections from apex to base with an inconspicuous groove on one side and with a small flat horizontal corona of irregular spines at the apex.

DISTRIBUTION: Collected only twice, both times in the state of Pará, Brazil. The collections were made either slightly before or after flowering in September and December.

Brazil. PARÁ: Oriximiná, bas Trombetas, *Ducke 10988* (BM, G, US); Rio Mapuera affl. Trombetas super cataractam Caraná, *Ducke 9050* (BM, F — photo. and fragment, G, RB — lectotype, U, US).

In the original description of this species no type was designated although two specimens, *Ducke 10988* and *9050*, were cited. I have seen three sheets of *Ducke 10988*: a specimen from Geneva with old inflorescences but lacking flowers, a specimen from the British Museum with very young flowers and a specimen from the Smithsonian Institution with a single mature flower. The collection of *Ducke 9050* is more widely distributed with the most complete sheet at Rio de Janeiro. This specimen consists of leafy shoots, old inflorescences and a single mature fruit. On this basis, I choose *Ducke 9050*, the specimen at the Jardim Botânico of Rio de Janeiro, as the lectotype.

The name *Lophostoma dinizii* has appeared, to my knowledge, twice before being validly published, first in Bull. Soc. Géographie 20: 105. 1909; and the following year in Bol. Mus. Goeldi 7: 163. 1910. In both instances the name appeared without description and must be considered as a *nomen nudum*.

3. **Lophostoma ovatum** Meissn. in DC. Prodr. **14**: 600. 1857 (TYPE: *Spruce 1461*!).

Linostoma albifolium Barbosa Rodrigues, Vellosia ed. 2. **1**: 67. 1891 (TYPE: *Barbosa Rodrigues 63*), ex char.

Lophostoma albifolium (Barbosa Rodrigues) Gilg, in Engl. Nat. Pflanzenfam. III. **6a**: 232. 1894.

Lophostoma bolleanum Domke, Notizbl. **11**: 350. 1932 (TYPE: *Ducke 23469*!).

Scrambling shrub becoming a climber; young stems terete, reddish brown, short puberulent and soon glabrescent, sparsely lenticellate; axillary branches normal or modified and unciform. Leaves opposite or subopposite, the blade ovate to elliptic or oblong-elliptic, 2–4.5 cm. long, 1–2.5 cm. broad, acute and sometimes minutely mucronulate at the apex, cuneate to obtuse at the base, thin-coriaceous, glabrescent above, somewhat papillate beneath, darker above than beneath, the costa plane to immersed above, slightly elevated beneath, the primary lateral veins, inconspicuous, parallel and more or less straight, the submarginal vein coinciding with the margin; petiole canaliculate, rugose, glabrous, 2–3 mm. long. Inflorescences terminal on young shoots, bi- or trifurcately compound; each inflorescence 8–15-flowered, racemiform, puberulent, the primary peduncle 2–7 mm. long, the rachis 6–30 mm. long, the secondary peduncles 0.5–1.5 mm. long, the true bracts absent, the bracteole borne at the summit of the primary peduncle, minute and ephemeral, the reduced leaf of the subtending node borne near the base of the primary peduncle, bract-like, minutely golden woolly (white in nature), caducous. Calyx tube cylindric, 12–15 mm. long, ca. 1.5 mm. in diameter at the orifice, white, tomentose to puberulent without, villous within except the glabrous upper third; calyx lobes oblong to lanceolate, 2.5–3.5 mm. long, ca. 1.5 mm. broad, glabrous within, spreading; petals cleft to the base, the lobes obtusely squamelliform, ca. 0.5 mm. long and broad, erect, subexserted, comose on outer surface, glabrous on inner surface, trichomes exserted beyond the orifice; filaments filiform, 1–2 mm. long, glabrous, the anthers oblong, 0.5–1 mm. long, 0.25–0.5 mm. broad, exserted, the antisepalous whorl inserted just below the petals, the alternisepalous whorl inserted about one-half anther's length below the antisepalous one; disc minute, annular, lobed, glabrous; ovary ellipsoid, 1.5–2.0 mm. long, short-sericeous, sessile, the style terminal, filiform, 10–15 mm. long, glabrous, the stigma capitate, included to exserted; pedicel ca. 2 mm. long, enlarging to 4 mm. in fruit. In fruit the calyx accrescent, ampulliform, ca. 7 cm. long, ca. 2.5 cm. in diameter, glabrescent except for the extreme apex; the drupe ellipsoid, ca. 4.5 cm. long, ca. 1.5 cm. in diameter at base of the wings, glabrescent, bicornate at the apex and with 10 strongly serrate vertical wings which are truncated at the lower third of the drupe, the style persistent.

ILLUSTRATION: Vellosia ed. 2. 3: *pl. 20.* 1891, as *L. albifolium.*

DISTRIBUTION: Brazil, known with certainty only from the vicinity of Manaus. A. Glaziou collection (*Glaziou 14080*) is labelled from Rio de Janeiro but I believe this to be an error. *Index Kewensis* gives the citation "Venezuela" for this species but as previously indicated by Ducke (1915) this record is in error. The plant has been collected in flower and fruit in February and May. According to Ducke, the plants are found in swampy and periodically inundated woods (see also introduction). Barbosa Rodrigues noted that he encountered the species on the left bank of the Rio Negro.

Brazil. AMAZONAS: Barra [Manaus] *Spruce 1461* (K; LE; NY — fragment of holotype; P), *Fróes 20527* (F, NY), *Ule 8953* (G, GH, K, L), *Ducke 704* (F, GH, NY, MO, US), *23469* (isotypes of *L. bolleanum*: G, U, US), *24036* (RB). Locality doubtful: "environs Rio Janeiro," *Glaziou 14080* (C, K, P).

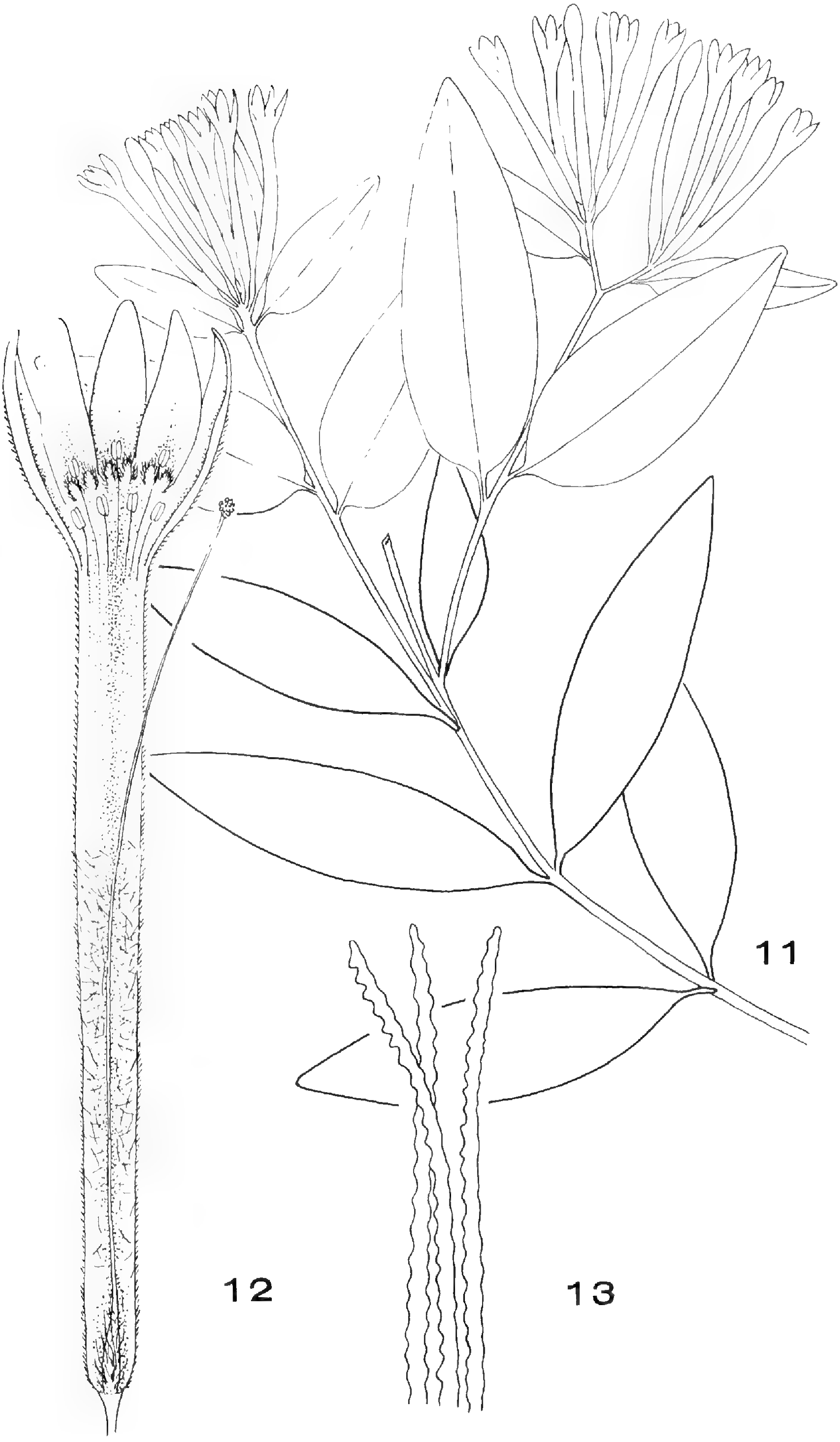
Barbosa Rodrigues, in the original description of *Linostoma albifolium*, admits some apprehension because he is acquainted with only one South American species (*L. calophylloides*) of the genus. He has not seen the other species and therefore he poses the rhetorical question whether it might not be the same as his new species. It is. I have not seen a type specimen but his very complete description and a well executed illustration leave little doubt that *L. albifolium* belongs in synonymy here.

Domke described *Lophostoma bolleanum* from a Ducke collection. As principal features to distinguish it from *L. ovatum* he gave larger, more oval and somewhat thicker leaves, shorter calyx tube, obtuse bud apex, multiflowered inflorescence and exserted stigma. Examination of the isotypes of this taxon shows all these statements to be true provided the specimens are contrasted solely with the types of *L. ovatum*. If one considers also the additional collections of *L. ovatum* now available it seems apparent that the characteristics which Domke mentions fall well within the total range of variation of a single species. Only the character of the exserted stigma cannot be demonstrated in other specimens positively referable to this species and this characteristic is now known to be unreliable (Nevling, 1961a, b). Domke gives the leaf position as alternate but the isotypes which I examined have opposite leaves. However, one leaf of the opposite pair often was shed giving the false impression of an alternate arrangement.

4. Lophostoma amoenum Nevl. sp. nov.

Vitis, ramis juvenibus pubescentibus usque glabrescentibus. Folia plerumque opposita coriacea glabra ovata usque elliptica 3.5–5.5 cm. longa 1–3 cm. lata apice acutis usque obtusis basi cuneatis; petiolo 2–4 mm. longo glabro. Inflorescentia compositae racemiformae pubescentes; pedunculo primario 1–5 mm. longo; rhachide 3–6 mm. longo; pedunculis secundariis usque 1 mm. longis. Bracteae roseae pubescentes. Flores hermaphroditi 10–16 per inflorescentem; pedicello ca. 3.5 mm. longo; calyce cylindrico 15–16 mm. longo 1.5–2 mm. lato roseo extus pubescente; calycis lobis subequalibus intus glabris; petalis 10 squamelliformis ca. 0.5 mm. longis dense barbatis; staminibus 10 in planis 2, antheris oblongis 0.5 mm. longis 0.25–0.5 mm. latis; disco nullo; pistillo 1, ovario ellipsoidale 1.5 mm. longo, sericeo, stigmate capitato exserto. Fructus non vidi. HOLOTYPUS: *Wurdack & Adderley 43208* (A). (FIGS. 11–13.)

Vine to 2.5 m., young stems minutely puberulent and glabrescent, light brown becoming grayish; axillary branches sometimes curved or recurved. Leaves opposite or sometimes alternate on vigorous shoots, the blade ovate to elliptic, 3.5–5.5 cm. long, 1–3 cm. broad, acute to obtuse at the apex, cuneate at the base, coriaceous, glabrous, darker above than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beneath, the costa immersed above, elevated beneath, the parallel lateral nerves conspicuous and slightly arcuate beneath; petiole slightly canaliculate, rugose, glabrous, 2–4 mm. long. Inflorescences borne terminally on young shoots, compound, two or three appearing as a single inflorescence; each inflorescence 10–16-flowered, racemiform, puberulent, the primary peduncle 1–5 mm. long, the rachis 3–6 mm. long, the secondary peduncles to 1 mm. long, the bracteole minute, caducous, the displaced leaf of the subtending node near the summit of the primary peduncle, bract-like, rose-colored, minutely puberulent, the leaves of two or more subtending nodes usually similar. Calyx tube cylindric, 15–16 mm. long, 1.5–2 mm. in diameter at the orifice, minutely puberulent without, pink, the tube interior glabrous in upper half, villous in lower half; calyx lobes elliptic or lanceolate, 4–4.5 mm. long, ca. 1.5 mm. broad, glabrous within; petals 5, completely cleft to the base and appearing as 10, squamelliform, spatulate, fleshy, ca. 0.5 mm. long, 0.25–0.5 mm. broad, densely comose on outer surface, glabrous or comose on inner surface; filaments filiform, glabrous, ca. 0.5 mm. long, the anthers oblong, 0.5 mm. long, 0.25–0.5 mm. broad, the antisepalous whorl inserted immediately below the petals, exserted, the alternisepalous whorl inserted 1 or 2 anther's lengths below the antisepalous, included to exserted, sometimes slightly exceeding the petals; disc absent; ovary ellipsoid, 1.5 mm. long, sericeous, the style somewhat eccentric, filiform, glabrous, the stigma capitate, small, papillate, exserted; pedicel ca. 3.5 mm. long. Fruit unknown.

This attractive vine was collected in flower on June 27, 1959, at an elevation of 120 meters. The collectors indicate that it is "occasional" on the Caño San Miguel.

Venezuela. AMAZONAS: Caño San Miguel near Limoncito 15 km. from Río Guaiana [2° 41′ N, 67° 25′ W], elev. 120 m., *Wurdack & Adderley 43208* (A, NY).

This new species resembles most closely *Lophostoma ovatum* from which it may be distinguished in gross morphology by the following characteristics: leaf shape; more numerous bract-like leaves, rose colored and minutely puberulent beneath; pink to rose-colored calyx tube which is slightly larger than that of *L. ovatum*; small anthers; absence of a disc; excentric style. The fruit, unfortunately, is not known up to now, but one can scarcely help wondering whether the fruit of *L. ovatum* will differ as much from that of the species presently known as their fruits differ from each other.

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FIGS. 11–13. Illustration of *Lophostoma amoenum*. FIG. 11, habit × 1.5. FIG. 12, detail of flower, × 6. FIG. 13, detail of trichomes from petal, × 12. All figs. from type.

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CAMBIUM AND VASCULAR DERIVATIVES OF GINKGO BILOBA

LALIT M. SRIVASTAVA[1]

NUMEROUS PAPERS AND MONOGRAPHS have been written about the habit, geographical and historical distribution, morphology and life history of *Ginkgo biloba* L. Most of this literature has been reviewed by Seward and Gowan (1900) and Sprecher (1907); and, in recent years, an extensive bibliography of papers published on different aspects of *Ginkgo* has been compiled by Franklin (1959). The structure of vascular tissues in the stems and roots of this plant has been described by several workers — in general, it resembles that of the conifers. However, there are some important differences, and certain anatomical details are not clear. The secondary xylem of *Ginkgo* is unique among gymnosperms in having parenchyma cells that accumulate druses of calcium oxalate, but whether these parenchyma cells occur in the axial tissue (Sprecher, 1907; Penhallow, 1907, p. 109–111) or also in the rays (Göppert, 1850, p. 266; Seward and Gowan, 1900) is not known. Tupper (1911) emphasized that the axial files of parenchyma cells containing druses were always in spatial contact with the rays. Penhallow (1907, p. 209) mentioned two types of tracheids in the xylem; but his observations were cursory and, to the best of my information, have not been reported in subsequent literature. Greguss (1955, p. 125) remarked on the irregular arrangement of tracheids in radial files of xylem, but he did not explain why it was so. The secondary phloem has been better described on the whole (Moeller, 1882; Strasburger, 1891; Sprecher, 1907), but the structure of fibers and the origin and distribution of albuminous cells are not clearly understood.

In order to understand thoroughly the structure of xylem and phloem and to determine the interrelationships of various cell types composing these tissues, detailed ontogenetic studies are essential. Since the xylem and phloem elements are derived from the cambium, a study of cambial phenomena is necessary also. The present investigation was undertaken, therefore, to study the developmental changes in the cambium and to relate these changes to the anatomical features of xylem and phloem. Relevant aspects of cambial activity are reviewed and described first; this is followed by the structure and ontogenetic relationships of the cell types in the vascular tissues.

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MATERIAL AND METHODS

Material was collected from short shoots, young rapidly growing long shoots and the old trunk of a tree in Boston[2] in Dec., 1961, and from an old branch of a tree in Cambridge in April, 1962. An earlier collection made in Feb., 1958, included samples of long shoots from a young tree in the Botanical Gardens of the University of California at Berkeley.[3] Most of this material was killed and fixed in Craf III (Sass, 1951, p. 18), softened in equal parts of 95 per cent ethyl alcohol and hydrofluoric acid for 16–20 hours, embedded in celloidin, and sectioned on a sliding microtome. Serial cross, radial, and tangential sections were obtained. They were tied to slides with thread (see Cheadle and Esau, 1958), and stained with tannic acid-ferric chloride and lacmoid (see Cheadle, Gifford and Esau, 1953). The sections were mounted in Harleco resin. In addition, some material from Boston and Cambridge collections was sectioned fresh and some after being killed in Regaud's fluid (Davenport, 1960, p. 168). These sections were stained in different ways and served for checking some histological features. The slides of *Ginkgo* available in the wood collections of the Arnold Arboretum, Harvard University, were examined also. They served to confirm several details of xylem structure and as subjects for some photomicrographs of that tissue.

As is well known, the cambial initials produce xylem and phloem derivatives by periclinal divisions. The radial files of vascular elements derived by periclinal divisions in single cambial initials are termed tiers. Periodically, the cambial initials divide in an anticlinal plane to form two daughter initials, which in turn divide periclinally, and some cambial initials decline and are lost from the initial layer through maturation into a xylem or a phloem derivative. The radial extent of a tier comes to an end with an anticlinal division in, or with a decline and loss of, its cambial initial. A study of tiers, although laborious and time consuming, yields valuable data regarding the developmental changes in the cambium and the origin of vascular elements. For details of method, the reader is referred to Bannan (1950) and Srivastava (1962).

Tiers, particularly those formed by fusiform initials, were studied in the present work by the use of serial tangential and radial sections. They were studied in xylem as well as phloem. The xylem derivatives of fusiform initials showed some apical intrusive elongation during their differentiation (FIG. 3), but this elongation was not excessive and was sometimes absent. The study of tiers in phloem was rather difficult because the collapse and crushing of sieve elements and albuminous cells occurred close to the cambium and obscured the pattern of cell lineages. Consequently, the tiers were followed in phloem only as far as it was possible to do so with reasonable certainty.

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[2] I acknowledge the assistance and cooperation of Mr. John Coob, and Mr. Robert McDonough and his associates of the Boston Park Division in the collection of this material.

[3] I am grateful to the authorities of these Gardens for their permission and help in procuring this material.

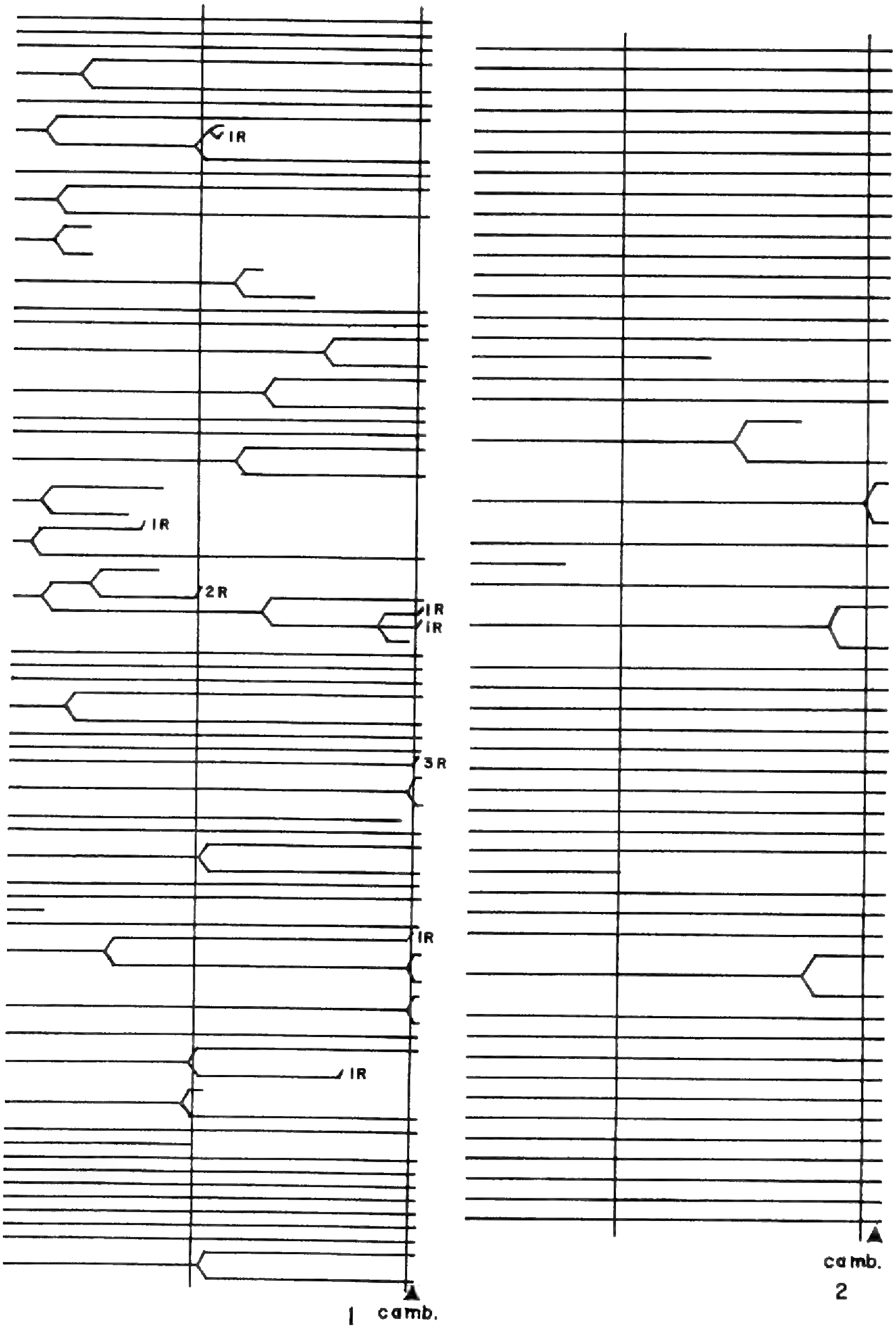
The terms used in the present study have been defined earlier (see Cheadle and Esau, 1958; Srivastava, 1962). However, a few are defined again for clarity. The daughter initials, formed after an anticlinal division in a fusiform initial, grow intrusively at their tips until they attain the length common to the fusiform initials of that region; during this growth, they divide periclinally also. The initials that are growing are called *growing initials*; they become *regular initials* after they have stopped elongating. Their tiers are called *growing* and *regular tiers*, respectively. The fusiform initials that are lost from the cambial layer are called *declining initials* and their tiers *declining tiers*. The terms *phloic* and *xylary initial* are used to denote the daughter cells formed toward the phloem and xylem, respectively, after a periclinal division in the cambial initial. The phloic and xylary initials either directly, that is, without any further divisions, or after a few divisions, produce the various cell types in the vascular tissues.

OBSERVATIONS AND RESULTS

Cambium

In order to understand the activity of fusiform initials in the cambia of young and old stems, 50 tiers in each of the two kinds of stems were followed from the inner xylem to the cambium. A radial distance of ca. 0.8 mm. and almost two growth increments was involved in each case. The tiers were selected at random in the first section of the tangential series and I had no idea what would eventually happen to the fusiform initials of the tiers selected. The results of this study are shown in a diagrammatic manner in FIGURES 1 and 2. In these figures the horizontal lines represent tiers; a bifurcation means an anticlinal division in the fusiform initial and the end of its tier; a line that stops short of the cambial level means the end of the tier through the loss of the fusiform initial; and small oblique lines with numerals by their side represent the number of new ray initials added to the cambium. Vertical lines demarcate the growth increments.

A comparison of these two figures reveals that the number of anticlinal divisions per unit of xylem increment is higher in young than in old stems. In the young stem 19 initials divided anticlinally, and of the 38 daughter initials 4 divided again. In the old stem, in contrast, only 4 initials divided anticlinally. Taking all tiers that were followed, in the young stem there was a net increase of 5 initials, over the original 50, after 23 anticlinal divisions. In the old stem there was no increase in the number of fusiform initials because the number of new initials that was added by anticlinal divisions was balanced by the number of initials that was lost from the cambium. (These figures must not be interpreted to mean that in this sector of the old stem there was no increase in the number of fusiform and ray initials with increasing diameter of the wood cylinder. Probably there was such an increase, but it did not become apparent in the tiers that were followed through the short radial distance of xylem.)



FIGS. 1, 2. Diagrammatic representation of the history of 50 fusiform initials and their daughter initials in a young (ca. 4 year old, FIG. 1) and an old (ca. 50 year old, FIG. 2) stem.

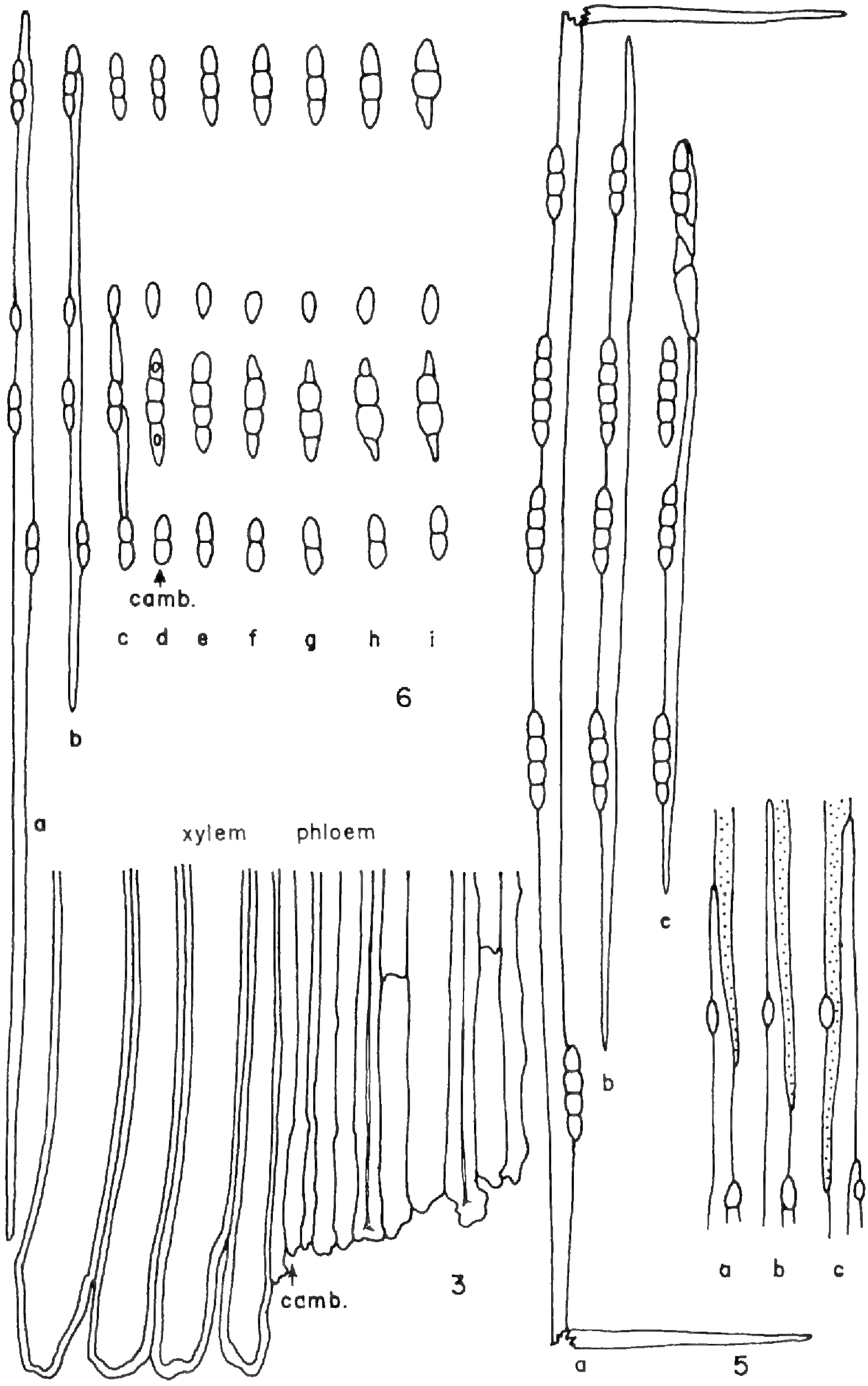
The results presented here are based on a very small sample and cannot be used statistically; however, they support the conclusion reached by Bannan (1960b) for conifer cambia that the frequency of anticlinal divisions and the survival of daughter initials are higher in young rapidly growing stems than in old stems.

It may appear from these figures that the relative frequency of anticlinal divisions in *Ginkgo* is less than in comparable material of conifer cambia (cf. Bannan, 1950, 1960a; Whalley, 1950; Srivastava, 1962). Among the 50 initials followed through almost two years growth, 27 initials in the young stem and 43 in the old stem divided only in the periclinal plane. (The initials that declined are omitted from this consideration.) It must be emphasized, however, that the results obtained in the present survey are based on a very small sample of the material of *Ginkgo* and the radial distances of xylem followed were not extensive. These results will have to be substantiated by a much wider sampling than was possible here before valid comparisons between the cambia of conifers and *Ginkgo* can be drawn.

The planes of anticlinal walls as seen in the cambium and as interpreted from the xylem derivatives show varying degrees of obliquity, but transverse or nearly transverse anticlinal walls seem to be rather rare. The oblique anticlinal walls may be very long, sometimes extending through one-fourth to one-third of the length of the original initial. The anticlinal divisions occur more or less near the middle of the dividing initial but in some cases, particularly in young stems, they are placed more toward one end and form daughter initials of unequal lengths.

During the elongation of daughter initials following an anticlinal division a curious phenomenon was noted. FIGURE 4 shows successive xylem derivatives of two fusiform initials. Only the tips of the derivatives are drawn and the derivatives of one initial are stippled. It will be noticed that the tips of the derivatives appear in different positions relative to one another at b and c. A simple explanation of this phenomenon would be that the xylem derivatives of the two fusiform initials elongated intrusively in different directions during their differentiation. If the intrusive elongation of differentiating tracheids is ignored, two other possibilities may account for the phenomenon. First, the fusiform initials of the two tiers underwent some shortening (see asymmetric periclinal divisions, below) after the periclinal divisions that produced the derivatives at b and elongated in different directions before they divided periclinally to produce the derivatives at c. Second, the tips of the two fusiform initials shifted their position relative to one another between the time they produced the derivatives at b and c. This explanation would involve actual "physical movement" of the tips of the two fusiform initials relative to one another. It was not possible to determine which of these explanations was true, but the phenomenon is indicative of the high degree of mutual adjustment among and between the fusiform and ray initials and their derivatives.

The decline of fusiform initials in the cambium of *Ginkgo* occurs essen-



FIGS. 3–6. Selected tiers in radial and tangential view. 3, Old stem, radial view of a tier in xylem and phloem; only one end of the tier is drawn, × 195. 4, Young long shoot, tangential sections; successive tracheary derivatives of two fusiform initials, only the tips of the derivatives are drawn, × 95. 5, Old stem, tangential sections; successive xylem derivatives of a fusiform initial that declined without leaving any ray initials, × 95. 6, Young long shoot, tangential

tially in the same manner as described for conifers (see Bannan, 1953; Srivastava, 1962); and results either in a total loss of the initial from the cambial layer by maturation into a xylem or a phloem derivative, or in its conversion to one or more ray initials. The periclinal divisions in the declining initials are usually asymmetric and so oriented that the shorter cell is left in the cambial layer and acts as the initial for the next division. The results of these divisions are seen in the xylem and phloem and are marked by a progressive shortening of the succeeding derivatives in the declining tier. FIGURE 5 shows the last few xylem derivatives of a declining fusiform initial which was lost from the cambium without leaving any ray initial. FIGURE 6 shows a declining tier in xylem and the remnants of its initial in cambium, which appear as two new ray initials attached to the margins of a two-celled ray. The new ray initials yielded derivatives toward the phloem side only (FIG. 6, i–e).

In several instances, the declining fusiform initial divides transversely, or obliquely, one or more times and the individual segments are lost by maturation or undergo further shortening by asymmetric periclinal divisions. The individual segments may further divide transversely (transverse divisions of second order), the same process being repeated until nothing is left of the original initial, or parts of it remain in the cambial zone and become new ray initials. As a result of transverse segmentation of the fusiform initial and maturation of some segments and shortening of others, the declining tier breaks up into segments which may be discontinuous in the axial direction. The xylem derivatives shown in FIGURE 7 illustrate the segmentation of the declining initial, loss of the upper and lower segments, and the formation of a ray initial by the middle segment. As in FIGURE 6, the derivatives of this ray initial appeared only in the phloem (see one-celled ray at the bottom, FIG. 8, f–d). The decline of the tiers shown in FIGURES 6 and 7 could not be traced from the phloem side.

The decline of several tiers was followed from the phloem side and the relevant stages in xylem studied. The drawings in FIGURE 8, f–d, illustrate an anticlinal division in a fusiform initial followed by the decline of the upper daughter initial, which is present in the cambium (at c) as three axially discontinuous segments. The evidence for the anticlinal division is seen in the phloem and xylem derivatives at f and b, respectively. It will be noticed that the transverse segmentation and the breakup of the upper daughter initial into axially discontinuous portions is obvious in the phloem (e–d), but not in the xylem (b). The lower daughter initial was still present in the cambium; it is possible that it would have declined later. In FIGURES 9 and 14, likewise, the evidence for the breakup of the declining fusiform initial into axially discontinuous segments is seen in the phloem but not in the xylem. In FIGURE 9 two new ray initials are present in the cambium but, although the last axial derivative of the

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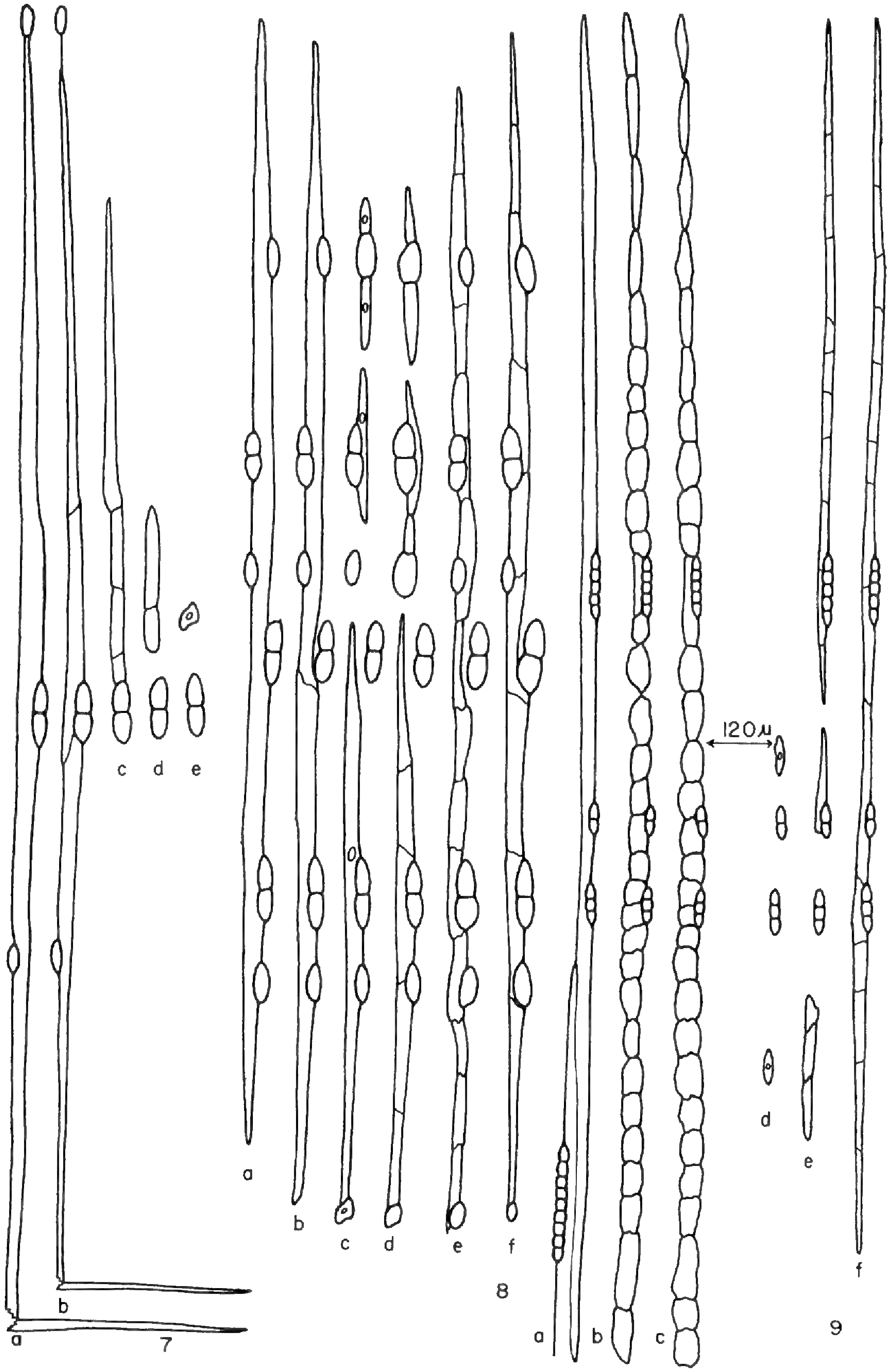
sections; successive xylem derivatives (a–c) of a declining fusiform initial that left two new ray initials (shown with nuclei) in the cambium (d). The new ray initials produced derivatives only toward phloem (i–e), × 95.



FIGS. 7–9. Selected tiers drawn from tangential sections. 7, Young long shoot; successive xylem derivatives (a–d) of a declining fusiform initial which left one ray initial in the cambium (at e, cell with nucleus), × 120. 8, Young long shoot; successive xylem (a–b) and phloem (f–d) derivatives of a fusiform

declining fusiform initial occurred ca. 120 μ internal to the cambium, no derivatives of the new ray initials were encountered in the xylem.

From these examples and several others of tiers that were followed both in phloem and xylem, it seems that the transitional stages in the decline of fusiform initials are often more clearly seen in the phloem than in the xylem. But these stages occur in the xylem also (FIGS. 6, 7). It is possible, as Bannan (1953) has suggested, that the declining fusiform initials produce xylem and phloem derivatives in varying amounts — sometimes more phloem elements are produced, at other times more xylem elements.

During their decline, the fusiform initials and their segments may divide periclinally at irregular intervals with the result that their derivatives appear radially discontinuous. In the present study such radial discontinuities in declining tiers were recorded only in the xylem (FIG. 10). They were particularly evident between the last axial derivatives, and the first derivatives of the new ray initials (FIG. 11). Several such examples were recorded. That these new ray initials had been left in the cambium by the declining fusiform initial was supported by the study of other declining tiers both in the phloem and xylem (FIGS. 8, 9, 14) and by the presence of transitional stages in the xylem (FIGS. 6, 7, 10). The observation of declining fusiform initials in the cambium further supported this conclusion. Possibly, in these instances of radial discontinuity between the last axial and the first radial derivatives, the declining fusiform initials and their segments did not produce any xylem derivatives after their length had fallen below a certain value — they produced only phloem derivatives until they were converted to ray initials.

Sometimes the early derivatives of newly established ray initials are produced toward phloem only (FIGS. 6, 7 and 8). Whether these ray initials would have produced xylem derivatives at a later date could not be determined. It is, of course, possible that some ray initials produce derivatives toward phloem only and form what are known as phloem rays.

Reference has been made earlier to anticlinal divisions that set off daughter initials of unequal lengths. Such divisions were very common in the material of young stem. The shorter initials often declined and were converted to ray initials, or were lost by maturation into xylem or phloem elements.

The occurrence of radial divisions, in which the dividing wall twice intersects the same radial wall, near the middle of fusiform initials was recorded in the cambium and interpreted from a study of xylem and phloem

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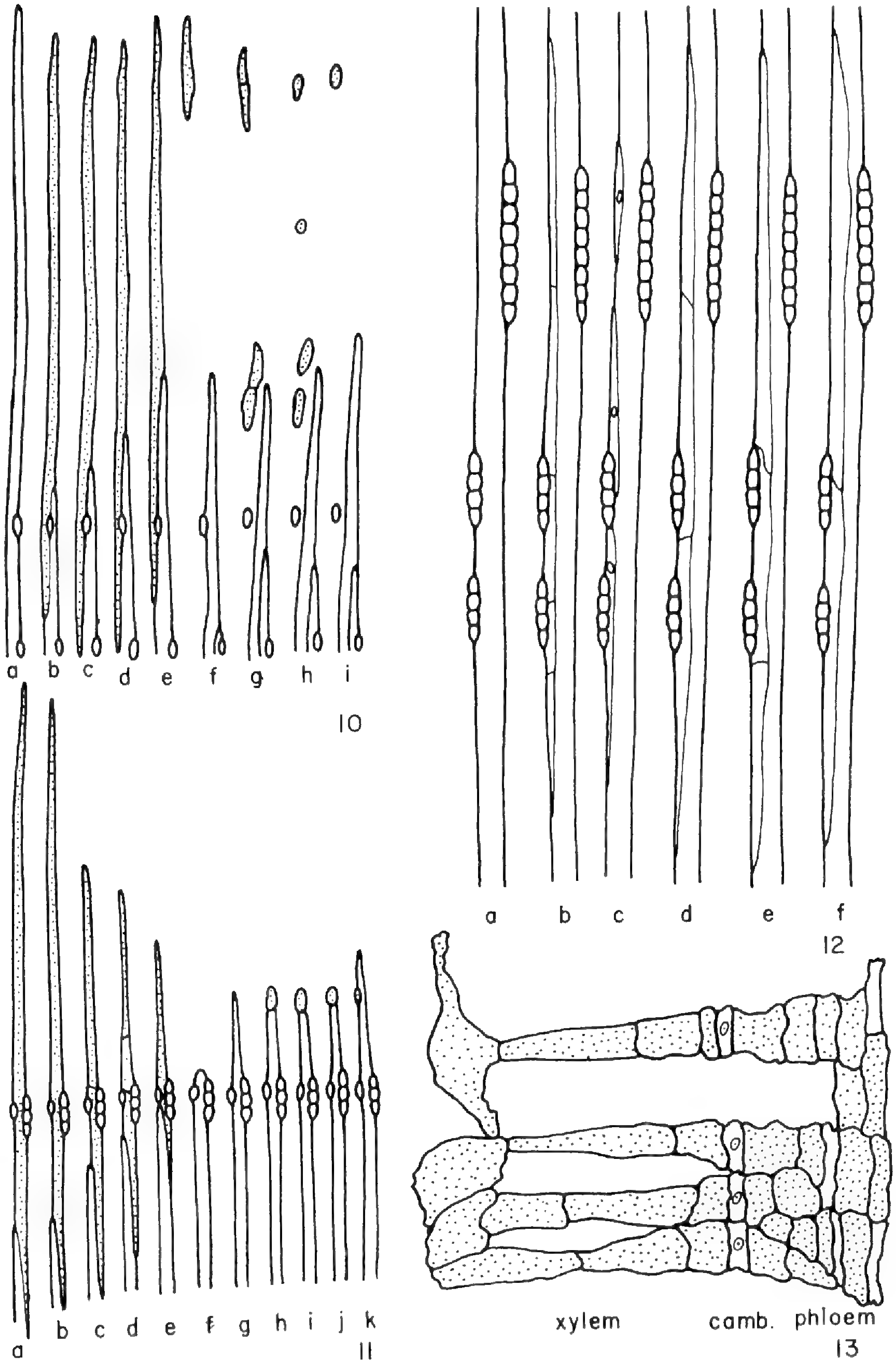
initial which divided anticlinally. The upper daughter initial declined and was present in the cambium as three axially discontinuous segments (at c, cells with nuclei), × 120. 9, Old stem; successive xylem (a–c) and phloem (f–e) derivatives of a fusiform initial which declined and left two new ray initials in the cambium (at d, cells with nuclei). A radial distance of 120 μ intervened between the last xylem derivative (at c) and the cambium (at d); during this time neighboring fusiform and ray initials produced xylem derivatives. The anticlinal division represented in the xylem derivative at a was picked up in the phloem derivative that occurred ca. 80 μ external to the derivative at f, × 60.



FIGS. 10–13. Selected tiers in tangential and radial view. 10, Young long shoot, tangential sections; successive xylem derivatives (stippled) of a declining tier and a ray. The figure also shows radial discontinuities between the derivatives of the declining tier. The derivatives of the subjacent tier are shown also,

(FIG. 12). Only a few radial divisions were seen, however, and it was not possible to determine whether they led to the formation of ray initials. In the literature on conifers, new ray initials are reported to be formed in this manner (Bailey, 1920a; Barghoorn, 1940; Bannan, 1957).

Addition of new ray initials at the margins of existing rays is a constant source of an increase in the height of rays (FIG. 6). Parts of declining initials often occur near the middle positions of the rays, but these parts usually do not become established in the cambium as new ray initials. This phenomenon is responsible, in part at least, for the generally uniseriate arrangement of rays in *Ginkgo*. Similar observations were made earlier in the Pinaceae (Srivastava, 1962).

Xylem

The secondary xylem of *Ginkgo* shows discernible growth increments. But in some specimens the amount of late wood formed in a year may be small — limited to one or two tangential layers of cells — and the boundaries between successive growth increments not very obvious (FIG. 16). In these specimens the progressive decrease in the radial diameter of tracheids during the transition from spring to summer wood seems to be absent also. Apparently, these phenomena, like the ring width, vary with the growth conditions and the age of a plant. (For seemingly conflicting reports in the literature about the discernibility of boundaries between growth increments and the amount of summer wood formed in a year in *Ginkgo*, cf. Göppert, 1850, p. 54; Nakamura, 1882; Strasburger, 1891, p. 10; Sprecher, 1907; Penhallow, 1907, p. 209; Greguss, 1955, p. 125; Cheng, 1958.)

The tracheids, as is usual in gymnosperms, are long prismatic cells. Bailey and Tupper (1918) found that the average length of tracheids in *Ginkgo* increased from 0.9 mm. in the first annual ring to 3.5 mm. in increments more than 60 growth rings away from the pith. Some measurements of the length of tracheids in young long shoots and old stems in the present work yielded similar results. In a fossil specimen of *Ginkgo* wood (courtesy of Prof. E. S. Barghoorn, Jr.) the tracheids were as much as 8–9 mm. long. The age of the tree from which this sample came was, of course, unknown.

The tracheids have circular bordered pits in one or more rows on their radial walls. The tracheids of spring wood have only occasional pits on their tangential walls, whereas those of summer wood have them commonly. Some summer wood tracheids, particularly in the young stems,

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× 70. 11, Young long shoot, tangential sections; successive xylem derivatives (stippled) of a declining fusiform initial and the ray initial that it formed. The derivatives of the subjacent tier are drawn also, × 70. 12, Old stem, tangential sections; successive xylem (a–b) and phloem (f–d) derivatives illustrating a radial division in the fusiform initial. The shorter cell formed after the radial division declined and was present in the cambium (at c) as three axially discontinuous segments (shown with nuclei), × 80. 13, Old stem, radial view of part of a declining tier and ray in xylem and phloem. Starch-containing cells are stippled, albuminous cells in outline, cells in cambial zone with nuclei, × 150.

had one or more transverse walls which were distinctly pitted (FIG. 18). The bordered pits in *Ginkgo* generally appear to have no torus on their membranes. However, a small torus is discernible at high magnifications in the membranes of unaspirated pit pairs (see also Wright, 1928). The diameter of the torus is usually smaller than that of the pit pores. (For details of pitting between tracheids and tracheids and rays, crassulae or bars of Sanio, and trabeculae, see Kleeberg, 1885; Müller, 1890; Seward and Gowan, 1900; Sprecher, 1907; Bailey, 1919, 1925; Kanehira, 1926; Greguss, 1955, p. 126; Cheng, 1958.)

A peculiar phenomenon noted in the xylem of *Ginkgo* is the presence of two more or less distinct types of tracheids in the spring wood. The two types of tracheids differ in their cross sectional diameters, thickness of their secondary walls, and the manner of pitting on their walls. For convenience, they are referred to as wide and narrow tracheids (FIGS. 17, 19).

The chief difference in the cross sectional diameters of these two tracheids is in their radial dimensions. Occasionally, the narrow tracheids have smaller tangential dimensions also. These overall size differences in cross sections are accentuated because the narrow tracheids as a rule have thicker secondary walls than the wide tracheids. With phloroglucin-HCl, however, the walls of these tracheids stain with equal intensity (FIG. 17). The wide tracheids have circular bordered pits in one or more rows along their radial walls, and well developed crassulae frequently separate individual or groups of pits. These tracheids are connected with the cells of the xylem rays by a combination of bordered pits and primary pit fields. In contrast to the wide tracheids, the narrow tracheids have very few pits on their radial walls, and these pits are generally confined to those areas of the wall that are in contact with the cells of the xylem rays (FIGS. 19, 20).

The samples examined in the present study came from different trees and were of different ages. Among these samples there was considerable diversity with regard to the occurrence of narrow tracheids. They were particularly common in old specimens with wide growth increments, and rather poorly represented in young specimens (cf. FIGS. 21–23). They are present in young specimens, however, and may be seen even in the first one or two years of xylem growth. Within a growth increment, the narrow tracheids appear to be relatively more abundant in the wood formed later in the spring.

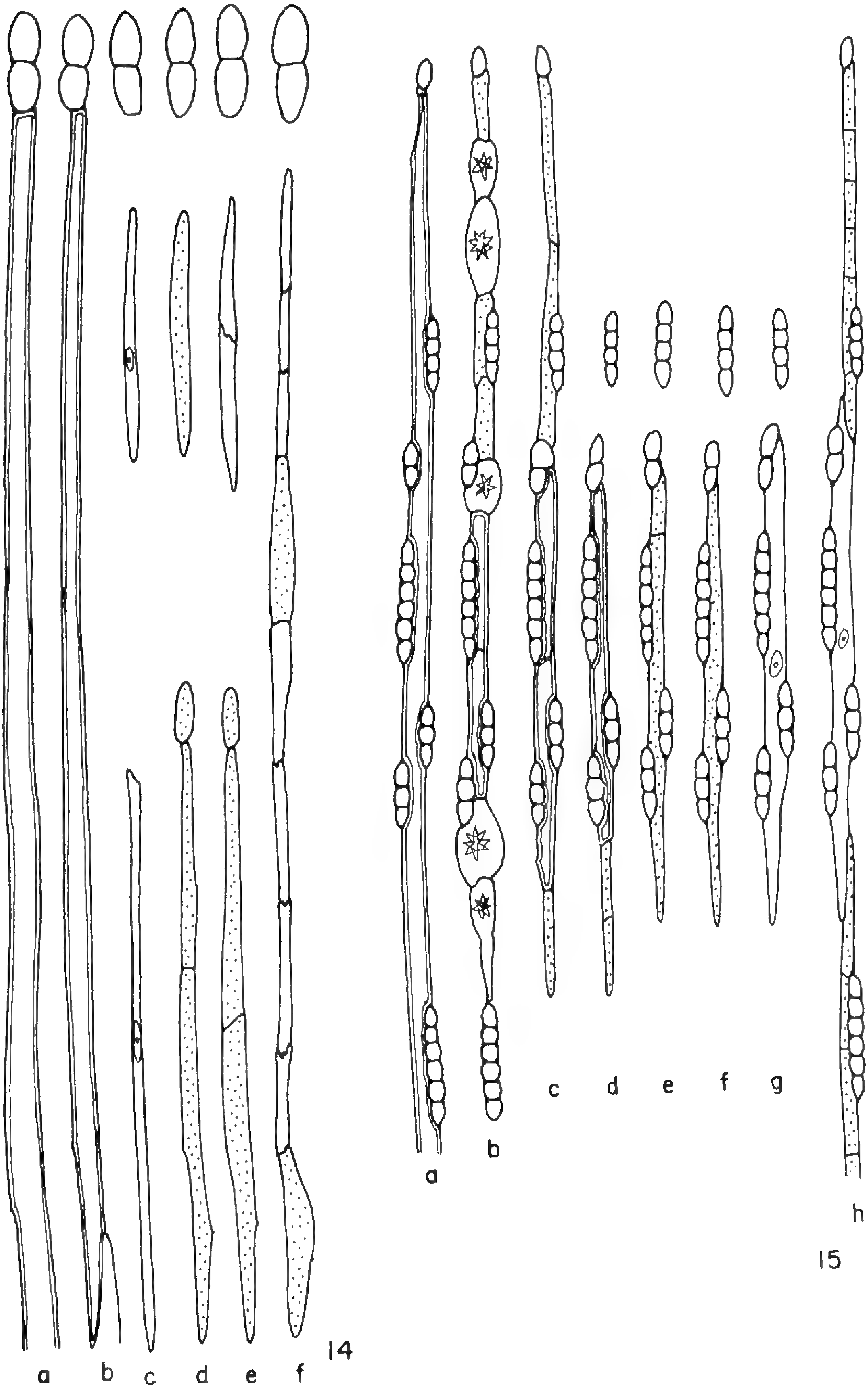
The wide and narrow tracheids occur interspersed in the same radial file — a variable number of wide tracheids alternating with an equally variable number of narrow tracheids (FIGS. 17, 20, 21). These tracheids are the usual xylem derivatives of growing and regular fusiform initials; their lengths within a tier correspond to the length of the fusiform initial responsible for that tier. Small differences in the length of tracheids within a tier are common; these differences are probably related to the varying degrees of intrusive apical elongation of the differentiating xylem tracheids. No direct relationship is evident, however, between the extent of apical elongation and the differentiation of narrow or wide tracheids. Within a tier some narrow tracheids may be longer, others shorter, than the wide tracheids (FIG. 20).

The presence of wide and narrow tracheids within the same tier indicates that the differences between these tracheids are brought about during their differentiation. The difference in radial diameter of these tracheids is probably the result of differential expansion — the wide tracheids expanding more than the narrow tracheids. The difference in tangential diameter, when present, is more difficult to explain. Lateral compression, due to expansion of derivatives in adjacent tiers, seems to be most likely. Some tangential shrinkage is also possible. In some instances, a radial division in the xylary initial may also occur.

Several workers have recorded the presence of axial parenchyma cells in the secondary xylem of *Ginkgo*. Some of these cells accumulate druses of calcium oxalate. Among the samples that I examined, the occurrence of parenchyma cells was rather variable and seemed to be related to the age of the sample. In young twigs parenchyma cells may not be formed for the first 3–4 years of xylem increment. Later they are formed and store starch. Parenchyma cells with druses of calcium oxalate generally do not appear until the 7th or 8th year of xylem growth.

The analysis of tiers revealed that the differentiation of parenchyma cells in the axial system is related primarily to the decline of fusiform initials. It is, of course, possible that some derivatives of growing and regular initials differentiate as parenchyma strands, but such an occurrence seems to be rare. The xylem derivatives of declining fusiform initials often become transversely divided and form strands of cells. These transverse or oblique divisions apparently occur in the xylary initials. They are more common in the declining tiers of old stems than of young, possibly because the fusiform initials, and hence the xylary initials, are much longer in the older material. Some of these cells in the declining tiers acquire pitted secondary walls like ordinary tracheary elements. Other cells remain parenchymatous.

In young twigs the xylem derivatives of declining tiers differentiate predominantly as tracheary elements, although some parenchyma cells storing starch may be formed also. In older material, some cells of declining tiers differentiate as tracheary elements, others as parenchyma cells storing starch, and still others accumulate druses of calcium oxalate (FIGS. 15, 21, 25, and 26). The cells that accumulate druses expand and become almost globular, and their differentiation is completed very close to the cambial zone (FIG. 27). The axial and the ray derivatives that are tangentially and radially adjacent to the expanding parenchyma cells become laterally displaced. Several declining tiers occur in the neighborhood of xylem rays — some segments of declining tiers may indeed be present between two axially adjacent rays (FIG. 15). In such instances it is difficult to distinguish between the ray cells and the derivatives of the declining fusiform initial and its segments in isolated tangential and radial sections; therefore it is possible to conclude that some ray cells accumulate druses. An examination of serial sections is necessary in these



FIGS. 14, 15. Tangential sections showing derivatives in declining tiers. 14, Young long shoot; successive xylem (a–b) and phloem (f–d) derivatives, cambium at c, × 195. 15, Old stem; successive xylem (a–f) and phloem (h) derivacases to determine the correct relationship between the axial and the ray elements.

The conversion of declining fusiform initials to ray initials is often accompanied by intermittent periclinal divisions toward xylem. Radial discontinuities frequently occur between the last axial and the first ray derivatives and, as a consequence, the xylem derivatives usually show a sharp and somewhat abrupt transition from an axial to a radial structure (FIGS. 10, 11). This transition is reflected in the nature of the xylem derivatives also. The last axial derivatives store starch or druses of calcium oxalate, or may even be tracheary; however, the ray derivatives seem to store starch only (FIG. 13). In some instances of extended decline of fusiform initial represented in the xylem, it is possible that some early derivatives of ray initials accumulate druses. I have not recorded this phenomenon, however.

Phloem

The secondary phloem of *Ginkgo* consists of sieve elements, parenchyma strands and fibers in the axial system and the rays (FIG. 16). Fibers were absent in the secondary phloem of short shoots examined by me (FIG. 24), but it appears from the literature that this may not be generally true (cf. Seward and Gowan, 1900; Sprecher, 1907; Gunckel and Wetmore, 1946). As noted in the literature, however, druses were abundant in the phloem-parenchyma cells of the short shoots.

The sieve elements, as in gymnosperms, are elongated prismatic cells with sieve areas confined mostly to radial walls. The sieve areas in *Ginkgo* may be elliptical, oval, or round; but they are usually broken up into numerous small pore groups (FIGS. 27, 28). Typical sieve plates are lacking and, in conformity with the accepted terminology (see Esau, 1950), the sieve elements in *Ginkgo* can only be considered as sieve cells. The sieve elements have thin walls; they lack the secondary, or nacré, wall typical of the sieve elements of Pinaceae (cf. Abbe and Crafts, 1939; Srivastava, 1962). The walls are weakly birefringent under polarized light.

As is typical for this type of cell, the mature sieve elements are enucleate. They have a thin layer of parietal cytoplasm and plastids. "Sieve element starch" that stains red with IKI is present.

The sieve elements are generally characterized by the presence of callose cylinders around the connecting strands in the sieve areas (see Esau, 1939, 1950). The material of *Ginkgo* examined by me was specially stained to detect the presence of callose. Only very small traces of callose were seen, however, even in the sieve elements close to the cambium. Most of the material was collected during periods of dormancy; the material from Cambridge was collected at a time when new leaves were just coming

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tives, cambium at g, × 95. Tracheary cells with double line, crystal cells with druses, starch-containing cells stippled, albuminous cells without nuclei, cells in cambial zone and undifferentiated cells with nuclei, ray cells in outline.

out. It is possible to assume, therefore, that in *Ginkgo* callose is present in the sieve elements only during periods of active growth, and that it disappears with the onset of dormancy. Detailed seasonal studies must be made, however, before the presence of callose can be related to the period of active growth.

Individual cells in phloem-parenchyma strands are distinguished on the basis of their contents, some contain starch, some accumulate druses of calcium oxalate, and some are specialized as albuminous cells (FIGS. 29–31). (For albuminous cells, see Strasburger, 1891, p. 55–62; Srivastava, 1962.) Some cells that store starch also accumulate tannins. These different cell types occur interspersed singly or in small chains in the same parenchyma strand. Occasional parenchyma strands may be composed of one type of cell only.

The cells that accumulate druses expand considerably. Strasburger (1891, p. 79–80) and Sprecher (1907) recorded the presence of crystal druses in some parenchyma cells of the youngest phloem, next to the cambium. I have not seen such an early deposition of druses in the phloem; although in xylem, as mentioned above, they are deposited in the youngest tissue. In the phloem of old stems that I examined the druses became evident ca. 8–10 layers of cells away from the cambium and it appeared that some starch-containing cells became modified as crystal-bearing cells.

The albuminous cells were distinguished in the present study by the lack of starch (FIG. 29) and by their collapse and crushing in the old phloem (FIGS. 27, 30). The albuminous cells, like the companion cells in angiosperms, are connected with the sieve elements by one-sided sieve areas (see Strasburger, 1891, p. 61, 65; Esau, 1939). However, as mentioned earlier, callose was not present in detectable quantity in the material of *Ginkgo* examined by me and, consequently, the sieve-area connections between the sieve elements and the albuminous cells were not very clear. The albuminous cells, like the sieve elements, have plastids and do not store starch that stains blue with IKI.

The fibers are elongated tapering elements that are flattened tangentially (FIGS. 16, 31). They usually have a very small lumen. Their thick secondary walls are distinctly lamellated and appear to be composed principally of cellulose. With phloroglucin-HCl they do not give a positive reaction for lignin (see also, Tobler, 1938). They are strongly birefringent under polarized light. Seward and Gowan (1900) mentioned that the fibers in *Ginkgo* are septate. I have not seen any evidence of transverse walls in these fibers. In tangential sections, because of their narrow radial diameter, the transverse walls of the radially adjacent parenchyma strands often appear to belong to the fibers. Also, the "slip lines" (Robinson, 1920; Frey-Wyssling, 1953), produced during sectioning, may be mistaken for transverse or oblique walls, or pore canals. A correct idea about the structure of fibers is obtained in macerations. In these preparations, cross walls are not observed; also, the pits seem to be very infrequent.

The sieve elements, parenchyma strands, and fibers are the usual derivatives of growing and regular fusiform initials. Within a tier and among neighboring tiers, the production of sieve elements, parenchyma strands and fibers is somewhat irregular; and any resemblance to the four-cyclic alternation of the tangential bands of sieve cells, parenchyma strands, sieve cells, and fibers, typical of several species of Cupressaceae and Taxaceae, is rather vague (see also, Moeller, 1882, p. 33; Strasburger, 1891, p. 77–78; Seward and Gowan, 1900).

With the decline of fusiform initials, particularly in later stages of decline, the phloem derivatives are usually strands of parenchyma cells, some of which store starch while others differentiate as albuminous cells (FIGS. 13, 14). Accumulation of druses in the derivatives of declining tiers was not observed, but it is possible. With the transition of declining fusiform initials and their segments to ray initials, the derivatives no longer differentiate as albuminous cells and only starch-containing cells are produced. But since the decline of fusiform initials and their conversion to ray initials is a continuous process, albuminous cells often appear among the earliest derivatives of ray initials; and in isolated tangential sections these albuminous cells may be interpreted as parts of rays.

DISCUSSION

The results obtained in the present survey indicate that the cambial phenomena in *Ginkgo*, that is, the planes of anticlinal divisions in fusiform initials, the growth and decline of fusiform initials, and the formation of new ray initials, are similar to those recorded in conifers (see Bailey, 1923; Bannan, 1953, 1957; Srivastava, 1962). Minor differences of a quantitative nature may perhaps be present. Thus, it is possible that the relative frequency of anticlinal divisions in a lineal series per unit of xylem (or phloem) increment is more in conifers than in *Ginkgo*. It is important here to discuss the role of anticlinal divisions in an increase in the girth of cambium.

As Bailey (1923) has mentioned, the multiplicative anticlinal divisions in fusiform initials are only one, among several, means by which the cambium is accommodated to the increasing girth of wood cylinder. Other means include an increase in length and tangential diameter of the fusiform initials and an increase in the number and tangential diameter of the ray initials. From the data presented by Bailey (1917, 1920b, 1923), Bannan (1960b), and in this paper, it seems reasonable to infer that in young stems of conifers and *Ginkgo* all the above-mentioned factors are operative in effecting an increase in the girth of the cambium. In old stems, however, the increase in length and tangential diameter of the fusiform initials and increase in the tangential diameter of the ray initials play only an insignificant role; the increase in the girth of cambium is effected primarily by an increase in the number of fusiform and ray initials. To achieve this increase in the number of fusiform and ray initials, anticlinal divisions are necessary.

The work of Bannan (1950) and Whalley (1950) on conifer cambia has shown that the number of anticlinal divisions in fusiform initials far exceeds the number actually required to accommodate the cambium to increasing diameter of the wood cylinder, and is accompanied by the loss of a large number of new initials. Thus, it is only a very small percentage of anticlinal divisions that is directly involved in increasing the girth of the cambial cylinder. It is of interest in this connection to recall that Priestley (1930) calculated from the data given by Bailey (1920b) that individual fusiform initials needed to divide anticlinally only once every fifteen years to accommodate the cambium to the increasing diameter of wood cylinder. These calculations have only a theoretical significance. However, they do emphasize that a high frequency of anticlinal divisions, as is seen in the conifer cambia, is not really essential for adjusting the cambium to the increasing circumference of wood cylinder. It is conceivable, therefore, that quantitative differences in the frequency of anticlinal divisions in fusiform initials may exist between the cambia of different plants. But large quantities of comparable material must be examined before such differences, if they are present, would be revealed.

Since the anticlinal divisions in fusiform initials of conifer cambia occur at a frequency far greater than is actually required, one wonders at the possible significance they might have, besides the fact that they result in an increase in the number of cambial initials. Bannan (1960a, b) has discounted the possibility that the frequency of anticlinal divisions may be directly related to the growth rate of the stem or to the length of the fusiform initials. He has concluded that the frequency of anticlinal divisions in fusiform initials apparently is geared neither to the circumferential expansion nor to the number of periclinal divisions in the cambium, but rather seems to be related to linear radial increment as determined by periclinal divisions both in cambial and xylary initials. It is possible to consider in this connection a role of anticlinal divisions that has not been mentioned so far. The anticlinal divisions confer upon the cambium a greater degree of plasticity than is possible with periclinal divisions (symmetric and asymmetric) and intrusive apical elongation only. Frequent anticlinal divisions and the loss of large portions of the new initials are phenomena of great significance in the mutual adjustments of the cambial initials and their derivatives. They are also of significance in adjusting the cambium to changes in the growth conditions of a plant. This increased degree of plasticity attained as a result of anticlinal divisions in the fusiform initials may have had a survival value in the course of evolution.

In the literature on the cambia of gymnosperms, new ray initials are reported to be formed by cutting off of large or small segments from the fusiform initials[4] (Velten, 1875; Schmidt, 1889; Klinken, 1914; Bailey, 1920a; Barghoorn, 1940; Braun, 1955). The divisions that separate these new ray initials may be radial, transverse, or of various degrees of

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[4] New ray initials are also formed by transverse, or anticlinal, divisions in existing ray initials.

obliquity and may occur near the middle or near one end of the fusiform initial. The ontogenetic work of Bannan and his associates (Bannan, 1950, 1953; Bannan and Bayly, 1956) and myself (Srivastava, 1962) has clarified the details of this process. As has been mentioned earlier, several fusiform initials are lost entirely, or in part, from the cambial zone. This loss, or decline, of fusiform initials is frequently brought about by a combination of asymmetric periclinal divisions and transverse segmentation. As a result, small segments of the original fusiform initial are left in the cambial zone and act as new ray initials. Ray initials are also formed by radial divisions in the fusiform initials — the shorter cells frequently persisting in the cambium as new ray initials.

These observations on the conifer cambia have been further substantiated in the present study. A few points may be emphasized briefly, however. In several instances of decline, the stages in the conversion of fusiform initials and their segments to ray initials are better represented in the phloem than in the xylem (Figs. 8, 9, and 14). Also, occasionally, the first derivatives of new ray initials are produced only toward phloem (Figs. 6, 7, and 8). Comparable literature, relating the extent of declining tiers in the xylem with that in the phloem, is lacking. But from the data presented here and my limited observations in the Pinaceae (Srivastava, 1962), it appears that during the transition of several fusiform initials and their segments to ray initials, periclinal divisions occur predominantly toward phloem and intermittently toward xylem. As a result, radial discontinuities appear in the xylem not only among the derivatives in the declining tier (Fig. 10) but also between the last axial derivatives of the declining fusiform initials and the first radial derivatives of the new ray initials (Fig. 11). These phenomena would explain the somewhat abrupt beginning of rays described by Bannan (1934) in the secondary xylem of *Ginkgo*.

The general resemblance of the secondary xylem and phloem in the long shoots of *Ginkgo* to those of conifers is obvious. There are some striking differences, however. These differences include the presence of narrow tracheids and crystal-bearing parenchyma cells in the xylem and cellulose fibers and crystal druses in the phloem. It must be pointed out in this connection that the presence of crystal druses in phloem and the manoxylic structure of the short shoots of *Ginkgo* are features shared by the cycads (see Mettenius, 1861; Strasburger, 1891, p. 154; Seward and Gowan, 1900).

In their cross sectional diameter and the thickness of their secondary walls the narrow tracheids in the spring wood resemble the summer wood tracheids. But, unlike the latter, the narrow tracheids generally have pits only on those areas of their walls that are in contact with the cells of xylem rays. A rough analogy with the fibers in the angiosperm woods would not be out of place; however, these tracheids have bordered pits on their walls, they also do not show any special intrusive apical elongation during their differentiation. As mentioned earlier, the narrow and the wide tracheids within a tier may show some apical elongation during their differentiation, but, on the whole, their length corresponds to the length of the fusiform initial of the tier and there does not seem to be any correlation between the degree of apical elongation and the nature of the tracheid. It has been indicated by Bailey (1920b) that fluctuations in the length of tracheids in a tier may occur within a growth increment and from one growth increment to another. These fluctuations may be related to varying degrees of apical elongation of individual tracheids during their differentiation.

The indefinite arrangement of tracheids in radial files and occasional presence of groups of small tracheids interspersed among larger tracheids (FIG. 21) seem to be features typical of *Ginkgo* wood. The study of tiers reveals that these features have their basis in a combination of several factors — the presence of narrow tracheids interspersed among wide tracheids in the same tier, occasional radial divisions in the xylary initials and the differentiation of derivatives as narrow tracheids, presence of narrow tracheids in tangentially adjacent tiers, differential intrusive growth of the tips of the derivatives in a tier, and differential expansion of the wide tracheids during their maturation.

It has been shown in the present study that the axial parenchyma in the xylem of *Ginkgo* is formed with the decline of fusiform initials. The radial files of parenchyma cells are only the declining tiers in xylem and their appearance as radial plates of cells depends on the duration of time through which a fusiform initial declines and divides periclinally toward xylem. The declining tiers have no particular spatial relationship with the rays, as Tupper (1911) thought; parts of these tiers may be in contact with existing rays, other parts may not be so connected. Tupper's (1911) observation that the crystal-containing cells are modified parenchyma cells is acceptable, if one bears in mind that the differentiation of these cells is completed very close to the cambium. The lateral expansion of the crystal-containing parenchyma cells would be possible only in the plastic zone of differentiating tracheids, not in the mature wood.

A detailed study of the bark, including the cytology of sieve elements and albuminous cells, changes in the old phloem, seasonal changes, and the structure of the periderm was beyond the scope of the present work. Emphasis was placed upon the origin and the interrelationships of the phloem elements as they are derived from the cambial initials. These have been described in detail elsewhere in this paper. In the following paragraphs, therefore, only a few points concerning the declining tiers and the rays in the phloem of *Ginkgo* and Pinaceae are mentioned briefly.

Although the decline of fusiform initials and their conversion to ray initials is often well represented in the phloem of *Ginkgo*, it does not seem to be as extended as in the phloem of Pinaceae. As a result, the "radial plates of cells," described in the literature and later interpreted as the declining tiers in phloem (see Srivastava, 1962), are usually not as clearly marked in the phloem of *Ginkgo* as they are in the phloem of Pinaceae. However, such radial plates do occur and their derivatives, as in Pinaceae, include starch-containing and albuminous cells (FIG. 13).

It was shown in the Pinaceae (Srivastava, 1962) that the differentiation of albuminous and starch-containing cells is rather irregular among the early derivatives of new ray initials; but as the ray initials become well established, the derivatives of marginal initials differentiate preferentially as albuminous cells, while those of submarginal initials differentiate as starch-containing cells. With addition of new initials at the margins of existing rays, the derivatives of initials that now become submarginal start to differentiate as starch-containing cells. In *Ginkgo* the derivatives of ray initials as a rule do not include albuminous cells. The derivatives of marginal and submarginal initials differentiate as starch-containing cells only. It appears that in *Ginkgo*, in comparison to Pinaceae, not only is the decline of fusiform initials and their conversion to ray initials more abrupt, but the change from a production of albuminous cells to starch-containing cells is rather abrupt also.

A discussion of the inappropriate term *albuminous cell* has already been given and is not repeated (see Srivastava, 1962).

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EXPLANATION OF PLATES

The following symbols have been used consistently in all the plates: a, albuminous cell; c, cambial zone; cc, crystal cell; dt, declining tier; f, phloem fiber; nt, narrow tracheid; r, ray; s, sieve element; sc, starch-containing cell; sw, summer wood; wt, wide tracheid.

PLATE I

Figs. 16–19. Transverse and tangential views of xylem, cambium and phloem. 16, Transverse section of old stem (Boston, 1961), × 70. 17, Transverse section of xylem of old stem (Boston, 1961) stained with phloroglucin–HCl and mounted in glycerine. Pith toward the bottom of the plate, × 115. 18, Tangential section of xylem of a young long shoot (Boston, 1961) showing transverse wall in a summer wood tracheid, × 390. 19, Radial section of xylem of old stem (A [wood coll.] 11353), × 190.

PLATE II

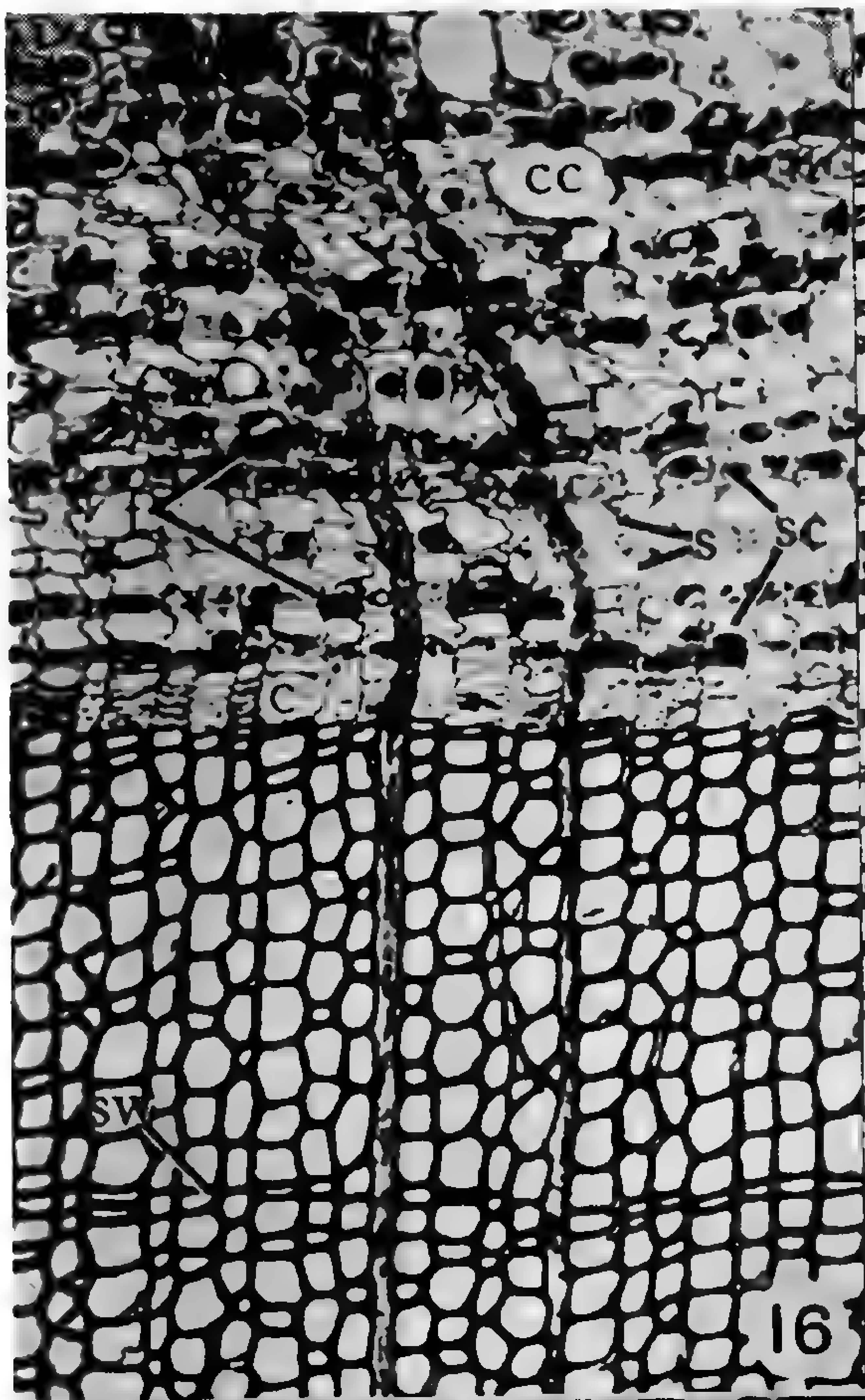
Figs. 20–23. Xylem of old and young stems. 20, A radial file of tracheids isolated during maceration from an old stem (Boston, 1961). A variable number of narrow tracheids alternate with a varying number of wide tracheids, × 115. 21, Transverse section of xylem of old stem (A [wood coll.] 10138) showing a declining tier and narrow tracheids interspersed among wide tracheids; pith toward the bottom of the plate, × 80. 22, Transverse section of xylem of a young long shoot (A [wood coll.] 12048); pith toward the bottom of the plate, × 80. 23, Transverse section of a young long shoot (Boston, 1961), × 115.

PLATE III

Figs. 24–27. Transverse, tangential, and radial sections of xylem and phloem. 24, Transverse section of a short shoot (Boston, 1961), × 115. 25, Radial section of xylem of an old stem (Boston, 1961, Regaud's fixative) stained with IKI and mounted in glycerine. The section shows axial xylem parenchyma with crystal and starch-containing cells, × 85. 26, Tangential section of xylem of an old stem (Boston, 1961, Regaud's fixative) stained with Regaud's hematoxylin and showing axial parenchyma with crystal and starch-containing cells, × 70. 27, Radial section of latest xylem, cambium and phloem of an old stem (Boston, 1961, Regaud's fixative) stained with IKI and mounted in glycerine. Axial file of xylem-parenchyma cells containing druses of calcium oxalate and starch are seen next to the cambium. In the phloem, sieve elements and parenchyma strands with starch-containing cells and albuminous cells are seen, × 190.

PLATE IV

FIGS. 28–31. Radial and tangential sections of phloem of old stem. 28, Radial section (Boston, 1961, Regaud's fixative) stained with Hotchkiss method (see Glick, 1949, p. 44) showing sieve areas, × 780. 29, Tangential section of phloem close to the cambium (Boston, 1961, Regaud's fixative) stained with aniline blue and mounted in glycerine. The section shows albuminous cells and starch-containing cells in parenchyma strands, × 190. 30, Tangential section of old phloem (Boston, 1961, Regaud's fixative) stained with IKI and mounted in glycerine. Albuminous cells appear empty and some are collapsed; the starch-containing cells remain alive, × 190. 31, Tangential section of old phloem (Boston, 1961) showing phloem fibers and parenchyma strands, some cells of which contain druses of calcium oxalate, × 70.



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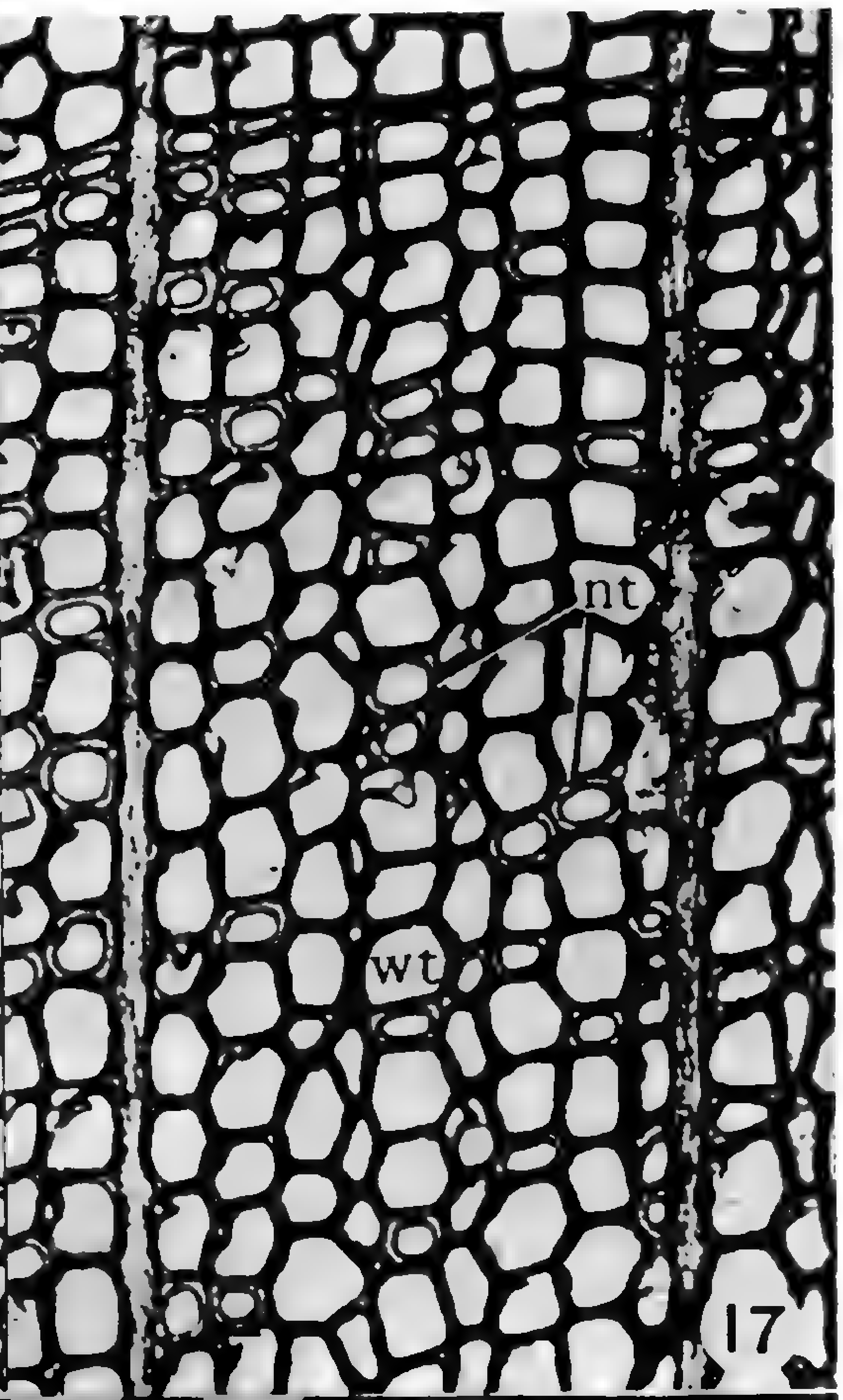

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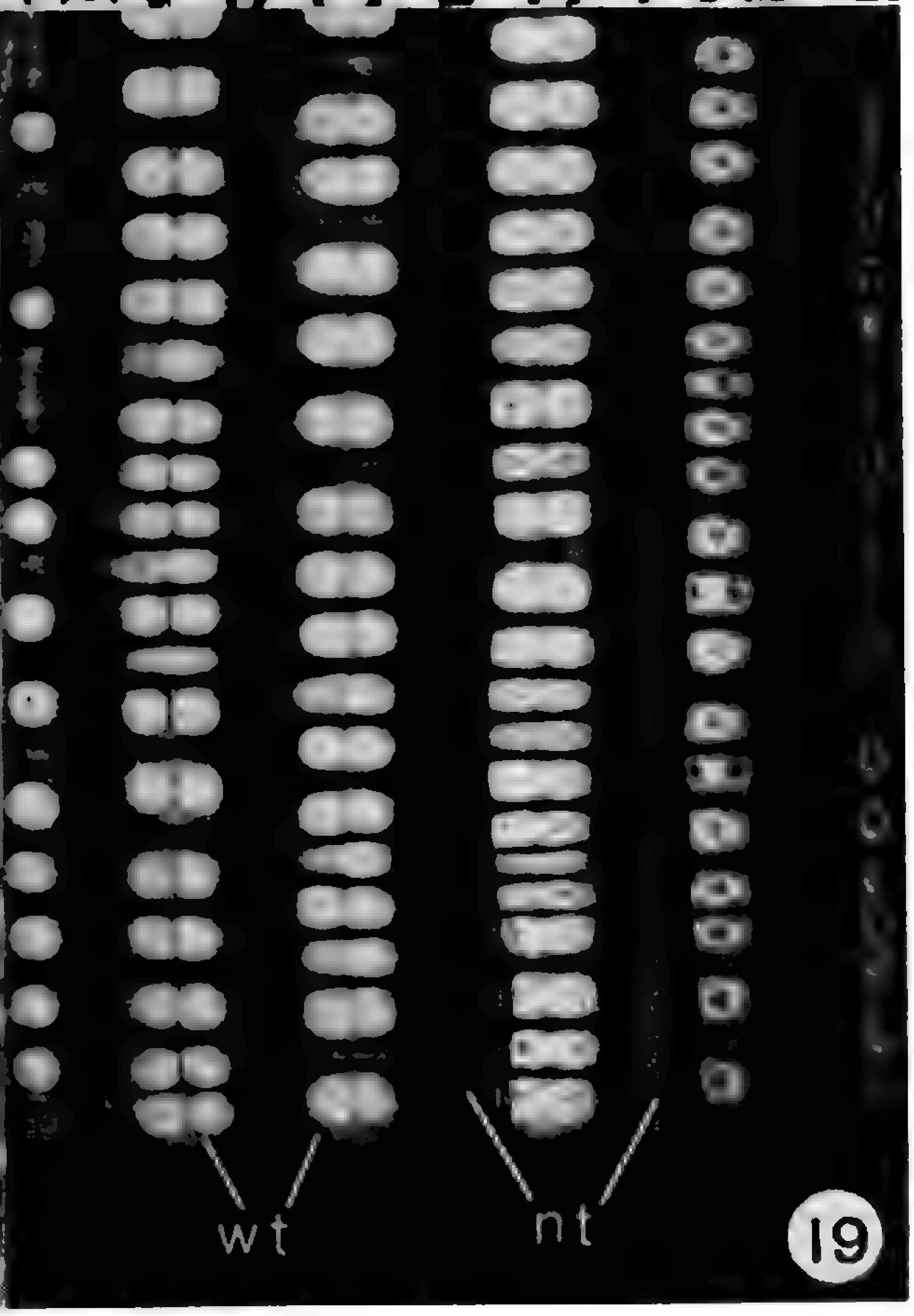

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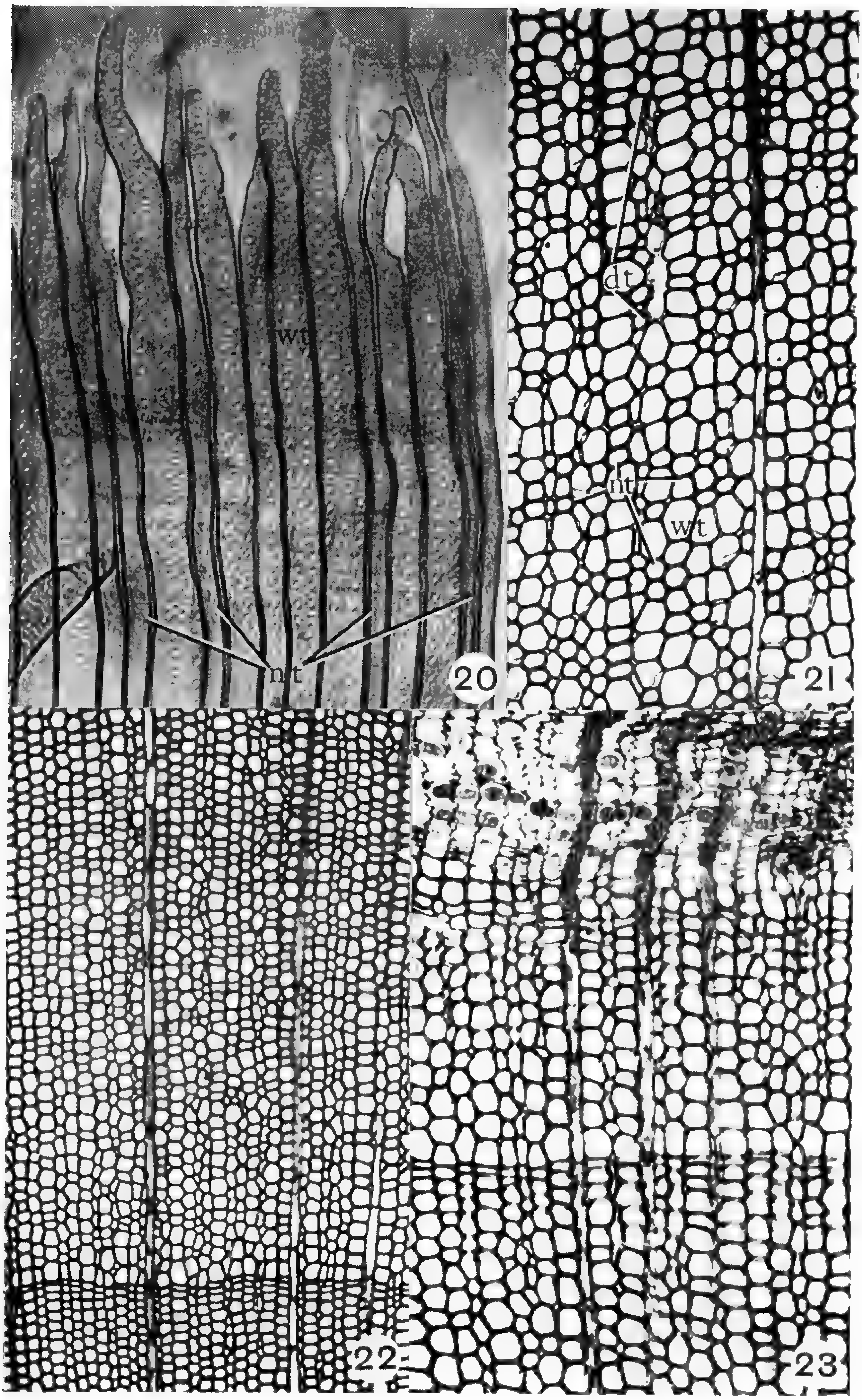
SRIVASTAVA, GINKGO BILOBA



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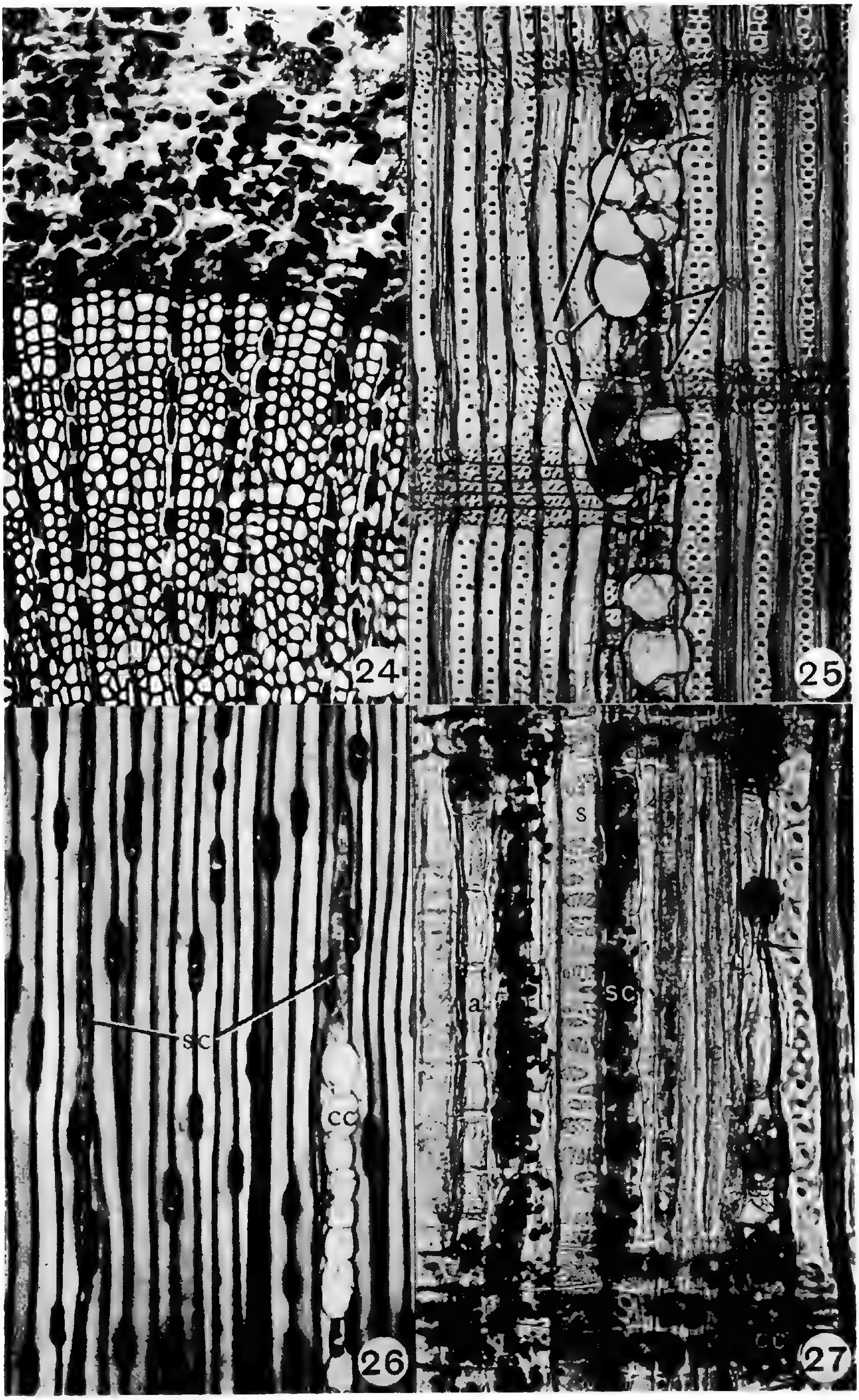

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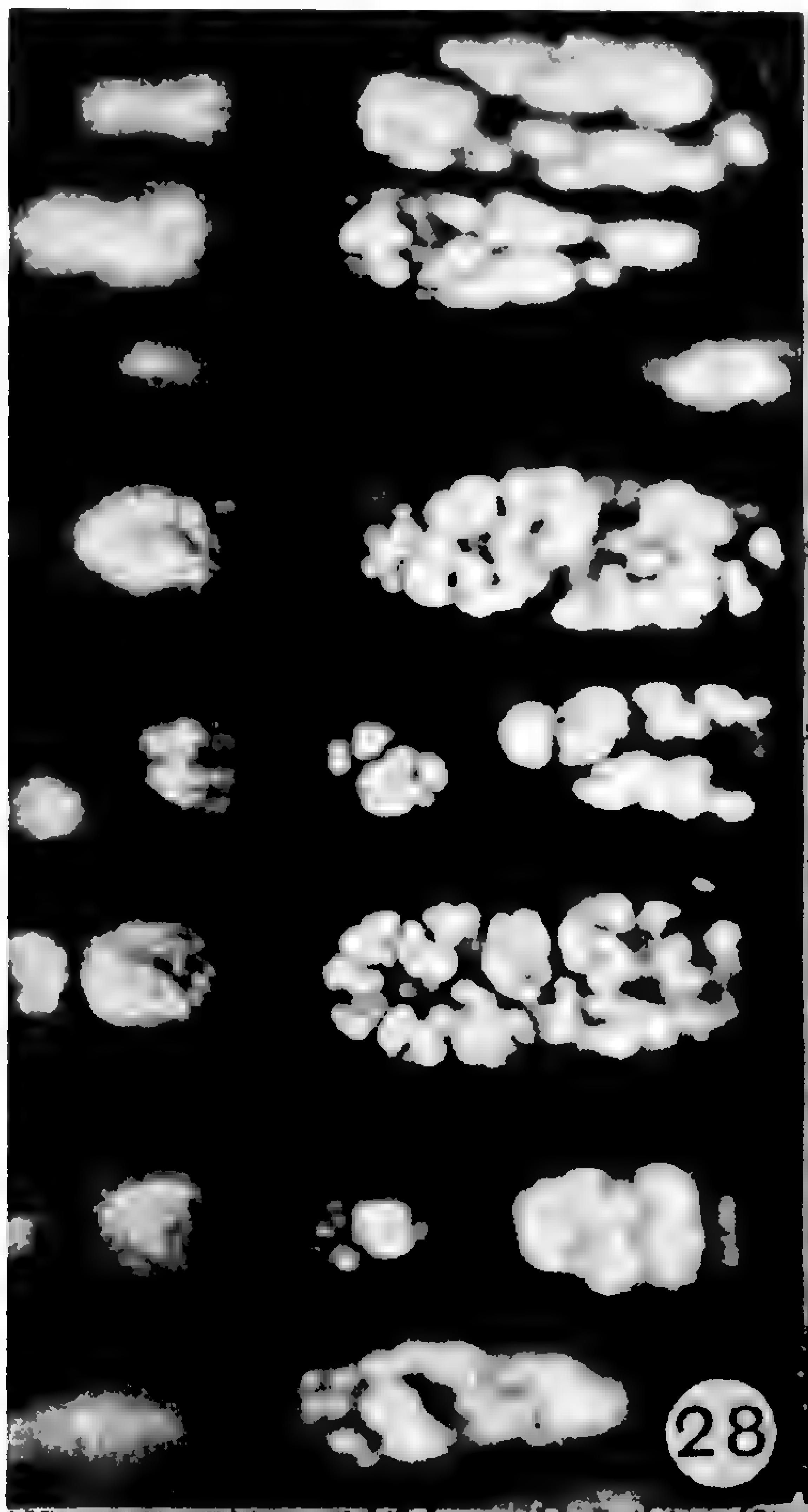

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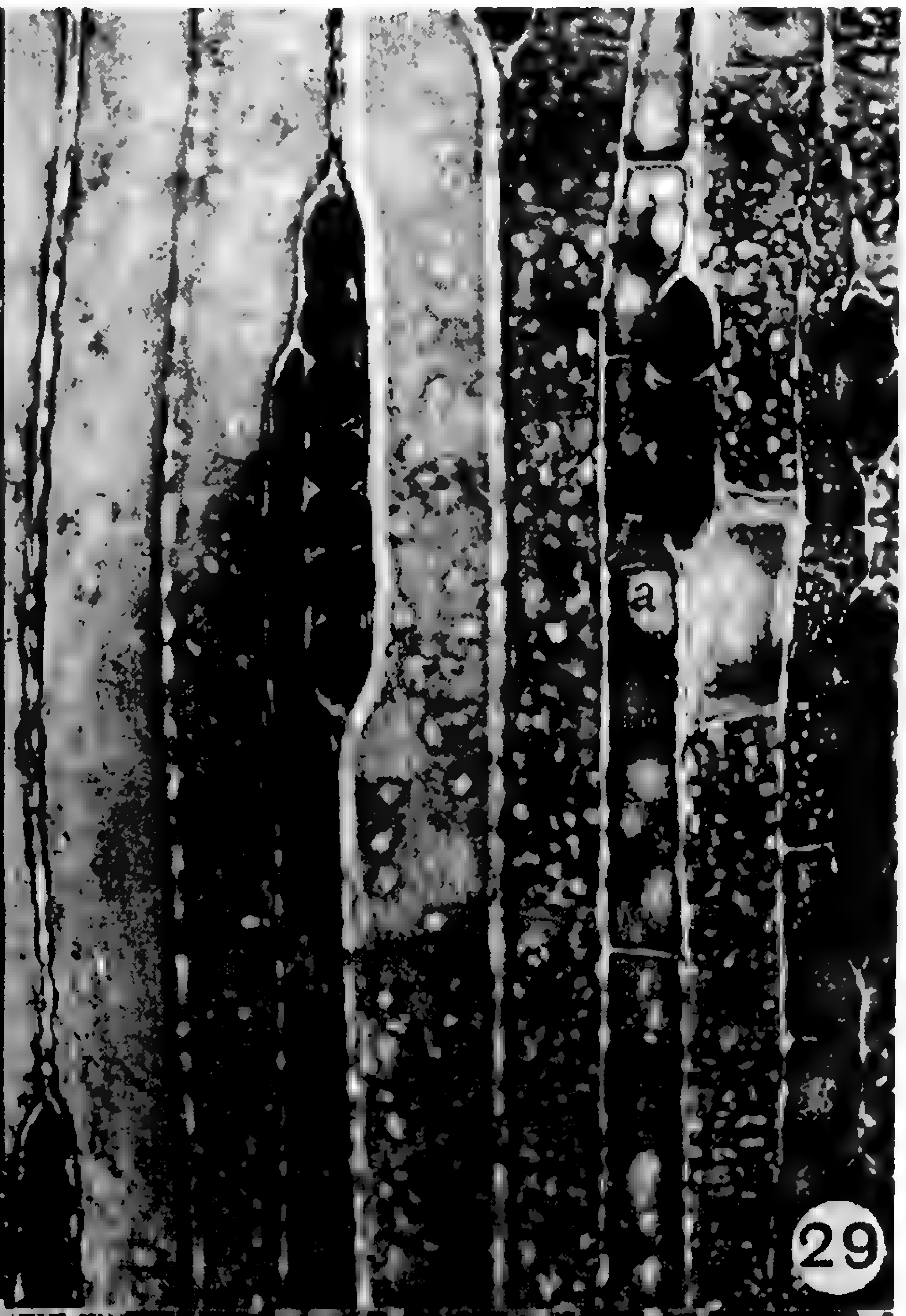

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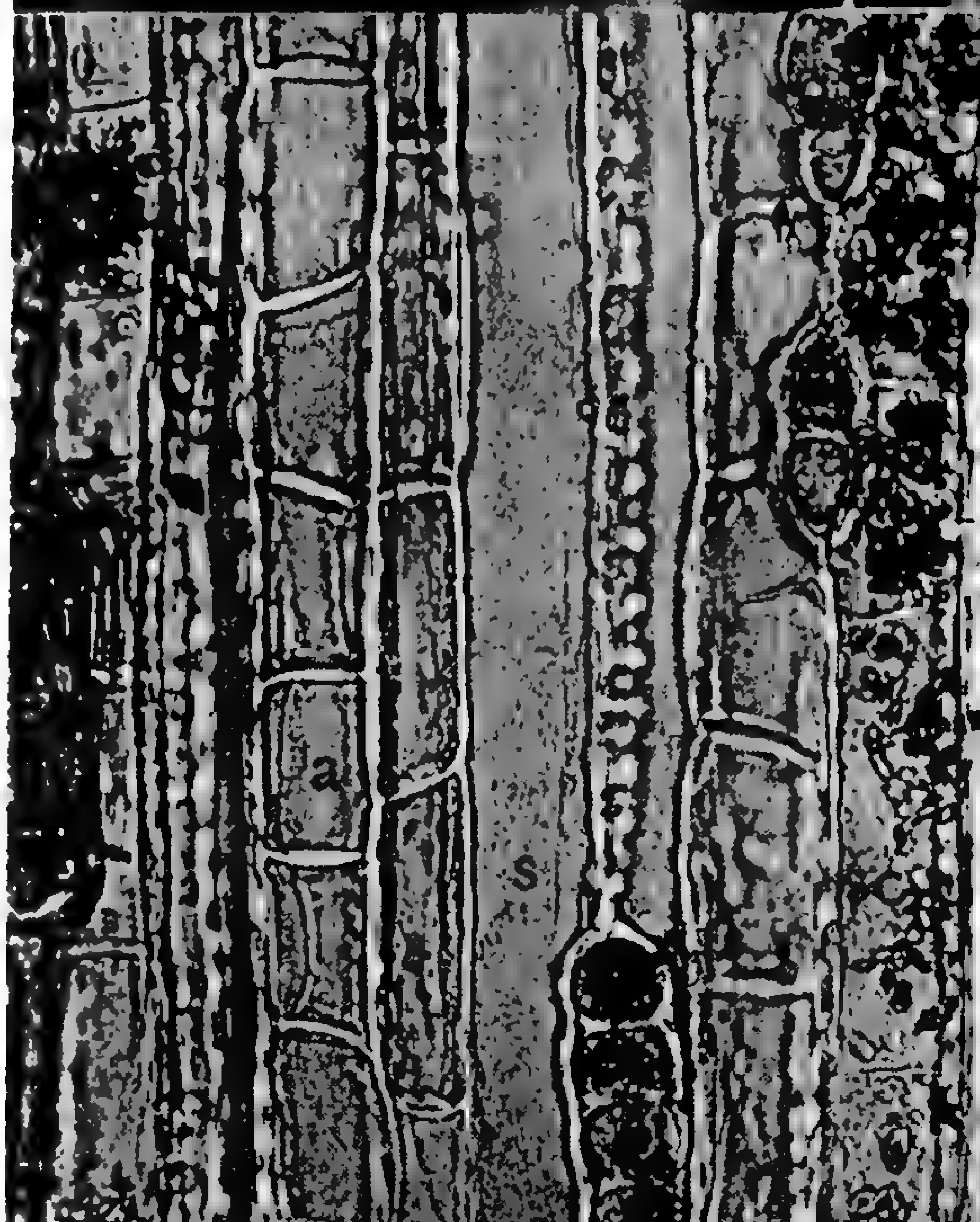

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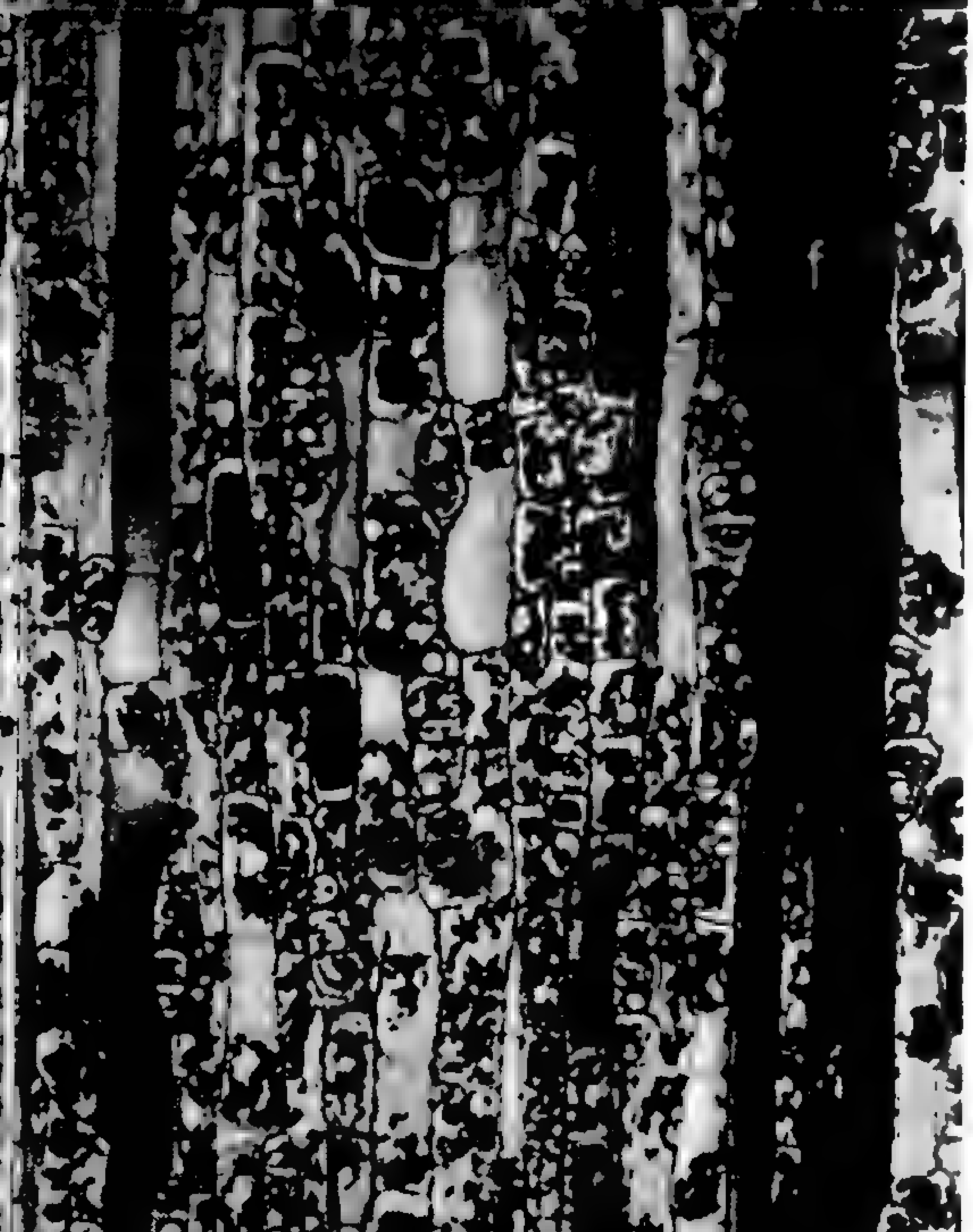

31

SRIVASTAVA, GINKGO BILOBA

THE GENERA OF HAMAMELIDACEAE AND PLATANACEAE IN THE SOUTHEASTERN UNITED STATES[1]

WALLACE R. ERNST

HAMAMELIDACEAE R. Brown in Abel, Narr. Journ. China 374. 1818, "Hamamelideae," nom. cons.

(WITCH-HAZEL FAMILY)

Deciduous [or evergreen], ± pubescent trees or shrubs. Leaves simple, usually with deciduous stipules [or stipules fused or rarely absent], petiolate, alternate [or opposite], pinnately (or palmately) veined [sometimes dimorphic]; stomata abaxial, paracytic. Hairs usually nonglandular, stellate or tufted, the individual members unicellular (or hairs simple). Inflorescences bracteate, axillary or terminal, ± capitate or spicate (or ± racemose). Flowers ± regular, subhypogynous to subepigynous, bisexual or unisexual (the plants then monoecious [rarely dioecious]); perianth 4(5)-merous, cyclic, 1- or 2-seriate, often reduced or ± absent. Calyx apparently united, 4- or 5(7)-lobed, usually persistent and ± adnate to the fruit or ± absent [or sepals connate or circumscissile]. Corolla apopetalous or absent. Stamens 4, alternipetalous, with alternating staminodia, or many and indefinite; [connective often conspicuous;] anthers usually basifixed, with 2 or 4 pollen sacs, becoming 2-locular at anthesis; dehiscence longitudinal by a simple slit, or by 1 or 2 vertical valves; pollen mostly 3-colpate (or polyporate). Gynoecium ± syncarpous, usually 2-carpellate; stigmas terminal or introrsely decurrent; styles free, usually spreading; ovary 2-locular, usually somewhat embedded in the receptacle [to inferior]; placentation ± axile; ovules 1 (2) in each locule and apical (or many), anatropous, pendent, 2-integumented, the micropyle upward. Fruits partly inferior or somewhat inclosed by the calyx, with leathery exocarp and bony endocarp, often appearing to separate apically into 4 persistent valves; dehiscence loculicidal, the fruits 2-seeded (or septicidal

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[1] Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium, made possible through the support of the National Science Foundation and George R. Cooley, and under the direction of Reed C. Rollins and Carroll E. Wood, Jr. This treatment follows the style established in the first paper of the series, Jour. Arnold Arb. **39**: 296–346. 1958 (and continued through volume 44). The area covered, as in earlier treatments, is bounded by and includes North Carolina, Tennessee, Arkansas, and Louisiana. The descriptions apply primarily to the plants of this area with supplementary information in brackets. References not seen by the author are marked with an asterisk. The illustrations were prepared by Mrs. Dorothy H. Marsh under the direction of Dr. George K. Brizicky; the manuscript was prepared by Mrs. Gordon W. Dillon. Helpful information on *Hamamelis* in Texas was provided by Dr. Lloyd H. Shinners. New cytological information on *Fothergilla* was supplied by Dr. Joab L. Thomas. Generous assistance from both Dr. Brizicky and Dr. Wood is gratefully acknowledged.

with most of the many seeds per locule aborted). Seeds oblong, lustrous, hard, often with a pale region merging with the apical hilum and decurrent on 2 sides (or seeds winged and the hilum lateral); embryo straight; endosperm present. (Including Altingiaceae Lindley.) TYPE GENUS: *Hamamelis* L.

About 23 genera and 100 species, concentrated in China, absent from western North America, the West Indies, South America, Polynesia, and Europe. Perhaps 13 genera are monotypic; about five are native to the New World. Several taxa are widely represented in northern fossil deposits.

Among the unifying landmarks of Hamamelidaceae are pinnately veined leaves, bicarpellate, ± bilocular, usually 2-seeded, loculicidal fruits with leathery exocarp, bony endocarp, lustrous seeds with characteristic apical marking associated with the hilum, and predominantly tricolpate pollen (cf. *Liquidambar*). Also characteristic of the family, and of interest morphologically, are the diversity of staminal structure and the often intermediate conditions of capitate, spicate, or somewhat catkin-like inflorescences; of reduction of perianth; of suppression of one sex (polygamy); and of epigyny, perigyny, and subhypogyny.

Placing primary emphasis on the number of ovules per locule, Niedenzu divided Hamamelidaceae into subfam. Bucklandioideae Niedz. (including *Liquidambar*) and subfam. Hamamelidoideae, both with two tribes. In the latter, tribe Hamamelideae, with short staminal filaments and capitate inflorescences, was separated from Parrotieae Gardn. (including *Fothergilla*), with spikelike inflorescences and long staminal filaments. Later, Harms recognized five subfamilies, among them Liquidambaroideae and Hamamelidoideae, the latter comprised of five tribes, including Hamamelideae and the apetalous Fothergilleae DC. In either system, the bulk of the taxa is referred to Hamamelidoideae. (See Gardner for an additional taxonomic scheme.)

In contrast to the apparently reduced floral morphology of many Hamamelidaceae, the tracheary structure is relatively unspecialized, the vessels having exclusively scalariform perforation plates. On the one hand, anatomical affinities are with some Magnoliales, and, on the other, with Casuarinales, Fagales, and Urticales (Tippo). Hamamelidaceae are similar to, but structurally more primitive than, Buxaceae, Platanaceae (*q.v.*), and Urticaceae. Anatomically, Rosales, from which Hamamelidaceae sometimes are considered derived, are more advanced. (For more details see Tippo and Tang.)

Chromosome numbers of $2n = 24, 30, 32, 48$, and 72 have been reported.

Several arborescent species provide useful timber; a fragrant exudate, styrax, is obtained from *Liquidambar* and *Altingia*; an extract of bark and leaves of *Hamamelis virginiana* is the source of witch-hazel. Handsome representatives of several genera are cultivated and often are valued for their vivid autumn coloration.

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KEY TO THE GENERA OF HAMAMELIDACEAE

General characters: *shrubs or trees with simple, alternate, deciduous leaves; flowers clustered, various, ± regular, subhypogynous to subepigynous, unisexual or bisexual; perianth ± reduced; ovary 2-carpellate, ± 2-locular with ± axile placentation; ovules pendent with micropyle upward; fruits with bony endocarp ± half inferior, loculicidal and 2-seeded (or septicidal, the fertile seeds winged).*

A. Leaves pinnately veined; flowers usually bisexual; ovules 1 per locule; fruits loculicidal, often appearing 4-valved, seeds not winged; usually shrubs.
  B. Inflorescences axillary, capitate, 1–5-flowered; petals yellow to red; stamens 4; fruits maturing in the fall. .... 1. *Hamamelis*.
  B. Inflorescences terminal, spicate, many flowered; petals absent; stamens many, the filaments white and conspicuous; fruits maturing in the summer, the inflorescence soon deciduous. .... 2. *Fothergilla*.
A. Leaves palmately veined and lobed; flowers mostly unisexual, in separate

inflorescences; perianth obsolete; ovules many per locule; fruits septicidal; fertile seeds few and winged; forest trees. .... 3. *Liquidambar.*

Subfam. HAMAMELIDOIDEAE

Tribe HAMAMELIDEAE

1. **Hamamelis** Linnaeus, Sp. Pl. 1: 124. 1753; Gen. Pl. ed. 5. 59. 1754.

Shrubs (or trees); leaves pinnately veined, ± unequal at the base. Inflorescences ± axillary, ± capitate, pedunculate, with a few bracteoles, usually of 3 (1–5) flowers. Flowers bisexual (or functionally unisexual, the plants then polygamous). Calyx deeply 4(5)-parted. Petals 4 (5), ligulate, with circinate vernation, yellow to dark red. Fertile stamens 4, alternipetalous, included; anthers introrse, 2-locular at anthesis, dehiscing by 2 valves hinged adaxially at the connective; pollen 3-colpate; staminodia 4, short, antipetalous. Ovary ± slightly recessed in the receptacle, 2-locular below, deeply 2-parted above into 2 styles; ovules pendent from the apex of the locule, 1 (2) in each locule. Fruits maturing in the fall, ± woody, partly inferior, fused ± to the middle with the persistent tubular calyx. Seeds usually 1 per locule, oblong, lustrous, forcibly discharged after dehiscence; hilum apical and surrounded by a pale area decurrent on 2 sides. TYPE SPECIES: *H. virginiana* L. (Ancient Greek name for a plant with apple-like fruits; perhaps derived from *hama*, together, and *melon*, fruit.) — WITCH-HAZEL.

Perhaps six species of temperate eastern Asia and eastern North America; in our area widely distributed.

Hamamelis virginiana, $2n = 24$, distributed from Florida to Texas, northward to Ontario and Nova Scotia, tends to flower on the autumn side of winter, often as the leaves are falling (sometimes as late as December), has only weakly fragrant flowers with long yellow petals, and usually grows in a woodland habitat. Fertilization of the ovules occurs five to seven months after pollination (Shoemaker); the fruits mature during the next blooming season. The var. *macrophylla* (Pursh) Nutt. (*H. macrophylla* Pursh), of uncertain status (see Sargent, 1920), the leaves smaller and with tuberculate surface, flowering from December through February, has been reported to a height of 15 m. and nearly a foot in diameter. The vars. *angustifolia* Nieuwl., *orbiculata* Nieuwl., and *parvifolia* Nutt. (f. *parvifolia* (Nutt.) Fernald) are based on characteristics of the leaves; f. *rubescens* Rehder has light-red petals. Resembling *H. virginiana* is the little-known *H. mexicana* Standl., of Nuevo León, Mexico, which has yellow petals and apparently blooms in July.

Of more limited distribution, *Hamamelis vernalis* Sarg., $2n = 24$, is restricted, perhaps ecologically, to the Ozark Region in an area extending from southeastern Missouri through Arkansas to southeastern Oklahoma. It tends to be a lower, stoloniferous, thicket-forming shrub of gravelly margins of streams that blooms on the spring side of winter and has fragrant flowers with shorter petals. The fruits mature in the first summer

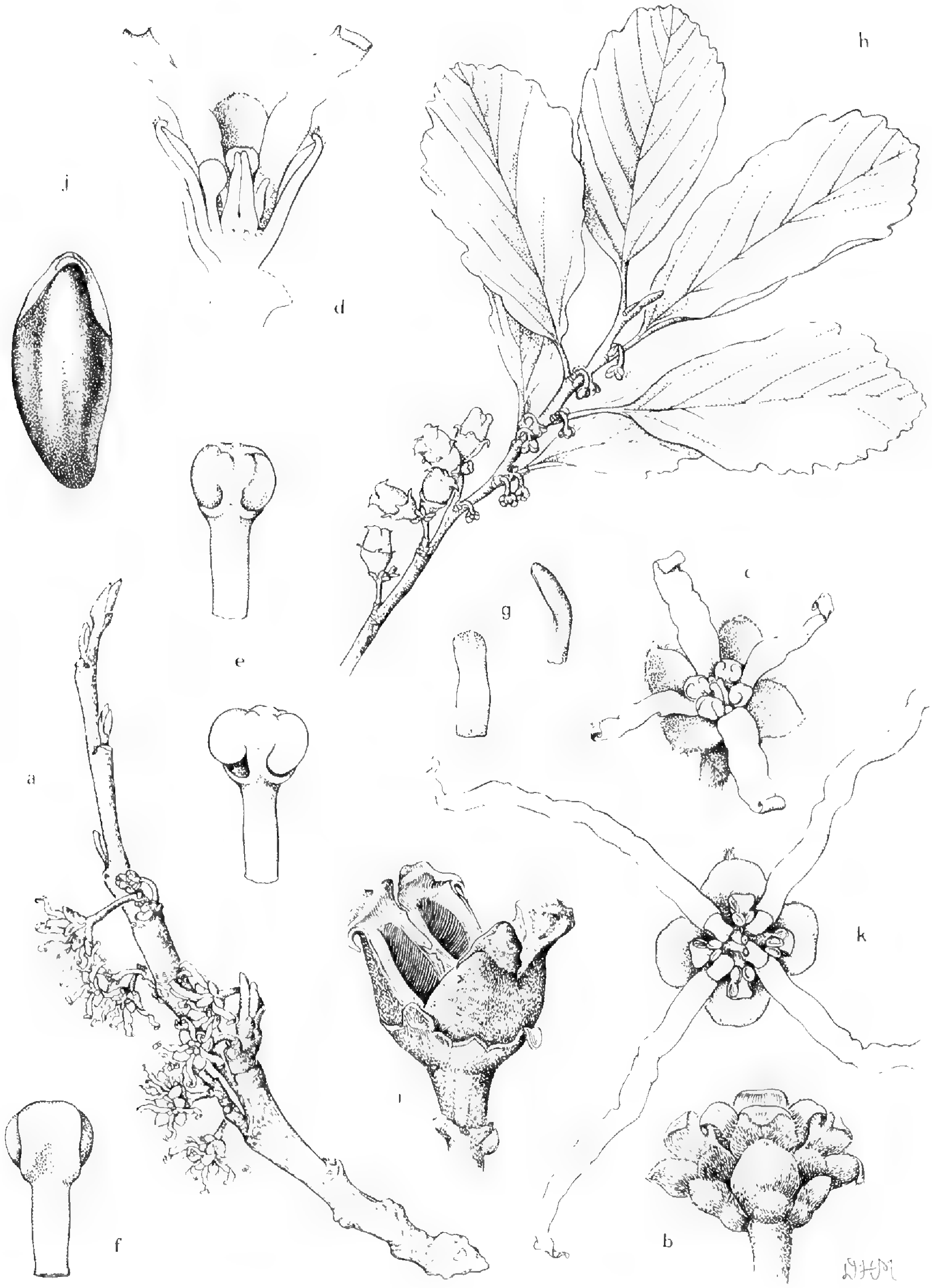

FIG. 1. **Hamamelis.** a–j, *H. vernalis*: a, vernal branch, with flowers, × 1; b, inflorescence of three flowers, petals removed to show involucre-like bracts and sepals, × 4; c, flower at anthesis, the anthers closed, × 4; d, flower in vertical section, stamen at right removed to show staminodium opposite petal, × 5; e, two stamens, showing valves and dehiscence, × 14; f, stamen, showing connective, × 14; g, two views of staminodia, × 14; h, autumnal branch, with ripening fruits and nodding inflorescences with flower buds, × ½; i, loculicidally dehiscent fruit, seeds discharged, × 2; j, seed — note apical characteristics, × 4. k, *H. virginiana*: flower — note petal proportions, staminodia opposite petals, and open anthers, × 5.

or autumn. The lower surface of the leaves tends to be glaucous-pubescent and the calyx red within, but the species is variable in most respects. Plants with pure yellow petals and plants with red petals (nearly every bush having its own petal hue) may grow side by side; the color patterns are constant in cultivation (Anderson, 1933). The leaves persist into winter, the fragrance of the flowers is diminished by low temperatures, and the petals recoil on cold days (Anderson, 1934). Forma *tomentella* Rehd. (var. *tomentella* (Rehd.) E. J. Palmer) is especially pubescent; f. *carnea* Rehd. has dark red petals.

In Missouri, the habitats of *Hamamelis vernalis* (flowering in February) and *H. virginiana* (flowering in November) overlap, but interspecific crossing apparently is precluded by the disparate periods of anthesis (Steyermark, 1934). *Hamamelis vernalis* shows a high degree of intraregional variability, but interregionally, *H. virginiana* perhaps is as variable (Anderson, 1933). The interrelationship of these species requires further study.[2]

The native variability of *Hamamelis* not withstanding, speciation apparently has affected primarily blooming season and petal length and color; determination of strictly vegetative material is often difficult. Our species usually have yellow autumnal leaves, while the species of Asia, all spring flowering, sometimes have reddish or orange leaves in autumn. *Hamamelis* × *intermedia* Rehd. originated in cultivation, presumably as a hybrid between *H. japonica* Sieb. & Zucc., of Japan, and *H. mollis* Oliv., of central China. The genus is valued in horticulture for its unusual blooming season. Some branchlets have close, distichous nodes and appear zigzag.

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[2] Sargent (Trees & Shrubs **2:** 137, 138. *pl. 156.* 1911) gives the petal color of *Hamamelis vernalis* as light yellow and shows a flowering twig that could pass for *H. virginiana.* The most distinctive element of this complex, however, appears to be *H. vernalis* f. *carnea,* which has red petals. The nomenclatural type of *H. vernalis,* viz., f. *vernalis,* may be an intermediate of some kind between the distinctive f. *carnea* and *H. virginiana.* This points out a conflict between the biological and nomenclatural aspects of our taxonomic method which perhaps is accountable for some of the apparent confusion in the identity of these two species.

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Tribe FOTHERGILLEAE DC.

2. **Fothergilla** Murray, Linn. Syst. Veg. ed. 13. 418. 1774.

Shrubs; leaves pinnately veined, ± unequal at the base. Inflorescences erect, ± terminal, many flowered, racemose, deciduous. Flowers bisexual or the lowest flowers ♀-sterile, weakly perigynous, apetalous; receptacle shallowly campanulate with 5–7 stubby, calyx-like teeth. Stamens indefinite (about 24), unequal, exserted; filaments expanded, ± clavate, white, conspicuous; anthers with 4 pollen sacs, becoming 2-locular at anthesis; dehiscence of each locule I-shaped, the locule opening by 2 flaps. Ovary slightly recessed in the receptacle, 2-locular below, 2-parted above into 2 styles, the stigmas introrsely decurrent; ovules solitary, pendent from the apex of each locule. Fruit partly inferior, fused ± to the middle with the receptacle-calyx, loculicidal (and ± septicidal), maturing in summer. Seeds 1 per locule, oblong, lustrous, hilum apical and surrounded by a pale area that usually is decurrent on 2 sides. TYPE SPECIES: *F. Gardenii* Murray. (Named for John Fothergill, 1712–1780, English physician and champion of the American colonists during the Revolution, in whose garden many American plants were first cultivated in the Old World.)

Two or three species endemic to our area, distributed from Alabama to Kentucky, North Carolina, and southeastern Virginia. *Fothergilla Gardenii* (*F. alnifolia* L. f., *F. carolina* (L.) Britt., *F. parvifolia* Kearney in Small), $2n = 72$,[3] dwarf witch-alder, is a low (usually less than 1 m.), stoloniferous shrub of wet, sandy soils of the Coastal Plain from southeastern Virginia (?) and southeastern North Carolina to Alabama. *Fothergilla major* (Sims) Lodd. (*F. alnifolia* var. *major* Sims), $2n = 72$,[3] with leaves glaucous and pubescent beneath, is an upright shrub (to 3 m.) of the southern Appalachians in North Carolina, Tennessee, Georgia, and Alabama; *F. monticola* Ashe, $2n = 48$,[3] with leaves only sparingly pubescent beneath, is distributed with the latter and appears to be almost in-

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[3] Chromosome number determined by Dr. J. L. Thomas from cultivated plants of the Arnold Arboretum. The number for *Fothergilla Gardenii* (Arnold Arb. no. 684–50) is reported here for the first time. Counts of *F. major* (Arnold Arb. no. 694–34) and *F. monticola* (Arnold Arb. no. 4163A) verify the earlier reports of Anderson & Sax. The determinations were made from pollen mother cells.

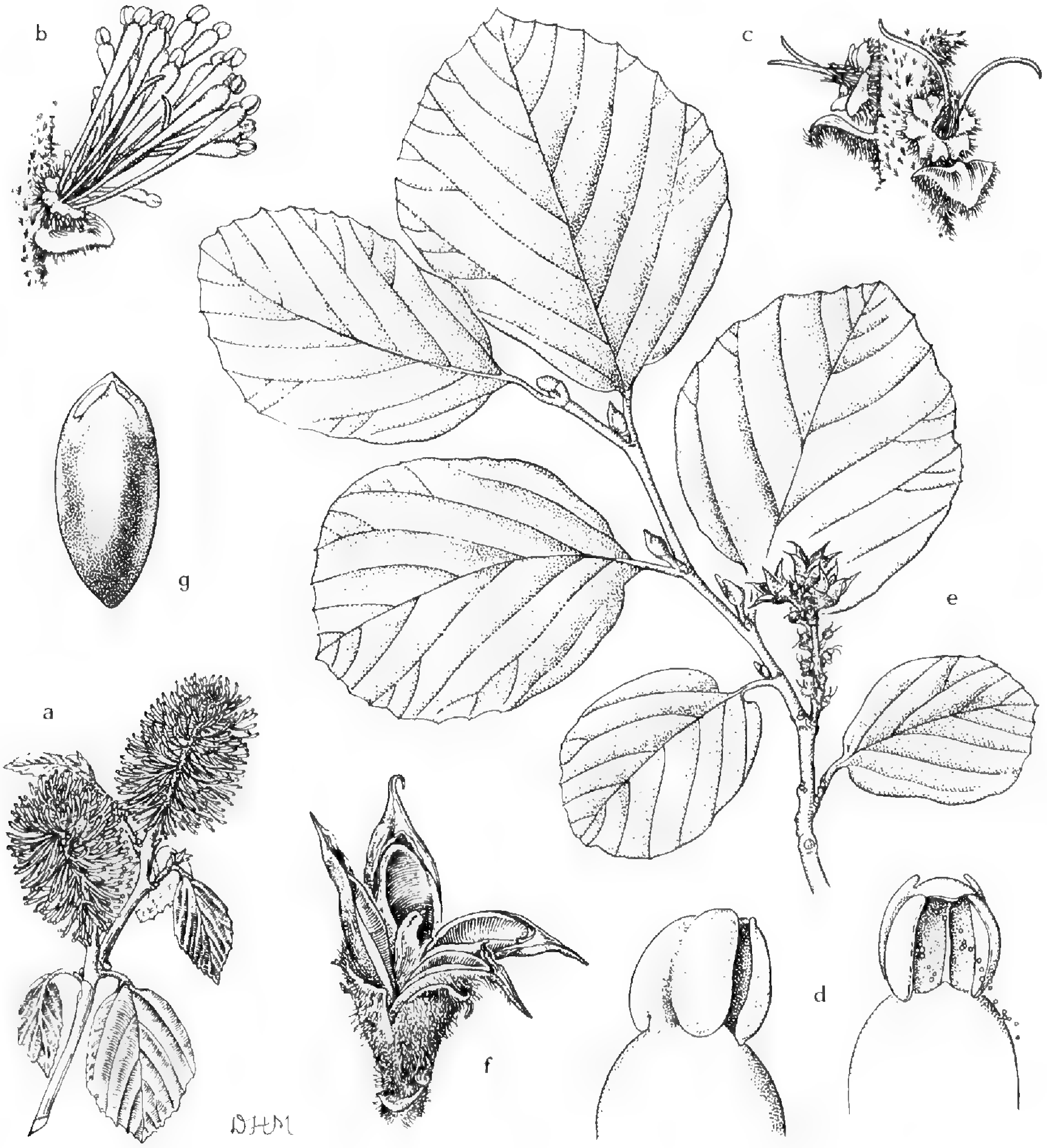

FIG. 2. **Fothergilla.** a–g, *F. major*: a, flowering branch, × ½; b, bisexual flower after anthesis, showing styles near center, × 2; c, two flowers, stamens removed to show diverging styles with decurrent stigmas, × 2; d, two anthers, showing mode of dehiscence, × 18; e, summer shoot with mature fruits, × ½; f, open fruit, seeds discharged, showing loculicidal and partially septicidal dehiscence, × 2; g, seed, color pattern omitted — note apical characteristics, × 4.

distinguishable from it. The interrelationships of the species are uncertain and in need of study.

The species of *Fothergilla* are handsome, spring-flowering shrubs with distinctive upright spikes of apetalous flowers with conspicuous white stamens; the leaves sometimes develop brilliant crimson autumnal coloration. In the vegetative stage *Fothergilla* and *Hamamelis* sometimes are surprisingly similar, but the characters common to both genera also are common to the nucleus of hamamelidaceous genera; both genera have some affinities with Old World taxa.

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Subfam. LIQUIDAMBAROIDEAE Harms in Engler & Prantl

3. **Liquidambar** Linnaeus, Sp. Pl. 2: 999. 1753; Gen. Pl. ed. 5. 434. 1754.

Trees to about 35 m. tall, usually with excurrent branching; bark often forming corky wings on twigs. Leaves palmately veined, [3- or] 5(7)-lobed, pubescent beneath when young, smooth, glandular, serrate, pleasantly scented when crushed, variously colored in autumn. Hairs simple. Inflorescences at ends of branchlets, bracteate, mostly unisexual, the plants monoecious, the perianths ± absent. Staminate inflorescences elongate, ± racemose, composed of globular masses of numerous stamens, these not organized into distinct flowers; each stamen mass pediceled and subtended by a deciduous bract or sessile; anthers on short filaments, 2-locular at anthesis, longitudinally dehiscent; pollen polyporate; ovaries absent. Carpellate inflorescences many flowered, spherical, long peduncled, pendent, 1(or more)-bracteate; receptacle of each flower ± campanulate and ± connate with adjacent flowers, broadly notched, with 4–5 [8–9] perigynous, usually ? rudimentary stamens; ovary partly inferior; stigmas introrsely decurrent; styles spreading; ovules numerous, ± in 4 rows in each locule, mostly aborting, only the basal 1 (2) ovules functional. Fruits ± connate, septicidal; maturing in autumn. Seeds few, 1 (2) per locule, winged apically, the hilum ± lateral. LECTOTYPE SPECIES: *L. Styraciflua* L.; see Aiton, Hort. Kew. 3: 334. 1789. (Name from Latin, *liquidus*, fluid, and Arabic, *ambar*, resin.) — SWEET GUM, RED GUM, STAR-LEAVED GUM, BILSTED, ALLIGATOR-TREE.

Three arborescent species of the Northern Hemisphere, occurring in Asia Minor, eastern Asia, and eastern North America and Central America. Section LIQUIDAMBAR (§ *Euliquidambar* Harms), is represented with us by *L. Styraciflua* (including var. *mexicana* Oerst. and *L. macrophylla* Oerst.), $2n = 30, 32$, a common forest tree distributed from Texas to

Florida northward to Connecticut and in the Mississippi drainage to southern Illinois, Indiana, and Ohio, mostly at lower altitudes. It occurs discontinuously in Mexico and southward to Honduras at higher altitudes (to 2200 m.). The leaves usually are 5(7)-lobed with ± straight, serrated margins. Forma *pendula* Rehd. (Arkansas) and f. *rotundiloba* Rehd. (North Carolina) were based on single trees. The leaves of *L. orientalis* Mill., $2n = 32$, of Turkey (?), also are 5(7)-lobed, but the margins usually are subdivided further. Leaves of *L. formosana* Hance (§ CATHAYAMBAR Harms), of Taiwan and China, usually are simply 3-lobed, and the ♀ flowers are separated from one another by elongate, pointed scales which are lacking in the other species.

With its palmately veined and lobed leaves, numerous ovules, septicidal fruits, winged seeds, and polyporate pollen, *Liquidambar* appears discordant in Hamamelidaceae. This remoteness has led some authors to place it along with *Altingia* Noronha, a genus of southeastern Asia, usually with pinnately veined leaves, in Altingiaceae. Although crystals and secretory elements (including individual cells and canals) appear to be widespread in the family, it is in *Liquidambar* and *Altingia* that vertical, traumatic-type medullary canals are found close to the protoxylem. (See Metcalf & Chalk, and Tippo, 45.) The familial affinities of *Liquidambar* cannot be evaluated solely by comparison with *Hamamelis* and *Fothergilla* but perhaps can be understood by comparison with other genera in Asia.

Styrax or liquid storax (not to be confused with storax from *Styrax officinale* L.), a balsamic resin exudate of trunk wounds on *Liquidambar,* originally obtained from *L. orientalis*, is pleasantly scented and has been used in incense, perfumery, medicine, and chewing gum. Valued for its fall color, rate of growth, and trim lines, *L. Styraciflua* is frequently cultivated for ornament. The wood has some desirable qualities and is known as satin walnut.

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PLATANACEAE Dumortier, Anal. Fam. 11, 12. 1829, "Plataneae," nom. cons.

(PLANE-TREE FAMILY)

A distinctive, monogeneric, arborescent family of uncertain affinity, easily recognized by the characteristic mottled bark; the axillary buds inclosed by the base of the petiole; the fragrance of the broad, palmately lobed leaves; and the pendent, unisexual globes of numerous, minute flowers with reduced, ± cyclic, hypogynous perianth, apocarpous gynoecium, and fruit of several bristly achenes.

1. **Platanus** Linnaeus, Sp. Pl. 2: 999. 1753; Gen. Pl. ed. 5. 433. 1754.

Large trees with pale, ± smooth, mottled bark, exfoliating in irregular, darker scales at least on the upper branches; young leaves, twigs, inflorescences, and most floral members copiously pubescent. Hairs long, multicellular-uniseriate, and bristly, or shorter, with whorls of unicellular branches, and matted, sometimes appearing almost stellate. Leaves deciduous, petiolate, alternate, pleasantly fragrant, broad, palmately veined, 3- or 5[7]-lobed [or oblong, pinnately veined and entire in *P. Kerrii*], the base of the petiole concealing the conical axillary bud; stipules paired or united, foliaceous or scarious. Plants monoecious; inflorescences at ends of branchlets, long-pedunculate, pendent, usually unisexual, of 1 (2) [or more] globes of numerous flowers; each globe subtended by a circular bract and with bractlets interspersed among the flowers. Staminate inflorescences disintegrating after anthesis; ♂ calyx minute, cup shaped, ± shallowly 3–6(8)-lobed [absent in *P. racemosa*]; petals 3–6, glabrous, ± fleshy, 3-pronged, sometimes ± connate, fitting ± between the stamens in *P. occidentalis* and *P.* × *acerifolia* (here resembling the staminodia of the ♀ flowers) [or petals sometimes low, rounded knobs in *P. racemosa*]; stamens 3–5 (8), alternate with the petals; filaments very short; anthers elongate, with characteristic, polygonal, truncate apex, 2-locular at anthesis, the dehiscence longitudinal; pollen 3–colpate; rudimentary carpels occasionally present. Carpellate inflorescences persisting in fruit; ♀ flowers hypogynous; calyx minute, cup shaped, shallowly 4(3–6)-lobed [aposepalous and resembling bracts in *P. orientalis* and *P. racemosa*]; apetalous (?) [or apopetalous in *P.* × *acerifolia* and *P. orientalis*]; gynoecium apocarpous, of 5–9 carpels ± in 2 or 3 series, the outer carpels alternating with a series of 3 or 4 staminodia; stigmatic region introrse and decurrent from the apex of the elongate style; ovaries superior, unilocular; ovules usually solitary (or 2 or more and rudimentary), ± orthotropous, 2-integumented, pendent, the micropyle downward. Fruit of 5–9 achenes each with 1 (2) seeds, narrowly angular-clavate, ± truncate [to attenuate], tapering into the narrow style, surrounded from the base by long bristles; seed spindle shaped; radicle downward; cotyledons ± unequal; endosperm scanty. LECTOTYPE SPECIES: *P. orientalis* L.; see N. L. Britton, N. Am. Trees 415. 1908. (Name Greek, probably from *platys*, broad, in reference to the leaves.) — PLANE TREE, SYCAMORE, BUTTONWOOD, BUTTONBALL.

Perhaps eight or nine species, mostly of the North Temperate Zone, distributed in Eurasia, North America south to Guatemala, and Indochina. Two or three species, usually of riparian associations and at lower altitudes, are indigenous to the United States. About five species are native to Mexico and Central America, where they occur at somewhat higher altitudes (to 6000 ft.). Fossil traces are reported as early as the Cretaceous and as far north as Greenland.

Platanus occidentalis L., $2n = 42$, usually with only one globe of flowers on a peduncle, the largest of our deciduous trees (to ca. 45 m. tall, and 3.5 m. in diameter), is distributed from Florida to Texas and north to Nebraska, Ontario, and Maine; var. *glabrata* (Fern.) Sarg., and f. *attenuata* Sarg. are based on leaf characters.

Platanus × *acerifolia* (Ait.) Willd. (pro sp.), $2n = 42$, London plane, hardy, and widely cultivated as a street tree, in some respects combines characters of *P. orientalis*, $2n = 42$, a native of southern Europe and western Asia, and *P. occidentalis*. It is said to be of hybrid origin and to have originated in 1670 in England (Henry & Flood), although *P. orientalis* may not be hardy in England (Li). The pollen of *P.* × *acerifolia* is 90% fertile (Sax); "first generation hybrids" are mixed and variable (Henry & Flood); however, no one seems to have attempted to resynthesize the hybrid experimentally.

The taxa of *Platanus* mostly are circumscribed on characteristics of the leaves and inflorescences rather than on floral structure. Contradictory accounts of the flowers are given by several authors.[4] Accountable are both the minute, mostly rudimentary and variable perianth requiring microscopical methods for effective study and the possible misdetermination of study specimens. The calyx and corolla, consisting (when present) of regular, alternating series, are devoid of vasculature, while the staminodia, stamens, and gynoecia receive tracheary tissue. Unlike other floral organs, the petals are glabrous; they are present in all staminate flowers, and here they may have fragments of vascular tissue beneath them. Staminate flowers are more consistent in structure than carpellate flowers (Boothroyd). The flowers are occasionally unilateral, with the floral members in imperfectly alternating series, and staminate flowers sometimes are separated with difficulty (Clarke).

Anatomically, *Platanus*, having vessels with simple perforations, is more advanced than Hamamelidaceae but less specialized than Rosaceae (Tippo). The genus probably is without close relatives. A direct relationship with Hamamelidaceae is not suggested by the floral morphology. The discovery of *Platanus Kerrii* Gagnep. in Laos is interesting, since it is the only representative of the genus in eastern Asia and the ovate-lanceolate leaves are pinnnately veined with entire margins. Seedling leaves of other species apparently are pinnately veined.

The wood of *Platanus*, sometimes known as lacewood, usually is not durable but has been used for miscellaneous objects. The hairs sometimes are claimed to be irritating to mucous membranes.

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[4] This presentation of *Platanus* is based primarily upon that of Boothroyd which sometimes is not very clear.

417. 1924. [Considers Platanaceae monotypic (with *P. acerifolia*, *P. occidentalis*, and *P. orientalis* only forms of one sp.), standing between Rosaceae and Hamamelidaceae. Chromosome number of "*Platanus acerifolia?*" $n = 10$ and 11. Bibliography.]

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COMPARATIVE ANATOMY OF THE LEAF-BEARING CACTACEAE, VIII[1]

THE XYLEM OF PERESKIAS FROM SOUTHERN MEXICO AND CENTRAL AMERICA

I. W. BAILEY [1]

AS DEMONSTRATED IN the second paper of this series (Bailey, 1961a), there are three distinct categories of pereskias that can be differentiated by consistent differences in the form and distribution of sclereids in their secondary phloem. *Pereskia conzattii* Britt. & Rose of southern Mexico, *P. autumnalis* (Eichlam) Rose of Guatemala and *P. nicoyana* Web. of Costa Rica belong in one category which includes *P. aculeata* Mill. and such pereskias of Peru and Bolivia as *P. humboldtii* Britt. & Rose, *P. vargasii* H. Johnson, *P. weberiana* K. Schum. and *P. diaz-romeroana* Cárd. It is of interest, both morphologically and taxonomically, to determine whether there is cogent evidence in the various organs and parts of these plants, other than in their syncarpous ovaries, which justifies separating them in independent genera, viz. *Pereskia* and *Rhodocactus* (Berg.) Knuth. In this paper evidence from the xylem will be described and discussed.

The pereskias of southern Mexico, Guatemala and Costa Rica are trees which attain heights of eight to ten meters at maturity. They are characterized by forming relatively massive trunks which at times attain diameters of as much as forty centimeters. My collections of *Pereskia conzattii* [2] are numerous, stems of varying sizes having been kindly collected and preserved for anatomical investigation by Norman Boke (5 collections), Duncan Clement, R. L. Dressler, King and Diboll, H. E. Moore, Jr. (two collections) and Sharp and Hernández. For comparison I have two collections of *P. autumnalis* made by Dr. Moore and one of *P. nicoyana* sent to me by Dr. Rodríguez. The xylem of the secondary body in stems and roots of the three pereskias is similar, exhibiting comparable ranges of structural variability in different parts of a mature tree.

The most characteristic and significant trend of diverging anatomical specialization occurs in the basal parts of the trunks of *Pereskia conzattii*,

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[1] This investigation was financed by a grant from the National Science Foundation. I am indebted to the American Philosophical Society for the loan of a Wild microscope.

[2] This species may prove to be the same as *Pereskia pititache* Karwinsky. Britton and Rose (1919) in reducing Karwinsky's species to synonymy with *Pereskiopsis pititache* evidently based their description upon a plant sent to the New York Botanical Garden by M. Simon of Paris. This particular clone appears to have differed from Karwinsky's plant in being a representative of *Pereskiopsis* rather than of *Pereskia*.

P. autumnalis and *P. nicoyana.* In preceding papers of this series I noted that in the larger young stems of *P. sacharosa* Griseb. and *P. aculeata* (Bailey, 1962), and likewise in those of Andean pereskias (Bailey, 1963), there is a tendency toward increase in the circumference of the primary vascular cylinder and in the diameter of the pith subsequent to the initiation of cambial activity in the fascicular parts of the eustele. In stems of these species broadening of the parenchymatous gaps in the eustele may or may not involve concomitant broadening of the inner parts of the first-formed, lignified, multiseriate rays of the secondary body. In dissecting the main stem and branches of *P. conzattii*, one finds that the basal part of the trunk has a much enlarged pith (up to five centimeters or more in diameter at times) having what appears superficially to be stellate projections which extend outward for varying distances into the xylem of the secondary body. Similar structures occur in the trunks of *P. autumnalis* and *P. nicoyana.* That such projections of soft tissue are not parts of the primary body is shown in FIGS. 1, 2, 4, 11, and 14.

When cambial activity is initiated in the broadening interfascicular parts of the eustele, its derivatives have thin, unlignified walls and retain a capacity for division and enlargement (note the transverse expansion of ray cells in FIG. 11). This broadening of multiseriate rays, concomitant with lateral expansion of the parenchymatous gaps in the eustele, facilitates continued increase in the diameter of the pith for more or less extended periods of time. In fully matured stems, the expanded rays may contain patches of lignified ray cells (FIGS. 1, 4, and 14). Although their outward extensions are lignified, the rays tend at least for a time to be conspicuously broader than the multiseriate rays of secondary xylem that is subtended by fascicular parts of the eustele (FIGS. 1, 2, 11, and 14). It should be noted in this connection that, as in stems and roots of *Pereskia aculeata* and in roots of the Andean pereskias, the thin-walled unlignified parenchyma of the secondary xylem contains characteristic druses of calcium oxalate (FIGS. 1, 2, and 4), resembling those that occur so commonly in unlignified tissue of the pith, phloem and cortex of the leaf-bearing Cactaceae (Bailey, 1961b).

The first-formed secondary xylem in branches and smaller stems from the upper part of mature trees of *Pereskia conzattii*, *P. autumnalis* and *P. nicoyana* tends to be of more nearly normal dicotyledonous structure. For example, in FIG. 3, the multiseriate rays which extend radially outward from parenchymatous gaps of the eustele are lignified throughout and are only slightly broader than those in wedges of secondary xylem subtended by fascicular parts of the primary body. There obviously has been some lateral expansion of the interfascicular parts of the eustele during earlier ontogenetic stages of development, but the tangentially enlarged parenchymatous cells of these parts have become lignified. By comparing sections from upper parts of a mature tree with others from successively lower levels various stages in the ontogenetic and phylogenetic modification of first-formed multiseriate rays may be reconstructed.

Turning to the structure of fully lignified parts of the secondary xylem, one finds similarities to that of *Pereskia sacharosa* in stems of comparable diameter from equivalent parts of a tree. The vessels occur singly and in small clusters and are diffusely distributed (FIG. 3), or may at times exhibit more or less conspicuous zonation (FIG. 5). The wood parenchyma is scanty paratracheal (FIG. 9). The libriform fibers are slender, thick-walled and function in the storage of starch. The lignified multiseriate rays, except in the first-formed secondary xylem of the trunk, are not excessively broad and exhibit ranges of variability in form and internal structure comparable to those which occur in *P. sacharosa*. The first-formed multiseriate rays in wedges of secondary xylem subtended by fascicular parts of the eustele are comparatively narrow (FIGS. 1, 2, and 3), and are vertically extensive (FIGS. 11, 14, and 15). As in *P. sacharosa* and many other dicotyledonous trees (Bailey, 1962), the multiseriate rays become dissected sooner or later into lower rays during their radial extension outward (FIG. 13). Such derivative parts tend to become somewhat broader and tangentially displaced during increase in circumference of the cambium (FIGS. 13 and 16). The cells of the rays vary conspicuously in size, form and orientation even in comparable parts of the stems of a single plant. The first-formed parts of the multiseriate rays, at least in small branches from the upper part of a tree, tend to be composed of somewhat vertically elongated cells, i.e. of "erect" orientation. The subsequently formed outward extensions of the rays, as in *P. sacharosa*, commonly are composed of more or less isodiametric cells or of varying mixtures of isodiametric and radially elongated or "procumbent" ones. In some cases (FIGS. 13 and 15), erect cells may occur along the sides of the multiseriate rays, as in *P. sacharosa*.

The most conspicuous differences in the lignified secondary xylem of such pereskias as *Pereskia conzattii* and *P. autumnalis*, in comparison with that of *P. sacharosa*, occur in the outer tissue of large trunks of the former species which greatly exceed the largest stems of *P. sacharosa* in diameter. In this tissue the vessels are jacketed by abundant wood parenchyma (FIGS. 10 and 12). Furthermore, the vessels and parenchyma occur in concentric patterns alternating with dense zones composed largely of libriform fibers (FIGS. 6 and 12). In addition, the multiseriate rays tend to be composed internally of conspicuously procumbent cells (FIGS. 10 and 12). Although the vessels frequently are larger (200 millimeters or more in diameter) than in earlier formed secondary xylem (compare FIGS. 9 and 10), this is not invariably the case. In some smaller stems there may be precocious enlargement of vessels to equivalent size (compare outer part of FIG. 5 with FIG. 6). Nor are the multiseriate rays invariably wider than in the xylem of all smaller stems (compare FIGS. 5 and 6, 13 and 16). The width and the abundance of multiseriate rays in the secondary xylem is highly variable as in stems of *P. sacharosa*.

My collections of roots of *Pereskia conzattii* and of allied taxa from Guatemala and Costa Rica are limited in number, but in those that I have, the secondary xylem is of normal dicotyledonous structure, resembling that which occurs in roots of *P. sacharosa*. In none of them are there indications of multiseriate rays composed of unlignified cells or of the occurrence of patches or zones of unlignified parenchyma. The rays which may broaden more precociously than in stems are lignified throughout their radial extension. The vessels, which frequently tend to be more numerous and larger than in equivalent tissue of stems, occur singly and in small crowded clusters (FIG. 7). The wood parenchyma is scanty paratracheal, but may at times exhibit a tendency to become more abundant in the outermost xylem of very large old roots.

DISCUSSION

Pereskia conzattii, *P. autumnalis* and *P. nicoyana* occur in a category of leaf-bearing cacti that exhibit consistent similarities in the form and distribution of sclereids in their secondary phloem (Bailey, 1961a). *Pereskia aculeata* and the Andean pereskias likewise occur in this distinct anatomical category. On the contrary, *P. sacharosa* falls into a second category with *P. grandifolia* Haw., *P. bleo* DC., *P. corrugata* Cutak and *P. tampicana* Web., whereas *P. colombiana* Britt. & Rose, *P. guamacho* Web., *P. cubensis* Britt. & Rose and *P. portulacifolia* Haw. belong in a third distinct category.

In *Pereskia aculeata*, in contrast to *P. sacharosa* (Bailey, 1962), the secondary xylem exhibits conspicuous trends of anatomical modification in both stems and roots. Therefore, this species cannot be considered to be one of the most, if not the most, primitive living representatives of the Cactaceae, except possibly in the supposedly "superior" position of its syncarpous ovary. Similarly, the excessive structural modifications of the roots of the Andean pereskias (Bailey, 1963) negates the conclusion that these species have retained comparatively primitive morphological features throughout both their reproductive and vegetative organs.

In the case of the pereskias from southern Mexico and Central America, although the secondary xylem in general tends to resemble that of *Pereskia sacharosa,* there obviously are excessive modifications of part of the first-formed multiseriate rays in the basal parts of the trunks of these trees. Similar trends of excessive divergent phylogenetic specialization do *not* occur in other pereskias that have been included in the putative genus, *Rhodocactus,* as will be demonstrated in the next two papers of this series, but do occur in *Pereskiopsis aquosa* (Web.) Britt. & Rose and possibly in other species of *Pereskiopsis* and *Quiabentia* as will be shown subsequently. Thus, there is no cogent complementary anatomical evidence which justified placing *P. conzattii*, *P. autumnalis*, and *P. nicoyana* in *Rhodocactus* as at present constituted. It should be noted in this connection that in preliminary investigations of immature and mature flowers of these three species Professor Boke and I find no conclusive evidence that the ovaries are much more deeply depressed in the tissue of the torus than, for example, in the case of *P. aculeata*. Rather, we have found that the flowers of the supposedly most primitive cacti need to be reinvestigated in detail by modern methods of clearing and serial sectioning.

In the case of the Cactaceae as a whole there obviously are many trends of parallel evolution. Relatively close similarities are not always indicative of close genetic relationship. Conversely, morphological differences in one organ or part, which frequently are quantitative rather than qualitative, may not necessarily be indicative of remote relationship when evidence from other organs or parts is taken into consideration. A more rational division of the family into subfamilies, tribes, genera and species may possibly be attained only by synthesizing and harmonizing evidence from all organs and parts of the plants.

Anatomical evidence presented thus far indicates that *Pereskia sacharosa* has retained a normal type of secondary xylem which may possibly have characterized ancestral Cactaceae. This structural form of xylem is retained in certain parts of the stems of *P. aculeata*, but has been drastically modified in other parts of its stems and in its roots. It tends to persist in stems of the Andean pereskias, but has been highly modified in the roots of these plants. It has tended to persist in the roots and most parts of the stems of pereskias from southern Mexico, Guatemala and Costa Rica, but has been extensively modified in the basal parts of their trunks. At present, such anatomical evidence by itself and without strong corroborative support from other parts of the plants is of uncertain reliability in determining genetic relationships.

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EXPLANATION OF PLATES

PLATE I

FIGS. 1–4. Transverse sections of stems showing incipient stages in the formation of multiseriate rays. 1, *Pereskia conzattii* [*Dressler*] stem 10 cm. in diameter, pith 2 cm. diameter, × 11. 2, *P. conzattii* [*Sharp & Hernández*] stem 7 cm. in diameter, pith 3 cm. in diameter, × 11. 3, *P. autumnalis* [*Moore 8210*] stem 7 cm. in diameter, pith 3.5 cm. in diameter, × 11. 4, *P. nicoyana* [*Rodriguez 662*] stem 7.5 cm. in diameter, pith 2 cm. in diameter, × 22.

PLATE II

FIGS. 5–8. Transverse sections of secondary xylem. 5, *P. conzattii* [*Sharp & Hernández*] stem 7 cm. in diameter, × 11. 6, *P. autumnalis* [*Moore 8210*] stem 18 cm. in diameter, × 11. 7, *P. conzattii* [*Sharp & Hernández*], old root, × 11. 8, *The same*, × 34.

PLATE III

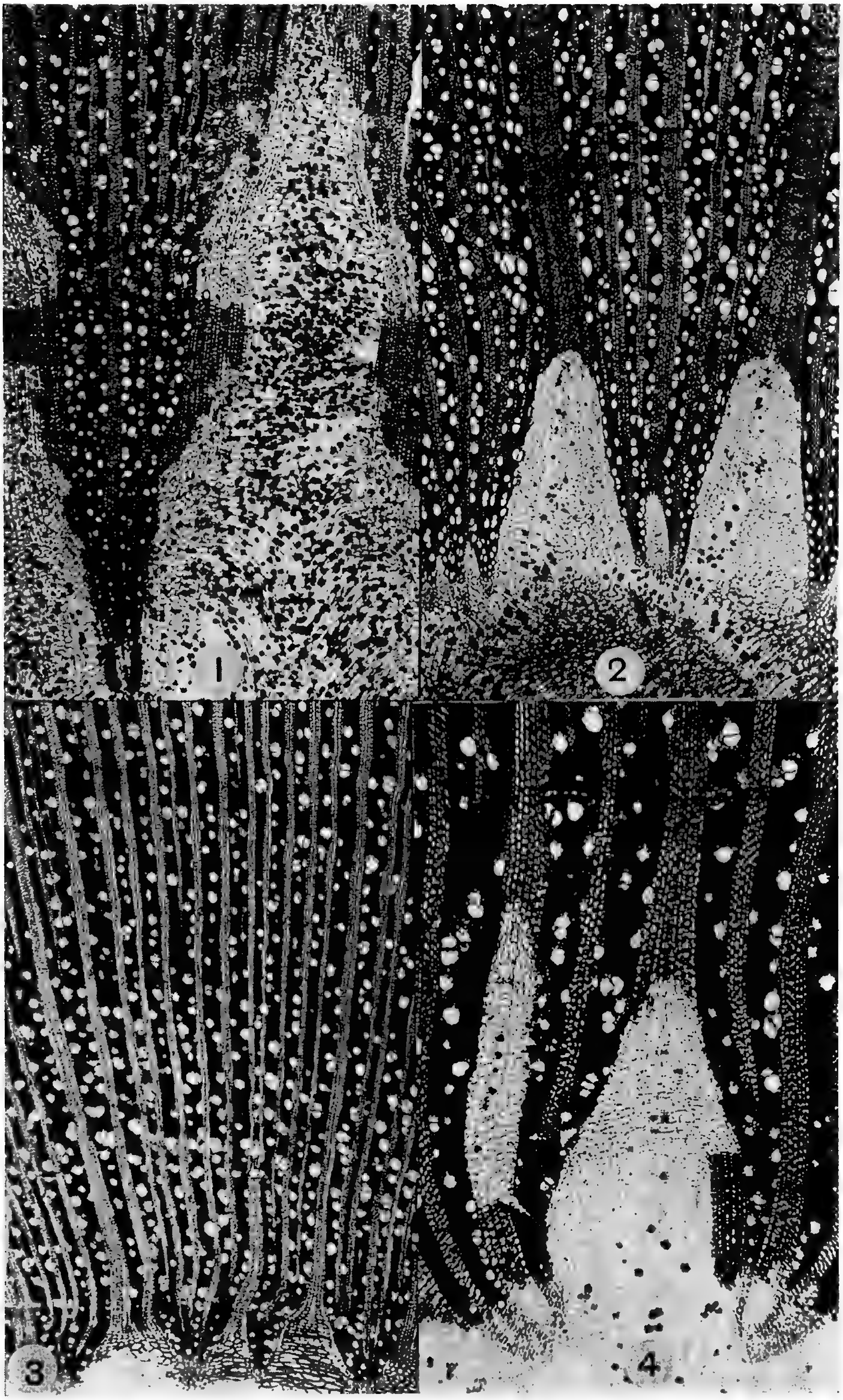
FIGS. 9, 10. Transverse sections of secondary xylem, × 88. 9, *P. autumnalis* [*Moore 8210*] wood from stem 7 cm. in diameter. 10, *The same*, wood from stem 18 cm. in diameter.

PLATE IV

FIGS. 11, 12. Tangential longitudinal and transverse sections of secondary xylem. 11, *Pereskia nicoyana* [*Rodríguez 662*] tangential section of first-formed secondary xylem showing variation in multiseriate rays, × 43. 12, *Pereskia conzattii* [*Boke B-9*] transverse section of outermost xylem of a very large stem, × 34.

PLATE V

FIGS. 13–16. Tangential longitudinal sections of secondary xylem. 13, *P. conzattii* [*Boke B-9*] showing form of multiseriate rays in outer xylem of a very large stem, × 43. 14, *Pereskia nicoyana* [*Rodríguez 662*] showing form of rays in innermost secondary xylem, × 11. 15, *Pereskia conzattii* [*King & Diboll*] form of rays in a stem 5 cm. in diameter, × 43. 16, *Pereskia conzattii* [*Sharp & Hernández*] form of rays in a stem 7 cm. in diameter, × 43.



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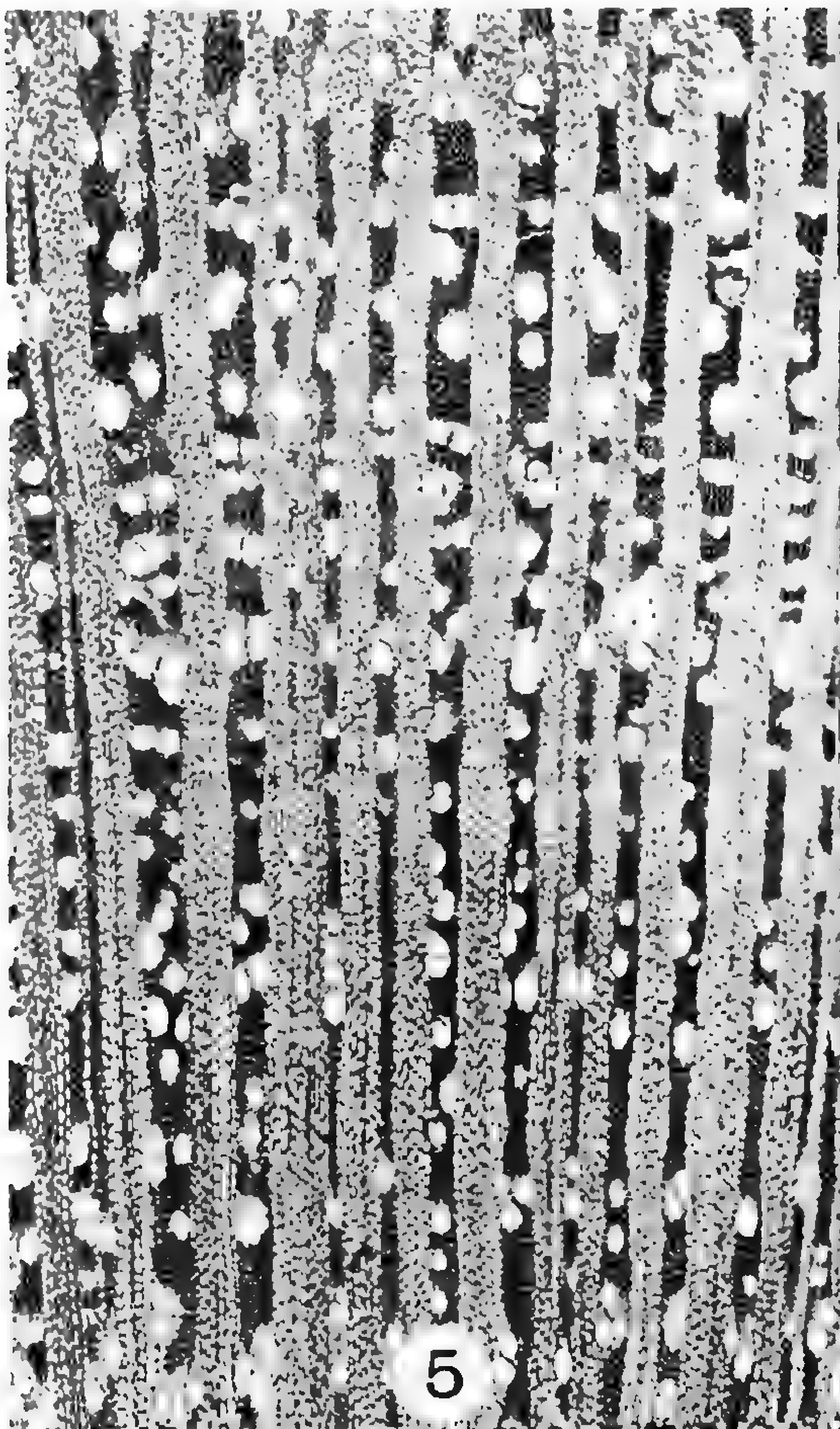
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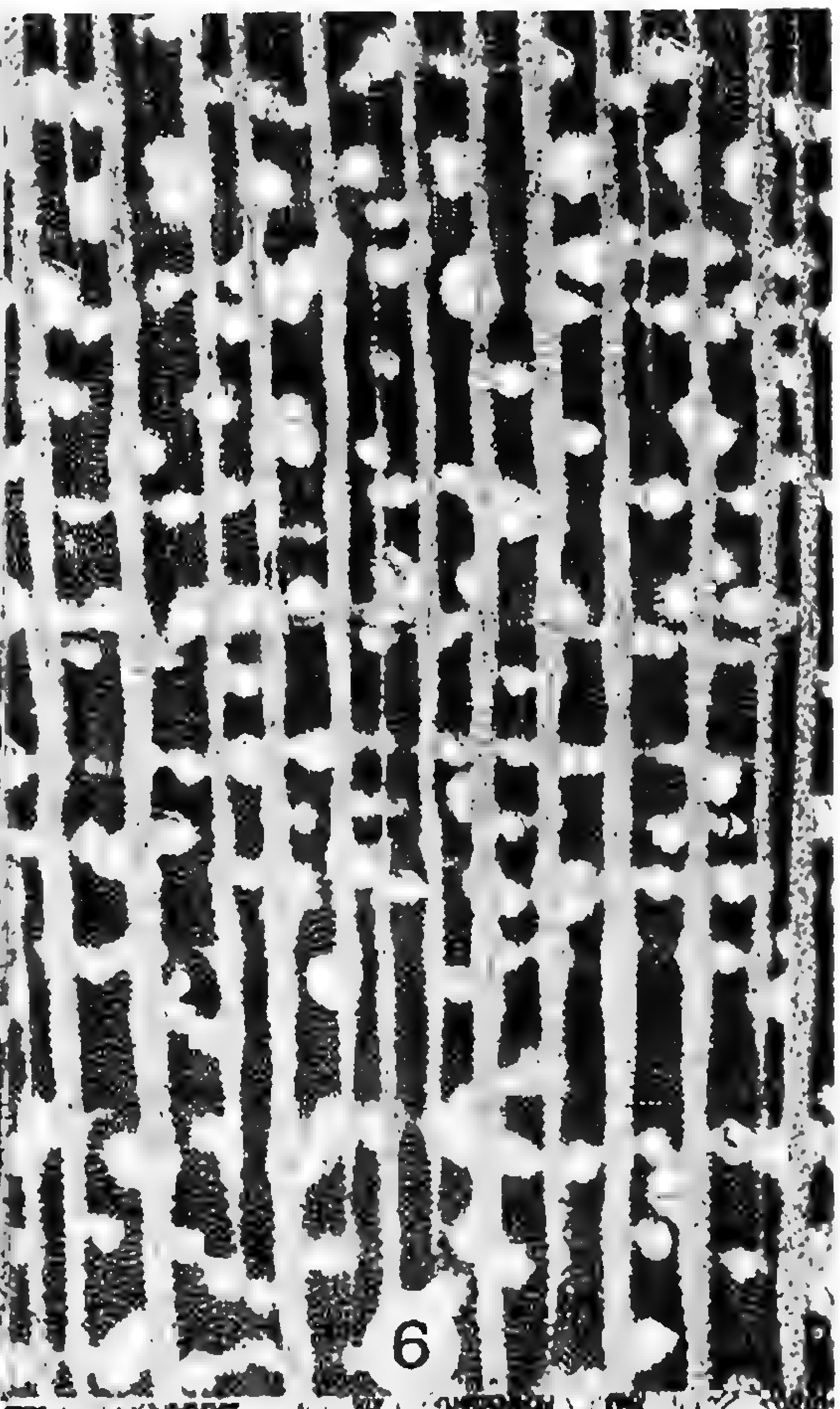
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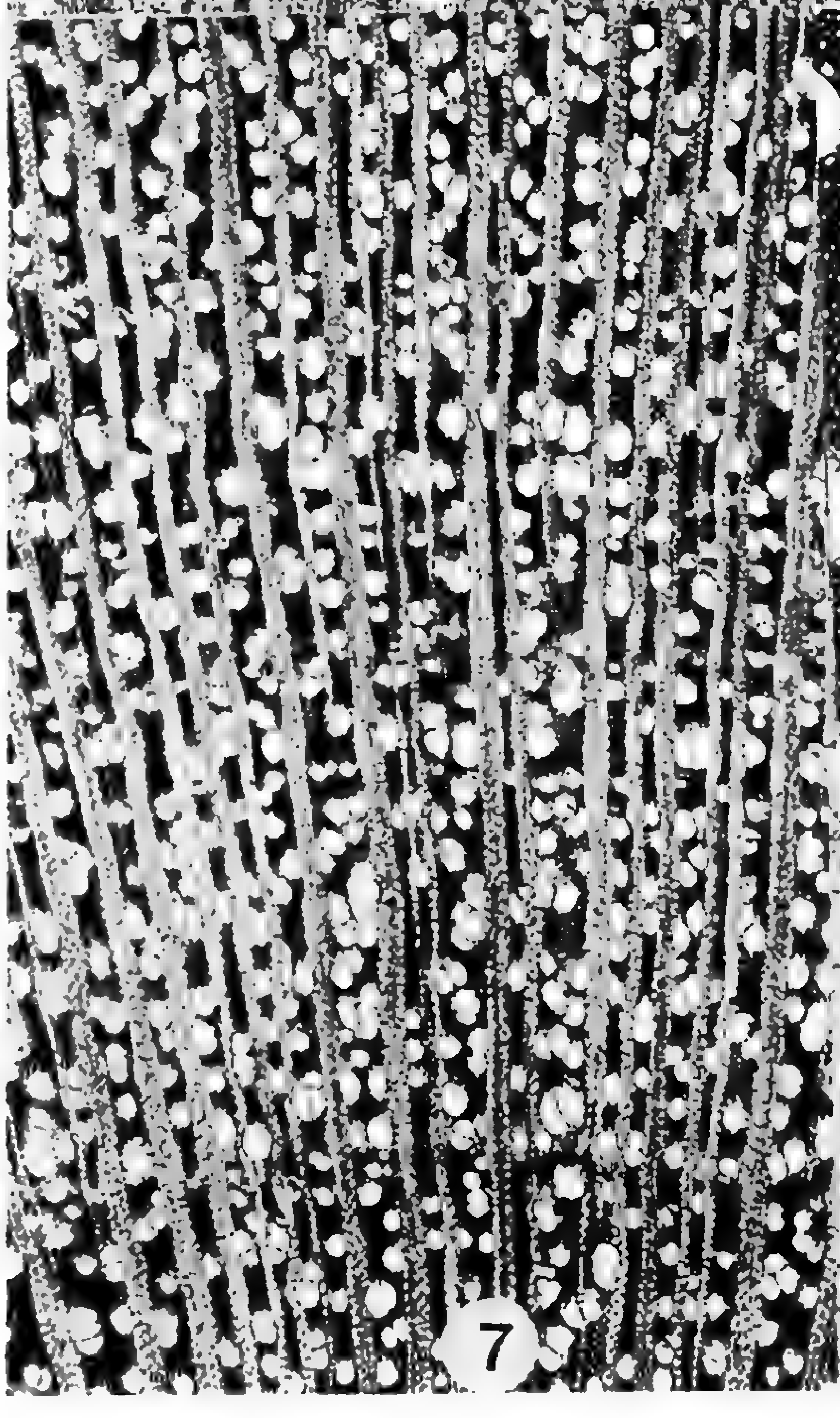
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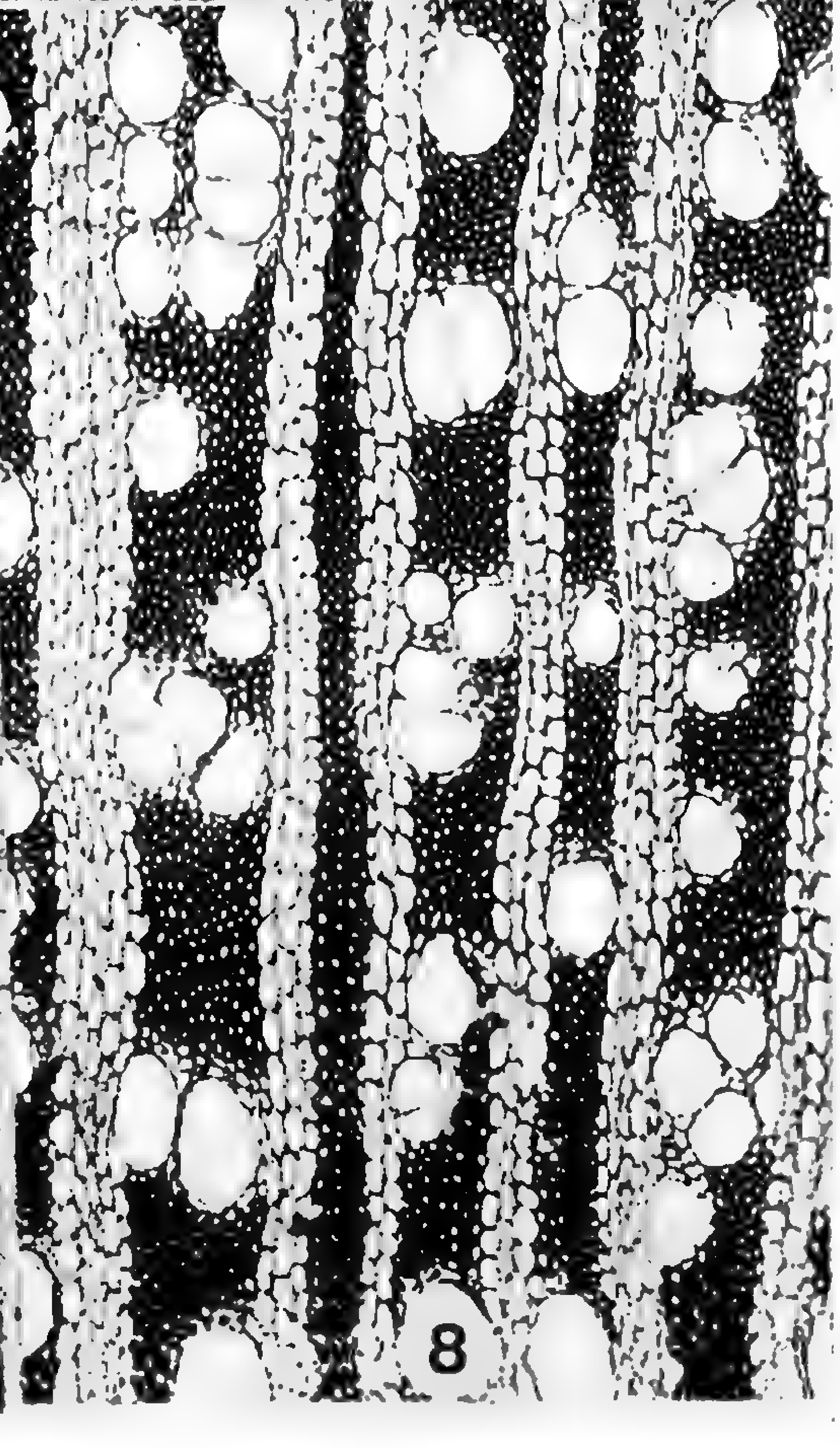
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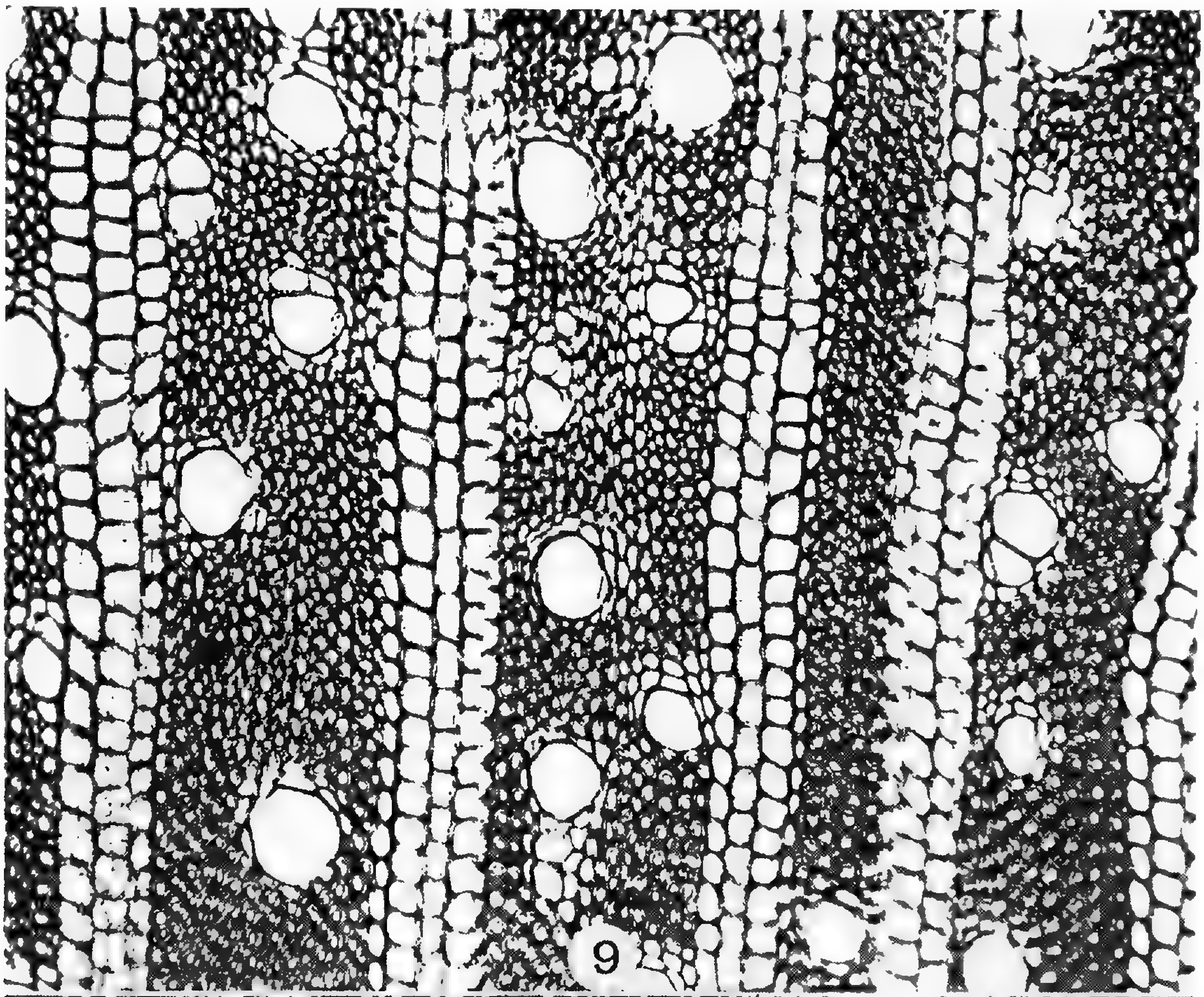

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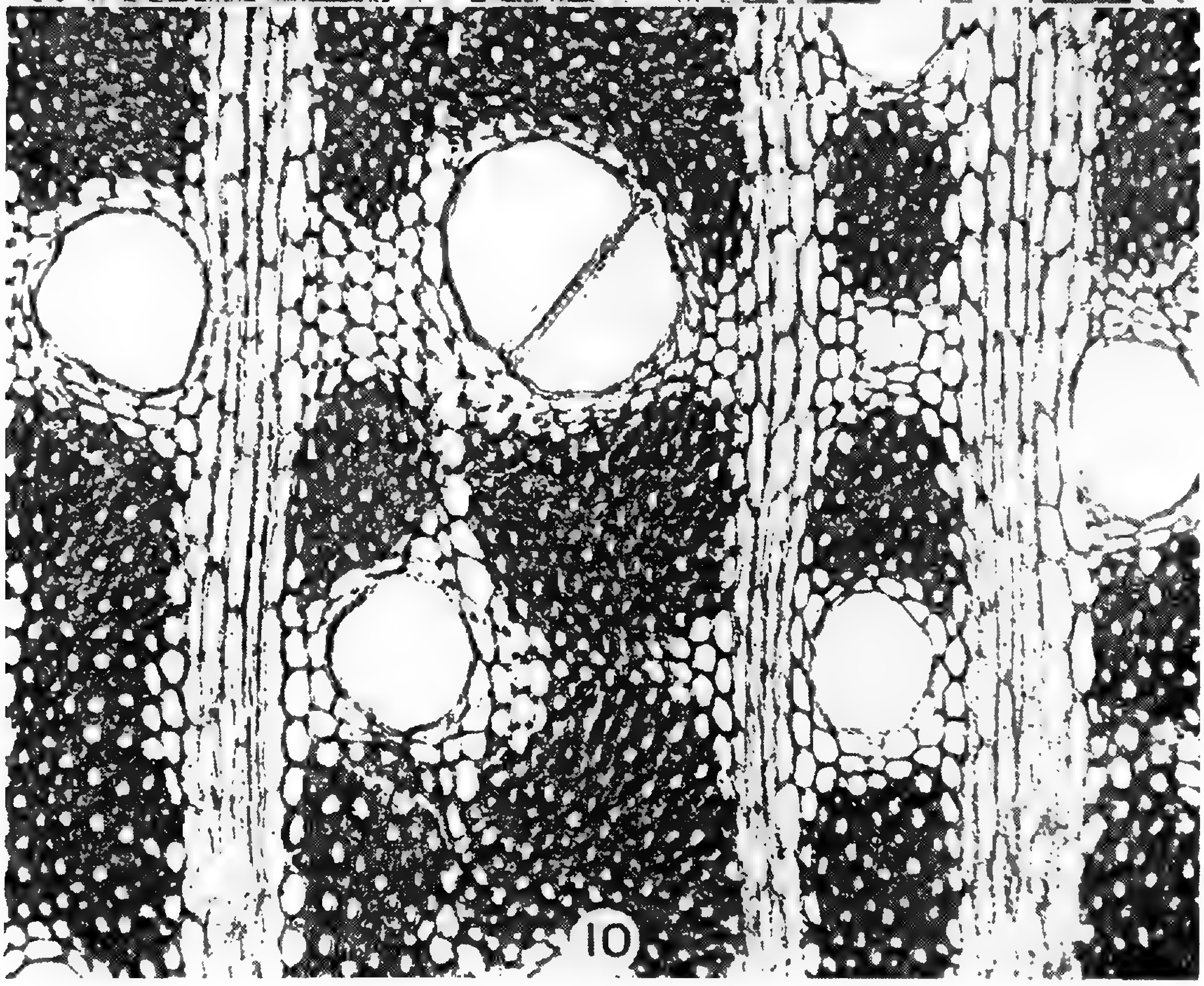

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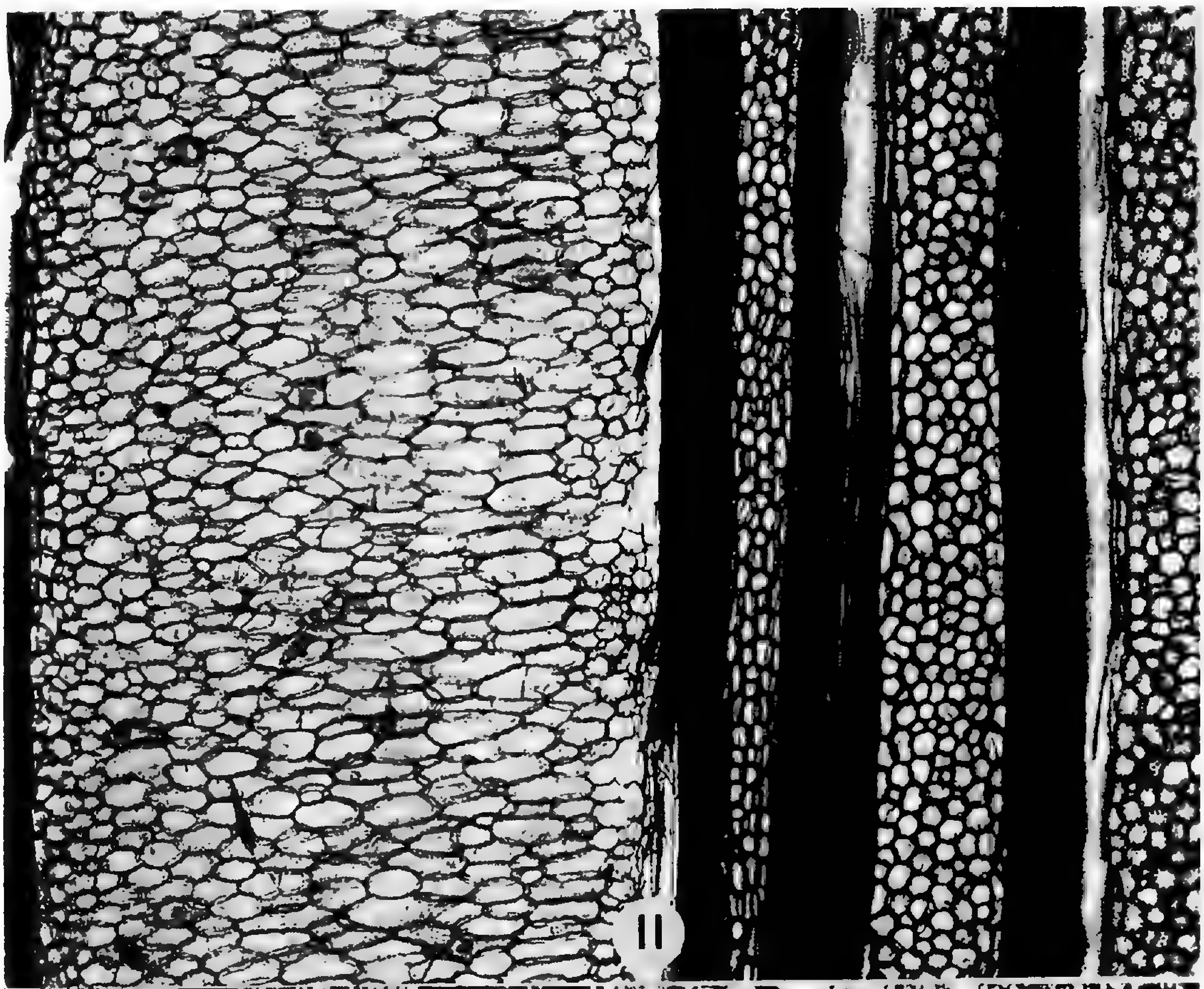

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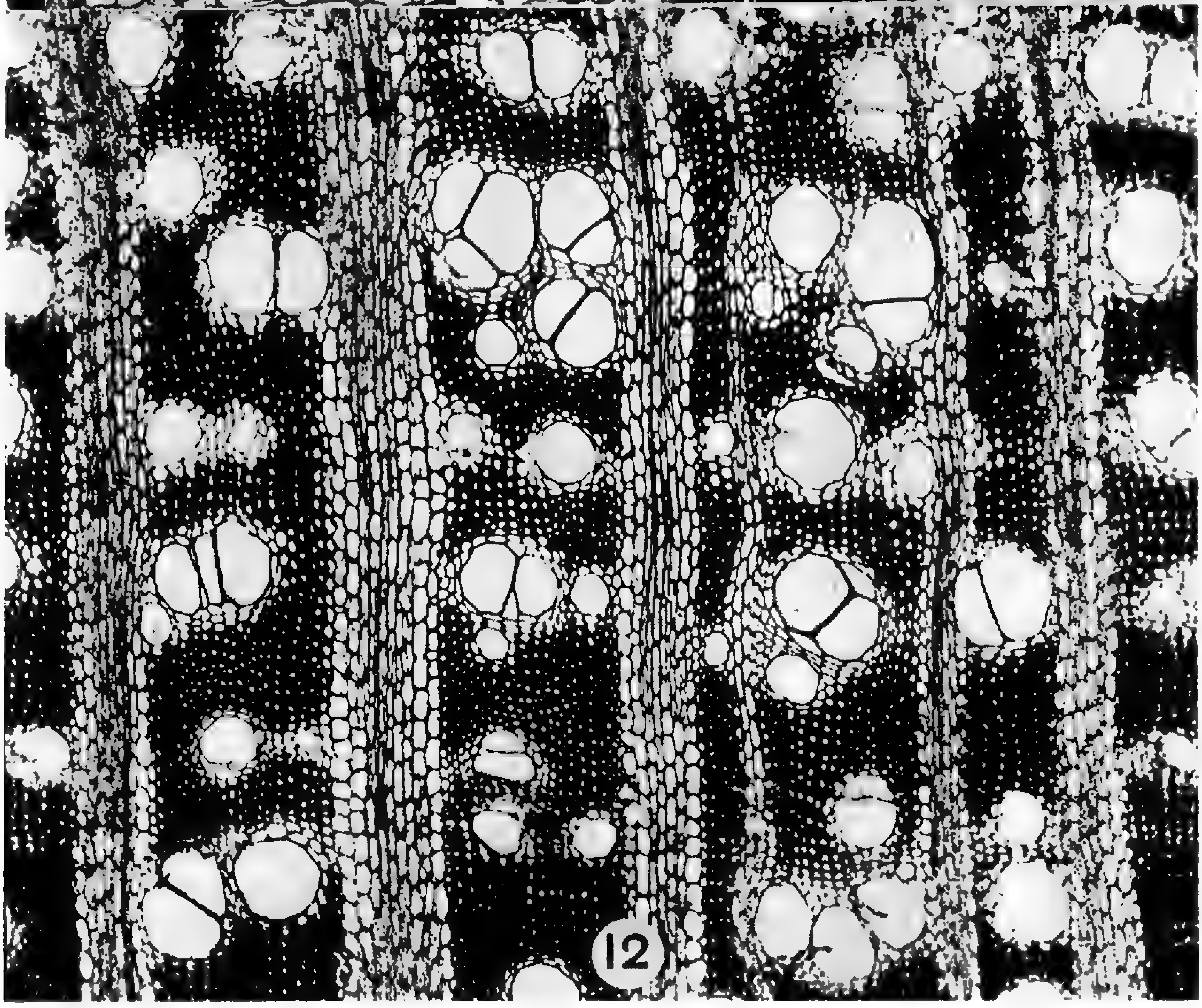

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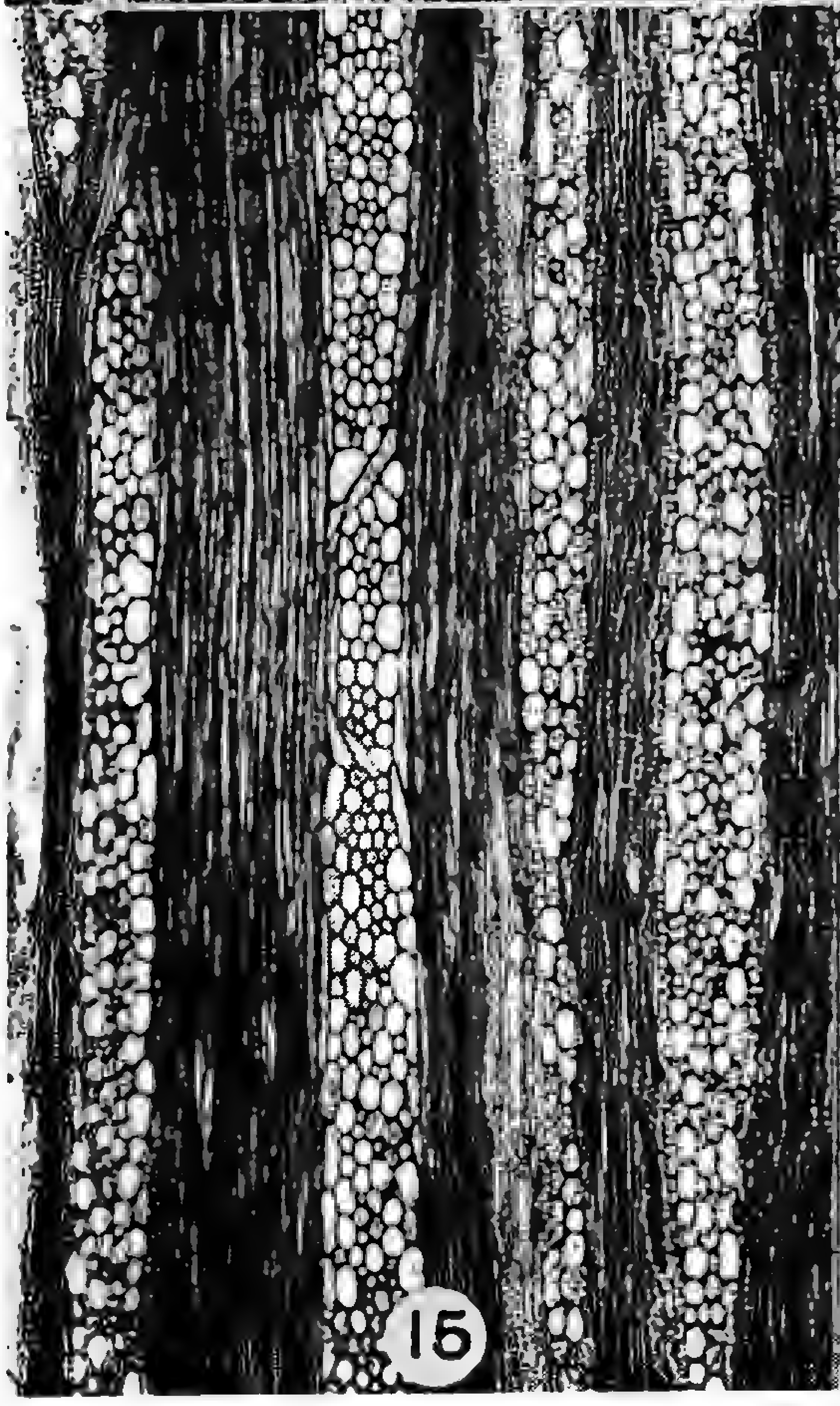
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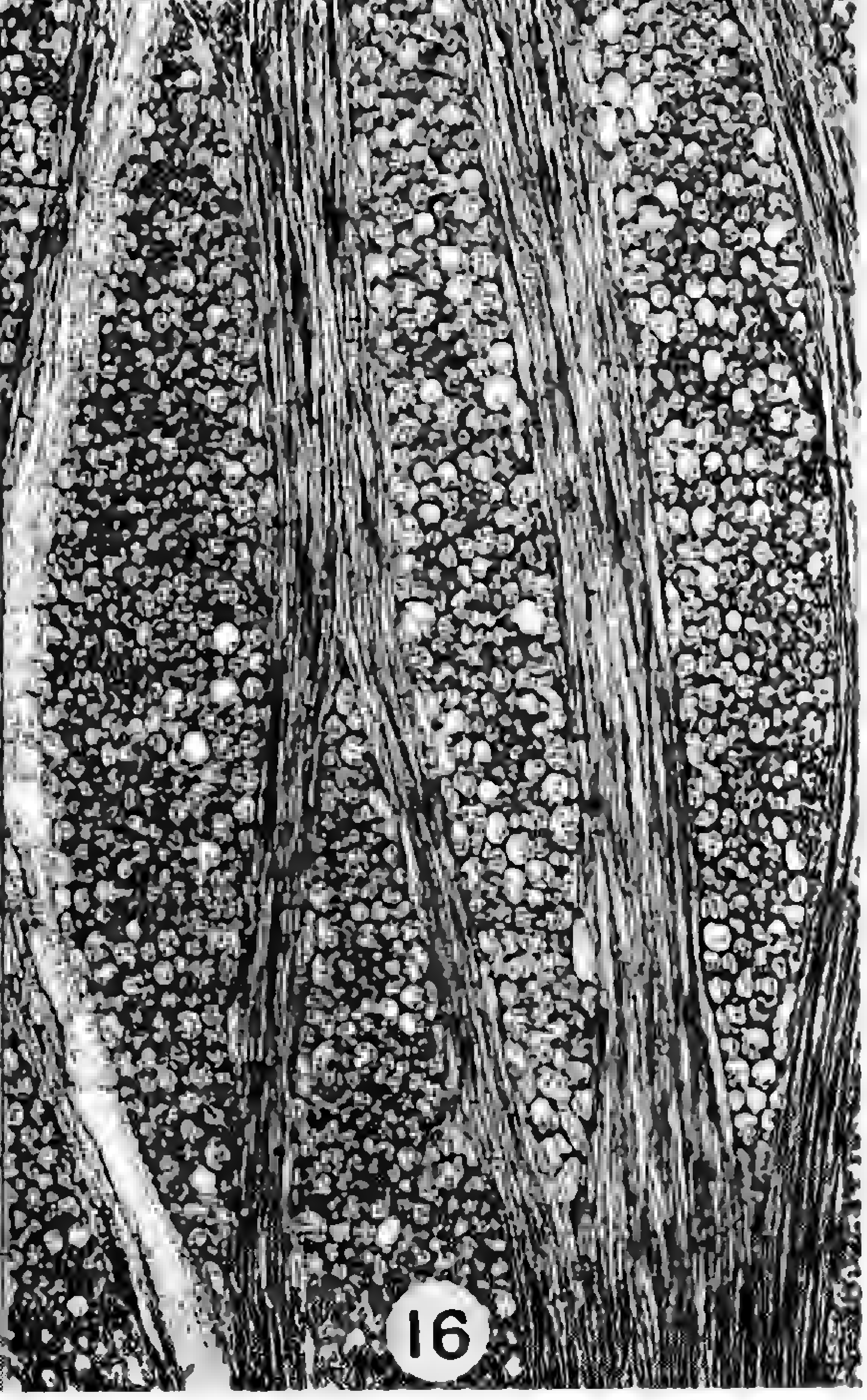
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COMPARATIVE ANATOMY OF THE LEAF-BEARING CACTACEAE, IX

THE XYLEM OF PERESKIA GRANDIFOLIA AND PERESKIA BLEO

I. W. BAILEY [1]

THE TWO SPECIES OF *Pereskia* treated in this paper, *P. grandifolia* Haw. and *P. bleo* DC., have been considered to be closely related, the former occurring in Brazil and the latter in northwestern South America and Panama. It is of interest in this connection that Dr. Rodríguez reports (personal communication) that trees closely resembling *P. bleo* occur in dense forests at elevations of 1400 meters in Costa Rica. He is convinced that these trees, now growing in the wild, do not belong to a species which was originally introduced by man and subsequently escaped from cultivation.

These putative species, which may ultimately prove to be geographical races of a single species, are woody shrubs or small trees which may attain a height of five to seven meters at maturity. When growing in isolation they tend to form a single main stem or trunk which may attain a diameter of ten centimeters or more. However, as in the case of other leaf-bearing cacti their form may be modified by close crowding in hedges and by pruning or other mutilation by man.

The xylem of *Pereskia grandifolia* and *P. bleo* exhibits similar ranges of anatomical variability, which in turn closely resemble those that occur in the xylem of *P. sacharosa* Griseb. (Bailey, 1962). The vessels occur singly and in small clusters (FIGS. 1–8). Although commonly diffusely distributed, particularly in the first-formed secondary xylem, the vessels may at times be aggregated into more or less conspicuous zonal or concentric patterns (FIGS. 1, 2, 3). However, in some cases appearances of zonation are due solely to varying intensities of lignification in the thick secondary walls of the libriform fibers (FIG. 8). The libriform fibers which may be septate or nonseptate function in the storage of starch. The wood parenchyma is scanty paratracheal (FIGS. 5–8).

The abundance and width of the multiseriate rays, as seen in transverse sections of stems and roots (FIGS. 1–4), are highly variable, those of the roots tending to broaden more precociously and extensively than those of the stem, as in *Pereskia sacharosa*. The particular structural details (illustrated in FIGS. 1 and 2) of *P. grandifolia* and (FIGS. 3 and 4) of *P. bleo* do not provide reliable diagnostic criteria for differentiating the

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[1] This investigation was financed by a grant from the National Science Foundation. I am indebted to the American Philosophical Society for the loan of a Wild microscope.

two species, for each form of anatomical structure occurs in either species when numerous stems and roots of each species are examined. In fact, they may be more or less closely duplicated in the ranges of structural variability of *P. sacharosa.*

As in certain of the larger young stems of *Pereskia sacharosa* (Bailey, 1962), comparable stems of *P. grandifolia* (FIG. 7), and *P. bleo* (FIG. 5), exhibit evidences of lateral expansion of the parenchymatous, interfascicular parts of the eustele by cell enlargement during later stages in the maturation of the primary body, thus facilitating increase in the diameter of the pith. Owing to the broadening of the interfascicular parts of the eustele and retardation in the initiation of cambial activity within them, the first-formed parts of the multiseriate rays tend to be broader than in their subsequent extensions outward. However, the first-formed parts of the rays are lignified and their cells are in normal radial seriation, differing markedly from those in the basal parts of the trunks of *P. conzattii* Britt. & Rose, *P. autumnalis* (Eichlam) Rose, and *P. nicoyana* Web. (Bailey, 1963), where they are unlignified and their cells exhibit a conspicuous capacity for transverse enlargement. In other words, the pereskias of southern Mexico and Central America exhibit exaggerated ontogenetic and phylogenetic modifications in their multiseriate rays which facilitate greatly prolonged increase in the diameter of the pith.

In *Pereskia grandifolia* and *P. bleo,* as in *P. sacharosa* and in many other dicotyledonous shrubs and trees, the first-formed multiseriate rays in close proximity to the primary body tend to be vertically extensive. These rays sooner or later become dissected into lower rays (FIGS. 9–12) which become laterally displaced in the outer secondary xylem during increase in the circumference of the cambium. During the outward extension of the rays, their cells become more or less conspicuously modified in size, form, and orientation. In the first-formed part of the rays, at least in some stems, the cells tend to be more or less vertically elongated or "erect" whereas in subsequently formed parts of the rays they become more nearly isodiametric or radially elongated, i.e. "procumbent." At times the rays, as in *Pereskia sacharosa,* may have more or less numerous erect cells along their sides and margins (FIGS. 9 and 11). In outer secondary xylem, the rays of roots (FIGS. 10 and 12) usually are conspicuously broader than in comparable secondary xylem of stems (FIGS. 9 and 11).

In *Pereskia grandifolia* and *P. bleo,* as in *P. sacharosa,* the multiseriate rays of the stem have lignified secondary walls throughout their extension. They commonly contain more or less abundant starch. When crystals of calcium oxalate occur within them, they occur singly or as a few independent ones; aggregation into druses, such as occur characteristically in the unlignified parts of the multiseriate rays of *P. aculeata* Mill. (Bailey, 1962) and *P. conzattii* (Bailey, 1963), being absent.

The multiseriate rays in roots of *Pereskia grandifolia* and *P. bleo,* as in the roots of *P. sacharosa,* commonly are lignified throughout. However, in some cases the innermost parts of the first-formed rays of the three species are composed of parenchymatous cells having thin unlignified walls (FIG. 15). In the limited number of specimens available to me, these parts differ from the unlignified ray tissue of *P. aculeata* and the unlignified parenchyma in roots of the Andean pereskias in being devoid of druses of calcium oxalate. The cells contain little if any starch but are packed with isotropic granular contents. The granules which vary considerably in size and form give a red color in Millon's reagent and a positive cytochemical coloration for protein in mercuric bromophenol blue (FIG. 16). For a description of the latter test see Mazia, Brewer and Alfert (1953). These tests suggest that the granules may be at least partly of proteinaceous composition.

It is of interest in this connection that Molisch (1885) found protein bodies of highly diversified forms in the parenchymatous cells of stems of *Epiphyllum*. He considered them to be reserve substances, whereas Chmielewsky (1887) subsequently concluded that they are products of excretion. However, the latter investigator agreed with Molisch that the protein bodies are formed in the protoplasm of living cells rather than in vacuoles or plastids.

In living cells of *Epiphyllum* the protein bodies occur in highly diversified forms of spindles, rings, and slender filaments variously contorted and aggregated. When sections containing living cells are transferred to hydrochloric, sulphuric, nitric, and acetic acids, ammonia, potassium hydroxide, or glycerin, the protein bodies are stated to contract, expanding laterally to form spheres which ultimately dissolve after more or less prolonged treatments. All of my specimens of stems and roots of *Pereskia*, *Pereskiopsis*, and *Quiabentia* were preserved by collectors in formalin-acetic-alcohol fixative. This raises the question whether the globular bodies illustrated (in FIG. 16) were derived during fixation from filamentous forms.

In sections of roots which contain globular bodies in the first-formed unlignified cells of the multiseriate rays many of the vessels in the xylem contain filamentous forms of protein bodies. They also occur in vessels of the stems of *Pereskia sacharosa*, *P. grandifolia*, *P. bleo*, and *P. tampicana* Web. The more slender filaments which grade down to less than half a micron in diameter may be diffusely distributed in the lumen of a vessel (center of FIG. 13) or aggregated in compact masses (FIG. 13, lower left and upper right). These filaments and their aggregations resemble those that occur in living cells of *Epiphyllum* (Molisch, figs. 3 and 5). In *Epiphyllum* the individual filaments may attain a length of 2.4 millimeters, but are variously contorted within the confines of a single cell. In my material individual threads commonly attain equivalent lengths but pass longitudinally through the lumina of a number of contiguous vessel members. Short, broad, spindle-shaped bodies of the forms illustrated by Molisch (figs. 1 and 4) are of relatively infrequent occurrence in vessels, but coarse strands of varying diameter are frequently present (FIG. 14 center). Such strands up to 10 micra in diameter may at times extend longitudinally in the lumen of a vessel for a distance of more than two millimeters. Granular forms of protein bodies are of infrequent occurrence in the vessels of *P. sacharosa*, *P. grandifolia*, *P. bleo* and *P. tampicana*, but may be present in parenchyma adjacent to vessels which contain filamentous forms. Furthermore, filamentous, stellate, and other forms of protein bodies occur in the phloem parenchyma of these four species of *Pereskia*. Such occurrences as these in different parts of a single transverse or longitudinal section make it difficult to conclude that the globular forms are necessarily due to changes that occurred during fixation in F.A.A. It should be noted in this connection that Chmielewsky found that the solubility of protein bodies of *Epiphyllum* in 10% NaCl is inhibited after prior fixation in alcohol.

In my extensive collections, filamentous forms of protein bodies do not occur in the vessels of other pereskias, nor in those of *Pereskiopsis* and *Quiabentia*.

CONCLUSIONS

Pereskia sacharosa, *P. grandifolia*, *P. bleo*, and *P. tampicana* form a group of species characterized by a constantly distinctive form of sclerenchyma in their secondary phloem (Bailey, 1961). A conclusion that this structural similarity is *not* due to parallel or convergent evolutionary changes in distantly related species is strengthened by evidence presented in this paper. The structure of the xylem is remarkably similar in the stem and roots of the four species, and the multiseriate rays exhibit much less conspicuous phylogenetic trends of specialization than in other pereskias. Furthermore, the occurrence of filamentous forms of protein bodies in the vessels of these four species appears to be an additional indication of relatively close genetic relationship.

Preliminary observations indicate that globular forms of proteinaceous bodies occur at times in the parenchyma of the xylem and phloem of other pereskias. The occurrence of protein bodies of diversified forms is of considerable significance from cytological, biochemical, and physiological, as well as purely taxonomic points of view. For example, are protein bodies formed by protoplasm, which persists during late stages of maturation of vessels or do they intrude into the lumina from jacketing parenchyma? More extensive and detailed investigations starting with living tissues will be initiated and reported upon in a subsequent paper of this series.

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EXPLANATION OF PLATES

PLATE I

FIGS. 1–4. Transverse sections of the secondary xylem, × 11. 1, Stem of *Pereskia grandifolia* [*Castellanos*]. 2, *The same*, root. 3, Stem of *P.* aff. *bleo* [*Rodríguez 640*]. 4, *The same*, root.

PLATE II

FIGS. 5, 6. Transverse sections of first-formed and outer secondary xylem of stems, × 34. 5, First-formed secondary xylem of *Pereskia bleo* [Atkins Gard.]. 6, Outer secondary xylem of *P.* aff. *bleo* [*Rodríguez*].

PLATE III

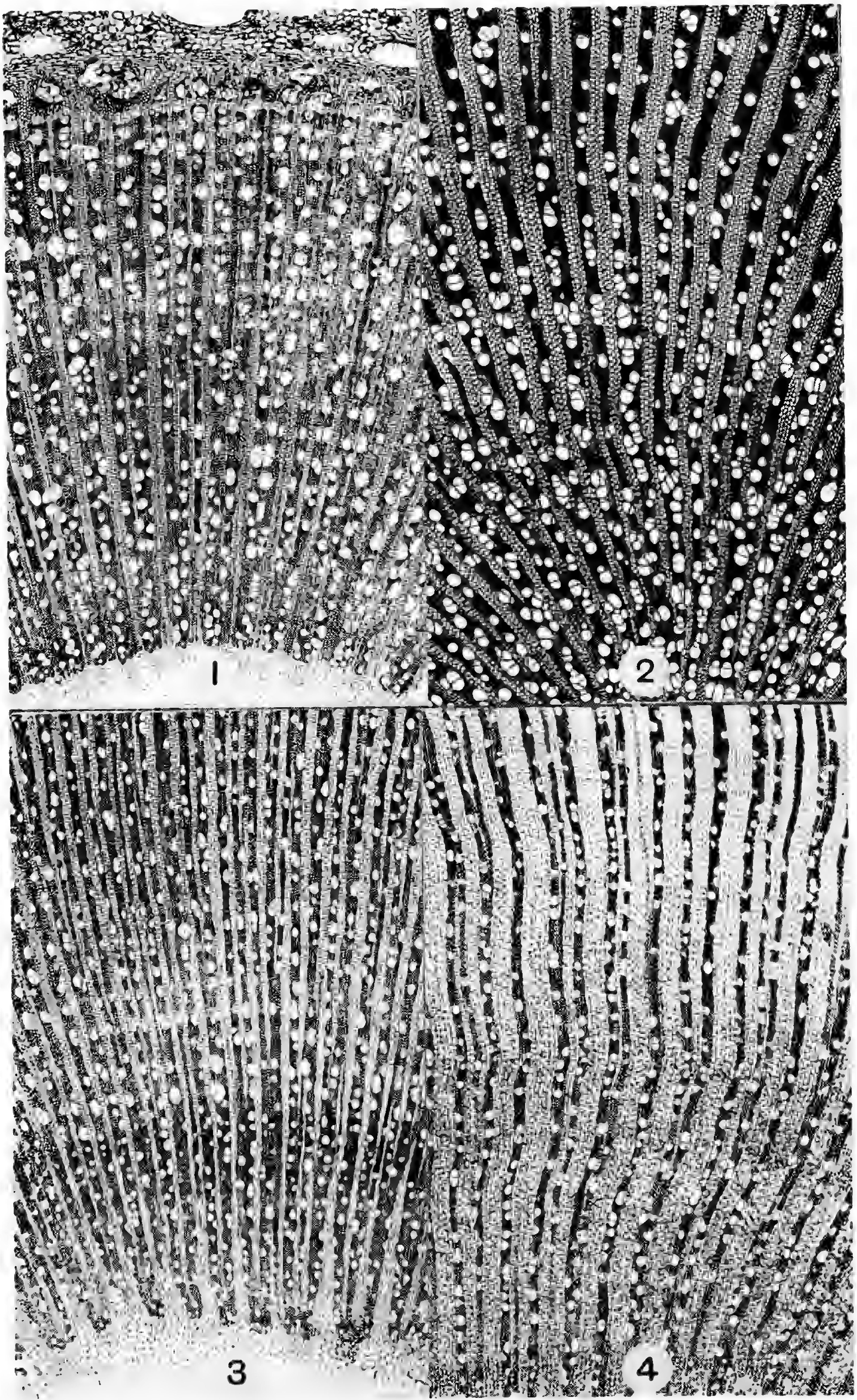
FIGS. 7, 8. Transverse sections of first-formed and outer secondary xylem of stems, × 34. 7, First-formed secondary xylem of *Pereskia grandifolia* [*Steyermark*]. 8, *The same*, outer secondary xylem showing zonation due to varying intensities of lignification.

PLATE IV

FIGS. 9–12. Tangential longitudinal sections of secondary xylem, × 43. 9, Stem of *Pereskia* aff. *bleo* [*Rodríguez 640*]. 10, *The same*, root. 11, Stem of *P. grandifolia* [*Castellanos*]. 12, *The same*, root.

PLATE V

FIGS. 13–16. Longitudinal and transverse sections of stems and roots. 13, *Pereskia grandifolia* [*Castellanos*], longitudinal section of a stem showing slender filamentous forms of "protein bodies"; long individual filaments, center; compact aggregations of shorter filaments, lower left and upper right, × 510. 14, *The same*, showing coarser strands of "protein bodies," × 510. 15, *P.* aff. *sacharosa* [*Cárdenas*], transverse section of the central part of a root treated with phloroglucin-HCl, showing unlignified part (white) of first-formed multiseriate rays, × 34. 16, *P. grandifolia* [*Steyermark*], transverse section of the unlignified inner part of a multiseriate ray, showing granular forms of "protein bodies," × 510.



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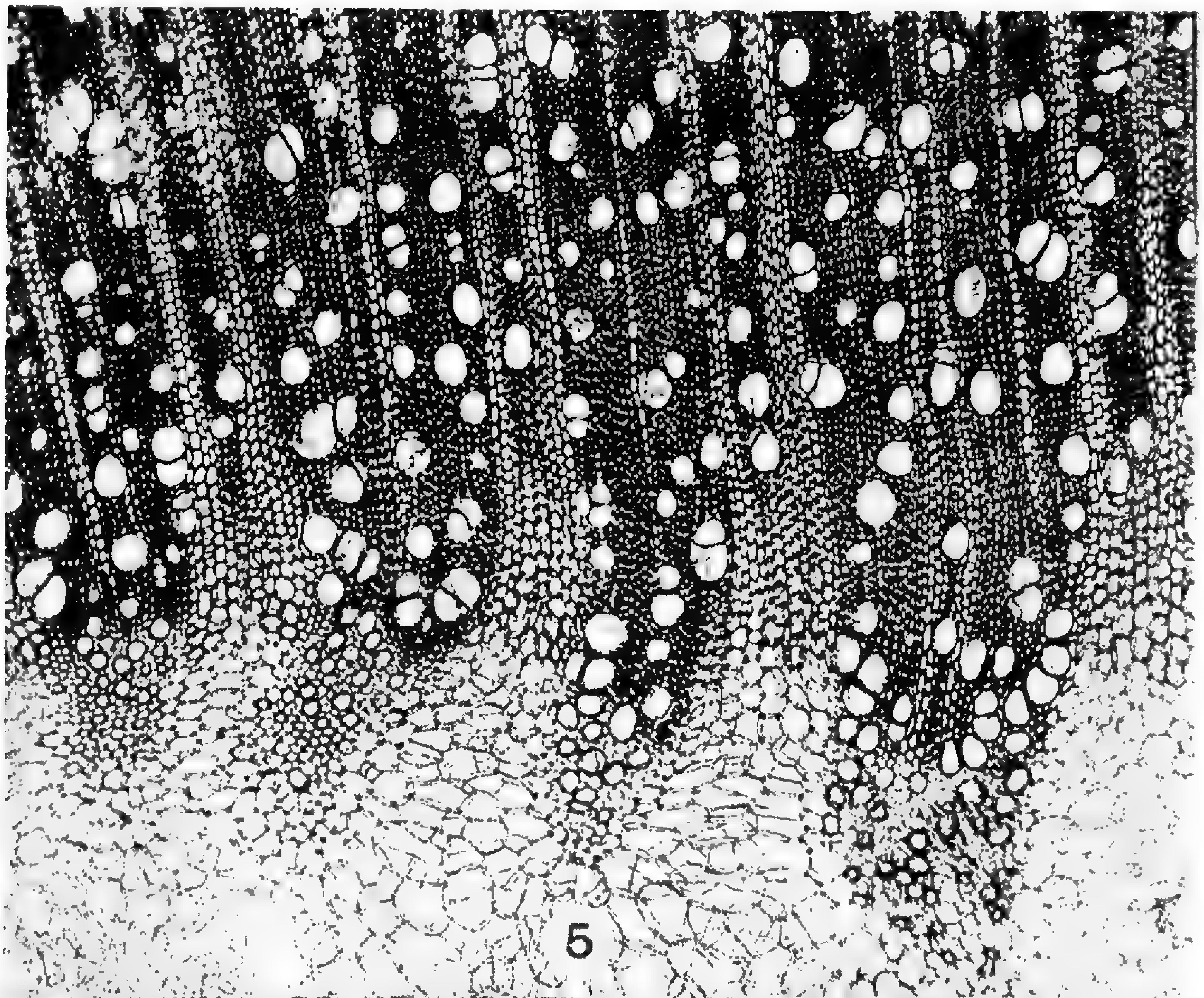

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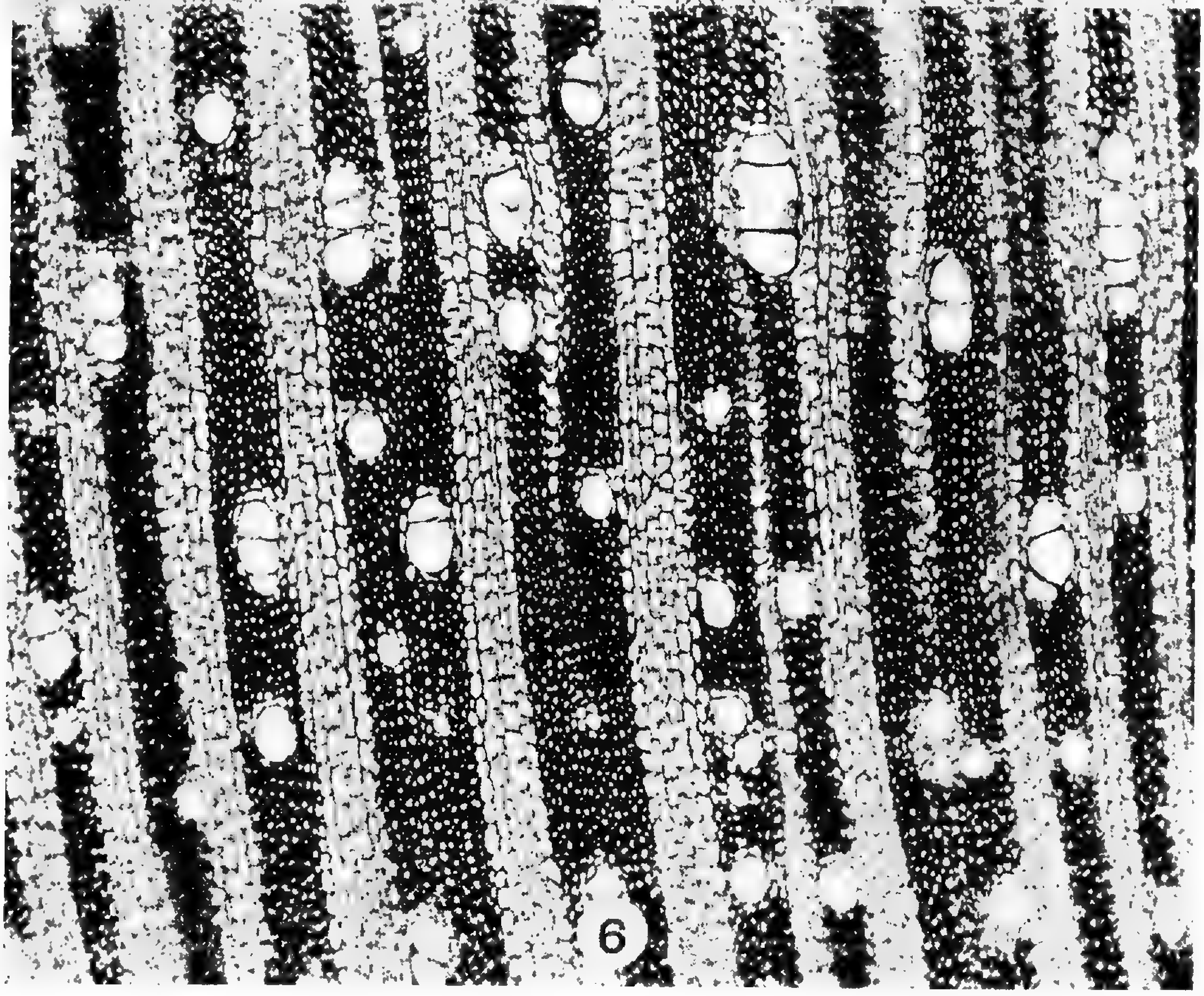

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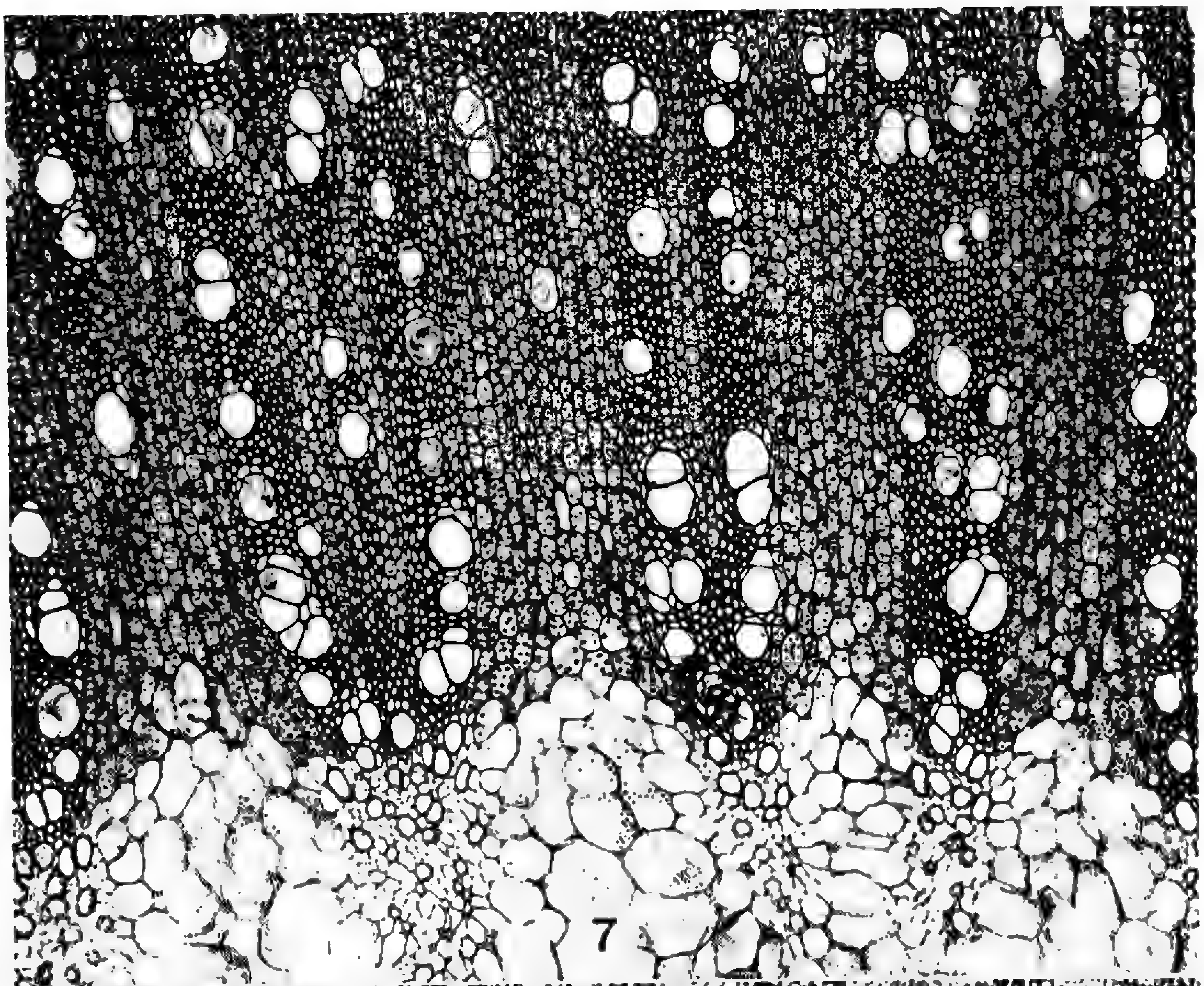

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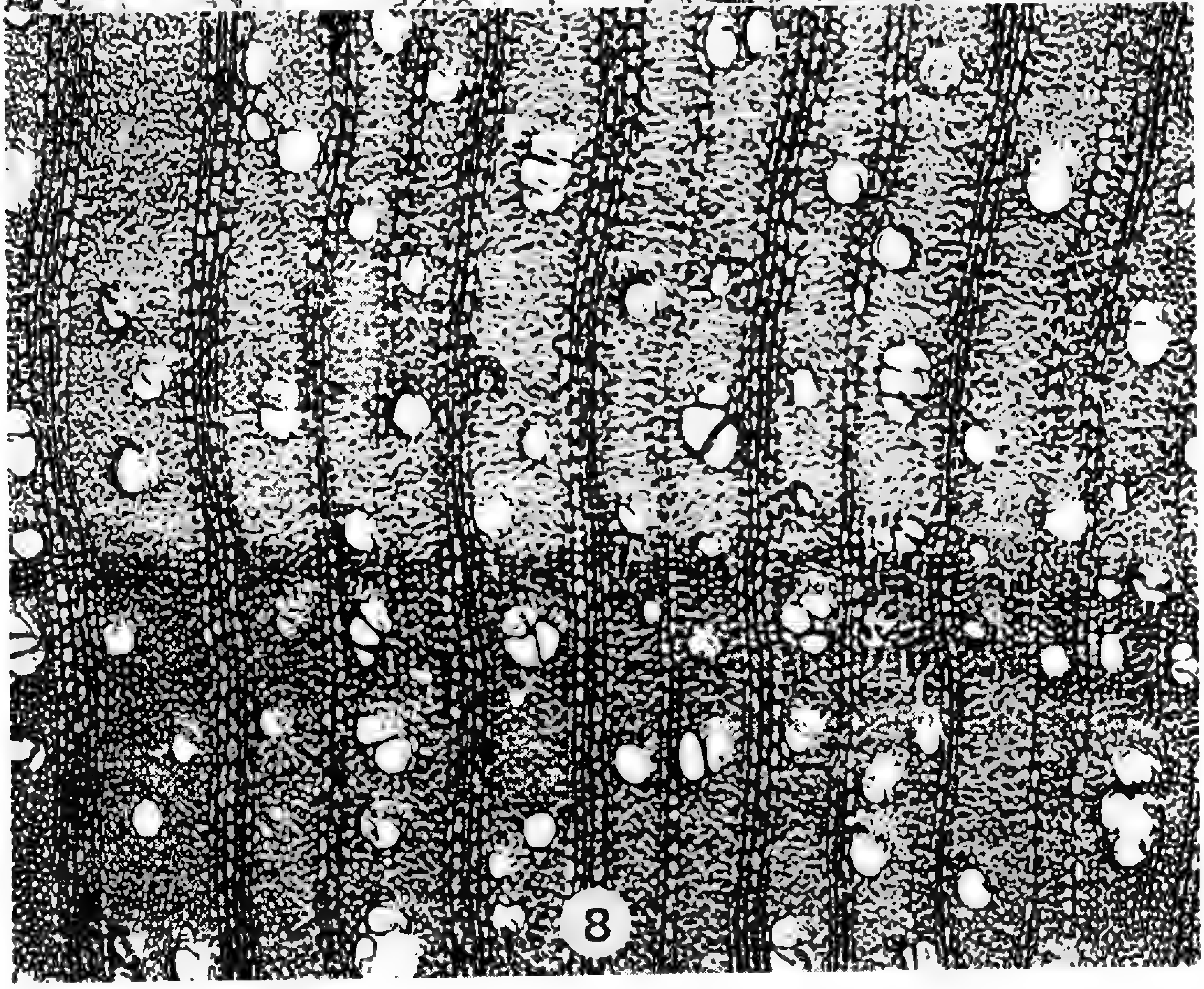

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BAILEY, LEAF-BEARING CACTACEAE, IX

PLATE IV

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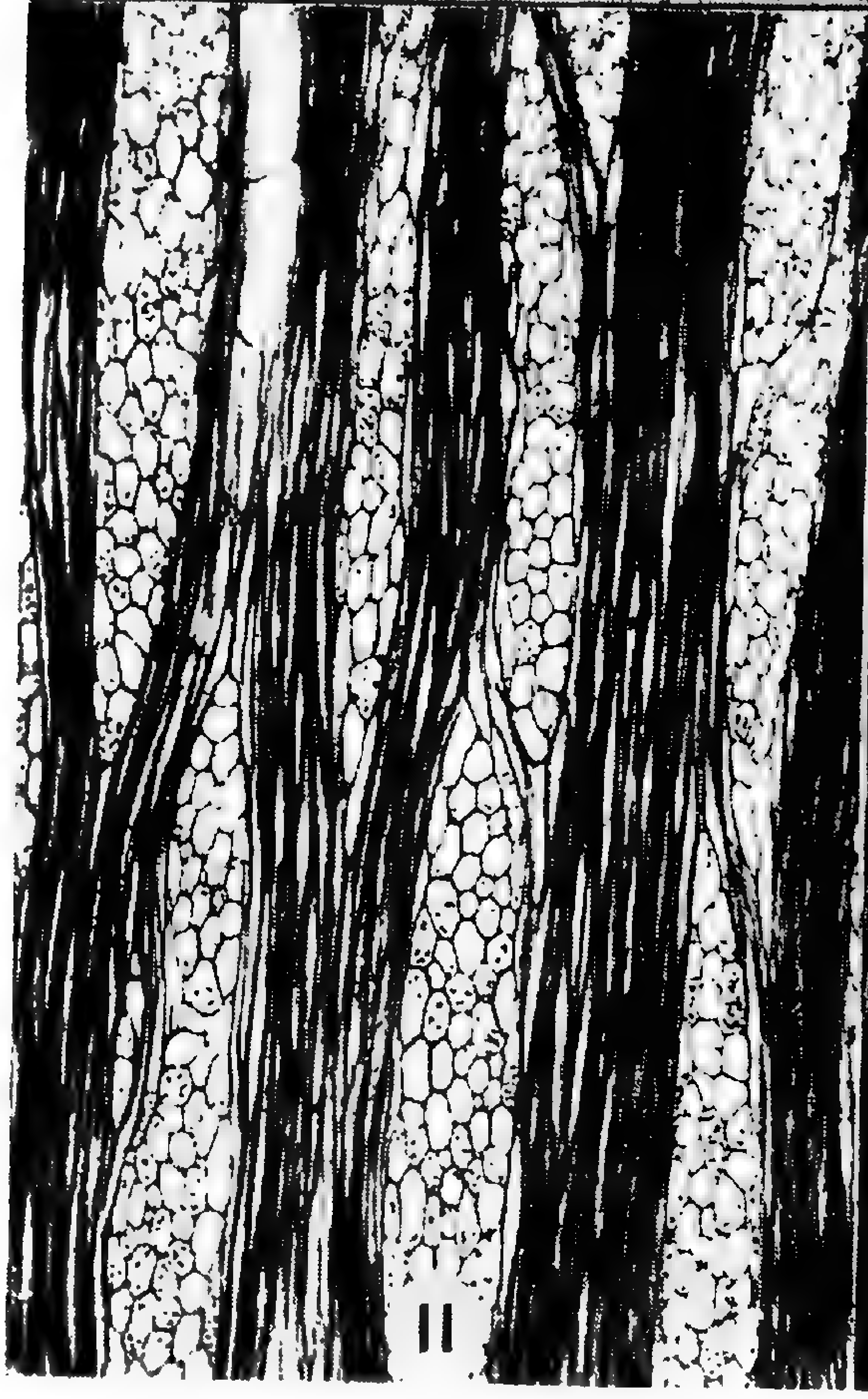

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BAILEY, LEAF-BEARING CACTACEAE, IX

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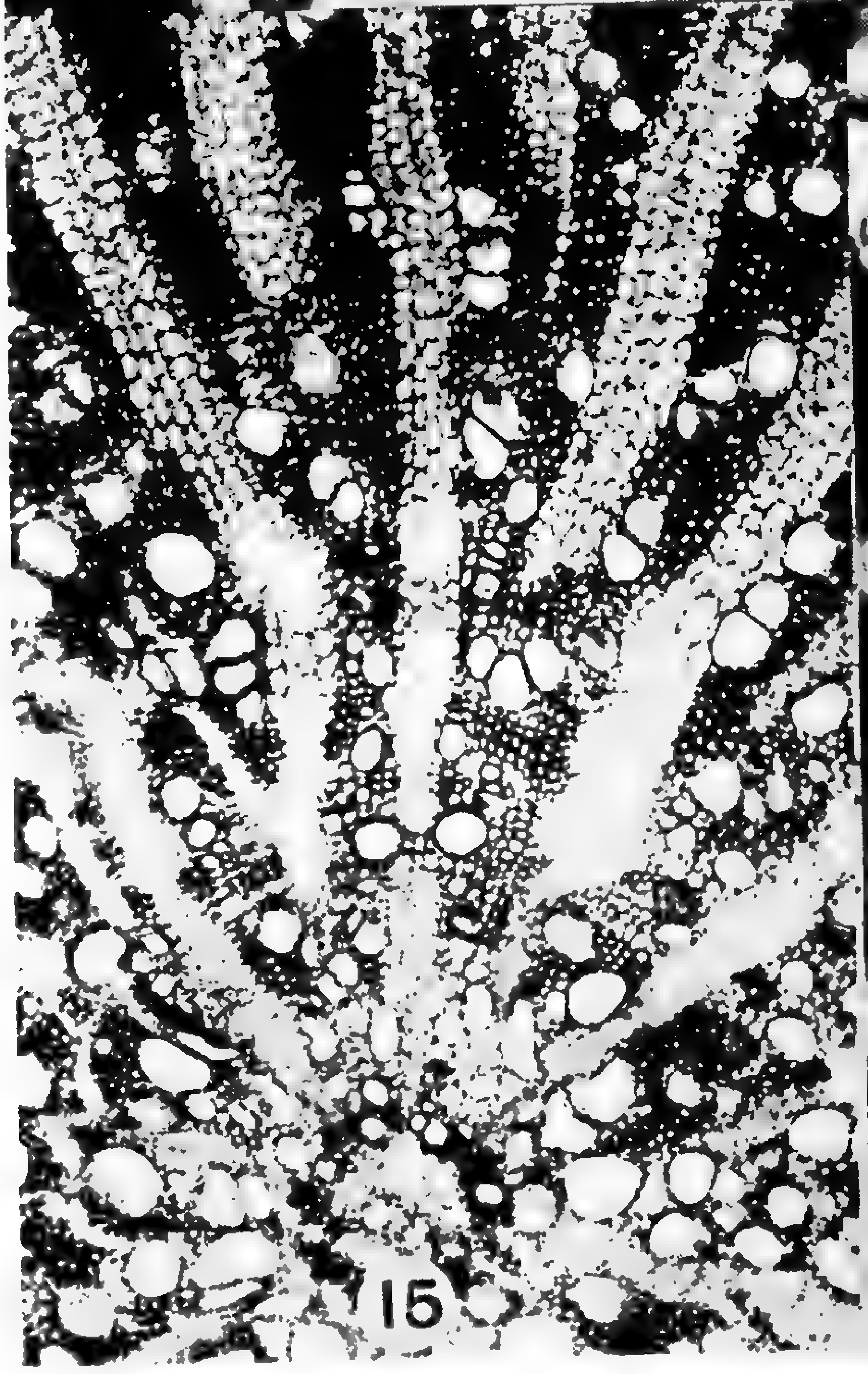

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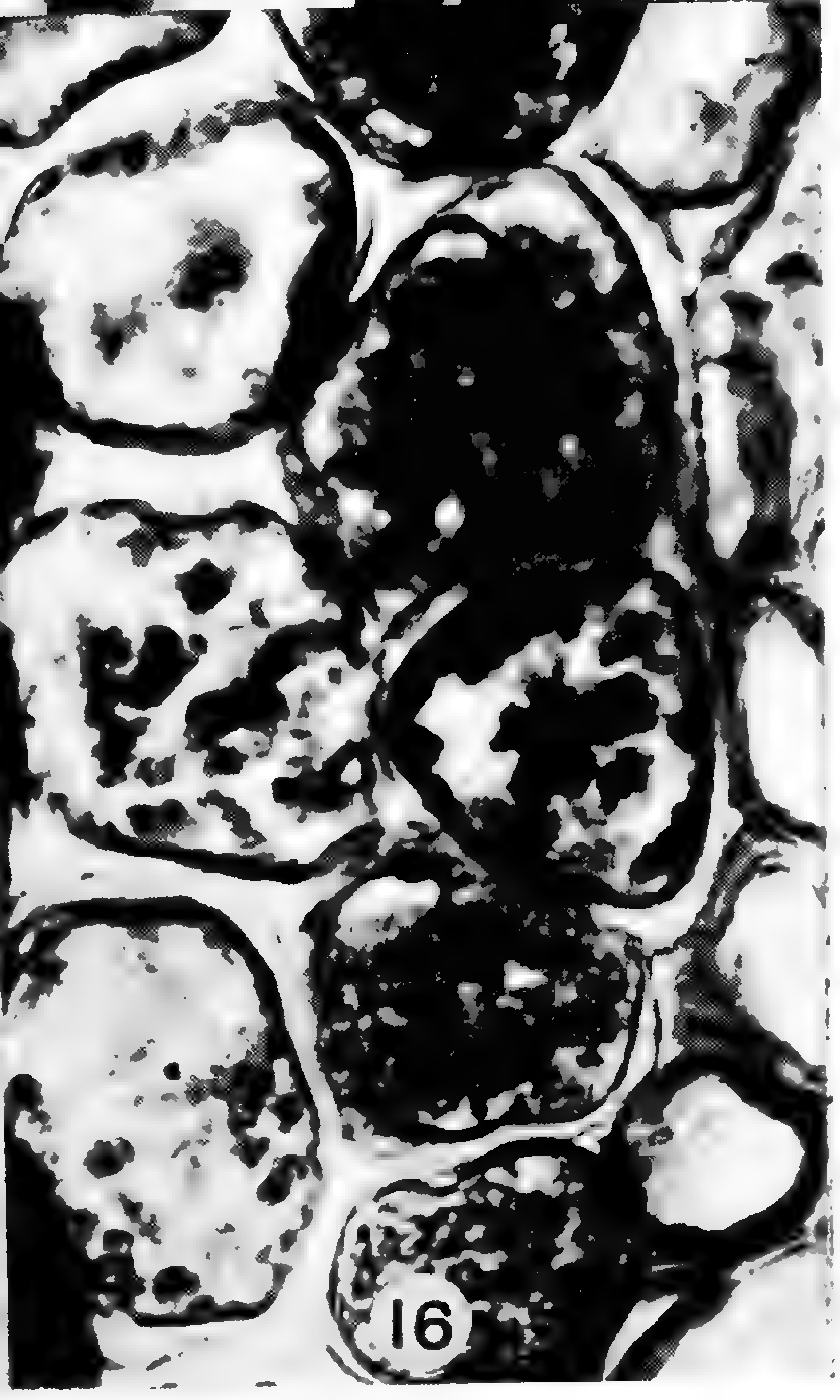

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BAILEY, LEAF-BEARING CACTACEAE, IX

THE RUBIACEOUS GENUS MUSSAENDA: THE SPECIES OF INDIA AND CEYLON

DON M. A. JAYAWEERA

IN A PREVIOUS PAPER,[1] *Mussaenda*, a genus of the Rubiaceae including some 190 species of the tropics of the Old World, was treated from the morphological point of view with special emphasis on the characteristics and range of variability of the Asiatic species. In the present paper, the species of India and Ceylon are treated from a taxonomic standpoint, and, in a paper to follow, the species of the Philippine Islands will be similarly considered.

Of the fifteen species treated in this study only two are found in Ceylon, one of them being endemic. The other species are distributed in the Western Ghats and neighboring hills and in the Himalayan range in India and Assam. Between these two areas there is a wide gap extending from West Pakistan to Orissa and Andhra Pradesh in which the genus does not occur at all. The species growing in the Western Ghats are of the *Mussaenda frondosa* group with somewhat diffuse inflorescences. Those growing in the Himalayan range belong to the *Mussaenda roxburghii* group with generally compact inflorescences. The plants of both groups bear tufted hairs in the mouth of the corolla tubes, an essentially Indian character. *Mussaendra glabra*, with a very wide range, has its center of distribution in the East Indies, extending to India through Malaysia, and seems to mix freely with indigenous species as shown by the presence of *M. glabra* characters observed in them.

Two new species are described in this paper: *Mussaenda samana*, from Ceylon, and *M. intuspilosa*, from Assam and Burma. These two species were considered by previous workers as within the limits of *M. glabrata* and *M. glabra* respectively. *Mussaenda pentasemia* Fischer is reduced to the status of a form of *M. macrophylla* Wall. var. *macrophylla*.

The characters of the stipules, hairiness within the corolla tube, and the spininess of the seed are used for the first time in the classification of the species. Heterostyly and its association with the hair-length in the corolla tube are amply demonstrated in all species studied.

Since a description of the genus with a discussion of the characters used was given in my previous paper,[1] a repetition here would be redundant. For the sake of brevity, citation of the dates of the collections examined is deliberately omitted and the field notes of collectors are summarized under the distribution of each species. The geographical subdivisions and arrangement of specimen citations are essentially as given on the labels

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[1] The rubiaceous genus *Mussaenda*: Morphology of the Asiatic species. Jour. Arnold Arb. **44**: 111–126. 1963.

and have not been changed to conform with modern political boundaries.

I am very grateful to the officers of the institutions from which material was borrowed for my study. The institutions, indicated in the citations of specimens by the standard abbreviations of Lanjouw and Stafleu, are those cited by me in the first paper.

ARTIFICIAL KEY TO THE SPECIES OF MUSSAENDA IN INDIA AND CEYLON

A. Calyx lobes equal, none enlarged into petaloid sepals; branchlets and leaves densely soft white-tomentose; leaves 4.5–7.5 cm. long; stipules 0.4–0.6 cm. long, lanceolate, deeply bifurcate at apex into two subulate lobes; cymes sessile, flowers large; corolla tube 2–2.5 cm. long, velvety, broad at the top, lobes orbicular; berry obovoid, 9 mm. long, puberulous, with persistent calyx teeth; seeds 0.7–0.72 mm. long, testa with 3–10 foveae in each areole. . . . . 1. *M. tomentosa.*

A. Calyx lobes unequal, one calyx lobe enlarged in some flowers to form a petaloid sepal.

- B. Calyx lobes persistent or subpersistent on the fruit.
  - C. Inflorescence glabrous, cymes almost capitate with filiform calyx lobes.
    - D. Leaves glabrous above, densely tomentose beneath, thick and leathery, 9.5–23.5 cm. long; stipules 1.6 cm. long, very broad, ovate, hairy along the midline of the outer surface, many-veined; calyx lobes scantily pubescent; corolla lobes small, lanceolate; berry ovoid 8 mm. long, seeds 0.36–0.46 mm. long, testa with 2–5 foveae in each areole. . . . . 11. *M. keenanii.*
    - D. Leaves glabrous above and minutely puberulous beneath, 8–16.5 cm. long; stipules large, 1.3–1.8 cm. long, hairy along the midline of the outer surface, glands numerous in a continuous band at the base within; calyx lobes glabrous; corolla lobes ovate-lanceolate; berry (immature) oval, 7–8 mm. long, seeds (immature) 0.43–0.46 mm. long, testa with 4–7 foveae in each areole. . . . . 10. *M. corymbosa.*
  - C. Inflorescence a crinite softly tomentose or villous cyme; stipules triangular, acuminate, hairy on the outer surface.
    - E. Corolla tube completely hairy within, tufted at the base, 2.4–2.8 cm. long, lobes oblong-lanceolate; inflorescence a somewhat capitate cyme; calyx lobes lanceolate-filiform, glabrous within with a tuft of hairs at the base; leaves 9–28 cm. long, oblong-lanceolate; stipules 0.75–2.3 cm. long, hairy within at the base; berry 8–13 mm. long; seeds 0.6–0.67 mm. long, testa with 4–10 foveae in each areole. . . . . 9. *M. roxburghii.*
    - E. Corolla tube not completely hairy within, glabrous at the base, 2–2.3 cm. long, lobes ovate-lanceolate, acuminate; cymes subsessile, densely hairy; calyx lobes linear, hairy; leaves 3.5–11(–18) cm. long, ovate-oblong, densely villous on both surfaces, almost sessile; stipules 0.7–0.95 cm. long, tapering from a broad base, glabrous within, with few glands; berry 13–15 mm. long; seeds 0.9–1.16 mm. long, testa with 2–7 foveae in each areole. . . . . 7. *M. incana.*

B. Calyx lobes deciduous from the fruit.

F. Seeds spiny.

G. Calyx lobes very small, 0.12–0.35 cm. long, lanceolate-acuminate; leaves 4–9.2 cm. long, glabrous on both surfaces; stipules 0.35–0.55 cm. long, bifid at apex, appressed pubescent; corolla tube 2.1–3.1 cm. long, lobes broadly lance-ovate; berry ovoid, 13–15 mm. long, seeds 0.83–1.33 mm. long, testa with 4–12 foveae in each areole. . . . . 14. *M. samana.*

G. Calyx lobes large, 0.55–1.1 cm. long, linear; leaves 5.5–10.5 cm. long, glabrous above, minutely villous only on nerves beneath, nerves conspicuous, transverse nervules parallel; stipules 0.5–0.6 cm. long, hairy on the outer surface, glabrous within except at the base, bifurcate from apex ⅖–½ their length; corolla tube 2.5–3.3 cm. long, hairy, lobes orbicular-ovate; berry obovoid, 10–12 mm. long, seeds 0.7–0.77 mm. long, testa with 4–11 foveae in each areole. . . . . 3. *M. glabrata.*

F. Seeds not spiny.

H. Leaves glabrous on both surfaces.

I. Corolla tube hairy within with a tufted ring of hairs at the base, 2.5–3 cm. long, hairs long in both long-styled and short-styled forms, lobes lanceolate, 4.5–8 mm. long, acuminate; calyx lobes 0.45–0.9 cm. long; berry (immature) small, 7.5–9 mm. long, glabrous or pubescent, seeds 0.53–0.73 mm. long, testa with 3–10 foveae in each areole. . . . . 12. *M. intuspilosa.*

I. Corolla tube hairy within as far as the bases of the anthers, 1.4–2.5 cm. long, hairs short in long-styled forms, lobes short, lanceolate, broadly ovate or orbicular; calyx lobes short, 0.1–0.75 cm. long; berry ovoid-elliptic, 10–12 mm. long, glabrous; seeds 0.67–0.83 mm. long, testa with 2–7 or 3–14 foveae in each areole. . . . . 15. *M. glabra.*

H. Leaves minutely or densely pubescent on one or both surfaces.

J. Stipules large 1–1.4 cm. long, ovate, densely hairy on both surfaces or on the outer surface only, bifid or bifurcate from apex ⅙–½ their length with numerous or few glands at the base.

K. Calyx lobes broadly oblong-lanceolate, 0.85–1.4 cm. by 0.12–0.4 cm.; leaves 8–20 cm. long, broadly elliptic, minutely hairy on the upper surface, hirsute beneath with 9–11 pairs of lateral veins, stipules 1.2–1.35 cm. long; corolla tube 2.4–3.2 cm. long, hairy, lobes broadly ovate or orbicular, acute; berry broadly ellipsoid, 10–12 mm. long, sparsely hirsute with a broad nectariferous disc, seeds reticulate, 0.9–1.03 mm. long, testa with 2–6 foveae in each areole. . . . . 5. *M. macrophylla.*

K. Calyx lobes linear or linear-lanceolate, subulate.

L. Leaves scantily pubescent with short hairs on both surfaces, 7.5–23 cm. long, ovate or elliptic-ovate, acuminate, cuneate with 8–10 pairs of lateral veins, calyx lobes linear, setose-ciliate, glabrous on the inner surface; corolla tube 2.9–3 cm. long; berry 10–13 mm. long, globular, glabrescent; seeds 1.1 mm. long, testa with 2–10 foveae in each areole. . . . . 6. *M. treutleri.*

L. Leaves densely hirsute with long hairs on both surfaces, 4.5–11 cm. long, ovate-elliptic to elliptic-lanceolate with 7–9 pairs of lateral veins, petiole very short and hirsute; calyx lobes lanceolate, hirsute on the outer surface, glabrous on the inner surface with a tuft of hairs at the base of each lobe; corolla tube 2.3–3.2 cm. long, lobes ovate; berry globose, 12 mm. long, sparingly hirsute; seeds 1.1–1.16 mm. long, testa with 4–8 foveae in each areole. . . . . 8. *M. hirsutissima.*

J. Stipules small, 0.35–1 cm. long.

- M. Seeds few (about 80) in the fruit; leaves 8–15.5 cm. long, elliptic, scantily long haired on both surfaces with 7–9 pairs of lateral veins; stipules 0.4–0.67 cm. long, lanceolate, hairy on the outer surface, bifurcate from apex more than ½ their length; cymes sessile, pubescent; calyx lobes linear-ensiform; corolla tube 2.1–2.5 cm. long, lobes suborbicularly ovate; berry 7–8 mm. long, subglobose, scantily pubescent; seeds few, reticulate, 0.9 mm. long, testa with 5–18 foveae in each areole. 13. *M. parryorum.*
- M. Seeds numerous (several hundred) in the fruit.
  - N. Leaves loosely pubescent on both surfaces, broadly ovate, 6–12 cm. long with 7–9 pairs of lateral veins; stipules 0.45–1 cm. long, glabrous inside, bifurcate from apex ⅔–½ their length, lobes curved outwards; inflorescence a lax cyme; corolla tube 2.5–3.2 cm. long, lobes ovate, caudately acuminate; berry obovoid, 10–12 mm. long, sparsely hirsute; seeds 0.67–0.76 mm. long, testa with 4–9 foveae in each areole. . . . . . . 4. *M. laxa.*
  - N. Leaves densely and softly hirsute especially beneath, variable in shape, 4.4–13 cm. long with 6–10 pairs of lateral veins; stipules 0.35–0.65 cm. long from a broad base, hairy on both surfaces, bifurcate from apex ¼–¾ their length, lobes erect; cyme densely hirsute; corolla tube 2–2.7 cm. long, lobes broadly ovate, apiculate; berry nearly globose, 10 mm. long, slightly scabrous; seeds 0.6–0.8 mm. long, testa with 3–10 foveae in each areole. . . . . 2. *M. frondosa.*

1. **Mussaenda tomentosa** Wight in Wall. Cat. 6265. 1832 (TYPE: *Wallich 6265*).

Erect or straggling shrub with pubescent, lenticellate stems; internodes 2.3–4 cm. long, hairy. Leaves 4.5–7.5 cm. long, 2.2–4.5 cm. broad, velvety-tomentose on both surfaces, more densely so beneath, ovate-elliptic or -lanceolate, acute or obtuse, narrowed at the base, with 6–10 pairs of lateral veins; petiole 1–1.3 cm. long, velvety. Stipules lanceolate, 4–6 mm. long, about 2 mm. broad, hairy on both surfaces, deeply bifurcate at apex, lobes subulate. Inflorescence cymose, terminal and with axillary cymes from the terminal pair of leaves extending beyond the primary cyme, contracted, with no petaloid sepals; bracts and bracteoles elongated, subulate, hairy on both surfaces, caducous, bracteoles trilaciniate, lobes linear. Flowers large, on stout, hairy pedicels shorter than the ovaries. Calyx lobes linear, subulate, 6–12 mm. long, 1 mm. broad, hairy on both surfaces. Corolla tube 2–2.5 cm. long, hairy on both surfaces, hairs tufted at the mouth; corolla lobes somewhat orbicular, 8 mm. long and broad, apiculate, acute, hairy on the outer surface, papillate within. Ovary 3.5 mm. long, broadly obconic-fusiform, hairy, stigma lobes emerging beyond the mouth through the tuft of hairs (long-styled form). Berry obovoid, about 9 mm. long, 6 mm. in diameter, puberulous, with persistent calyx teeth; seeds minute, reticulate, oblong, oval or triangular-ovate, 0.7–0.72 mm. long, 0.5 mm. broad, testa with 3–10 foveae in each areole.

DISTRIBUTION. This species grows in the Gingee Hills of Arcot, among rocks in the shade, and along the Western Ghats at Kannikatti, Tinnevelly, between 500 and 750 meters elevation.

India. CARNATIC: *Wallich 6265* (K–holotype); *Herb. Wight 1271A* (K).

Only two specimens, one of which is the type, were available for examination. Both collections are of the long-styled form. The presence of long hairs tufted at the mouth of the corolla tube indicates that this species belongs to the *Mussaenda frondosa* group in which throat hairs in both long-styled and short-styled forms are long and equal in length. It is safe to infer that heterostyly exists in the species.

Mussaenda tomentosa may be distinguished by its sessile cymes without petaloid sepals, velvety tomentum on stems and leaves, deeply bifurcate lanceolate stipules hairy on both surfaces, and obovoid fruits with persistent calyx segments.

2. **Mussaenda frondosa** L. Syst. Nat. ed. 10. 2: 931. 1759 (TYPE: *Hermann*). FIGS. 1, O, and 4.

M. fr[uctu] frondoso L. Sp. Pl. **1**: 177. 1753.
M. zeylanica, flore rubro, fructu oblongo, polyspermo, etc. Burm. Thesaurus Zeyl. 165. *pl. 76.* 1737.
M. formosa L. Mantissa Pl. ed. 6. 45. 1767.
M. fruticosa L. Syst. Nat. ed. 12. 168. 1767.
M. sumatrensis Roth, Nov. Pl. Sp. Indiae Orient. 152. 1821.
M. flavescens Buch.-Ham. Trans. Linn. Soc. **14**: 203. 1824.
M. dovinia Buch.-Ham. *ibid.*
M. belilla Buch.-Ham. *ibid.*
M. macrophylla sensu Kurz, Forest Fl. Brit. Burma **2**: 57. 1877, non Wallich.
M. ingrata Wall. ex Hook. f. Fl. Brit. India **3**: 89. 1880.
M. tomentosa Wight ex Hook. f. *ibid.* 88.
M. villosa Wall. ex Hook. f. *ibid.* 91.
Cercophyllum grandiflorum Meyen, Reise um die Erde **2**: 234. 1835.

Scandent shrub; young stems hirsute, curving gracefully over other shrubs, older stems glabrate, reddish or blackish brown, lenticellate. Leaves opposite, lamina ovate, elliptic, orbicular, lanceolate, oblong or obovate, 4.4–13 cm. long, 2–8.3 cm. broad, short-acuminate, acute, base cuneate, obtuse or rounded, rather scantily hirsute on the upper surface, densely and softly white tomentose on the lower surface; primary lateral veins

6–10 pairs, more prominent on the lower surface and more hairy; petiole 0.35–2.1 cm. long, densely hirsute with gray or brownish hairs. Stipules 3.5–6.5(–9.5) mm. long, oblong-ovate, broadly triangular or oblong from a broad base narrowing toward the apex and bifurcate 1/4–3/4 their length, lobes straight, not curved, hairy on both surfaces, with few to many glands in two groups at the base inside. Inflorescence terminal, of small, contracted, dichotomously branched, densely hirsute, few-flowered cymes; bracts and bracteoles subulate, pubescent and caducous, bracteoles trifid. Flowers heterostylous, on stout, pubescent pedicels as long as the ovaries. Calyx lobes deciduous, narrowly linear, 6.5–15 mm. long, 0.5–1.5 mm. broad, pubescent on the outer surface, usually glabrous within (rarely pubescent) with one pair of glands at the base of each; petaloid sepal creamy white, ovate or oblong-ovate, 3.7–12 cm. long, 2.2–8.9 cm. broad, acuminate, subacute at apex, short or long attenuate or cuneate at base, puberulous on the upper surface, hirsute below, 3- or 5-veined, hairs denser on veins, "petiole" 0.9–2.5 cm. long, hirsute. Corolla tube 2–2.7 cm. long, hairy on the outer surface, hairs denser toward the broader apex, densely hairy within as far as the bases of the anthers, lower down scantily short hairy, as far as 1/10–1/4 of the tube from the base, hairs ligulate, linear, 1.2–1.5 mm. long in both long-styled and short-styled forms, tufted at the mouth, shorter below the anthers; corolla lobes broadly ovate, 3–4.5 mm. long, 4–5 mm. broad, apiculate, hairy on the outer surface, papillate within. Stamens with short filaments inserted 1/2 way on the tube in long-styled forms, 3/4 way up in short-styled forms; anthers linear, dorsifixed, introrse, 4.5–5.5 mm. long, bilobed at the sterile base, pollen grains of short-styled forms larger. Ovary 3–4 mm. long, obconical or turbinate, hairy, 2-locular, with numerous ovules on cushion-shaped axile placentae; style and stigma lobes 1.6–2.5 cm. and 2–5.5 mm. long respectively in long-styled forms, 1–1.5 cm. and 2.5–4 mm. long in short-styled forms. Berry nearly globose, 1 cm. long, sparsely hirsute; seeds minute, reticulate, 0.6–0.8 mm. long, 0.5–0.6 mm. broad, somewhat rounded or pyriform, albuminous, testa with 3–10 foveae in each areole; germination epigeal.

ILLUSTRATIONS. Burmann, Thesaurus Zeyl. *pl. 76.* 1737; Lindley, Bot. Reg. 6: *pl. 517.* 1820; Wight, Illust. Indian Bot. 2: *pl. 124.* 1850; Beddome, Fl. Sylv. S. India 2(Anal. Gen.): *pl. 16, fig. 3.* 1873.

DISTRIBUTION. The actual geographical range of this species is in doubt. Merrill (1910) says that "none of the Ceylon material matches any of our Philippine specimens and our Philippine specimens apparently closely match some Javan and Caroline Islands material distributed as *M. frondosa* Linn. and *M. glabra* Vahl." Further he says that "the typical form of the Linnaean species does not extend to the Archipelago." These observations are confirmed by an examination of collections from the Malayan Archipelago and the Pacific Islands distributed as *Mussaenda frondosa.* Valeton (1926), basing his observations on Konig's collection from Ceylon, excludes *M. frondosa* from New Guinea and Java. The plant

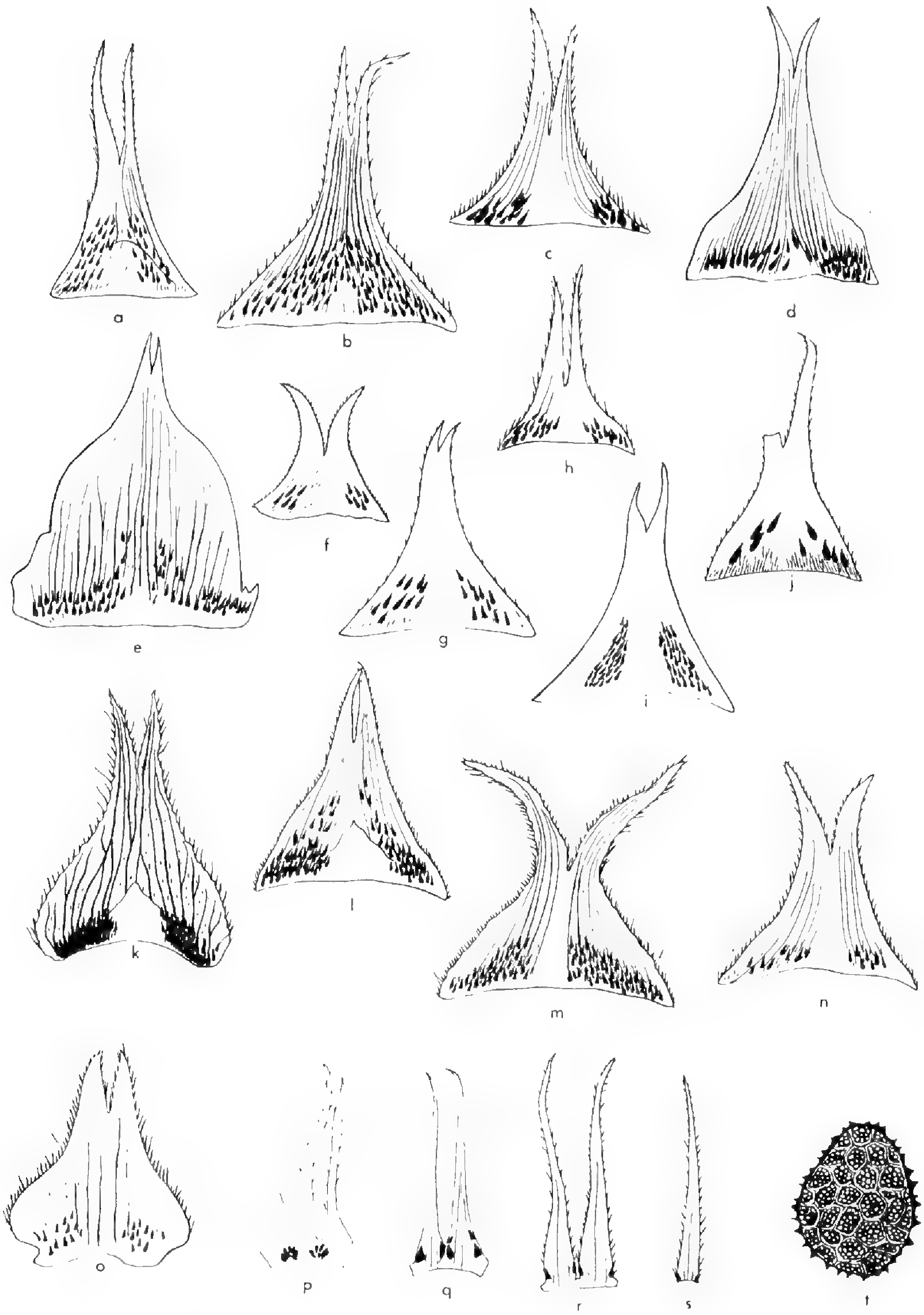

FIG. 1. a–o, stipules of some Indian species of *Mussaenda* spread out and viewed from the adaxial surface to show distribution of hairs and glands; p–s, calyx lobes from within; t, seed. a, *M. roxburghii* (*Wallich G 6252*), × 2½; b, *M. roxburghii* (*Gamble 10476*), × 3; c, *M. incana* (*Herb. Griffith 2781*), × 3½; d, *M. corymbosa* (*Herb. Wallich 954*), × 2½; e, *M. corymbosa* (*Herb. East India Co. 2779/1*), × 2½; f–j, *M. glabra* showing variation in hairiness and in bifurcation at apex (f, *Hooker & Thomson 17*, Chusa, Khasia, × 4⅓; g, *Rock 712*, × 4; h, *Siedenfaden 2696*, × 4½; i, *Herb. Helfer 2778*, Burma, × 3½, note glabrousness; j, *Henry 3118*, × 4, note large glands); k, *M. macrophylla* (*Parry 274*), × 2; l, *M. treutleri* (*Hooker & Thomson 20*), × 1¾; m, *M. hirsutissima* (*Barnes 120*), × 2½; n, *M. glabrata* (*Hooker & Thomson 23*), × 3½; o, *M.*

described as *M. frondosa* from the Moluccas is in his opinion *M. reinwardtiana* Miq. In addition, he does not think that collections from Fiji, the Caroline Islands, and the Samoan Islands distributed as *M. frondosa* are this species.

Stapf (1894) in assigning the collection *Haviland 1355* from Kinabalu to *Mussaenda frondosa* was not quite sure of the specimens he had examined. Short-styled and long-styled flowers never occur together in an inflorescence nor on the same plant. He seems to have examined a flower in which the throat hairs had been eaten by an insect, shown by the presence of its excrements. I have come across several specimens in similar condition from India, the Philippine Islands, and New Guinea.

Pitard's (1923) description of *Mussaenda frondosa* from Annam and Indo-China does not agree with typical material. He seems to be describing a glabrous-leaved form with sepals 2–2.5 mm. long and petals oblong, 4 mm. long, 2.5 mm. broad.

Mussaenda frondosa therefore occurs in India, extending as far as Nepal, Assam, the Khasia Mountains, and the Andaman Islands, and southward along the Western Ghats from Concan as far as Ceylon. Unfortunately no material was available for examination from Nepal, Assam, the Khasia Mountains, and the Andaman Islands.

India. Kodaikanal Region, Pulney Hills, *Fr. Anglade* (A); Yellapur-Karwar District, *Nana 5816* (K); *Herb. Wight 1267* (NY), *1305* (C); Concan, *Herb. Hooker & Thomson* (GH); *Herb. Rottboell* (C); *Herb. Schum.* (C); *Herb. Hofman Bang*, *Wallich* (C); Calcutta, *Wallich 434* (C).

Ceylon. MID-COUNTY WET ZONE: *Konig* (C); Peradeniya, *Gardner 333* (K); *De Silva 38* (A), *210* (NY); *Jayaweera 8, 12–15* (A); Dolosbage, *Jayaweera 1* (A); *Thomson 1845* (K); *Fraser 135* (US); *Rostrup 99* (C). LOW-COUNTRY WET ZONE: *Hermann* (BM–lectotype, upper specimen; syntype, lower specimen on same sheet as lectotype); Ratnapura District: ("*J*" designates *Jayaweera*, all in A) Kotamulla, *J2*; Idellana, *J3*; Elapatha, *J4*; Algoda, *J5*; Kohiladeniya, *J7*; Foot of Adam's Peak, *J29*; Gilimale, *J22*. WET MONTANE ZONE: Labookelle, *J16*; Ramboda, *J17*, Rangala *J18*, *J19*; Hewaheta, *J20*; Ginigathhena, *J27*; Palugama, *J30–34*; Peragala, *J35*. DRY MONTANE ZONE: Welimada, *J41*. DRY ZONE: Nalanda, *J9*; Pannampitiya *J10*, *J38*, *J40*; Ritigala, *J11*; Weragantota, *J23*; Bibile, *J24–26*; Dambulla, *J36*; Kurunegala, *J37*; Kodikaragamuwa, *J39*; Sigiriya, *Cooley & Siyambalagastenne* (US). **China.** Kwangtung University Campus (probably cultivated), *Metcalf 17245* (A).

It is difficult to determine the characters of the type from a photograph of Hermann's original specimen but a drawing in Burmann's *Thesaurus Zeylanicus*, supported by a large number of dissections from Ceylonese material, brings out the characters very clearly.

Mussaenda frondosa has been the subject of much discussion, and in the absence of clearly defined characters many collections from Assam,

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frondosa (*Jayaweera*), × 4. p–s, calyx lobes of *M. keenanii*, × 2; *M. corymbosa*, × 2¾; *M. treutleri*, × 2½, and *M. glabrata*, × 2¼, respectively. t, seed of *M. glabrata*, × 25, note spininess.

Burma, Siam, China, Malacca, the Nicobar Islands, the Moluccas, Sumatra, Java, Borneo, Celebes, Fiji, the Philippines, and the Caroline Islands have been erroneously referred to this species. These are correctly referred to various others, including *M. macrophylla*, *M. sanderiana*, *M. erosa*, *M. villosa*, *M. laxiflora*, and *M. philippica*.

Frère Anglade's collection from the Kodaikanal Region, Nana's collection from Karwar, Hooker and Thomson's from Concan, and Wallich's from Calcutta agree with the typical material from Ceylon, the only difference being the longer stipules which are hairy within at the base only, a character of *Mussaenda glabrata*. Voigt's collection (C) from Calcutta, presumably from cultivated specimens is, I think, *M. glabra* with its characteristic glabrous leaves with 4–6 pairs of lateral veins, small stipules, glabrous within with few glands, short, lanceolate calyx lobes, glabrous petaloid sepals and lanceolate or oblong-lanceolate corolla lobes. Both Merrill and Bremekamp, however, have annotated this as *M. frondosa*.

The collection *Erlanson 5614* (NY) from Travancore is of special interest. The character of the leaves and stipules are typically those of *Mussaenda glabrata* while the floral characters are distinctly those of *M. frondosa*. It was gathered from an area where the two species overlap. *Kamphovener 528* (C) from Calcutta and Serampore has similar characters, but the corolla tube is much shorter (1.9 cm. long), the leaves elliptic and entirely glabrous above, pubescent on veins beneath, and the stipules glabrous within except at the base. In Calcutta and Serampore the two species concerned do not occur in the natural state.

I do not agree with Bentham (1861) that the plant figured in Curtis' *Botanical Magazine* (*pl. 2099*) as *Mussaenda pubescens* Ait. is *M. frondosa*. It differs much from the material of *M. frondosa* examined and figured elsewhere, in its glabrous stems, leaves and inflorescence, and its diverging, linear, stipular teeth, which are characteristic of *M. pubescens*.

Mussaenda frondosa differs from other species in habit and pubescence and is easily distinguished by its straight stipular teeth; long, deciduous calyx lobes which are linear and more than twice the length of the ovary (or about half the length of the corolla tube) bearing a single pair of glands at the base of each; in the dense hairiness of the corolla tube within, as well as on the outer surface; and in the hairs of the throat equal in length and equally dense in both the long-styled and short-styled forms, but tufted at the mouth.

USES. *Mussaenda frondosa* is used medicinally in India and Ceylon. Different parts of the plant are used for the treatment of different diseases. In India the root is used for the treatment of white leprosy, the petaloid sepals for jaundice, the flowers for asthma, intermittent fevers, and dropsy; also, the leaves are used externally as a detergent for ulcers. In Ceylon, on the other hand, the plant is not used internally but, the leaves and flowers are employed externally in the form of a decoction to remove inflammations.

3. **Mussaenda glabrata** (Hook. f.) Hutch. ex Gamble, Fl. Madras 2: 610. 1921 (TYPE: *Herb. Wight 1269*). FIG. 1, n, s, t.

M. frondosa var. *glabrata* Hook. f. Fl. Brit. India 3: 90. 1880.

Climbing shrubs; stems nearly glabrous except at nodes or scantily pubescent, lenticellate. Leaves opposite, lamina narrowly or broadly elliptic, 5.5–10.5 cm. long, 3.3–6 cm. broad, glabrous or subglabrous on the upper surface, sparingly hairy and villous on conspicuous nerves beneath, short acuminate, somewhat cuneate at base, primary lateral veins 6–8 pairs, transverse nervules parallel; petiole 0.6–2.5 cm. long, pubescent. Stipules ovate, 5–6 mm. long, 3.5–5 mm. broad at the base, hairy on the outer surface, glabrous on the inner surface except at the base, hairs of medium length dispersed among numerous glands (about 22 pairs) at the base, bifurcate from apex about 2/5–1/2 their length, lobes diverging. Inflorescence a terminal, rather spreading, dichotomously branched, pubescent cyme; bracts and bracteoles lanceolate, hairy, caducous, bracteoles broader at base, trifid at apex. Flowers heterostylous on stout, pubescent pedicels shorter than the ovaries. Calyx lobes 5.5–10.7 mm. long, 0.8–1 mm. broad, linear, narrowing to a point at the apex, hairy on the outer surface, glabrous within with one or two pairs of glands at the base of each; petaloid sepal ovate, 3.3–9.5 cm. long, 3.3–5.3 cm. broad, shortly acuminate, cuneate, puberulous above and below, hirsute on veins on the lower surface, "petiole" 2–2.7 cm. long. Corolla orange, the tube 2.5–3.3 cm. long, hairy on the outer surface, more densely so towards the broader end, rather densely hairy within as far as the bases of the anthers, farther down the hairs shorter and scantier to 1/5–1/4 the length of the tube from the base, hairs equal in length (1.5–2 mm. long), tufted at the mouth in both the long-styled and short-styled forms; corolla lobes orbicular-ovate, 2.5–5.5 mm. long, 5–5.5 mm. broad, apiculate, hairy on the outer surface, papillate within. Stamens with short filaments inserted halfway on the tube in long-styled forms and 3/4 way up in short-styled forms; anthers linear, dorsifixed, introrse, 6.2–7 mm. long, bilobed at the sterile base. Ovary 3.5–4 mm. long, broadly fusiform, hairy, 2-locular, ovules numerous on cushion-shaped axile placentae; style and stigma lobes 2.7 cm. and 3.5 mm. long respectively in long-styled forms, 1.6 cm. and 4.5 mm. long in short-styled forms [measurements taken from flowers with corolla tubes over 3.2 cm. in length]. Berry obovoid, 1–1.2 cm. long, glabrous, calyx lobes deciduous; seeds oblong or ovate, 0.7–0.77 mm. long, 0.56 mm. broad, testa spiny with 4–11 foveae in each areole.

DISTRIBUTION. *Mussaenda glabrata* occurs along the Western Ghats extending from North Kanara through Malabar, Nilghiri and Tinnevelly hills from sea level upwards. I have not seen it in Ceylon, and it is very doubtful whether its distribution extends that far. Two collections of *M. glabrata* from the Botanic Gardens, Calcutta, presumably from plants under cultivation as *M. corymbosa* and *M. frondosa* were examined, one labelled as from Ceylon and the other as from Malabar.

India. MYSORE: Karwar, North Kanara District, *Bell 7807* (K); *Puri 1158* (BSI); Mangalore, *Hohenacker 170* (C, K). KERALA: Mount Nilghiri & Kurg, (*Herb. Hook. & Thomson*) *Thomson 22* (GH), *23* (GH, K); *Herb. Wight 1307* (GH), *Herb. Wight* (GH); *Herb. Wight 1269* (K–lectotype; C, NY); *Herb. Wight 1270* (K–syntype; NY). CULTIVATED: Bot. Gard. Calcutta, *Herb. Torrey* (NY), ? Ceylon & Halabar, *Voigt* (C).

The collection *Thomson 23* seems to be from more than a single shrub, for both long-styled flowers (with longer calyx lobes) and short-styled flowers are represented. Voigt's collection has leaves which are puberulous on the upper surface and conspicuously hirsute on the veins and parallel venules on the lower surface. The stipules and flowers are characteristic of *M. glabrata*. The other sheet from the Calcutta Botanic Garden has two mounts, the top specimen being *M. roxburghii* and the lower one probably *M. glabrata*.

The collection *Jacob 17518* (K), from Madura, is of doubtful identity; it differs from *M. glabrata* in the deeply bifurcate stipules which are pubescent within, long-petioled leaves, and doubtfully spiny seeds.

Heterostyly is clearly displayed in this species, but the throat hairs in both the long-styled and short-styled forms are long and dense.

Mussaenda glabrata may be distinguished by its glabrous berries with spiny seeds (a character separating it from the other Indian mussaendas); glabrous leaves, villous on conspicuous nerves beneath; small, hairy stipules glabrous inside except at the base and bifurcate at the top; and larger anthers.

4. **Mussaenda laxa** (Hook. f.) Hutch. ex Gamble, Fl. Madras 2: 610. 1921 (TYPE: *Herb. Wight*, 1836).

M. frondosa var. *laxa* Hook. f. Fl. Brit. India 3: 89. 1880.

Climbing shrub; stems hirsute, lenticellate. Leaves opposite, lamina broadly ovate, 6–12 cm. long, 3–7.2 cm. broad, abruptly short-acuminate, cuneate or rounded at the base, sparsely pubescent on the upper surface, loosely pubescent on the paler lower surface, more densely so on the veins, hairs usually long (sometimes short), loosely dispersed and not matted together, primary lateral veins 7–9 pairs, prominent on the lower surface, transverse nervules not prominently parallel; petiole 0.6–3.5 cm. long, slender or stout, subglabrous or hirsute. Stipules 4.5–10 mm. long, 2.5–5 mm. broad at the base, ovate, densely hairy on the outer surface, glabrous within except at the base where long hairs form a screen over the few glands, bifurcate from apex for about 2/5–1/2 their length, lobes curved outwards. Inflorescence a terminal, very lax, few-flowered di- or trichotomous, pubescent cyme; bracts and bracteoles lanceolate, hairy, 5.5–8 mm. long, bracteoles broader at the base and trifid at the apex, caducous. Flowers heterostylous, on short, pubescent pedicels shorter than the ovaries. Calyx lobes deciduous, narrowly linear, 6–17(–19) mm. long, 1–1.5 mm. broad, hairy outside, glabrous or hairy inside with 1–3 pairs of glands at the base of each; petaloid sepal ovate, 7.5–10 cm. long, 3.5–6.5 cm. broad, short-acuminate, cuneate at base, subglabrous or puberulous on the upper surface, minutely pubescent or sparsely hirsute on the lower surface, more densely so on the veins, 5-veined, "petiole" 1.3–2.5 cm. long, pubescent. Corolla tube 2.5–3.2 cm. long, hairy on the outer surface, more densely so toward the broader end, hairy within, densely so in short-styled forms and sparsely in long-styled forms as far as the base of the anthers, hairs equal in length (1.5 mm. long) in both forms and tufted at the mouth, hairs below the anthers shorter and scantier as far as 1/5–1/4 the length of the corolla tube from the base; corolla lobes ovate, 5.5–7 mm. long, 6 mm. broad, caudate-acuminate, hairy on the outer surface, papillate within. Stamens with short filaments inserted midway on the tube in long-styled forms and 4/5 way up in short-styled forms; anthers linear, dorsifixed, introrse, 6–6.8 mm. long, straight or slightly curved, bilobed at base. Ovary 3.7–4.5 mm. long, obconical or broadly fusiform, hairy, 2-locular, with numerous ovules on cushion-shaped axile placentae; style and stigma lobes 2.8 cm. and 3.5 mm. long respectively in long-styled forms, 1.65 cm. and 4.5 mm. long in short-styled forms. Berry obovoid, 1.1–1.2 cm. long, sparsely hirsute; seeds minute, reticulate, ovate, oblong or oval, 0.67–0.76 mm. long, 0.39–0.67 mm. broad with 4–9 foveae in each areole of the testa.

DISTRIBUTION. This species grows along the west coast of India and in the Western Ghats from sea level to about 1000 meters elevation. It extends from Konkan southward as far as Travancore, and inland from Mysore to Tinnevelly and Nilghiri hills. It has been collected in flower from April to July, October, and November; in fruit in June, October, and November.

India. BOMBAY: Malabar, Concan, etc., *Herb. Hooker & Thomson, Stocks, Lau,* etc. (C); Ram Ghat, *Richie 242* (K); Yellapur-Sahasarali, *Fernandes 1642* (A); Manchikeri, *Fernandes 1565* (A); Samkhand Sirsi Taluka, *Garade* (BSI). MYSORE: Maisor & Carnatic, *Herb. Hooker & Thomson, Thomson* (K); Mangalor, *Hohenacker 170* (K). KERALA: *Anstead 30* (A); Quilon, *Herb. Wight,* 1836 (K–holotype). MADRAS: Nilghiri, *Gamble 20541, 12180, 15598* (K); Biligirirangan Hills, *Barnes 403* (A). Ind. Orient: *Herb. Wight 1306* (C, GH in part), Kew distribution 1866–7; *Wallich,* 1816 (A).

Gamble's description of *Mussaenda laxa* does not seem to have included collections from Bombay Presidency. Stocks' collection, however, differs from the type in its narrow elliptic leaves, attenuate at the base and with long petioles, while *Fernandes 1642* and *1567,* annotated by Razi as *M. glabrata,* agree with the type material rather closely but for the smaller leaves and more prominent veins on the lower surface. I think this material is *M. laxa.* The collection *Hohenacker 170* has leaves which are more or less glabrous on the upper surface and minutely pubescent on the veins beneath but agrees with the type in the pubescent stems, lax inflorescences, and stipular and floral characters, while *Anstead 30* from the coast of Kerala has smaller and less hairy leaves and shorter stipules. In *Barnes 403* the bifurcation of the stipules varies from 2/5 to 1/2 their length from the apex. In all these collections both short-styled and long-styled forms have in the throat of the corolla tube long hairs of equal length which are tufted at the mouth of the tube; the hairs in the long-styled forms are less dense.

The chief distinguishing characters for *Mussaenda laxa* are, therefore, the loosely pubescent stems and leaves; lax inflorescences; stipules bifurcate about 1/2 their length, lobes curving back and glabrous inside, fewer glands and long basal hairs forming a screen over them; broadly ovate, caudate-acuminate corolla lobes; longer anthers and sparsely obovoid, hirsute fruits.

5. **Mussaenda macrophylla** Wall. in Roxb. Fl. Indica ed. Carey & Wall. 2: 228. 1824 (TYPE: *Wallich 6255*). FIG. 1, k; FIG. 3, j–l.

M. hispida D. Don, Prodr. Fl. Nepal. 139. 1825, non Engl.
M. calycina Wall. Cat. 6253. 1830 (*nomen nudum*).
M. frondosa sensu Wall. Cat. 6250A. 1830, non L.

A large, subscandent shrub with stout branches densely pubescent with grayish hairs remaining gray or becoming rufous brown when dry. Leaves elliptic, broadly ovate, or elliptic-lanceolate, 8–20 cm. long, 3.8–10.5 cm. broad, subglabrous or pubescent on the upper surface, entirely hirsute or hairy on veins and venules only on the lower surface, short acuminate, cuneate at the base with 9–11 pairs of primary lateral veins arcuate and conspicuous on the lower surface; petioles 0.8–4 cm. long, densely hirsute. Stipules large, ovate, 1.2–1.35 cm. long, 6–9.5 mm. broad at the base, bifurcate from the apex 1/6–2/5 their length, lobes diverging, densely hairy outside, glabrous or hairy inside with few or numerous glands in two bundles at the base. Inflorescence a terminal, compact or spreading, trichotomously branched, pubescent, corymbose cyme; bracts and bracteoles large, very hairy, lanceolate, acuminate, bracteoles usually in opposite pairs, deeply divided into 2 or 3 lanceolate, acuminate lobes. Flowers large, heterostylous, nearly sessile or on very short, stout, pubescent pedicels. Calyx lobes narrowly or broadly oblong-lanceolate, 8.5–14 mm. long, 1.2–4 mm. broad, acuminate, margin smooth or irregular, hairy on the outer surface, scantily pubescent or glabrous within with 1–3 pairs of glands at the base of each sepal; petaloid sepal white with faintly green veins, ovate or broadly lanceolate, 6–9 cm. long, 2.5–6.7 cm. broad, glabrous on both surfaces except on veins below, or puberulous on the upper surface and hirsute below, "petiole" 1.7–2.5 cm. long, hirsute. Corolla tube greenish, 2.4–3.2 cm. long, hairy on the outer surface, hairs spreading horizontally or directed forward especially toward the broader end, tube hairy within at the throat as far as the bases of the anthers, and tufted at the mouth, hairs long in both long-styled and short-styled forms but less dense in the former, hairs shorter and scantier below the anthers extending as far as to about 1/12 to 1/4 the length of the corolla tube from the glabrous base; corolla lobes yellow, broadly ovate or orbicular, 4–5 mm. long, 4–6.5 mm. broad, acute, apiculate or caudate, pubescent on the outer surface, papillate within. Stamens with short filaments, epipetalous about 1/2 way up the tube in long-styled forms and 3/5–3/4 way up in short-styled forms; anthers linear, dorsifixed, introrse, 5–5.7 mm. long, bilobed at the base. Ovary 3.5–4.5 mm. long, broadly fusiform, hairy, 2-locular, with numerous ovules on cushion-shaped axile placentae; style and stigma lobes 1.65–2.3 cm. and 2.5–3.5 mm. long respectively in long-styled forms, 0.9–1.4 cm. and 3.5–4 mm. long in short-styled forms. Berry dark purple, oblong-ovoid, 1–1.2 cm. long, sparsely hirsute, with very board nectariferous scars, calyx lobes deciduous; seeds minute, reticulate, oblong-ovoid, 0.9–1.03 mm. long, 0.73 mm. broad, embedded in a soft, fleshy pulp, hilum conspicuous, testa with 2–6 foveae in each areole.

DISTRIBUTION. This species grows in the tropical Himalayan range of hills at an elevation of 300 to 1500 meters above sea level, extending from Nepal through Sikkim, Khasia, Assam, and Burma to Yunnan in China. Collections from the Andaman and Nicobar Islands were not available for examination. Collections from the Philippine Islands differ sufficiently from the typical to be treated as a variety. In connection with the distribution of the species Merrill (1908) says, "The exact identity of the Philippine forms referred to this species is doubtful." It has been collected in flower from May to August, and in October; in fruit in June, November, December, and January.

India. NEPAL: *Wallich* (C, GH), *Wallich Cat. 6255* (K–holotype; GH, NY–isotypes). SIKKIM: *Herb. Kuntze 7083* (NY); Darjeeling, *Cowan* (US). KHASIA: *Hooker & Thomson* (GH, K). ASSAM: Lushai Hills, *Parry 274* (K); Jotsoma, Naga Hills, *Bor 6360* (K); Kilomi, *Bor 5054* (K); Cachar Hills, Hajlong, *Craib*, 1909 (K); Kala Naga, *Watt 6926* (K); Jotsoma, *Prain*, 1886 (A); Pynursla, *Biswas 4038* (A); Margarata, *Prain's collector* (A); Manipur, *Watt 5050* (K); Tirap River Valley, *Juan 179* (K, US); *Belcher 145* (US); Namchik River Valley, *Belcher & Juan 73* (K, US); 19 miles from Ledo, *Juan 158* (A). **Burma.** Myitkyina, *White 2* (US). **China.** YUNNAN: Szemao, *Henry 12265* (A); Banchiou-chiam, Cheli-Hsien, *Wang 79595* (A); Fo-Hai, *Wang 74675* (A); Mienning, Gewanshuei, *Yu 17681* (A).

The type specimen described by Wallich obviously refers to *Wall. Cat. 6255*, although Hooker (1880) erroneously cited the number *6295* which refers to *Hopea wightiana*. Wallich's and Lindley's figures referred to by them (Pl. As. Rar. 2: *pl. 180*. 1832, and Bot. Reg. 32: *pl. 24*. 1846 respectively), are of *Mussaenda treutleri*, a species which had been confused with *M. macrophylla* but was distinguished and described by Stapf in 1909.

Mussaenda macrophylla has a wide range of variation in the characters of the leaves, pubescence, inflorescences, and flowers; its stipule character, however, seems to be more or less constant.

The collections from Assam, *White 2*, *Juan 158*, *Belcher 145*, *Juan 179*, *Belcher & Juan 73* referred to earlier as *Mussaenda frondosa*, show the greatest amount of variation. In these the leaves are lance-elliptic, somewhat glabrous, the stipules are glabrous within, and the inflorescences compact (*Belcher & Juan 73*) or diffuse (*Belcher 145*, *Juan 158*, *179*). The sepals are linear-lanceolate with ovate-caudate petals (*Belcher 73*) or broader and with ovate, acute, or apiculate petals (*White 2*, *Belcher 145*). The corolla tube in *Belcher 145* is hairy within to the base, indicating an affinity with *M. hirsutissima* and *M. roxburghii*. The Chinese collections agree well with those from India.

Heterostyly is demonstrated clearly in *Mussaenda macrophylla* with both long-styled and short-styled forms. As in *M. frondosa*, the throat hairs are long and tufted at the mouth in both forms. The affinities of the species are with *M. treutleri* from which it may be distinguished by the oblong-lanceolate calyx lobes, ovate stipules, bifurcate at apex and with diverging lobes, the hairs of the outer surface of the corolla tube somewhat horizontal and not appressed, the ellipsoid, rugose berry, and smaller seeds with fewer foveae in the areoles of the testa.

Mussaenda macrophylla is distinguished from other species of the genus by the hairiness of its stems, leaves, inflorescences, and flowers, by its larger stipules densely hairy on both surfaces, its broadly lanceolate sepals and its large, pubescent berries with broad nectariferous scars, as well as by its larger seeds with fewer foveae in the areoles of the testa.

Mussaenda macrophylla Wall. forma **grandisepala,** stat. et nom. nov.

M. pentasemia Fischer, Kew Bull. **1928:** 275. 1928.

Spreading shrub 2–3 m. tall, stems terete, pilose, branches densely villous. Leaves opposite, subequal, elliptic or ovate, 7–12 cm. long, 2.5–6 cm. broad, acute or acuminate, cuneate and more or less decurrent at the base, scantily pilose on the upper surface, appressed pilose on veins below with 7–9 pairs of lateral veins; petiole 0.5–1 cm. long, densely villous. Stipules broadly ovate, 5–10 mm. long, about 5 mm. broad, hairy on both surfaces and bifurcate at apex. Inflorescence a terminal, few-flowered, pubescent cyme; bracts and bracteoles lanceolate, densely hairy on both surfaces; bracteoles broader, trilobed, the midlobe linear, subulate, much longer than the lateral lanceolate lobes. Flowers (long-styled forms) subsessile on stout, hairy pedicels much shorter than the ovaries. Calyx lobes all petaloid, petiolate, elliptic-lanceolate or elliptic-oblong, 2–7 cm. long, 0.5–4 cm. broad, acuminate, attenuate at the base, scantily pubescent on the upper surface, setose on veins below, "petioles" 0–2.5 cm. long, setose. Corolla brownish yellow, the tube 2 cm. long, cylindrical, slightly broader at the top, hairy on the outer surface at the mouth and throat as far as the bases of the anthers, then the hairs becoming shorter and scantier, extending as far as 1/4 the length of the tube from the base; lobes orbicular-ovate, 3.5 mm. long, 4.5 mm. broad, apiculate, hairy on the outer surface, papillate within. Stamens with short filaments attached about halfway up on the tube; anthers linear, dorsifixed, introrse, 5.2 mm. long, bilobed at the base. Ovary infundibuliform, 4–5 mm. long, densely villous; style filiform, stigma bilobed. Berry not seen.

Distribution. This form of the species was collected in flower at Nhatial in the Lushai Hills, Assam, at an elevation of 925 meters, in July, 1927, by Mrs. N. E. Parry. It has not been collected since.

The collection *Parry 275* (K) which is the type specimen of *Mussaenda pentasemia* was available for examination. There seems to be no difference in characters between this and the typical *M. macrophylla* except in the petaloid development of all five calyx lobes. The specimen *Parry 274* (K) agrees with typical *M. macrophylla* rather closely in the form of the leaf and stipules and in the structure and pubescence of the corolla. Both collections were made in the Lushai Hills in Assam, and I have no doubt that this form is a variant of the species. This variation is comparable to *M. philippica* var. *aurorae* from the Philippine Islands and *M. whitei* S. Moore (*Brass 11682* [A]) from Dutch New Guinea. In the latter collection two specimens are mounted on the same sheet. Both specimens, probably from the same plant, are long-styled forms, the one at the top bearing large, petaloid calyx lobes.

6. **Mussaenda treutleri** Stapf, Bot. Mag. 135: *pl. 8254.* 1909. (Type: *Wallich 6250E*). Fig. 1, l, r.

M. frondosa var. *grandifolia* Hook. f. Fl. Brit. India 3: 90. 1880.
M. macrophylla sensu Kurz, Forest Fl. Burma 2: 57. 1877, non Wall. in Roxb. Fl. Indica ed. Carey & Wall. 2: 228. 1824.

Shrub 2–3 m. in height, sometimes scandent in its native habitat. Leaves ovate or elliptic-ovate, 7.5–23 cm. long, 3–14 cm. broad, short acuminate, cuneate, scantily pubescent on both surfaces, hirsute on the 8–10 pairs of veins beneath; petioles 0.8–5 cm. long, stout, hairy. Stipules broadly ovate or triangular-ovate, 1.1–1.4 cm. long, 5.5–10 mm. broad at the base, bifurcate from the apex for about 1/3 their length, densely hairy on the outer surface, less hairy within with numerous glands in two ascending groups. Inflorescence a terminal, trichotomously branching, compact, many-flowered, pubescent, corymbose cyme; bracts and bracteoles lanceolate, 5–10 mm. long, hairy, bracteoles trilaciniate, broader at the base. Flowers heterostylous, on stout, pubescent pedicels much shorter than the ovaries. Calyx lobes linear or subulate, 4.5–12 mm. long, 0.7–1 mm. broad at the base, tapering toward the apex, hairy on the outer surface especially along the midrib and the margins, glabrous within with two pairs of glands at the base of each; petaloid sepal ovate or oblong-ovate, 4.7–14.5 cm. long, 2.5–10 cm. broad, short acuminate, short cuneate at base, glabrous on both surfaces except on veins below or scantily hairy on the upper surface and hirsute below, hairs denser on veins, "petiole" 2.5–2.8 cm. long, scantily pubescent or hirsute. Corolla tube 2.9–3 cm. long, appressed pubescent on the outer surface, hairy within at the throat as far as the bases of the anthers, and tufted at the mouth, hairs long in both the long-styled and short-styled forms, less dense in the former, below the anthers the hairs shorter and scantier extending about 1/4 the length of the corolla tube from the glabrous base; corolla lobes 5.2–6 mm.

long, 4 mm. broad, ovate, caudate-apiculate, hairy on the outer surface, papillate within. Stamens with short epipetalous filaments, inserted 1/2 way on the tube in long-styled forms and 3/4 way up in short-styled forms; anthers 4–5.5 mm. long, linear, dorsifixed, introrse, faintly bifid at the base. Ovary broadly fusiform, 2.5–4 mm. long, hairy, 2-locular, with numerous ovules on cushion-shaped axile placentae; style and stigma lobes 2.7 cm. and 4 mm. long respectively in long-styled forms, 1.4 cm. and 4.5 mm. long in short-styled forms. Berry globose, 1–1.3 cm. long and as broad, glabrescent, with calyx lobes deciduous; seeds minute, reticulate, broadly ovate or pyriform, 1.1 mm. long, 0.8 mm. broad with a conspicuously protruding hilum, testa with 2–10 foveae in each areole.

ILLUSTRATIONS. Wallich, Pl. As. Rar. 2: *pl. 180.* 1831; Lindley, Bot. Reg. 32: *pl. 24.* 1846; Paxton, Mag. Bot. 12: 197. *pl. C.* 1846; Stapf, Bot. Mag. 135: *pl. 8254.* 1909.

DISTRIBUTION. This species grows in the tropical Himalayan range of hills in India, Sikkim, Bhutan, and Khasia, at elevations between 650 and 2200 meters above sea level. It was first collected by Wallich in the mountains of Nepal and later by Hooker in Khasia and Sikkim. It is said to flower during the rainy season and fruit in the winter months. It has been collected in flower in June and July and in fruit in December.

India. KUMAUN: Almora Div., *Biskam 2298* (NY). NEPAL: *Wallich* [*6250 E*], 1821 (K–lectotype), *Herb. Meisner, Basil,* 1853 (NY). BHUTAN: Trongsa to Tsanka, *Gould 629* (K). KHASIA: *Hooker & Thomson 20* (K). SIKKIM: *J. D. Hooker 20* (GH, K, NY); *Treutler 6500* (K–syntype); Darjeeling, *Gamble 3758A* (K), *9565* (K).

The type specimens of this species come from the original collection of Wallich from Nepal in 1821 and Treutler's collection from Sikkim Himalaya in 1874. *Wallich 6250E* is selected as the lectotype. The species was introduced into cultivation by Knight and Perry about 1840 as a form of *Mussaenda frondosa* from Nepal and was confused with *M. macrophylla* and figured as such by Wallich, Lindley, and Paxton until Sir Joseph Hooker pointed out that it was distinct and treated it in his *Flora of British India* as *M. frondosa* var. *grandifolia.* Stapf elevated the variety to the rank of species.

All figures match well with the species. Wallich figured a short-styled form and showed the characters of the stipules and sepals clearly, while Paxton and Stapf figured long-styled forms. Heterostyly is obvious in this species. Throat hairs are long and tufted in the mouth in both types of flowers but less dense in the long-styled forms. *Mussaenda treutleri* is distinguished from *M. macrophylla* by the large, ovate or elliptic-ovate, scantily pubescent leaves, cuneate from a broad base; the broader, triangular-ovate stipules; the linear or subulate sepals, hairy along the midrib on the outer surface and setose ciliate at the margin, glabrous within with two pairs of glands at the base of each; the corolla tube appressed-pubescent on the outer surface, lobes caudate-apiculate (recognized in the unopened flower by recurved tips at the top); and the glabrescent fruits and larger seeds. *Mussaenda treutleri* is distinguished from other species by its large leaves and stipules; its linear, setose-ciliate sepals; its ovate, caudate-apiculate petals; and its globular, glabrous berries and larger seeds with 2–10 foveae in each areole of the testa.

7. **Mussaenda incana** Wall. in Roxb. Fl. Indica ed. Carey & Wall. 2: 229. 1824; Hook. f. Fl. Brit. India 3: 87. 1880 (TYPE: *Wallich 6256*). FIG. 1, c; FIG. 3, d–f.

M. pubescens sensu Buch.-Ham. in Wall. Cat. 6257. 1832, non Ait.

Small, erect shrub less than 1 m. tall; stems simple, terete, pubescent, not commonly branched except at the top before flowering, internodes 6–11 cm. long. Leaves ovate-oblong, 3.5–11(–18) cm. long, 1.7–6(–10) cm. broad, tapering, acute or acuminate, the base acute or rounded, inequilateral; hairy above, villous and white beneath with 6–14 pairs of arcuate, parallel, lateral veins, prominent on the lower surface; petiole stout, 2–5 mm. long, densely hairy. Stipules triangular, tapering from a broad base, 7–9.5 mm. long, 4.5–6 mm. broad, erect, bifurcate from apex for about 1/3–1/2 their length, hairy on the outer surface, within glabrous with a few glands in two groups at the base, 6–19 glands to each group. Inflorescence a terminal, small, subsessile, few-flowered di- or trichotomous cyme, the terminal pair of leaves also producing axillary, long-stemmed cymes extending beyond the primary one, exceedingly hairy; bracts and bracteoles linear, subulate and hairy. Flowers heterostylous, subsessile or on very short, stout, hairy pedicels. Calyx lobes 4–5.5 mm. long, 0.8–1 mm. broad at the base, filiform, hairy outside, glabrous inside with a pair of glands at the base of each; petaloid sepal milky white, 5–7 cm. long, 2.8–3.6 cm. broad, ovate or broadly oblong, acute, cuneate at base, glabrous or hairy on the upper surface, pubescent below, 5- or 7-veined, "petiole" 2.5 cm. long, densely hairy. Corolla tube 2–2.3 cm. long, hairy on the outer surface, hairs scanty within, long, slightly shorter (1–1.2 mm. long) in long-styled flowers but tufted at the mouth in both forms; below the anthers hairs shorter, scantier, extending as far as 1/12–1/4 the length of the tube from the base; corolla lobes 4.5–5.5 mm. long, 2.5–3.2 mm. broad, ovate-lanceolate, acuminate, sometimes almost caudate, hairy on the outer surface, papillate within. Stamens with short filaments, epipetalous 1/2 way on the tube in long-styled forms and 3/4 way up in short-styled forms; anthers linear, dorsifixed, introrse, 3.7–4.3 mm. long, bilobed at base. Ovary broadly cup-shaped, 3–3.2 mm. long, hairy, 2-locular, with numerous ovules on cushion-shaped axile placentae; style and stigma lobes 2 cm. and 2.5 mm. long respectively in long-styled forms, 1.1–1.3 cm. and 2 mm. long in short-styled forms. Berry globose, 1.3–1.5 cm. long, hairy at first, later glabrous, nectariferous disc small with subpersistent calyx segments; seeds brown, numerous, minute, ovate, reticulate, 0.9–1.16 mm. long, 0.83 mm. broad, testa with 2–7 foveae in each areole.

DISTRIBUTION. This species occurs in the tropical Himalayan range between 600 and 1200 meters elevation, extending from Nepal (where the type was collected), through Sikkim, the Khasia mountains as far as Assam to the east, and southwards to Orissa. It has been collected in flower in July, in fruit in October.

India. NEPAL: *Wallich 6256* (K–holotype). SIKKIM: Darjeeling, *Gamble 840A* (K); *Herb. Griffith 2781* (K), Kew Distribution 1861–2. ASSAM: Khasia Mts., *Hooker & Thomson* (C, K, NY). ORISSA: Chota Nagpore, *Clarke 20344, 20455A* (K); Cult. Bot. Gard. Calcutta, *Voigt 136* (C).

This species seems to be allied to *Mussaenda hirsutissima* in many respects. The form and pubescence of the leaves and stem, the size of the fruits and seeds are characters common to both species. It differs, however, in the habit; the subsessile, small, few-flowered inflorescence; and the smaller stipules, flowers, calyx and corolla lobes. Heterostyly is demonstrated in the species; the throat hairs in the long-styled forms are slightly shorter and scantier than in the short-styled forms.

Mussaenda incana is distinguished by its short-petioled, hairy, ovate leaves; subsessile, few-flowered, densely hairy cymes; triangular-acuminate stipules glabrous within and with few glands; small linear-subulate calyx lobes glabrous within and with one pair of glands; short corolla tube; small lance-ovate corolla lobes; and large fruits and seeds.

8. **Mussaenda hirsutissima** (Hook. f.) Hutch. ex Gamble, Fl. Madras 2: 610. 1921 (TYPE: *Herb. Wight 1268*). FIG. 1, m; FIG. 3, m–o.

M. frondosa var. *hirsutissima* Hook. f. Fl. Brit. India 3: 90. 1880.

Large climbing shrubs; stems roughly hirsute-pilose. Leaves opposite, lamina ovate-elliptic, rarely elliptic-lanceolate, 4.5–11 cm. long, 2.5–5 cm. broad, acuminate, cuneate or rounded at base, shaggily hirsute on both surfaces, primary lateral veins 7–9 pairs, prominent on the lower surface; petiole 0–5 mm. long, densely hirsute. Stipules 10–12 mm. long, 4.5–8 mm. broad at the base, bifurcate from apex 1/2–2/3 their length, lobes spreading, hairy on the outer surface, glabrous or scantily pubescent within, usually hairy at the base within and among the numerous glands occurring in two groups, vascular strands about 5–7 pairs, branched. Inflorescence a terminal, close, hairy, dichotomously branched, few-flowered cyme; bracts and bracteoles 1–1.5 cm. long, lanceolate, hairy, bracteoles trifid at apex, broader at the base. Flowers large, heterostylous, on stout, densely hairy pedicels shorter than the ovaries. Calyx lobes 6.5–13 mm. long, 1–1.2 mm. broad, lanceolate, hirsute on the outer surface, glabrous or scantily pubescent within with a tuft of hairs and 1–3 pairs of glands at the base of each; petaloid sepal 5.5–10 cm. long, 2.7–6 cm. broad, ovate-elliptic, short acuminate, cuneate or even cordate, scantily pubescent or hirsute on both surfaces, hairs denser on veins below, "petiole" 1.7–3 cm. long, hirsute. Corolla tube 2.3–3.2 cm. long, hairs on the outer surface horizontally spreading, longer toward the broader end, hairy within at the mouth and throat as far as the bases of the anthers, densely so in short-styled forms and scantily hairy in long-styled forms, hairs in both forms long (1.5 mm.) and tufted at the mouth, below the anthers the hairs shorter, linear, and scantier, extending as far as the base in long-styled forms and to 1/4 the length of the tube from the base in short-styled forms; corolla lobes broadly ovate, 5–12 mm. long, 4.5–8 mm. broad, acuminate, hairy on the outer surface, papillate within. Stamens with short filaments inserted midway on the tube in long-styled forms and 3/4 to 4/5 way up in short-styled forms; anthers 4.2–6.5 mm. long, linear, dorsifixed, introrse, bilobed at the sterile base. Ovary 2.7–4.5 mm. long, turbinate, hairy, 2-locular with numerous ovules on cushion-shaped axile placentae; style and stigma lobes 2.35 cm. and 1.8 mm. long respectively in long-styled forms, 1.1–1.5 cm. and 2.5–3.5 mm. long in short-styled forms. Berry globose, 1.2 cm. long, and about equal in diameter, sparingly hirsute, calyx teeth deciduous; seeds minutely reticulate, triangular-ovate or oval, 1.1–1.16 mm. long, 0.87 mm. broad, some smaller (0.67 mm. by 0.5 mm.), testa with 4–8 foveae in each areole.

DISTRIBUTION. This species occurs along the Western Ghats in India confining itself to higher elevations (1200 to 2400 meters), extending from Mysore through the Nilghiri and Pulney hills to Madura, Tinnevelly, and Travancore. It has been collected in flower in March, April, May, and December; in fruit in January and June.

India. COONOOR: Nilghiri hills, *Bourne* (K); *Gamble 11393* (K); *Prain* (A), 1899; *Clarke 10704A* (K); *Cole 6* (K, NY); Mount Nilghiri & Kurg, *Thomson 9* (GH, K). KODAIKANAL REGION: Pulney Hills, *Anglade* (A); *Bourne 50* (K). MADURA: *Jacob 17568* (K). TRAVANCORE: Kovilur, Pambadi Shola, *Barnes 120* (A). Ind. Orient: *Herb. Wight 1306*, in part (GH), *1305* (C, GH, NY); *Herb. Wight 1268* (K–lectotype; NY).

Heterostyly may be seen clearly in this species. In both short-styled and long-styled forms the throat hairs are long and tufted at the mouth, but less dense in the long-styled form. Below the anthers the hairs are shorter and scantier extending through the entire length of the corolla tube in the long-styled forms as in *Mussaenda roxburghii*, but only 3/4 the length in short-styled forms, the base being glabrous. Another character present also in *M. roxburghii* is tufted hairs at the base of the calyx lobes within. The collection *Herb. Wight 1306* (GH) has two specimens mounted on it. The branch at the top is *M. hirsutissima*, while that below is *M. laxa*. The leaves of the Anglade collection from the Pulney Hills are less hairy than those of other collections. *Barnes 120* is remarkable for its large flowers, stipules, and long, almost lanceolate filiform calyx lobes.

Mussaenda hirsutissima is distinguished by its shaggy-pilose stems and leaves, the latter almost sessile, ovate-elliptic, and more or less rounded at the base; its larger flowers with rather horizontally placed hairs on the outer surface of the corolla tube, its throat hairs long and tufted within at the mouth in both forms, hairs less dense in the long-styled forms; and its larger seeds triangular-ovate and of two different sizes.

9. **Mussaenda roxburghii** Hook. f. Fl. Brit. India 3: 87. 1880 (TYPE: *Wallich 6252C*). FIG. 1, a, b; FIG. 3, a–c.

M. corymbosa sensu Wall. Cat. 6250C (in part), 6252A, B (in part), C, & D (in part). 1832, non Roxb.
M. frondosa sensu Wall. Cat. 6250E. 1832, non L.
M. pubescens sensu Wall. Cat. 6257B. 1832, non Ait.
M. corymbosa sensu Kurz, Forest Fl. Burma 2: 58. 1877, non Roxb.

Large, erect, spreading shrub, 2–9 m. tall with stems almost glabrous to densely hirsute. Leaves oblong-lanceolate, ovate or elliptic, 9–28 cm. long, 3.5–9.8 cm. broad, acuminate, cuneate at base, glabrous or minutely pubescent on the upper surface, pubescent on the lower surface and hirsute on veins, or densely hairy throughout, with 7–14 pairs of lateral veins; petioles 0.5–2.5 cm. long and hirsute. Stipules triangular-lanceolate, 7.5–23 mm. long, 4–9 mm. broad at the base, bifurcate from apex 1/3–1/2 their length, hairy on the outer surface, hairs concentrated on the body with the margin glabrous, hairy within at the base and between the few or many glands occurring in two groups, the lobes straight. Inflorescence a terminal, pubescent, many-flowered, somewhat capitate cyme; bracts and bracteoles small, lanceolate, hairy; bracteoles trilaciniate into short or long, linear segments, broader at the base. Flowers heterostylous on stout pedicels as long as or shorter than the ovaries. Calyx lobes lance-filiform, 6–12 mm. long, 1 mm. broad, hairy on the outer surface, glabrous within, usually with a tuft of hairs and 1–3 pairs of glands at the base of each; petaloid sepal white, oblong-lanceolate, 4–11.5 cm. long, 2–5.8 cm. broad, short-acuminate, cuneate, glabrous above, minutely pubescent and hirsute on veins below; "petiole" 1.5–4.5 cm. long, hairy. Corolla tube green, 2.4–2.8 cm. long, narrow, silky, appressed pubescent on the outer surface, within hairy throughout the entire length with a tufted ring of hairs at the base, hairs above the bases of the anthers longer (1.5 mm. long) in the short-styled than in the long-styled forms, tufted at the mouth, hairs scantier and shorter below the anthers; corolla lobes yellow to orange, oblong-lanceolate, 4–8 mm. long, 2–2.5 mm. broad, acuminate, filiform at the apex, pubescent on the outer surface, papillate within. Stamens with short filaments, epipetalous on the tube about 2/5–3/5 way up in long-styled forms and 3/5 way up in short-styled forms; anthers linear, dorsifixed, introrse, 5–5.5 mm. long, acute, bilobed at base. Ovary 2.5–4.5 mm. long, hairy, soon glabrous, 2-locular with numerous ovules on cushion-shaped axile placentae; style and stigma lobes 2 cm. and 2.5–3 mm. long respectively in long-styled forms, 1.25–1.35 cm. and 2.5–4 mm. long in short-styled forms. Berry globular, about 0.8–1.3 cm. long, glabrous, with persistent calyx lobes; seeds minute, numerous, reticulate, 0.6–0.67 mm. long, 0.53–0.56 mm. broad, oblong, oval or triangular-ovate, albuminous, testa with 4–10 foveae in each areole.

DISTRIBUTION. This species occurs in the tropical Himalayan range of hills up to an elevation of about 1500 meters above sea level, extending from Nepal through Sikkim, Bhutan, Khasia, E. Bengal, and Assam to

Arracan and Upper Tenasserim in Burma. It has been collected in flower from April to September, and in November; in fruit in September and October.

India. NEPAL: *Wallich* (C); *Clarke 26486* (K). EAST HIMALAYA & SIKKIM: Chungthan to Singhik, *Biswas 6968* (A); Simulbari-Tindharia, *Biswas 8697* (LWG), *Biswas s. n.* (A); *J. D. Hooker 18* (K, GH); *Herb. Kuntze 665* (NY); Darjeeling, *Gamble 3760A* (K), *3761A* (K); *Cowan Imp. For. 24466* (US); *Herb. Griffith 2780* (C, GH, K); *Herb. Kuntze 6643* (NY). BHUTAN: Kalimpong, *Gamble 10476* (K). KHASIA: Mairong, *Schlaginweit 507* (GH); *Hooker & Thomson 18* (C, NY); Mungklow, *Clarke 44821B* (US); *Hooker & Thomson 19* (GH, K); Shillong, *Clarke 44321A* (K). SILHET: *Wallich 6252C* (A–photograph of lectotype in K), *Wallich 6252G* (C). EAST BENGAL: Chittagong, *Hooker & Thomson 18*, in part (K), *Herb. Griffith 2780* (C, K). ASSAM: Cachar, *Keenan*, 1873 (K); Manipur, *Meebold 6287* (BSI); Kala Naga Hills, *Watt 7322* (K); Upper Assam, *Jenkins 496* (K); Namchik River Valley, *Juan 228* (US); 19 miles from Ledo, *Juan 178* (A); Barni Hat, *Ruse 96* (A); Kamakhya, Kamrup, *Nayar 51288* (LWG); *Chatterjee* (A, BSI, GH); Jacoba, *Prain's Collector 43* (A); Tura Mountain, *Parry 846* (K). **Cultivated:** Calcutta Bot. Gard., *Wallich 6250C* (in part), *6252A*, *6252D* (in part) (A–photographs of syntypes in K), *Voigt* (C), *136* (A, C, US), *360* (A, C); without locality, *Mus. Bot. Haun. 11538* (C, US). Pennsylvania, Longwood Gard., *Wikoff 1382* (GH).

Hooker's description of this species is based on Wallich specimens labeled *Mussaenda corymbosa* (see synonymy above), his own collections *18* and *19* from Sikkim and Khasia, *Herb. Griffith 2780*, and several other collections. Of these, one sheet of *Wallich 6252C* (K; photograph, A), from Silhet, is most characteristic and is chosen as the lectotype. In his discussion he remarks that this is "not the same plant described under that name by Roxburgh in the Flora Indica, which is stated to be native of Ceylon and Malabar." No plant answering Hooker's description nor that by Roxburgh has been collected from Ceylon and Malabar. Further, it is very unlikely that the distribution of this species extended so far without a trace of it among the collections from the Western Ghats.

Hooker distinguished two varieties: var. 1, representing the typical *M. roxburghii* with nearly glabrous branches, oblong-lanceolate leaves, and silky bracts and flowers; and var. 2, from higher elevations and possessing more or less villous branches, large, elliptic and hairy leaves, and villous bracts and flowers. The second variety is represented by Clarke's and Hooker's collections from Khasia and Parry's collection from Assam. Clarke distinguished this from *M. incana* "as sepals persistent a species next *incana*. It has spreading hairs on the stem, upper surface of leaves glabrous. Therefore it is not *incana*." Another worker, with the initials "DN,"[2] added to the same specimen in Oct. 1902, "I see no difference of importance between this and the Khasia specimens of *M. Roxburghii* Hook. f. with hirsute branches." I am inclined to agree with the latter statement as the sepal, petal, and internal characters of the flower are the same in both varieties.

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[2] According to Dr. R. C. Foster, "DN" represents the initials of Lady Dorothy Neville, a great horticulturist of this period.

The collection *Parry 276* (K) from the Lushai Hills, Assam, is of particular interest. The leaves are over 30 cm. long, the stipules broadly ovate, 17.5 mm. long, cordate at base, glabrous within, not bifurcate at apex, also the hairs in the corolla tube not extending to the base, characters common to *M. corymbosa*. In the leaf and sepal characters *Parry 276* resembles *M. roxburghii*. Another collection, *Kingdon-Ward 8455* (K), also from Assam at an altitude of 1500 m., resembles *M. treutleri* in all the external characters, such as the form and pubescence of leaves, inflorescence, and the internal hairs in the corolla tube, but differs from it in characters of the sepal and stipules, which are those of typical *M. roxburghii* with the characteristic tuft of hairs at the base of the sepal.

Mussaenda roxburghii is distinguished from other species by its compact or almost capitate cymes; pubescent and filiform calyx lobes, glabrous within with a tuft of hairs at the base of each; narrow, silky corolla tube, hairy within and with a tufted ring of hairs at the base, the lobes caudate; globose and glabrous fruits with persistent calyx segments; and leaves glabrous on the upper surface.

10. **Mussaenda corymbosa** Roxb. Fl. Indica ed. Carey & Wall. 2: 226. 1824, non Kurz, Forest Fl. Burma 2: 58. 1877; Hook. f. Fl. Brit. India 3: 91. 1880 (TYPE: *Wallich 6252D*, in part).

FIG. 1, d, e, q.

Stout, rigidly erect, branching shrub with glabrous stems. Leaves opposite, ovate- or oblong-lanceolate, 8–16.5 cm. long, 3.5–8 cm. broad, short acuminate, cuneate at the base, glabrous on the upper surface, minutely puberulous below, with 9–14 pairs of lateral veins conspicuous on the lower surface and pubescent; petioles stout, 0.3–4.2 cm. long, glabrous or pubescent. Stipules broadly oblong or triangular ovate, 13–18 mm. long, 7–12 mm. broad at the base extending to within the petioles, hairy along the midline on the outer surface, glabrous within with numerous glands in a continuous band at the base, apex abruptly acuminate terminating in an acute point or bifurcate at the tip only, margin entire or somewhat undulate, vascular strands many, parallel and branched. Inflorescence a terminal, compact, many-flowered, glabrous, di- or trichotomous cymose corymb; bracts and bracteoles lanceolate, glabrous, bracteoles becoming somewhat ovate and larger lower down. Flowers heterostylous on stout, glabrous pedicels shorter than the ovaries. Calyx lobes erect, filiform, 3.5–8.5 mm. long, 0.8–1 mm. broad at the base, glabrous on both surfaces with 2 or 3 pairs of glands at the base of each within; petaloid sepal white, 5–6.5 cm. long, 2.5–3.7 cm. broad, ovate or oblong-elliptic, glabrous on both surfaces except on veins below, acute at apex, narrowed at base, 5- or 7-veined "petiole" 3–3.5 cm. long, minutely pubescent. Corolla tube 2.2–2.6 cm. long, glabrous on the outer surface, hairy within, tufted at the mouth, hairs in the throat long and dense in both long-styled and short-styled forms, below the anthers the hairs shorter and scantier up to 1/5–1/4 the length of the tube from the base; corolla lobes deep, bright orange, greenish underneath, fleshy, ovate-lanceolate or oblong-ovate, 3.5–4 mm. long, 1.7–2.4 mm. broad, minutely pubescent along the midline of the outer surface, papillate within. Stamens with short filaments, epipetalous about 1/2 way up on the tube in long-styled forms and 2/3 way up in short-styled forms; anthers linear, dorsifixed, introrse, 4.5–5.3 mm. long, straight, blunt at the apex, faintly bifid at the base. Ovary 2.3–4.5 mm. long, broadly obconic-fusiform, glabrous, 2-locular with numerous ovules on cushion-shaped axile placentae; style and stigma lobes 1.65–2.05 cm. and 2–3.5 mm. long respectively in long-styled forms, 1.25 cm. and 3 mm. long in short-styled forms. Berry (immature) oval, 7–8 mm. long, glabrous with numerous seeds embedded in a fleshy pulp, calyx lobes subpersistent, seeds (immature) reticulate, 0.43–0.46 mm. long, 0.33–0.39 mm. broad, oblong or broadly triangular ovate, testa with 4–7 foveae in each areole.

ILLUSTRATION. Roxburgh's Fl. Indica drawing No. 1220 in Kew (Kew Bull. **1957**: 361), not seen.

DISTRIBUTION. The collections of *Mussaenda corymbosa* made so far have been from the Bengal-Calcutta area only. The localities of this species were erroneously reported by Roxburgh as Ceylon and Malabar. Hooker (1880) says that "no Ceylon or Malabar plant known to me answers to his [Roxburgh's] description or to a figure of a Calcutta Garden plant which bears this name in a collection of drawings at Kew made for Dr. Roxburgh." I have not come across this plant in Ceylon either, nor has it been collected from Malabar. It flowers during the rainy season.

India. BENGAL: *Herb. Griffith 2779/1* (GH); Calcutta, Galathea Expedition (1845–47), *Kamphovener 954* (C); *Herb. Didrichsen* (C); Hort. Bot. Calcutta, *Wallich 6252D* (A–photograph of lectotype at K; GH–isotype); H[ort]. B[ot]. Serampore [Calcutta], *Wallich 6252* ex Herb. Bentham (NY–isosyntype); Bot. Gard. Calcutta, *Wallich* (GH); cult. Hort. Bot. Calcutta (NY).

Mussaenda corymbosa is allied to *M. roxburghii* Hook. f., from which it differs in its large, persistent stipules and in having all parts of the plant glabrous. Its affinity to *M. keenanii* Hook. f. is closer still. The large stipules, compact, glabrous inflorescence, and filiform calyx teeth are characters common to both, in addition to the leaves with the upper surface glabrous. Heterostyly is demonstrated in the species. Kamphovener's collection bore only a cluster of miniature berries along with short-styled flowers. Throat hairs in both the long-styled and short-styled forms are long and of equal length, a character of *M. frondosa*.

The species is distinguished from others by the glabrous stems, leaves and inflorescences; the large persistent stipules, glabrous within and with numerous glands in a continuous band at the base; glabrous, filiform calyx lobes with two or three pairs of glands at the base of each; narrow corolla tube, glabrous on the outer surface with ovate-lanceolate, non-appendaged lobes; and glabrous, oval berries.

11. **Mussaenda keenanii** Hook. f. Fl. Brit. India 3: 87. 1880 (TYPE: *Keenan*, 1874). FIG. 1, p.

Herbaceous shrub, stems glabrous or scantily appressed pubescent, internodes 3.7–5.7 cm. long, stout. Leaves petioled, 9.5–23.5 cm. long, 4.7–11.3 cm. broad, broadly elliptic or oblanceolate, coriaceous, acuminate, rounded or narrowing towards the base, glabrous and shining above, densely tomentose or hirsute on veins below, the 9–12 pairs of lateral veins arcuate and very prominent on the lower surface; petioles 0.5–3 cm. long, stout, hirsute or appressed pubescent. Stipules broadly ovate, acuminate, 1.6 cm. long, 7 mm. broad at the base, many veined, hairy along the midline and the margin of the outer surface, glabrous within, faintly bifid at the apex, bases extending to within the petioles. Inflorescence terminal, glabrous, the almost capitate cymes about 5 cm. in diameter, on stout peduncles; flowers glabrous, on stout, glabrous pedicels shorter than the ovaries. Calyx lobes linear-filiform, 0.8–1.2 cm. long, 1 mm. broad at the base, scantily pubescent on the outer surface and along the margin, glabrous within, bases fused to form a short tube. Corolla tube about 2–2.5 cm. long, puberulous towards the top, lobes lanceolate, 5 mm. long, 2.2 mm. broad, fleshy, minutely puberulous on the outer surface, papillate within. Ovary about 3 mm. long, broadly fusiform, glabrous. Berry ovoid, 8 mm. long, glabrous, with persistent calyx segments; seeds minute, numerous, reticulate, 0.36–0.46 mm. long, testa with 2–5 foveae in each areole.

DISTRIBUTION. This species, occurring on the margins of flats, was collected by Keenan, in Cachar in 1874, and in Chittagong by Hooker.

India. Cachar, *Keenan* (K–holotype); up to 300 m. elevation, Chittagong, *J. D. Hooker & T. Thomson 18*, in part (K).

This species, *Mussaenda keenanii*, was noted by Hooker as "a remarkable plant, described by its finder as herbaceous, large and robust in all its parts, and flowering later than the other Cachar species." Hooker's collection from Chittagong has two specimens mounted on the same sheet, both with fruits. The top specimen collected from Seetakoond on Jan. 5, 1851, is *Mussaenda roxburghii*, while the specimen below, marked "Flagstaff 228" and collected on Dec. 29, 1850, has the characters of *M. keenanii*: leaves glabrous on the upper surface with 12 pairs of lateral veins, glabrous fruits with persistent calyx, smaller seeds and smaller number (2–5) of foveae in the areoles of the testa.

Mussaenda keenanii is allied to *M. roxburghii* in its almost capitate, glabrous cymes, filiform, crinite calyx teeth, and glabrous berries with persistent calyx segments, but differs from it in the glabrous stems, corolla tube, and the smaller seeds with fewer foveae in the areoles of the testa. I see no relationship to *M. incana* except in the persistent calyx.

From the other mussaendas, *M. keenanii* may be distinguished by its large, thick, leathery leaves, glabrous on the upper surface and tomentose beneath; its glabrous and almost capitate cymes; its glabrous corolla tube; and its berries with persistent calyx segments.

12. **Mussaenda intuspilosa,** sp. nov.

Frutex, caulibus et ramis glabris. Folia oblongo-lanceolata, acuminata, basi cuneata, supra glabra, subtus minute puberula, venis lateralibus 8–10 paribus; stipulae triangulari-lanceolatae, apice bifidae, extus basi et secundum medias pilosae. Cyma terminalis, trichotoma, diffusa. Flores heterostyli; calycis lobi lanceolati, acuminati, glabri vel pubescentes; corollae tubus 2.5–3 cm. longus, extus pubescens, intus totus pilosus vel pubescens et basi pilis penicillatis; corollae lobi lanceolati, acuminati; antherae lineares; bacca ovoidea calycis segmentis deciduis coronata, semina numerosa, minuta, reticulataque.

Shrub about 2.5 m. high with glabrous stems and branches. Leaves oblong-lanceolate or elliptic-lanceolate, 8.5–24 cm. long, 3–8 cm. broad, acuminate, cuneate at base, glabrous on the upper surface, minutely puberulous beneath with 8–10 pairs of lateral veins prominent on the lower surface; petiole 0.5–3 cm. long, glabrous or puberulous. Stipules triangular-lanceolate from a broad base, 6.5–8.5 mm. long, 3.5–6 mm. broad at the base, bifurcate at the apex, hairy at the base and along the middle on the outer surface, hairy within at the base and among the numerous glands. Inflorescence a terminal, glabrous or minutely appressed-pubescent, trichotomous, diffuse cyme; bracts and bracteoles small, lanceolate, glabrous or pubescent, bracteoles broader. Flowers heterostylous, on stout, glabrous or appressed-pubescent pedicels shorter than the ovaries. Calyx lobes five, lanceolate, 4.5–9 mm. long, 1–1.5 mm. broad, acuminate, glabrous or pubescent on the outer surface, within glabrous with one or two pairs of glands and a tuft of hairs at the base of each sepal; petaloid sepal ovate or elliptic-lanceolate, 6.5–10 cm. long, 4.5–6 cm. broad, short acuminate or acute, cuneate, glabrous on both surfaces, 5-veined, "petiole" 1.2–2.8 cm. long, minutely puberulous. Corolla tube 2.5–3 cm. long, glabrous or minutely pubescent outside, hairy inside from mouth to base of the tube; hairs long in both long-styled and short-styled forms, tufted only at the base; corolla lobes 5, lanceolate, 4.5–8 mm. long, 2–2.5 mm. broad, acuminate, glabrous on the outer surface and minutely papillate within. Stamens five, with short filaments, adnate to the corolla tube below the middle, 2/5 way up in long-styled forms and 3/5 way up in short-styled forms; anthers linear, dorsifixed, introrse, 5–6 mm. long, acute, bilobed at base. Ovary inferior, turbinate or globular, 3–4 mm. long, glabrous or minutely and scantily appressed pubescent, 2-locular, with numerous ovules on cushion-shaped axile placentae; style and stigma lobes 2–2.35 cm. and 2–2.5 mm. long respectively in long-styled forms, 1–1.1 cm. and 3.5 mm. long in short-styled forms. Berry (immature) ovoid, 0.75–0.9 cm. long, 6 mm. in diameter, glabrous or pubescent, with a deciduous calyx; seeds minute, reticulate, 0.53–0.73 mm. long, 0.36–0.53 mm. broad, oblong or broadly ovoid, testa with 3–10 foveae in each areole.

DISTRIBUTION. *Mussaenda intuspilosa* grows at the edge of semiopen glades or on roadsides in dense, heavy jungle in Assam and Burma at an elevation of 200–300 meters above sea level. It has been collected in flower in July, August, and October; in fruit in December.

India. ASSAM: 23 mi. on Ledo Road, Namchik River Valley, *Belcher*, U.S.A. Typhus Comm. *953* (US). **Burma.** UPPER BURMA: 40 mi. n. of Myitkyina, Malihka, Nsop Zup, *McKee 6242* (K); 26.2 mi. on Myitkyina-Sumpsabum Road, *Belcher*, U.S.A. Typhus Comm. *811-E* (US); Clegg Hill Traverse, e. bank of Irrawaddy, *Belcher*, U.S.A. Typhus Comm. *111*, Aug. 17, 1945 (US–holotype); *Belcher*, U.S.A. Typhus Comm. *869* (K); Katha District, Mohuyin Reserve, *Lace 5318* (K). LOWER BURMA: Myawaddi to Kawkereik Hills, *Rock 712, 714* (US).

These collections previously have been doubtfully assigned to *Mussaenda glabra* from which they differ in many respects: larger leaves; larger stipules glabrous or pubescent along the midline and base on the outer surface, pubescent within at the base with numerous glands; sepals larger, pubescent (*Lace 5318, Belcher 953*) or glabrous (*Belcher 111, 869*) on the outer surface, all glabrous within and carrying a tuft of hairs at the base of each, a character typical of *M. roxburghii*. Other characters of *M. roxburghii* are the pubescence of the corolla tube inside where hairs are long in both short-styled and long-styled forms and tufted at the base but not at the mouth. The species differs however, from *M. roxburghii* in the diffuse inflorescence, lanceolate sepals glabrous or minutely pubescent outside the corolla tube, and the calyx segments deciduous from the fruit. *Lace 5318* is more pubescent than other collections; *Belcher 953* from Assam differs slightly from the type in the longer corolla tube and banded glands at the base of the stipule. The collections of Rock from Lower Burma agree with the typical form in the leaf, stipule, fruit, and seed characters, though their petaloid sepals are somewhat lanceolate-elliptic and narrowed at both ends.

The species can be distinguished by the large elliptic-lanceolate leaves, triangular-lanceolate stipules with numerous glands, diffuse cymes, lanceolate sepals with a tuft of hairs at the base of each; corolla tube not tufted at the mouth, entirely hairy within and tufted at the base, and glabrous berries with deciduous calyx segments.

13. **Mussaenda parryorum** Fischer, Kew Bull. **1928**: 274. 1928 (TYPE: *Parry 359*).

Scandent shrub, stems terete, brown, appressed-pubescent, internodes 2.5–6.5 cm. long, lenticellate, lenticels white. Leaves opposite, equal, elliptic-lanceolate, 8–15.5 cm. long, 3.5–7 cm. broad, acuminate, cuneate at base, scantily pubescent with long hairs on both surfaces and 7–9 pairs of arcuate, lateral veins prominent below; petiole 0.3–1.5 cm. long, appressed-pubescent. Stipules caducous, triangular-lanceolate, 4–6.7 mm. long, about 3.5–4 mm. broad at the base, hairy outside, bifurcate from apex for about 1/2 their length, lobes subulate, straight. Inflorescence a terminal, trichotomous, many-flowered, diffuse, pubescent, sessile cyme; bracts and bracteoles linear-ensiform, pubescent on both surfaces, 4–8 mm. long, bracteoles trilaciniate. Flowers short, on stout, pubescent pedicels shorter than the ovaries. Calyx lobes 3–4 mm. long, about 0.8 mm.

broad, linear-ensiform, pubescent on both surfaces, caducous; petaloid sepal white with green veins, 4.5–6.5 cm. long, 2.2–3.5 cm. broad, elliptic, acute, narrowed and tapering to base, puberulous on the upper surface, hirsute on veins below, 5-veined, "petiole" 1–1.2 cm. long, hirsute. Corolla tube 2.1–2.5 cm. long, hairy on the outer surface, probably hairy within, tufted at the mouth, lobes yellow, small, suborbicularly ovate or reniform, 2–3 mm. long, 3.5 mm. broad, apiculate, hairy outside, papillate within. Ovary turbinate, 3–4 mm. long, hirsute, style filiform, stigma bilobed, lobes emerging through the tuft of hairs at the mouth (long-styled form). Berry subglobose, 7–8 mm. long, scantily pubescent, lenticellate, calyx lobes deciduous; seeds few, minute, reticulate, black, about 80 to a berry, consisting of large and small seeds embedded in the soft pulp, larger seeds 0.9 mm. long, 0.77–0.83 mm. broad, testa with 5–18 foveae to each areole.

DISTRIBUTION. This species was collected in flower and fruit, Oct. 1927, at an elevation of 1500 meters above sea level. It has not been collected since.

India. ASSAM: N. Vanalaiphai, Lushai Hills, *Mrs. N. E. Parry 359* (K–lectotype, in fruit; syntype, in flower).

The type collection consisting of two sheets, one in flower and the other in fruit, was available for examination. Fischer was of the opinion that *Henry 8270* from Hainan, China, is this species. *Mussaenda parryorum* is related to *M. pubescens*, but the two differ in the size of the leaves, number of lateral veins, size of fruits and seeds. The leaves of *M. pubescens* are smaller with 5–7 pairs of lateral veins, while those of *M. parryorum* bear 7–9 pairs and are more pubescent. The fruits of the former are larger and bear numerous, smaller seeds (0.77–0.8 mm. long). Further, the number of foveae in the areoles of the testa is 3–10 as against 5–18 in *M. parryorum.*

Mussaenda parryorum may be recognized by its elliptic-lanceolate, pubescent leaves and stems, sessile and diffuse cymes, smaller fruits, and larger and fewer seeds embedded in soft pulp.

14. **Mussaenda samana**, sp. nov. FIG. 2.

M. frondosa L. var. *β. glabrata* sensu Trimen, Hand-book Fl. Ceylon 2: 324. 1894, non Hook. f.

M. glabrata sensu Alston in Trimen, Hand-book Fl. Ceylon **6**: 150. 1931, non Hutch. ex Gamble.

Frutex scandens, caulibus et ramis longis tenuibus arcuantibus glabris. Folia oblonga vel obovato-elliptica, acuminata, utrinque glabra, venis lateralibus 5–9 paribus. Stipulae parvae, triangulares vel lanceolato-acuminatae, apice bifidae, extus pubescentes intus glabrae cum glandulis paucis. Cymae terminales dichotomae pauciflorae. Flores tenues heterostyli; calycis lobi parvi lanceolati, acuminati; corollae tubus 2.1–3.1 cm. longus, extus adpresso-pubescens, pili ad orem penicillati, lobi lanceolati

FIG. 2. *Mussaenda samana*: a, branch with inflorescence and petaloid sepals, × ½; b, stipule seen from adaxial surface, × 10; c, calyx lobes from within, × 4½; d, corolla lobe from within, × 4; e, longitudinal section of a long-styled flower, × 2; f, longitudinal section of a short-styled flower, × 2; g, young, mature berries, × ½, all from *Jayaweera 46*.

acuminato-caudati; antherae lineares epipetalae; ovarium fere cylindricum sparsim et minute adpresso-pubescens; bacca ovoidea glabra segmentis deciduis calycis coronata, semina numerosa, minuta, reticulata et spinulosa. (FIG. 2.)

Shrubby climber about 6–10 m. high with long, slender, glabrous, arching stems and branches. Leaves oblong, elliptic or obovate-elliptic, 4–9.2 cm. long, 1.5–4 cm. broad, acuminate, cuneate at base, glabrous on both surfaces with 5–9 pairs of lateral veins, veins prominent below and minutely appressed pubescent; petiole 0.5–1 cm. long, minutely appressed pubescent. Stipules small, 3.5–5.5 mm. long, 2.7–3 mm. broad at the base, triangular or lance-acuminate, bifid at apex, appressed pubescent on the outer surface, glabrous within with few, large glands in two groups at the base. Inflorescence a terminal, diffuse, dichotomous, few-flowered, slender cyme; bracts and bracteoles minute or small, triangular or lanceolate, hairy outside, within glabrous with one or two pairs of glands at the base, bracteoles larger, 3.5–4.5 mm. long, trifid at apex, the midlobe longer than the lateral lobes. Flowers heterostylous, on stout, minutely appressed-pubescent pedicels longer than the ovaries. Calyx lobes 5, small, lance-acuminate or triangular-subulate from a broad base, 1.2–3.5 mm. long, 0.6–1.5 mm. broad at the base, appressed pubescent on the outer surface, within glabrous with 1 or 2 pairs of glands at the base of each; petaloid sepal white, elliptic or ovate, 5.5–8.5 cm. long, 3.7–5 cm. broad, acute or rounded at apex, base cuneate, glabrous on both surfaces or minutely pubescent on the lower surface or on veins only, 5-veined; "petiole" 1–2.5 cm. long and pubescent. Corolla tube 2.1–3.1 cm. long, appressed pubescent on the outer surface; hairs on the inner surface long, tufted at the mouth, dense at the throat and between the anthers in both short-styled and long-styled forms, below the anthers the hairs shorter and scantier, extending as far as 1/7–1/5 the length of the corolla tube from base; corolla lobes 5, orange, broadly lance-ovate, 5.5–7.5 mm. long, 3.5–5.5 mm. broad, acuminate, caudate, pubescent on the outer surface, papillate within. Stamens 5, with short filaments, adnate to corolla tube 3/5 its length in long-styled forms and 2/3 its length in short-styled forms, filaments free for a short distance (about 2 mm.) midway on the corolla tube; anthers linear, dorsifixed, introrse, 5.3–7 mm. long, subacute or rounded at apex, bilobed at base. Ovary inferior, 3.5–5.5 mm. long, somewhat cylindrical, scantily and minutely appressed pubescent, 2-locular with numerous ovules on cushion-shaped axile placentae; style and stigma lobes 2–2.4 cm. and 2–3 mm. long respectively, in long-styled forms, 1.6–1.75 cm. and 4.5 mm. long in short-styled forms. Berry ovoid, 1.3–1.5 cm. long, 1 cm. in diameter, glabrous, calyx lobes deciduous; seeds minute, reticulate, spiny, oblong or irregularly triangular-ovate, 0.83–1.33 mm. long, 0.67–1 mm. broad; testa with 4–12 foveae in each areole.

DISTRIBUTION. This is an endemic species growing at Gilimale in the Ratnapura District in Ceylon at an elevation of 150 meters above sea level, extending on to the foot of Adam's Peak or Samana Kande (elevation 1350 meters), a locality sacred to Buddhists all over the world because of a rock carving of a foot of Buddha at its summit. The vegetation in this area is transitional between the Tropical Wet Evergreen Forests and Subtropical Montane Forests with a rainfall of over 250 centimeters a year. Species characteristic of this type of jungle are *Celtis cin-*

namomea Lindl., *Calophyllum calaba* L., *Garcinia echinocarpa* Thw., *Terminalia parviflora* Presl, *Kurrimia zeylanica* Arn., *Doona gardneri* Thw., *Semecarpus nigroviridis* Thw., *Myristica malabarica* Lam., and *Diospyros sylvatica* Roxb. *Mussaenda samana* flowers and fruits between September and January, the less rainy months of the year.

Ceylon. RATNAPURA DISTRICT: Gilimale, *Jayaweera 46*, Jan. 24, 1961, holotype (A), *Jayaweera 43, 47* (A); Foot of Adam's Peak, *Jayaweera 42, 44* (A).

This species was referred to *Mussaenda frondosa* var. *glabrata* by Trimen (1894), but it differs from that plant in its glabrous stems and leaves, smaller stipules, longer, lance-ovate corolla lobes, and larger fruits and seeds. The only common character is the spininess of the seed. It resembles *M. glabra* to a certain extent but differs from it in the large spiny seeds and in having in the throat of the corolla tube of long-styled forms long hairs which are tufted at the mouth of the tube, in contrast to *M. glabra* with its smooth seeds and short hairs in the corolla tube of the long-styled forms. This species stands distinct from *M. frondosa* var. *glabrata* and from *M. glabra* but is related to both of them. I describe this species as new, not only because of its distinctive characters, but also because of its isolation. Trimen says in reference to this, "Var. β, which looks quite distinct, is perhaps the *M. corymbosa* of Roxb. which he states (Fl. Ind. i. 556) to be a native of Ceylon, or possibly *M. glabra*, Vahl, which has a wide Malaya and Burma distribution but is not recorded for Peninsular India in Fl. B. Ind."

Mussaenda samana is easily distinguished from other species of the genus by its glabrous stems and leaves; small stipules; slender, few-flowered terminal cymes; small calyx lobes; lance-ovate, acuminate corolla lobes; throat hairs long in both long-styled and short-styled forms; glabrous berries with dehiscent calyx; and large, spiny seeds.

15. **Mussaenda glabra** Vahl, Symb. Bot. Pl. 3: 38. 1790; Hook. f. Fl. Brit. India 3: 90. 1880 (TYPE: *Vahl*). FIG. 1, f–j; FIG. 3, g–i.

M. frondosa sensu Wall. Cat. 6250B & E (both in part). 1832, non L.
M. setulosa Klotzsch, Ber. Akad. Wiss. Berlin **1853**: 499. 1853.
M. penangensis Miq. Fl. Ned. Indië **2**: 214. 1857.

Rambling or climbing shrub with almost glabrous branches. Leaves elliptic, oblong or elliptic-lanceolate, 5–14 cm. long, 1.6–5.5 cm. broad, acuminate, cuneate, acute or obtuse at base, usually glabrous on both surfaces and minutely pubescent on veins below or on both surfaces, or on the lower surface only, with 4–10 pairs of lateral veins; petioles 0.4–2.5 cm. long, glabrous or pubescent. Stipules triangular or lanceolate, 2.7–8.5 (–11) mm. long, 1.5–7 mm. broad at the base, pubescent on the outer surface, glabrous within or hairy at the base only, bearing a few glands in 2 groups, apex bifurcate 1/3–1/2 way, lobes straight or diverging. Inflorescence a terminal, di- or trichotomous, many-flowered, diffuse cyme; bracts and bracteoles lanceolate, deciduous, pubescent on both surfaces, bracteoles larger in opposite pairs, trifid about 1/2 way. Flowers small, slender, on pubescent pedicels as long as the ovaries. Calyx lobes lanceolate, 1–7.5 mm. long, 0.7–1.5 mm. broad, pubescent on both surfaces or on the outer surface only; petaloid sepal white, oblong or elliptic, 3–12 cm. long, 1.5–9.2 cm. broad, usually glabrous on both surfaces except on veins below or minutely puberulous on both sides, cuneate, 5-veined, "petiole" 0.8–2.5 cm. long and hairy. Corolla yellow or orange, the tube 1.4–2.5 cm. long, hairy on the outer surface (more densely so towards the upper half), hairy within at the mouth, the throat, and between the anthers as far as the anther bases; hairs long in short-styled forms and short in long-styled forms; corolla lobes 1.5–6 mm. long, 2–3.5 mm. broad, lanceolate, broadly ovate or orbicular, acuminate or apiculate, hairy on the outer surface, papillate within. Stamens with short filaments, epipetalous on the upper 2/5–1/2 of the tube in long-styled forms and 1/4–1/3 of the tube in short-styled forms; anthers linear, dorsifixed, introrse, 2.5–5.5 mm. long, bilobed at the base, shorter in long-styled forms. Ovary obconical or turbinate, 2–4 mm. long, glabrous or minutely pubescent, 2-locular, with numerous ovules on cushion-shaped axile placentae; style and stigma lobes 1.4–2 cm. and 4.5–7 mm. long respectively in long-styled forms, 1.6–6 mm. and 1.5–5 mm. long in short-styled forms. Berry ovoid-elliptic, 1–1.2 cm. long, glabrous, lenticellate, calyx lobes deciduous; seeds minute, reticulate, 0.67–0.83 mm. long, 0.46–6 mm. broad, testa with 2–7 or 3–14 foveae in each areole.

ILLUSTRATIONS. Loddiges, Bot. Cab. **13**: *tab. 1269*. 1827; Rumphius, Herb. Amboinense **4**: *tab. 51*. 1743.

DISTRIBUTION. Collected widely from Sikkim, Khasia, Assam, and Chittagong at elevations up to 2440 meters above sea level; in Burma mostly for the Mergui area with *Kingdon-Ward 22098* from the Triangle in North Burma between 900 and 1500 meters elevation; in Siam from the Chantaboon area; in Singapore from lower altitudes; also in Java, China, and the Ryukyu Islands. (The distinction between *Mussaenda glabra* and *M. erosa* Champ. from China is very little. Bentham (1861) says in reference to *M. erosa*, "It may however be a variety of *M. frondosa* or of *M. glabra* of Vahl, which Miquel unites with *M. frondosa*.") It has been collected in flower from January to June, September, October, and December; in fruit in January, April, June, and December.

India. SIKKIM: *J. D. Hooker 17* (GH, K); *Treutler*, 1874 (K); Darjeeling, *Schlaginweit 12385* (GH); *Cowan, Imp. For. 24464* (US); Choonbutte, *Clarke 26603B* (K). KHASIA: *Hooker & Thomson 17* (NY); Silhet, *Wallich 6250D* (C); *Hooker & Thomson 17* (NY); Mamloo, *Clarke 43821* (K); Chura, *Hooker & Thomson 17* (K). ASSAM: *Masters* (GH); *Jenkins* (K); *Jenkins 501* (NY); Naga Hills, Henima, *Bor 6471* (K); Mishmi Hills, Sadiya Plain, *Kingdon-Ward 18588* (A); Janakmukh, *Burkill 36467* (K); Lushai Hills, Chinchuk, *Parry 600* (K); Cachar, *Bazer 146* (K); Sittong, *Biswas 7473* (PNH); Ledo, *Juan 76* (A); Ind. Orient. *Herb. Wight 1266* (NY); Ind. Orient., *Vahl* (C–holotype); cultivated, Calcutta Bot. Gard., *Voigt* (C, A). **Burma.** NORTH TRIANGLE: *Kingdon-Ward 22098* (A). RANGOON: Mogok, *Dickason 5005, 3093* (A). MERGUI:

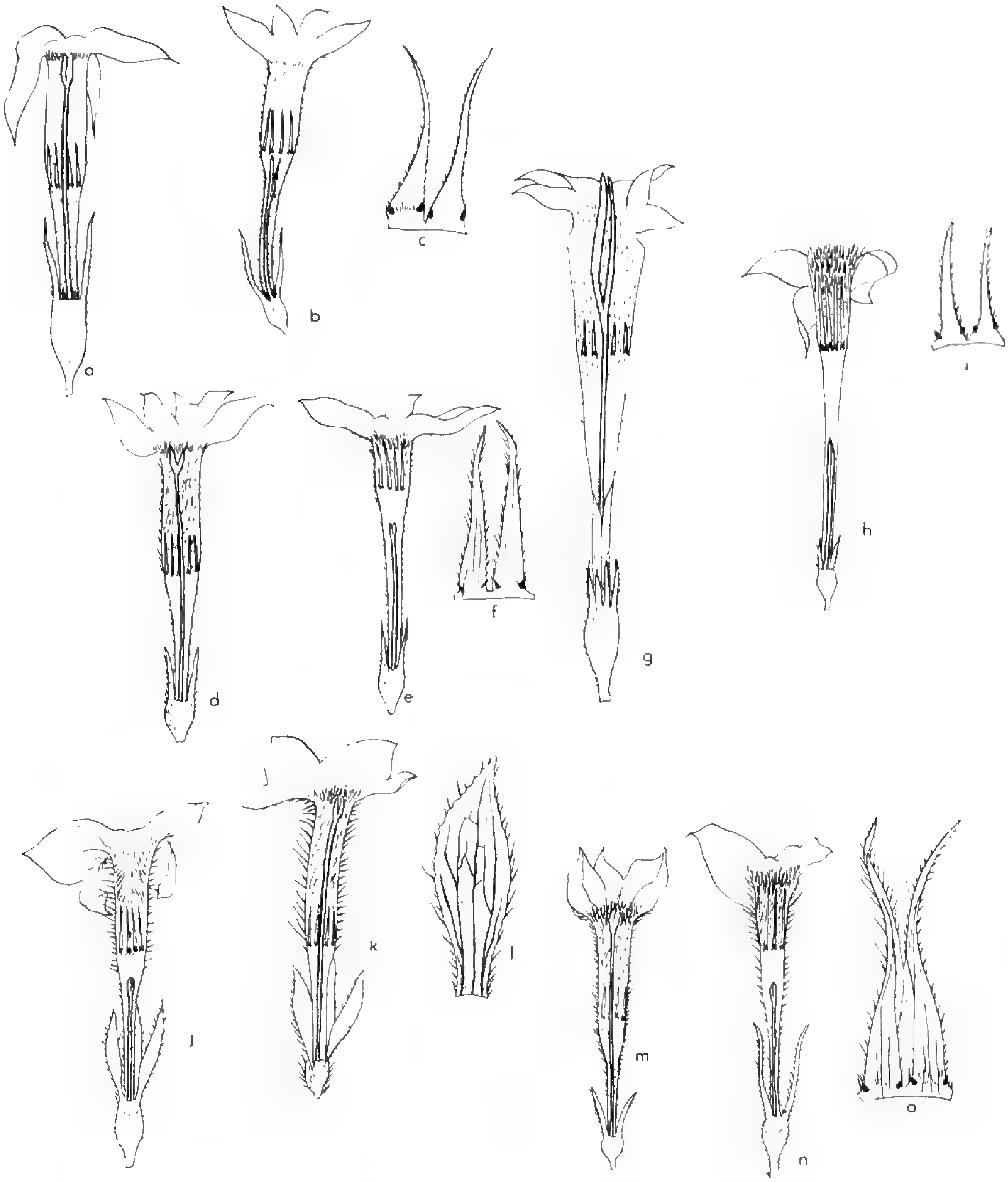

FIG. 3. Longitudinal sections of long-styled and short-styled flowers of some Indian species of *Mussaenda* and calyx lobes seen from within. a–c, *M. roxburghii*: a, (*Gamble 10476*), × 1; b, (*Wallich G 6252*), × 1; c, calyx lobes, × 3¼ (note tufted hairs at base of corolla tube and calyx lobes). d–f, *M. incana*: d, (*Voigt 136*), × 1; e, (*Herb. Griffith 2781*), × 1; f, calyx lobes, × 2⅓. g–i, *M. glabra* (*Siedenfaden 2696*): g, long-styled flower, × 1⅔; h, short-styled flower, × 1½; i, calyx lobes, × 5. j–l, *M. macrophylla*: j, (*Yü 17681*), × 1; k, (*Parry 274*), × 1; l, calyx lobes, × 2. m–o, *M. hirsutissima*: m, (*Gamble 11393*), × 1; n, (*Barnes 120*), × 1; o, calyx lobes, × 2½, note hairiness at base of calyx lobes.

Palauk, *Parker 3079* (NY); Palauk Chaung, *Parker 3137* (NY); Kwin-ta-bin taw, *Maung Po Khant 13290* (K); *Herb. Helfer 2778* (K), Kew Distribution 1861–2; *Griffith* (K). S. TENASSERIM: Kallin kwan chang, *Parkinson 1692* (K); Chaungnaukpyan, *Parkinson 1638* (K). **Siam.** Chantaboon, *Vesterdal 9B, 9E, K* (C); Chantabura, West of Kao Sabab, *Siedenfaden 2696* (C). **China.** KWANGTUNG: Lantau Island, Taai ue Shaan, *Tsang 16672* (A). KWANGSI: Shap Man

Taai Shan, *Tsang 22095* (A). **Japan.** Ryukyu Islands, *Wright 119* (GH, US). **Malaya.** Singapore, Pahang, Sungai Bera, *Henderson 24128* (NY); Bot. Gard., *Clemens 1013* (NY). **Java.** *Delessert* (C); *Blume* (NY); *Didrichsen 3926* (C); Depok, *Jensen* (C); *Soegandirerja 244* (A); *Reinwardt* (C); *Sargent* (A); *Mousset 230* (US); Goenoeng Boto, *Franck 93* (C, GH, US); Mount Salak, *Palmer & Bryant 371* (US); Nogosari, *Gandrup* (C).

There are two collections included in the type cover (C); one, which agrees with the description of Vahl, I select as the lectotype; the other, with large, oblong-elliptic leaves bearing 13 or 14 pairs of lateral veins, large flowers, and long, pubescent calyx lobes does not seem to belong to this species but rather to be a form of *Mussaenda macrophylla* Wall. Vahl did not mention the locality of the collection he described, but G. Don said it was a native of the East Indies. Delessert's collection from Java closely resembles the type.

Most of the collections from India have been made from elevations below 1500 meters, but *Schlaginweit 12385* was gathered from Darjeeling between 1830 and 2440 meters elevation.

Hooker divided the species into four varieties distinguished by the character of the leaf base and the proportion of the calyx lobes to the ovary. As there are a large number of transitional forms the boundaries between them can hardly be maintained. Therefore, the species is considered as a whole with variations.

Most of the leaves of gatherings bear 4–6 pairs of lateral veins, except *Herb. Wight 1266* which has the leaf bases long attenuate and nine pairs of lateral veins. The stipules in all collections are small, except Treutler's which bears stipules about 11 mm. in length with glands in a continuous band at the base. The calyx lobes vary in size but agree in shape and hairiness on the outer surface. In all Indian forms the calyx lobes are glabrous inside, while the type specimen bears short lobes, minutely appressed pubescent on both sides. Although the corolla tube is generally short, the lobes in some forms are broadly ovate or orbicular.

According to the number of foveae in the areoles of the testa of the seed, the specimens of this species fall into three groups which cannot, however, even be considered *formae.* The collections *J. D. Hooker 17,* from Sikkim, and *Burkill 36467* and *Parry 600,* from Assam, bear 2–7 foveae in each areole of the seed coat, while *Clarke 26603B,* from Sikkim, and *Jenkins 501,* from Assam, bear 3–10 foveae, and still others such as *Hooker & Thomson 17,* from Khasia, bear 3–14 foveae. The seed is reticulate and usually smooth, but there is a tendency toward spininess in some forms (such as *Herb. Wight 1266* and *J. D. Hooker 17*) but not sufficiently marked to be termed spiny.

Voigt's collections from Calcutta, probably from cultivated material, are of special interest. Of the ten specimens examined, three have been annotated by Bremekamp as *Mussaenda frondosa* and three as *M. glabra,* two specimens have been identified by Merrill as *M. frondosa* and the remaining two as *M. frondosa* by Voigt himself. All these specimens are of the short-styled form with stigmatic lobes as long as the styles. The throat hairs are long and not tufted at the mouth, a character which re-

FIG. 4. *Mussaenda frondosa*: Photograph of type-collection, from Ceylon (*Hermann*), left-hand specimen lectotype, right-hand specimen syntype. — By permission of the British Museum (Natural History).

moves them from the *M. frondosa* group. The leaves of those which Bremekamp and Merrill have named as *M. frondosa* are elliptic-lanceolate, acuminate, attenuate at the base, short petioled, very scantily hairy on both surfaces, and with 4–6 pairs of lateral veins not unlike Treutler's collection from Sikkim Himalaya. Stipules are small, appressed pubescent on the outer surface, glabrous within with few glands in two groups. The corolla tube is short (2 mm. long) and not tufted at the mouth, and the lobes are lanceolate. As they agree with the typical *M. glabra* in their stipule and floral characters I have reidentified them all as *M. glabra*.

The collections of Parker, Griffith, Helfer, and Parkinson from Burma are conspicuous in their sturdy, trichotomous, many-flowered, diffuse, cymose panicles, glabrous stems, leaves, and larger stipules (7–8.5 mm. long) bearing numerous glands in two groups at the base. The corolla tube is longer (2.2–2.5 cm. long) than in the typical form, the lobes ovate, and the anthers in long-styled forms do not seem to dehisce. Hairs inside the corolla tube of the long-styled forms are short (0.2 mm. long) extending to below the bases of the anthers as far as 1/5 the length of the tube from the base, a feature not observed in other forms. The specimens of *Kingdon-Ward 22098* from North Triangle are said to be abundant at elevations between 900 and 1500 meters. This is a long-styled form, but the corolla tube is shorter (1.5 cm. long) and the throat hairs extend as far as 1/3 the length of the tube from the base. The style is looped somewhat inside the tube and the stigmas protrude beyond the mouth. The anthers do not seem to have pollen. *Dickason 5005* from Mogok is a short-styled form with the anthers attached to the upper third of the tube. The stipules are typical of *M. glabra*, and the style and stigmas are well developed.

Vesterdal's and Seidenfaden's collections from Siam agree with *Mussaenda glabra* var. 1 of Hooker in the form of the leaves and pubescence, though the flowers are more slender. The stipules are narrow, densely pubescent outside and bifurcate at the apex to about 3/4 way. *Seidenfaden 2696* (c) has two specimens mounted, one belonging to the long-styled form and the other to the short-styled form. The flowers of the long-styled form bear large stigma lobes (7 mm. long) and reduced anthers (3.2 mm. long) placed lower down in the corolla tube. The ovary is about twice as long as that in the short-styled form.

There seems to be some confusion in the identities of *Mussaenda erosa* and *M. glabra* from China. Collections labeled as *M. erosa* are made up of the true *M. erosa* Ait. (e.g., the collections *Henry 10646, 13648, 13694* bearing linear calyx lobes more than twice as long as the ovary) and a form of *M. glabra* erroneously labeled as *M. erosa*. True *M. erosa* differs from *M. glabra* in its stipules bearing numerous glands in a continuous band at the base within and each calyx lobe bearing two or three pairs of glands at the base. *Wright 119* from the Ryukyu (Loo-choo) Islands agrees with true *M. glabra*, but the testa of the seed contains a larger number of foveae (7–17) in each areole.

Four collections from Singapore and Johore were examined. *Henderson 24128* and *Clemens 1013* agree with *Mussaenda glabra* except for their longer sepals and broadly ovate petals. They are short-styled forms, and their style, stigmas, and ovaries are much reduced. Clemens' collection seems to be from a cultivated specimen in the Botanic Gardens, Singapore.

The collections from Java show the greatest variation in the species. They differ from the type in the number of pairs of lateral veins in the leaf, which normally exceeds six, and in the broader corolla lobes. There is a considerable development of the styles and stigmas in the long-styled forms and conversely a reduction in size of these organs in the short-styled forms.

Mussaenda glabra can be distinguished by its glabrous stems and leaves, small stipules with fewer glands at the base within, hairs not tufted at the mouth of the corolla tube (very short in long-styled forms), glabrous fruits with dehiscent calyx lobes, and minute seeds with fewer foveae in the areoles of the testa.

ROYAL BOTANIC GARDENS,
PERADENIYA, CEYLON

A REVISION OF THE NEW CALEDONIAN SPECIES OF OSMANTHUS *

P. S. GREEN

THROUGHOUT MUCH OF THE OLEACEAE generic limits are obscure; particularly is this so in the Tribe Oleeae, and until detailed revisions on a world basis have been completed it is in many ways advisable to take a broad view of genera. In consequence of this the species included in this revision are treated as members of the genus *Osmanthus* Lour., notwithstanding the fact that Johnson, in his relatively recent review of the family (Contr. New S. Wales Natl. Herb. 2: 295–318. 1957), segregated them, along with some other Australasian species, in the resurrected genus *Nestegis* Raf. (*Gymnelaea* (Endl.) Spach). These New Caledonian species, however, differ from the other members of *Osmanthus* in their inflorescence characters and should be recognized as constituting a separate section. This is proposed and described below.

In addition to being treated in *Nestegis*, which has been characterized by the possession of a decussate inflorescence together with either no corolla or one in which the aestivation of the lobes is imbricate, these species have at times been classified in the genus *Notelaea* Vent. However, although the basic inflorescence type is similar throughout the whole Pacific complex, the true members of this last genus are distinguished by their induplicate-valvate corolla lobes. Three of the species maintained in this revision were first classified as *Notelaea* but other New Caledonian plants which have been described in this latter genus are excluded from *Osmanthus* by characters of the flowers. The first such species described was named *Notelaea brachystachys* and the type specimen, one of the only flowering specimens of this group, bears flowers with induplicate-valvate corolla lobes arranged in two pairs and appearing as though, when fully developed, they would be long in proportion to their breadth. This suggests the genus *Linociera* with many species in Malaysia and a few outliers in Australasia. The appearance of the other species, *N. francii* Guillaum. and *N. paniculata* Guillaum., would also suggest *Linociera*, as does that of *Sarlina cylindocarpa* Guillaum., a relatively newly described monotypic genus.

I should like to express my grateful thanks and appreciation to the directors and curators of the various herbaria cited in this revision, either for the loan of material or for facilities to study. All the material cited has been examined and the respective herbaria are indicated by the abbreviations published in the *Index Herbariorum*. I should particularly

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* Results of the Botanical Expedition to New Caledonia 1950–52 (French-Swiss Mission).

like to thank Dr. H. Hürlimann, of Basle, for help with information about the habitats of *Osmanthus austro-caledonicus*, and Miss Judith Kroll for the drawing and diagrams used to illustrate this paper.

Osmanthus Sect. **Notosmanthus** P. S. Green, sect. nov.

Ab aliis sectionibus inflorescentiis decussatis differt. Folia integra. Inflorescentiae axillares decussatae. Flores androdioecii. Corolla tuba brevicampanulata, lobis quattuor imbricatis. Antherae 1–2.2 mm. longae, appendice terminali parva.

Evergreen shrubs or small trees up to 10 m. in height, branches glabrous or puberulous when young. *Leaves* glabrous or minutely puberulous towards the base of the midrib when young, lamina thick coriaceous; margin entire, slightly thickened; apex acute to rounded; venation obscure or reticulate. *Inflorescence* axillary, decussate with terminal flower, 1–6 per axil from 1–2 superposed buds, 1.5–6 cm. long with 5–13 flowers per rachis, sometimes the five terminal flowers subumbellate; bracts narrowly triangular-linear to more or less ovate or subfoliaceous. *Flowers* androdioecious. *Calyx* 1–2.5 mm. long with 4 somewhat irregular more or less triangular lobes 0.5–1.5 mm. long. *Corolla* short campanulate, tube 1.2–2.8 mm. long, lobes 4, broadly ovate, rounded, imbricate in bud, 0.7–2.5 mm. long. *Stamens* 2, subsessile near the middle of the corolla tube, anthers 1–2.5 mm. long, the largest in male flowers, with a slight terminal appendage often barely discernible. *Ovary* 1.7–2.5 mm. long, triangular flask-shaped without differentiated style; terminal stigma more or less bilobed, 0.4–0.6 mm. long; in male flowers abortive, more or less conical 0.3–1.2 mm. long. *Drupe* ovoid or ellipsoid, often slightly asymmetrical, 7–12 mm. long by 4–8 mm. broad; endocarp hard, 0.2–1 mm. thick, sometimes slightly ridged.

TYPE SPECIES: *Osmanthus austro-caledonicus* (Vieill.) Knobl.

KEY TO SPECIES

1. Petioles up to 1.5 cm. long; inflorescence one per axil terminated by a single flower (FIG. 1, A & B). . . . . 2.
    2. Inflorescence bracts narrowly triangular or linear, 0.5–3 mm. long, more or less early deciduous; calyx 1–1.5 mm. long with lobes 0.3–1 mm. long; petioles 1–2 mm. broad, 2–10(–15) mm. long; lamina very narrowly to broadly elliptic or occasionally narrowly ovate or obovate, (1.8–)3–7(–9.5) cm. long; apex acute, obtuse or rounded, less commonly subacuminate. 3.
        3. Leaves very narrowly elliptic to elliptic or occasionally narrowly ovate or obovate, thickish, more or less coriaceous, (1.8–)3–7(–9.5) cm. long; apex acute, obtuse or rounded, sometimes subacuminate; venation usually with only primary veins visible, sometimes obscurely reticulate; petioles 2–10(–15) mm. long; found from sea level to 1000 m. alt. . . . . 1. *O. austro-caledonicus.*
        3. Leaves broadly elliptic, thick, coriaceous, 2.8–4.2 cm. long; apex subacuminate; venation with primary veins clearly visible, more or less

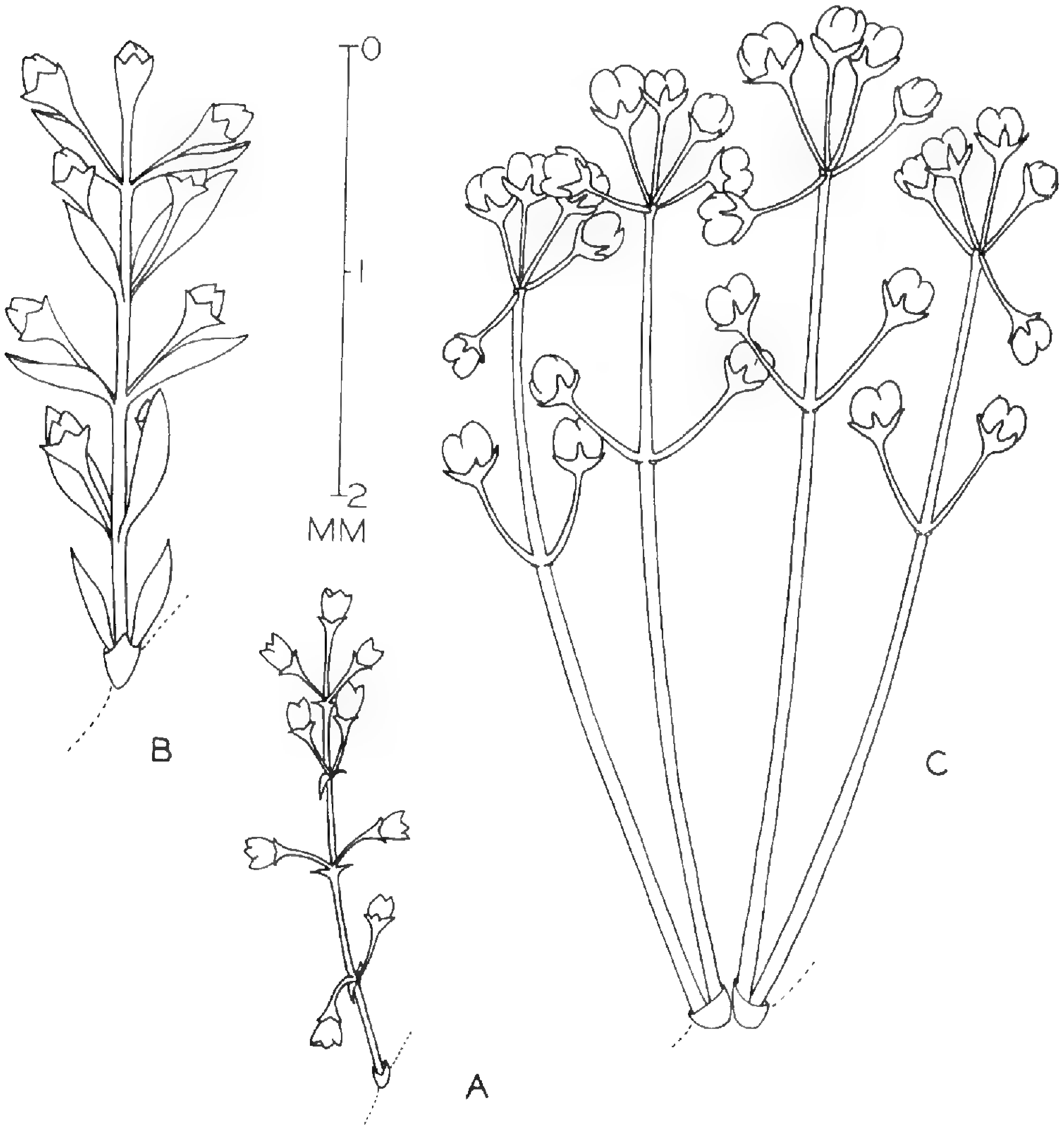

FIG. 1. Types of inflorescence in New Caledonian *Osmanthus*, semidiagrammatic. A, *Osmanthus austro-caledonicus* (*White 2184*); B, *O. monticola* (*Schlechter 15315*); C, *O. cymosus* (*Balansa 1222*).

reticulate below; petiole 3–4 mm. long; montane habitats, about 1400 m. alt. . . . . 2. *O. crassifolius.*

2. Inflorescence bracts subfoliaceous, ovate to lanceolate or elliptic, (2–)3–5 (–12) mm. long, more or less persistent; calyx 2–2.5 mm. long with lobes 1–1.5 mm. long; petioles 3–4 mm. broad, stout, 3–7(–10) mm. long; lamina elliptic to broadly elliptic (4.5–)6.5–9(–12.5) cm. long, apex short acuminate to subapiculate. . . . . 3. *O. monticola.*

1. Petioles 2.5–3 cm. long; inflorescences 3 to 6 per axil, the five terminal flowers subumbellate (FIG. 1, C). . . . . 4. *O. cymosus.*

1. **Osmanthus austro-caledonicus** (Vieill.) Knoblauch, Repert. Sp. Nov. **41**: 152. 1936; Guillaumin, Bull. Soc. Bot. France **89**: 232. 1942, Bull. Mus. Hist. Nat. Paris II. **15**: 454. 1943, *ibid.* **28**: 314. 1956, Fl. Nouv.-Caléd. 283. 1948 et Mém. Mus. Hist. Nat. Paris II (B). **8**: 161. 1959.

Notelaea austro-caledonica Vieillard, Bull. Soc. Linn. Normand. **9**: (Pl. Nouv.-Caléd. 16) 345. 1865; Guillaumin, Ann. Mus. Col. Marseille II. **9**: 192. 1911.

N. badula Vieillard ex Pancher & Sebert in Sebert, Not. Bois Nouv. Caléd. 184. 1872; Jeanneney, Nouv.-Caléd. Agricole, 115. 1894; Schlechter, Bot. Jahrb. **39**: *228*. 1906; Guillaumin, Ann. Mus. Col. Marseille II. **9**: 192. 1911, Bull. Mus. Hist. Nat. Paris. **18**: 40. 1912, *ibid.* **19**: 522. 1913, *ibid.* **25**: 291. 1919, *ibid.* **27**: 560. 1921, *ibid.* II. **2**: 169. 1930, *ibid.* **4**: 701. 1932, *ibid.* **5**: 323. 1933, *ibid.* **6**: 458. 1934, *ibid.* **13**: 476. 1941, in White, Jour. Arnold Arb. **7**: 100. 1926, Bull. Soc. Bot. France **89**: 232. 1942 et Not. Syst. Paris **11**: 55. 1943; Däniker, Viert. Naturf. Ges. Zürich **78** (Beibl. 19): 363. 1933.

N. collina Schlechter, Bot. Jahrb. **39**: 229. 1906; Guillaumin, Ann. Mus. Col. Marseille II. **9**: 192. 1911, Bull. Mus. Hist. Nat. Paris II. **4**: 693. 1932, *ibid.* **5**: 323. 1933.

N. eucleoides Schlechter, Bot. Jahrb. **39**: 229. 1906; Guillaumin, Ann. Mus. Col. Marseille II. **9**: 192. 1911, Bull. Mus. Hist. Nat. Paris **18**: 40. 1912, *ibid.* **25**: 652. 1919, *ibid.* II. **6**: 458. 1934; Däniker, Viert. Naturf. Ges. Zürich **78** (Beibl. 19): 364. 1933.

N. vaccinioides Schlechter, Bot. Jahrb. **39**: *230. fig 22*. 1906; Guillaumin, Ann. Mus. Col. Marseille II. **9**: 192. 1911, Bull. Mus. Hist. Nat. Paris **18**: 40. 1912, *ibid.* II. **5**: 323. 1933, in Sarasin & Roux, Nova Caledonia, Bot. **1**: 206. 1921 et in White, Jour. Arnold Arb. **7**: 100. 1926; Däniker, Viert. Naturf. Ges. Zürich **78** (Beibl. 19): 364. 1933; Guillaumin, Bull. Soc. Bot. France **89**: 232. 1942.

Osmanthus vaccinioides (Schltr.) Hochreutiner, Bull. New York Bot. Gard. **6**: 284. 1910; Moore, Jour. Linn. Soc. Bot. **45**: 356. 1921; Guillaumin, Bull. Soc. Bot. France **89**: 233. 1942, Bull. Mus. Hist. Nat. Paris II. **15**: 340, 454. 1943, *ibid.* **30**: 397. 1958, *ibid.* **31**: 179. 1959, Fl. Nouv.-Caléd. 283. 1948, et Mém. Mus. Hist. Nat. Paris II (B). **4**: 49. 1953; Virot, Vég. Canaque 175. 1956.

O. deplanchei Hochreutiner ex Guillaumin, Ann. Mus. Col. Marseille II. **9**: 192. 1911 et Bull. Soc. Bot. France **89**: 232. 1942; Nakai, Bot. Mag. Tokyo **44**: 15. 1930; *nomen nudum.*

O. badula (Vieill.) Hutchinson ex Moore, Jour. Linn. Soc. Bot. **45**: 356. 1921; Guillaumin, Bull. Soc. Bot. France **89**: 232. 1942, Bull. Mus. Hist. Nat. Paris II. **15**: 340, 454. 1943, *ibid.* **20**: 371. 1948, *ibid.* **23**: 648. 1951, *ibid.* **27**: 475. 1955, *ibid.* **30**: 397. 1958, Fl. Nouv.-Caléd. 283. 1948, Mém. Mus. Hist. Nat. Paris II (B). **4**: 48. 1953, *ibid.* **8**: 161. 1959, et Not. Syst. Paris **15**: 38. 1954; Virot, Vég. Canaque 211. 1956.

O. collinus (Schltr.) Knoblauch, Repert. Sp. Nov. **41**: 152. 1936; Guillaumin, Mém. Mus. Hist. Nat. Paris II (B). **8**: 161. 1959.

O. eucleoides (Schltr.) Knoblauch, Repert. Sp. Nov. **41**: 152. 1936; Guillaumin, Bull. Soc. Bot. France **89**: 232. 1942, Fl. Nouv.-Caléd. 283. 1948, Mém. Mus. Hist. Nat. Paris II (B). **4**: 49. 1953, *ibid.* **8**: 161. 1959 et Bull. Mus. Hist. Nat. Paris II. **27**: 475. 1955.

Gymnelaea badula (Vieill.) L. Johnson, Contr. New S. Wales Natl. Herb. **2**: 413. 1957.

G. collina (Schltr.) L. Johnson, *loc. cit.*

G. eucleoides (Schltr.) L. Johnson, *loc. cit.*

G. vaccinioides (Schltr.) L. Johnson, *loc. cit.*

Nestegis badula (Vieill.) L. Johnson in Degener, New Ill. Fl. Hawaiian Is. 300. Nestegis. 1958.

N. collina (Schltr.) L. Johnson, *loc. cit.*

N. eucleoides (Schltr.) L. Johnson, *loc. cit.*
N. vaccinioides (Schltr.) L. Johnson, *loc. cit.*

Evergreen *shrub* or *small tree* (microphanerophyte) 0.5–3(–7) m. tall; branches glabrous or puberulous, often minutely so. *Leaves* glabrous, sometimes minutely puberulous towards the base of the midrib when young; petiole 2–10(–15) mm. long, glabrous or puberulous, often minutely so; lamina thick or thickish, more or less coriaceous, very narrowly elliptic to elliptic or occasionally narrowly ovate or obovate (FIG. 5), (1.8–)3–7(–9.5) cm. long by (0.3–)0.5–2.5(–3.5) cm. broad; margin entire, slightly thickened, flat or slightly recurved; apex very acute to obtuse or rounded, sometimes subacuminate, tip blunt; base attenuate into the petiole, acute or rarely obtuse; venation usually more or less obscure, often only primary veins visible, 4–7(–8) per side, sometimes obscurely reticulate. *Inflorescence* axillary, decussate, 1.5–4(–6) cm. long, (5–)7–9(–13)-flowered with a single terminal flower (FIG. 1, A), glabrous or puberulous, often minutely so; bracts narrow triangular or linear 0.5–3 mm. long, deciduous. Flowers androdioecious, white (or yellowish-white, *Baumann-Bodenheim 6291*) scentless (*fide* Compton); pedicels 1–5(–13) mm. long. *Calyx* glabrous or puberulous, 1.5 mm. long, lobes 4, blunt-triangular, 0.3–1 mm. long, margins glabrous or ciliolate. *Corolla* short campanulate, tube (1.2–)1.5–2(–2.5) mm. long, lobes 4, imbricate in the bud, broadly ovate, rounded, (1–)1.5–2(–2.5) mm. long. *Stamens* 2, subsessile near the middle of the corolla tube; anthers 1–2 mm. long in hermaphrodite flowers and 1.5–2.2 mm. long in male flowers, broadly elliptic to slightly ovate, apex rounded with a very slight, blunt (sometimes barely discernible) appendage. *Ovary* in hermaphrodite flowers 1.7–2.2 mm. long, triangular-flask shaped without differentiated style; stigma terminal, more or less bilobed, 0.4–0.6 mm. long (FIG. 2,A); in male flowers abortive, 0.3–1 mm. long, more or less conical, often with a slightly notched apex (FIG. 2,B). *Drupe* dark purple or black when ripe, ovoid to ellipsoid, often slightly asymmetrical, 7–12 mm. long by 4–7 mm. broad, endocarp hard 0.2–0.7 mm. thick, sometimes slightly ridged.

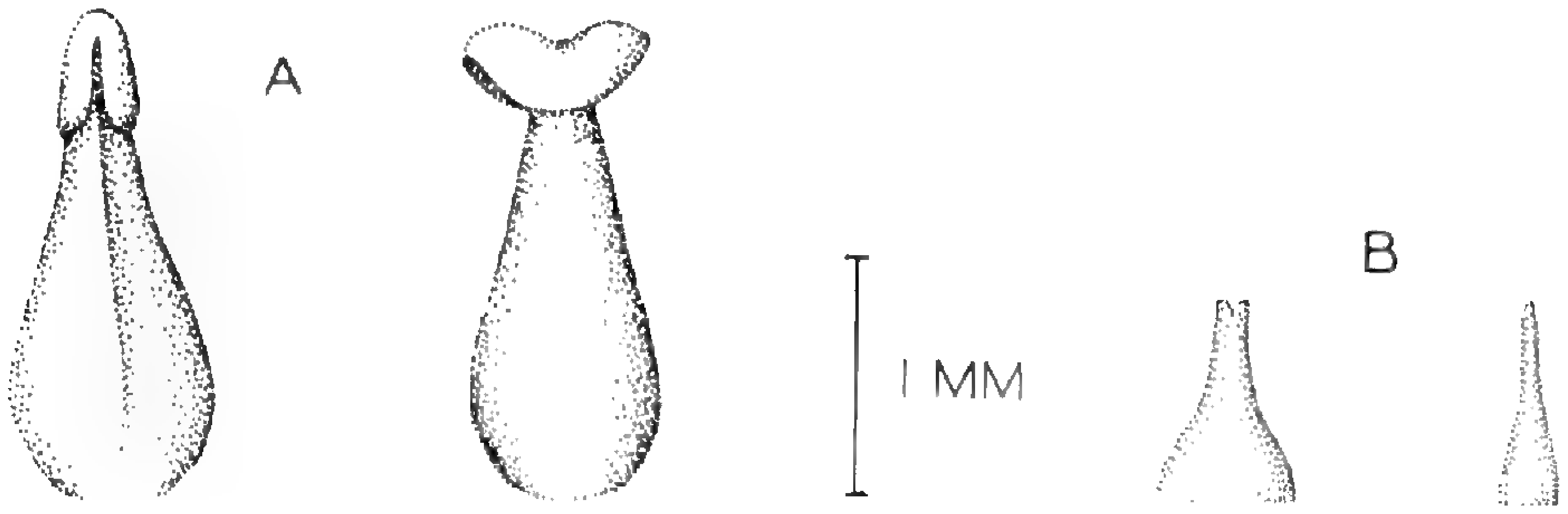

FIG. 2. Ovaries in *Osmanthus austro-caledonicus* from the front and side; A, from an hermaphrodite flower (*Däniker 255*); B, from a male flower (*Pancher 114*).

HABITAT: serpentine or ferruginous lateritic soils; river and stream banks, thickets or heath, scrub, and forest; from sea level to 1000 m. altitude.

Grande Terre: Montagnes de Balade, 1855–60, *Vieillard 327, 872 & 874* (P); Cap Tonnerre, 1861–67, *Vieillard 323* (BM, GH, P — as *Osmanthus deplanchei*); am Fusse des Piton Pandop bei Koumac, 20 Feb. 1925, *Däniker 1300 & 1325* (Z); an der nördlichen Erhebung im Kaala Massif bei Koumac, 26 Feb. 1925, *Däniker 3087a* and 19 May 1925, *Däniker 3087* (Z); Montagne de Temala près Gatop, 1861–67, *Vieillard 2062* (GH, K); Mt. Pouitchaté, on ridge between Upper Tipindjé and Upper Kamendoua, above Atéu, 29 Aug. 1956, *McKee 5169* (HULL); slopes of Mt. Koniambo, 31 Mar. 1956, *McKee 4263* (HULL) and *4265* (A, HULL); prope Wagap, *Vieillard 333* (isotypes: BM, G, K, L, LE, P); Poya valley, road to Roches d'Adio, 18 Oct. 1956, *McKee 5455* (A); slopes along ocean, 13 miles southeast of Ponérihouen on route to Houailou, 5 Aug. 1952, *McMillan 5213* (A, E); au point culminant de la route conduisant de Bourail à Canala, 9 Mar. 1869, *Balansa 1221* (P); collines entourant la Baie Duperré dans la rade de Canala, 2 Sept. 1869, *Balansa 1682* (P); Kanala, montagne du lac, 1861–67, *Vieillard 323* (A, GH, P); Canala, 23 Feb. 1912, *Sarasin 550* (Z); rive de la rivière Toou'du, baie de Tupiti, 1861–67, *Vieillard 328* (A, BM, G, K, LE, P); Île Grand Tupiti, 1861–67, *Deplanche 432* (G); auf den Bergen am Ngoyé, 31 Oct. 1902, *Schlechter 15164* (isotypes of *Notelaea eucleoides*: BM, E, K, LE, NSW, P, Z) and *15166* (BM, E, FI, GH, K, LE, NSW, P, Z); Riv. Ngoyé, 1914, *Compton 2049* (BM, NSW); north bank of Tontouta River near junction with Kalouéhola, 23 Oct. 1955, *McKee 3271* (HULL); Upper Tontouta Valley, near Mine Galliéni, 14 Oct. 1956, *McKee 5447* (NSW); auf der Südwestseite des Mt. Humboldt und an der Tontouta, 2 Nov. 1924, *Däniker 434* (Z); an der Kalouéhola auf der Südwestseite der Mt. Humboldt, 9 Nov. 1924, *Däniker 434a* (Z); im Tale des vom Mt. Humboldt kommenden zuflusses der Kalouéhola, 3 Nov. 1924, *Däniker 468* (Z); am Abhang der Südcrête des Mt. Humboldt, 6 Nov. 1924, *Däniker 468a* (Z); Mt. Dzumac, *Le Rat 155 & 1073* (P); bas du Mt. Dzumac, 28 Apr. 1951, *Guillaumin & Baumann-Bodenheim 12693* (A, Z); auf den Huegeln bei Paita, 28 Sept. 1902, *Schlechter 14834* (isotypes of *Notelaea collina*: BM, E, K, LE, NSW, P, Z); auf den Bergen bei Paita, 9 Oct. 1902, *Schlechter 14976* (isotypes of *Notelaea vaccinioides*: BM, E, FI, GH, K, LE, NSW, P, Z); le long des rivières Couvelée, 1 Nov. 1929, *Franc 2405* (A, BRI, E, K, NSW, NY, Z); ravin de la Couvalée, 1907, *Le Rat 2842* (P); Mts. Kouvelée moyens, 9 May 1951, *Guillaumin & Baumann-Bodenheim 13066, 13072, 13085 & 13170* (A, Z); Dumbéa, *Le Rat 2385* (A) & Sept. 1909, *Le Rat 924* (K, LE, P); rives de la Dumbéa audessus de Koé, 1868, *Balansa 531,* (LE, P), *531a* (A, P) *& 1220* (BM, E, FI, G, K, LE, NY, O); près de la dernière trémie de la mine Sunshine, concession Werquin, Haute Dumbéa branche Nord, 29 Nov. 1942, *Virot 903* (A); Dumbéa valley, north bank, 8 May 1955, *McKee 2477* (HULL); vallée de la Dumbéa-Nord, 14 Mar. 1951, *Hürlimann 1041* (A, Z); pente N. des montagnes entre le Pic de Casse-Cou et la Dumbéa, 7 Mar. 1951, *Hürlimann 1014* (A, Z); massif du Tchingou entre P 743 et P 1187, 17 Apr. 1951, *Hürlimann 1214* (A, Z); plaine de l'Odjijoni, 2 June 1951, *Hürlimann 1457* (A, Z); chaine du Mont Podchoumié, 27 July 1951, *Hürlimann 1626* (A, Z); bas de l'Oua Tilou, 13 Apr. 1951, *Guillaumin & Baumann-Bodenheim 12304* (A, Z); route vers la Montagne des Sources, 5 Dec. 1950, *Hürlimann 248* (A, Z) and 28 Jan. 1956, *McKee 3868* (HULL, K); Crête am Mt. Koghi, 1 Feb. 1926, *Däniker s. n.* (Z); summit ridge of Mt. Koghi, 25 Feb. 1956, *McKee 4008* (A, K); crête au SW. du Mt. Bouo (Koghis), 6 Nov. 1951, *Baumann-Bodenheim 15808* (A, Z); crête au SE. du Mt.

Bouo (Koghis), 20 Apr. 1951, *Guillaumin & Baumann-Bodenheim 12565, 12629 & 12631* (A, Z); à l'Est de la Conception, Dec. 1868, *Balansa 1220a* (P); Mt. Dore, 1861–67, *Vieillard 228* (GH) and 1 May 1955, *McKee 2457* (HULL); pente N. du Mt. Dore, 8 Nov. 1950, *Guillaumin & Baumann-Bodenheim 7861 & 7871* (A, Z); versant E. du Mt. Dore, 21 Mar. 1951, *Guillaumin & Baumann-Bodenheim 11338 & 11357* (A, Z); vallée de la Pouéta Kouré, 26 Aug. 1950, *Hürlimann 21 & Baumann-Bodenheim 5750 & 5754* (A, Z); Col de Volcain, 11 Nov. 1950, *Baumann-Bodenheim 8054, 8085, 8159, 8162, 8163, 8167 & 8267* (A, Z) and 24 Sept. 1951, *Baumann-Bodenheim 15542* (A, Z); sur la Rivière Blanche, 22 Feb. 1951, *Guillaumin & Baumann-Bodenheim 10837 & 10845* (A, Z); bord du Marais Kiki, 26 Sept. 1950, *Baumann-Bodenheim 6291* (A, Z); Mt. Kaféaté, 22 Dec. 1950, *Guillaumin & Baumann-Bodenheim 9627, 9667 & 9695* (A, Z); Col de Plum, 22 Aug. 1950, *Baumann-Bodenheim 5535, 5554 & 5599* (A, Z); vallée supérieure de la Rivière des Pirogues, 29 Mar. 1951, *Guillaumin & Baumann-Bodenheim 11605* (A, Z); crête ou SW. du P 247 (W. de la Baie des Pirogues), 17 Dec. 1950, *Hürlimann 380* (A, Z); Ria de Pirogues, Oct. 1923, *White 2184, 2200* (A, BRI, K) *& 2267* (A, BRI, K, O, P); Baie du Carénage, 22 July 1952, *McMillan 5132* (A, E); Le Carénage, 8 Apr. 1955, *McKee 2370* (A, HULL, NSW); Col d'Amieu, 13 Aug. 1950, *Baumann-Bodenheim 5468* (Z); Champ de Bataille in Tale des Ngo, 15 Oct. 1924, *Däniker 346* (Z); Prony, Sept. 1913, *Franc 1537A* (A, BRI, NY, Z), Mar. 1914, *Franc 114* (A, BM, BRI, E, K, LE, NSW, NY, O, P, Z) *& 114 A* (A, BM, GH, NY, P, Z) and 20 Jan. 1916, *Franc 2011* (P); Baie de Prony, Sept. 1910, *Godefroy 180* (P); Baie du Sud, 1903, *Le Boucher 1508* (NSW); Val Suzon, 30 July 1930, *Franc 2480* (A, BRI, E, K, NSW, NY, Z); Yaté, 16 Mar. 1912, *Sarasin 639* (P, Z); Plaine des Lacs und oberen Yaté, ges. im Yatétal, 8 Oct. 1924, *Däniker 255* (Z); in der Plaine des Lacs, 12 Oct. 1924, *Däniker 297* (Z); beim Lac en 8, Plaine des Lacs, 12 Oct. 1924, *Däniker 304* (Z). Without locality: *Baudouin 634* (P), *Deplanche 14* (A, K), *Franc 192* (Z), *Kay 26* (P), *Pancher 114* (A, K, P) *& s.n.* (? type collection, *Notelaea badula*, P) and *Vieillard 2861* (P).

Isle of Pines: creek sur la pente S. du Pic Nga, 29 May 1951, *Baumann-Bodenheim 13691* (A, Z); flanc NE. du Pic Nga, 1 June 1951, *Baumann-Bodenheim 13842* (A, Z).

The reduction of so many species to synonymy may at first appear somewhat drastic but from a thorough study of the numerous collections which have been assembled and cited above, I am convinced that they all represent facets of one and the same species.

When the flowers of each individual specimen were examined it soon became apparent that they were androdioecious, a condition also found in all the species of Section *Osmanthus* and in some species of related genera (e.g. *Olea dioica*). In the hermaphrodite flowers the ovary is fully developed and topped by a bilobed stigma (FIG. 2,A) whereas in those which are functionally male it is much smaller, more or less conical and lacks the stigmatic lobes (FIG. 2,B). Nor is the sex difference confined to the ovary alone for measurements were made of the length of the anthers and it was found that whilst the sizes for the two sex forms overlapped, those for the functionally male flowers were larger on the average (for dimensions see the description above). In all some 68 different collections bearing flowers were examined and of these 32 were hermaphrodite and

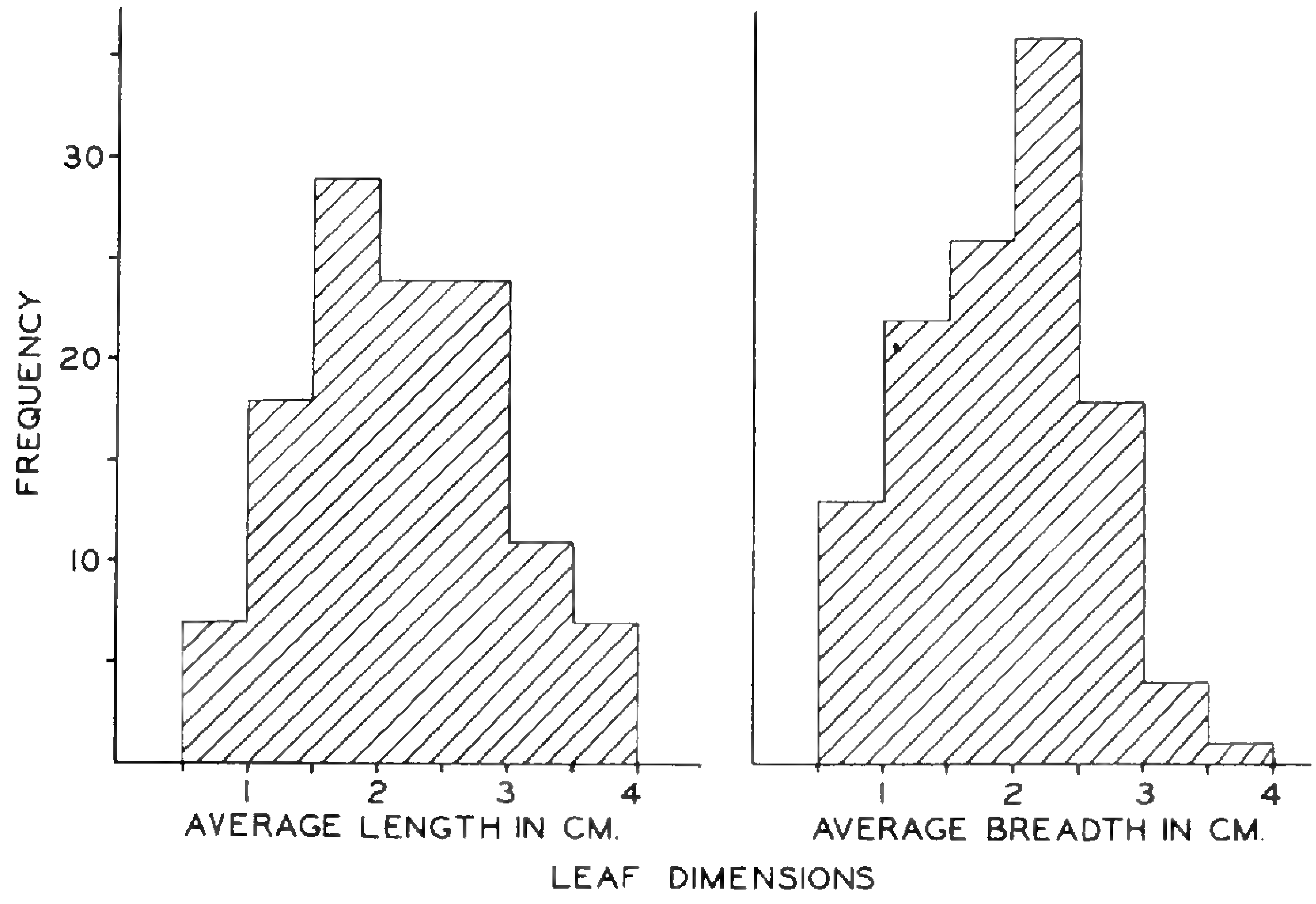

FIG. 3. Frequency histograms for leaf length and breadth in *Osmanthus austro-caledonicus.*

36 male; from this it may be safely assumed that the two forms occur in equal numbers, as might perhaps be expected. The failure to recognize that the ovaries of the type specimens of *Osmanthus austro-caledonicus* and *O. vaccinioides* were the abortive ovaries of male flowers led to their being contrasted with the larger functional ovaries possessing distinct stigmatic lobes in specimens named *O. badula* and *O. eucleoides.* Guillaumin in the Key presented in his *Flore de la Nouvelle-Calédonie* (p. 284) uses stigma size to separate these species. If, however, in the light of the occurrence of androdioecism, one discounts these differences then one is left with two instead of four possible species, and these are distinguished by leaf shape.

The diagnostic value of leaf shape was therefore considered, and the numerous collections cited above were analyzed for leaf length, breadth and outline. It soon became evident, as was suspected from a purely visual appraisal, that continuous variation exists between the two extremes of a very narrowly elliptic leaf on the one hand and a narrowly ovate to obovate outline on the other. Measurements of leaf length and leaf breadth for each collection when plotted in the form of a frequency histogram showed a normal variational spread (FIG. 3). Nowhere could the material be separated into discrete groups and the separation of species by leaf shape alone was found to be purely artificial. The specimens were also examined for other possible characters which could perhaps be used for the differentiation of separate taxa, e.g. characters of the petiole, leaf apex, base and venation, inflorescence and flowers, but nothing was found to justify any subdivision of the material. In fact, apart from androdioecism the flowers throughout were identical, which in itself is strong evidence that one is dealing with a single species.

Measurements of a leaf length–breadth factor (the length divided by the breadth) were plotted in the form of a frequency histogram (FIG.

4) and it was seen that relatively few specimens with proportionately broad and long leaves (FIG. 5,A) had been collected; generally they were either long and narrow (FIG. 5,B) or short and broad (FIG. 5,C). This observation led to an examination of the field notes accompanying the specimens and it was found that wherever the habitat was mentioned, the long and narrow-leaved specimens, in almost all cases, came from the banks or margins of streams, rivers, mountain torrents, etc., whereas most of those with the shortest and broadest leaves came from heath, maquis, scrub, forest, etc. This raised the question whether the narrow leaves might be an adaptation to periodic immersion in swiftly flowing water; in other words, could the plants be rheophytes? Van Steenis in an article on rheophytes (Proc. Roy. Soc. Queensland, **62**: 61–68. 1952) mentions *Notelaea* from New Caledonia, and Schlechter in his account of the vegetation of New Caledonia (Bot. Jahrb. **36**: 1. 1905) includes *N. badula* as an interesting species characteristic of river courses. In the introductory paragraph to the account of species he collected (Bot. Jahrb. **39**: 228. 1907) Schlechter remarks that *N. badula*, *N. collina*, and *N. eucleoides* seek the banks of water courses whereas the other species (including *N. vaccinioides*) are found in woods. But if, as I am convinced, one is dealing here with a single species and it is stenophyllous only when growing by the side of mountain torrents, etc., then one has a case of facultative rheophytism. Although Dr. van Steenis informs me, in correspondence, that in an overwhelming number of cases rheophytes are good species, from the material examined in this revision, any separation, even at the rank of variety, appears to be artificial. Facultative rheophytism would infer that the stenophyllous habit was phenotypic and develops only where the plant is subject to periodic inundation. Not only is it doubtful whether a strong but intermittent current of water could produce such an

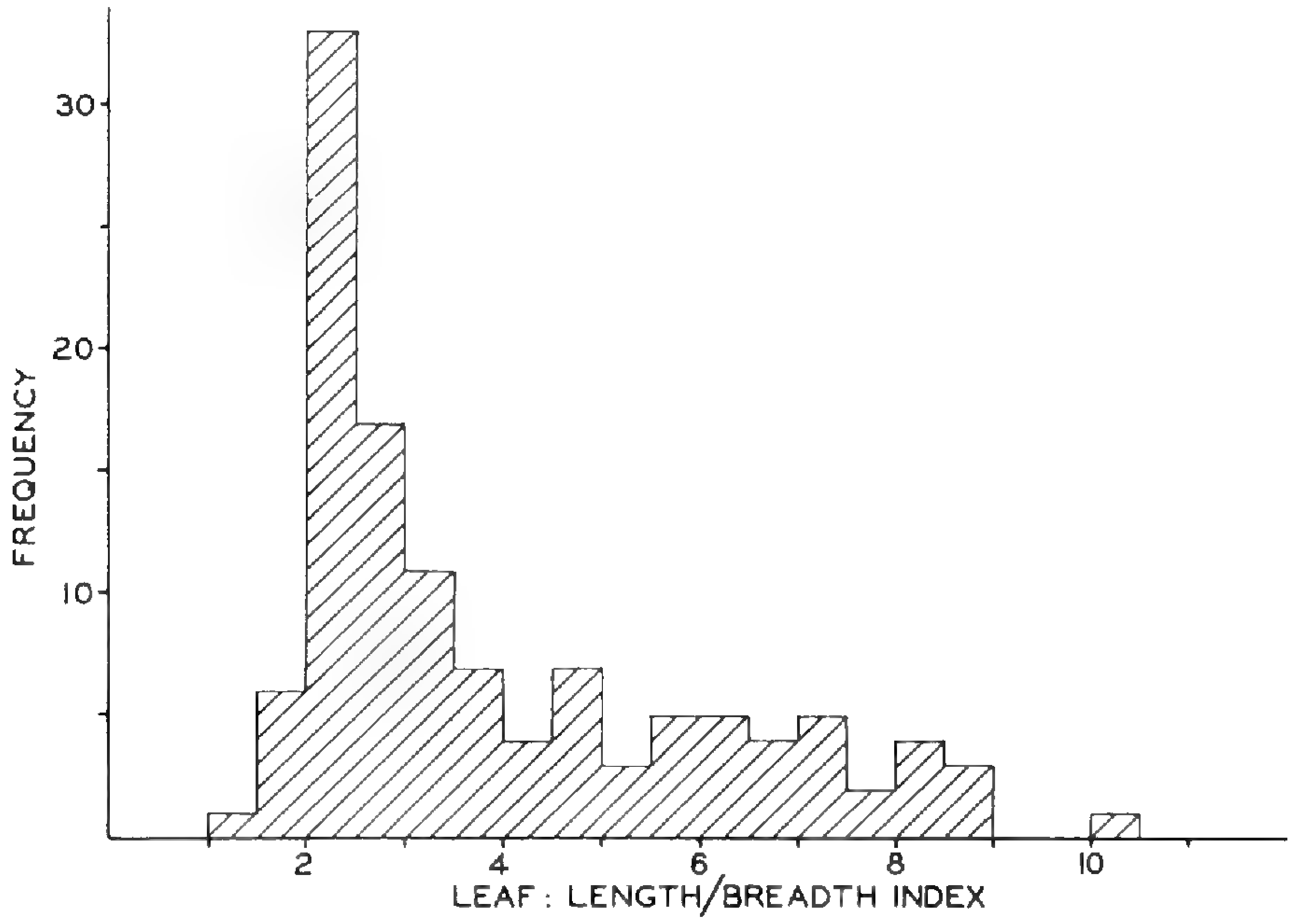

FIG. 4. Frequency histogram for leaf length/breadth factor in *Osmanthus austro-caledonicus*.

effect but amongst the many collections examined one might reasonably expect to find gatherings made from trees which bear more than one type of leaf, where the lower branches only are subject to immersion. In no case however, has such a condition been found in these collections. Moreover, there are occasional exceptions to the rule that the narrow-leaved specimens have been collected from river banks, etc.: *Baumann-Bodenheim 8159* is perhaps the best, for it was collected in serpentine maquis at the same locality and on the same day as numbers *8054, 8085, 8162, 8163, 8167* and *8267*, yet it is the only one of these numbers with extremely narrow leaves. *Guillaumin & Baumann-Bodenheim 13066, 13072, 13085* and *13170* all exhibit very narrow leaves, yet for all of them the field notes say "forêt mésophile sur serpentine."

An alternative explanation was suggested by my colleague Dr. Lorin I. Nevling who pointed out that stenophylly is one of the recognized features of plants growing in serpentine soils, in temperate regions at least. *Osmanthus austro-caledonicus* is a serpentine endemic. Could it be that in New Caledonia the serpentine effect is more intense in some areas than in others, due perhaps to severe leaching by the tropical rains, with the result that stenophylly tends to be greater in some local areas than in others? These areas might include those where the subsoil was continuously disturbed or exposed (such as river and stream banks), or the effect might be due to differences in the size of soil particles with all the physico-chemical effects that might be attributable to this (and on a stream bank the percentage of coarse soil particles is greater than in undisturbed soil). Most of the literature on the vegetation of serpentine soils deals with that of the temperate regions of Europe and North America and no published observations have been found to support the hypothesis that a differential effect on leaf shape based on edaphic factors may be found within a serpentine endemic. The problem of *O. austro-caledonicus* calls for studies in the field combined, if possible, with transplant and other experimental techniques.

The original holotypes of Schlechter's species were presumably destroyed in Berlin during the Second World War but fortunately duplicates of his collections were widely distributed and many isotypes are available. Neither has the holotype of *Notelaea austro-caledonica* been seen. Vieillard in his protologue cites one gathering, *Vieillard 333*, the holotype of which is suspected to be in the herbarium at Caen in Normandy; however, three duplicates have been examined in the course of this investigation. Although he only cited one gathering Vieillard must have examined other material as well when he drew up his description, for the flowers of *Vieillard 333* prove on examination to be functionally male whilst in his description he includes references to the style, stigma and fruit. No actual specimens or collections are cited for *N. badula* but an unnumbered specimen at Paris collected by Pancher in 1862 is annotated as "type collection." No locality is given, only "Massifs de la Calédonie et de l'Île des Pins" in Pancher's hand, together with "Olea convoluta de la corolle ou punctata des feuilles. Arbre de 5 metres, cime arrondie, dense.

FIG. 5. Shoots of: A, *"Osmanthus collinus"* (*Schlechter 14834*); B, *"O. badula"* (*Franc 2405*); C, *"O. vaccinioides"* (*Schlechter 14976*). (½ natural size.)

Fleurs blanches, Juin-Septembre, selon les localités. Bois très dur." Some of these phrases appear in the protologue and even though this may perhaps not be the type, since the epithet is attributed by Pancher to Vieillard, who does not appear to be associated with this specimen, and since as its flowers are functionally male it bears no fruit (as described in the protologue), it may nevertheless be taken as authentic and used to indicate the proper application of this name.

Finally, one or two specimens (e.g. *Däniker 8087* and *McKee 2370*) may be slightly confusing at first sight as they bear galled flowers in which the bud is attacked and never opens. The corolla tube enlarges and lengthens considerably and presumably persists, for some specimens show both fruit and galled flowers.

2. **Osmanthus crassifolius** Guillaumin, Mém. Mus. Hist. Nat. Paris II (B). **4**: 48. 1953; Virot, Vég. Canaque 218. 1956.

Evergreen glabrous *shrub* 5 m. tall. *Leaves* glabrous; petioles 3–4 mm. long; lamina coriaceous broadly elliptic, 2.8–4.2 cm. long by 1.7–2.5 cm. broad; margin entire, slightly thickened and recurved; apex short acuminate; base attenuate into the petiole; venation more or less reticulate below, primary veins only visible above, 7–8 per side. *Inflorescence* axillary, decussate, 1.5–2 cm. long, 7-flowered, with a single terminal flower, glabrous; bracts linear-triangular 1–2 mm. long. Flowers androdioecious, white; pedicels 1–2 mm. long. *Calyx* glabrous 1.5 mm. long, lobes 4, blunt, broadly triangular, 0.8–1 mm. long, margins glabrous. *Corolla* short campanulate, tube 1.5 mm. long, lobes 4, imbricate in the bud, broadly ovate-rounded, 1.5 mm. long. *Stamens* 2, subsessile near the middle of the corolla tube; anthers 1.4 mm. long in a male flower, very broadly elliptic, apex rounded with a very slight blunt appendage. *Ovary* not seen in hermaphrodite flowers, in male, abortive, 0.4 mm. long, slightly conical. *Drupe* unknown.

HABITAT: Serpentine, maquis, 1400 m. alt.

Arête méridionale du Humboldt, 12 Dec. 1940, *Virot 339* (holotype, P).

Osmanthus crassifolius is retained as a distinct species in this revision with a considerable measure of doubt. It is very similar to *O. austro-caledonicus* but in vegetative morphology it lies just outside the range of variation of this species and so until more material is available for study it seems advisable to maintain its separate recognition. In characters of the inflorescence and flower, however, there appears to be no differentiation at all; yet such a difference might reasonably be expected in two distinct species.

The type, *Virot 339*, was collected at an altitude of 1400 meters which is comparable with that for *Osmanthus monticola* and some 400 meters higher than any recorded altitudes for *O. austro-caledonicus*, although from the localities it is suspected that some Däniker specimens of the latter species may have been collected from above 1000 meters. It is possible that the thicker, broadly elliptic leaves are a response to altitude or, alternatively, that hybridization may occasionally occur between *O. austro-caledonicus* and *O. monticola.* Both species grow on Mount Humboldt and whilst the suggestion of hybridization, when so little is known about the species, is almost too facile a hypothesis, in leaf characters the type of *O. crassifolius,* the only known specimen, is intermediate between the two species.

The collection of Virot, however, is not the only one difficult to place; two others have been collected from montane, serpentine heath and are represented in the herbaria of the Arnold Arboretum and Zürich: *Baumann-Bodenheim 15361* (western summit of Mt. Humboldt, 1400 m. alt., 20 Sept. 1951) and *Hürlimann 1652* (slope to the N. E. of summit of Mt. Moné (Koghis), 1060 m. alt., 28 July 1951). These also show somewhat intermediate characters. In the former the leaves (3 to 6 cm. long) are too short to be *Osmanthus monticola,* and the remains of an inflorescence rachis shows bracts like those in *O. austro-caledonicus,* but the texture, shape, and general appearance of the leaves with their short acuminate apices is very strongly reminiscent of *O. monticola.* It is interesting, too, that on one of the sheets of *Däniker 468* (z), here named *O. austro-caledonicus,* there is one small shoot which does not conform with the rest of the material under this number, yet is an exact match for part of *Baumann-Bodenheim 15361.* It is perhaps also significant that this sheet is an obvious mixed collection since the remainder of the material contains both sex forms and was, in consequence, named *O. eucleoides* in part and *O. vaccinioides* in part by Knoblauch in 1935. No altitude is given for the gathering but it was collected on the slopes of Mt. Humboldt. The other anomalous specimen, *Hürlimann 1652,* was collected on Mt. Koghis, from which *O. monticola* has not been collected, and from as low as 1060 meters. However, although the smaller leaves resemble the short broad-leaved expression of *O. austro-caledonicus* the larger ones (up to 6 cm. long) are broadly elliptic, and thick in texture, resembling small leaves of *O. monticola.* It also bears very immature inflorescences (with large bracts which when mature may well be subfoliaceous) which certainly resemble immature inflorescences of *O. monticola* rather than of *O. austro-caledonicus.*

Clearly more collecting, mindful of the variation and altitudinal ranges of the known species, is required to elucidate the true status and exact differentiation of *Osmanthus crassifolius.*

3. **Osmanthus monticola** (Schltr.) Knoblauch, Repert. Sp. Nov. **41**: 152. 1936; Guillaumin, Bull. Soc. Bot. France **89**: 232. 1942, Fl. Nouv.-Caléd. 283. 1948, Mém. Mus. Hist. Nat. Paris II(B). **4**: 49. 1953, *ibid.* **8**: 161. 1959; Virot, Vég. Canaque 218. 1956.

Notelaea monticola Schlechter, Bot. Jahrb. **39**: 229. 1906. Guillaumin, Ann. Mus. Col. Marseille II. **9**: 192. 1911 et Bull. Mus. Hist. Nat. Paris **18**: 40. 1912.

Gymnelaea monticola (Schltr.) L. Johnson, Contr. New S. Wales Natl. Herb. **2**: 413. 1957.

Nestegis monticola (Schltr.) L. Johnson in Degener, New Ill. Fl. Hawaiian Is. 300. Nestegis. 1958.

Evergreen *shrub* or *tree*, 1–10 m. high; branches glabrous or minutely puberulous when young. *Leaves* glabrous; petioles stout 3–7(–10) mm. long, glabrous or minutely puberulous when young; lamina very thick, coriaceous, pale beneath and dark above even when dried, elliptic to broadly elliptic (4.5–)6.5–9(–12.5) cm. long by (1.5–)2–4.5(–6) cm. broad; margin entire, somewhat thickened, more or less recurved; apex acute, short, very short acuminate or subapiculate; base attenuate into the petiole; venation with reticulations more or less visible, primary veins visible above and below, 6–7(–10) per side. *Inflorescence* axillary, decussate, 2–4.5 cm. long, (7–)9–13-flowered, with a single terminal flower, minutely puberulous; bracts ovate to lanceolate or elliptic, subfoliaceous, (2–)3–5(–12) mm. long, more or less persistent (Fig. 1,B). Flowers androdioeceous, white; pedicels 2–5 mm. long. *Calyx* minutely puberulous or glabrate, 2–2.5 mm. long, lobes 4, bluntly and broadly triangular, 1–1.5 mm. long, minutely ciliolate. *Corolla* short campanulate, tube 2.5–2.8 mm. long, lobes 4, imbricate in the bud, broadly ovate-rounded, 1.6–2 mm. long. *Stamens* 2, subsessile near the middle of the corolla tube; anthers about 1.5 mm. long, in hermaphrodite flowers and 2.5 mm. long in male flowers, broadly elliptic to slightly ovate, apex with a barely discernible appendage. *Ovary* in hermaphrodite flowers 2.5 mm. long, triangular-flask shaped without differentiated style; stigma terminal, more or less bilobed, 0.5 mm. long; in male flowers abortive, 1–1.2 mm. long, slightly conical. *Drupe* ovoid-ellipsoid, 11 mm. long by 8 mm. broad (*Baumann-Bodenheim 15481*); endocarp hard, 1 mm. thick.

Habitat: Serpentine soils, rocky maquis or hygrophilous forest, montane, 1100 to 1600 m.

Auf den Abhängen des Mt. Humboldt, 16 Nov. 1902, *Schlechter 15315* (isotypes: BM, E, K, LE, P, Z); arête méridionale du massif du Humboldt, 12 Dec. 1940, *Virot 426* (A); crête S. et sommet secondaire du Mt. Humboldt, 23 Sept. 1951, *Baumann-Bodenheim 15481 & 15523* (A, Z); crête ouest du Mt. Humboldt, 19 Sept. 1951, *Baumann-Bodenheim 15344* (A, Z); à l'ouest du sommet du Mt. Humboldt, 21 Sept. 1951, *Baumann-Bodenheim 15433* (A, Z); Mt. Mou, Aug. 1908, *Le Rat 203* (P); sommet du Mont Mou, 13 Mar. 1951, *Guillaumin & Baumann-Bodenheim 11238* (A, Z).

Quite distinct from *Osmanthus austro-caledonicus*, this species is known only from higher altitudes on two of the higher mountains towards the southern part of the island. *O. crassifolius*, and the two specimens discussed under it, blur the differences between *O. monticola* and *O. austro-caledonicus*, whilst the great range in leaf variability in this last makes it difficult to distinguish and use diagnostic vegetative characters in a key for specific identification. The flowers of *O. monticola* are much larger in their various parts and the subfoliaceous bracts of the inflorescence give a ready character for differentiation, but even in purely vegetative specimens its leaves are distinctive. They are broadly or very broadly elliptic and generally longer than those of *O. austro-caledonicus*. The leaves are also very much thicker in texture than *O. austro-caledonicus*, and in contrast to this very variable species, are remarkably uniform in general shape, texture, and dimensions.

Schlechter in his protologue describes this species as a tree 10 m. tall but Virot (La Végétation Canaque, 218. 1952) classifies it as a nanophanerophyte and, in the field notes accompanying his specimen number *426*, describes it as a shrub 1 m. high. The recent collections of the 1950–52 Franco-Swiss Expedition, whilst indicating a height of as much as 4 m. for one of the gatherings (*Baumann-Bodenheim 15344*), state that two others are only 1 m. high. However, like the Virot specimen, they are mature enough to bear flowers and fruit. Within its family, the Oleaceae, this species is somewhat unique in reaching maturity at so low a stature yet with such relatively large leaves, but as a New Caledonian serpentine endemic it is probably no more remarkable in the field than many other unrelated plants growing together in the same vegetational communities.

4. **Osmanthus cymosus** (Guillaumin) P. S. Green, comb. nov.

Notelaea? cymosa Guillaumin, Bull. Soc. Bot. France **89**: 232. 1943 et Fl. Nouv.-Caléd. 283. 1948; Johnson, Contr. New S. Wales Natl. Herb. **2**: 411. 1957.

Shrub (?) or small tree (?); branches minutely puberulous when young, later glabrous. *Leaves* glabrous; petiole 2.5–3 cm. long, glabrous or minutely puberulous when young; lamina thickish, broadly elliptic or almost narrowly ovate, 6.5–11.5(–16) cm. long by 3.5–5.5(–7.5) cm. broad; margin entire, very slightly thickened, flat; apex rounded-obtuse; base attenuate into the petiole, more or less obtuse; venation more or less reticulate above and below, with 8–10 primary veins per side. *Inflorescence* axillary, decussate, 3–6 arising from 1–2 superposed buds, each 2.5–6 cm. long, slender, minutely puberulous, (5–)7–9-flowered, with usually 5 flowers borne together terminally (FIG. 1,C); bracts ovate, 1 mm. long, early deciduous. Flowers androdioecious (?), pedicels 4–12 mm. long. *Calyx* glabrous, 1–1.5 mm. long, lobes 4, blunt triangular, 0.5–1.7 mm. long, margins more or less ciliolate. *Corolla* short campanulate, tube 1.5–1.7 mm. long, lobes 4, imbricate in the bud, very broadly ovate, rounded, 0.7–1 mm. long. *Stamens* 2, subsessile near the middle of the corolla tube; anthers 1.6 mm. long in male flower, more or less orbicular, apex rounded with barely discernable terminal appendage. *Ovary* (male flower only examined) abortive, more or less conical, 0.5 mm. long. *Drupe* unknown.

HABITAT: montane forest.

Mont Mi, 9 March 1869, *Balansa 1222* (holotype [not seen] and isotype, P).

Most distinct because of its fasciculate inflorescence with slender relatively few-flowered rachises and usually five flowers arising together terminally (FIG. 1,C). The inflorescence is basically decussate as in the other species but the terminal subumbellate group of five pedicels would seem to be a contraction of the apical group of three, together with the penultimate pair normally (cf. *Osmanthus austro-caledonicus*) borne below. The large more or less elliptic leaves on relatively long petioles are also distinctive and it is a pity that for a more ample description and better assessment of this species, more adequate material is not available, the species having been collected once only, nearly one hundred years ago.

INDEX TO EXSICCATAE

The list is arranged alphabetically by the last name of the collector. Numbers in parentheses refer to the corresponding species in the text.

DESMODIUM: PRELIMINARY STUDIES — IV

BERNICE G. SCHUBERT

DURING THE DOZEN YEARS since the series *Desmodium: Preliminary Studies* (Schubert, 1940, 1941, 1950) was interrupted it has been possible for me to examine in some detail material of the species of several regions (including central and east tropical Africa and Panama), to photograph the types of many species, as well as to observe certain other species in the field in various localities in Latin America. As a result, the long-term project of a monographic treatment of *Desmodium*, though still a somewhat distant objective, now is more likely to be accomplished than it has been at some periods in the past. To avoid bibliographic confusion the series of *Preliminary Studies* will be continued and, as in the past, will include taxonomic and nomenclatural notes best published as a prelude to, rather than in, a floristic or monographic study.

In this paper there will be considered some problems concerning tropical American and African species. Many of the problems necessitating these notes arose during studies toward the preparation of a treatment of species of *Desmodium* for the *Flora of Panama*, others for the *Flora of East Tropical Africa*. Some of the conclusions presented here are, however, corrections of previous misinterpretations now clarified by a study of the types.[1]

The genus *Desmodium*, widespread and consisting of a large number of species, is distributed throughout most tropical and temperate regions of the world. One of its great centers of distribution is in Mexico where there is perhaps the largest number of species with the most diverse development of plant parts. The habit may vary from delicately herbaceous to tall frutescent or subarborescent. Each of the organs also has a wide range of diversity, probably the most conspicuous being in the loment.

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[1] The studies on which this paper is based (including the photographs taken in European herbaria) were carried on largely while I was a fellow of the John Simon Guggenheim Memorial Foundation (1950–51) and, to a lesser extent, during a trip sponsored by the Gray Herbarium of Harvard University (1946), and during a period in Belgium (1951–52) while serving as botanical consultant for the Economic Cooperation Administration under the auspices of I.N.E.A.C. at the Jardin Botanique de l'État in Brussels. Field observations in Latin America were made during various collecting trips while conducting a project, as botanist, for the New Crops Research Branch, Agricultural Research Service, U. S. Department of Agriculture and the National Heart Institute, National Institutes of Health.

To the friends and colleagues who facilitated field work and library studies and in various ways disposed of numerous difficulties I am most appreciative. To the directors and curators of the institutions in which I was able to study and take photographs and to those who kindly made material available on loan I am extremely grateful. The herbaria from which material is cited are indicated by the abbreviations of Lanjouw and Stafleu listed in *Index Herbariorum* (ed. 4, 1959).

FIG. 1. Holotype of *Hedysarum axillare* Sw., × ½.

The characters of the inflorescence and loment offer the best means for distinguishing species, as well as the best clues to discovering their relationships. Among the Mexican species of *Desmodium, sensu lato,* there are at least three subgenera. The species treated by Schindler as *Meibomia, sensu stricto*, would form the largest subgenus (although unfortunately in the subgeneric category this name will probably not be available). As a unit this group of species is composed of two sections, each of which contains several easily recognizable species groups probably best designated as series. The subgeneric classification will be considered in detail in a later paper. It is interesting to note, however, that within the two sections distinguished by characters of the inflorescence there are several occurrences of parallel development in the modification of the loments.

In tropical Africa, although many subgeneric categories of *Desmodium* are represented, there are many fewer species and far fewer species groups (Schubert, 1952, 1954). Endemics do occur, but there seems to be a much lower level of development in the genus in Africa than in America, and there are scarcely any unquestionably native species which have American relatives.

In Asia the genus reaches a far more interesting level of development with large numbers of species showing much diversity and modification. The Section *Podocarpium* Bentham (Isely, 1951) has three representatives in eastern North America. Also many of the widespread tropical species have an Asiatic origin.

DESMODIUM AXILLARE AND ITS VARIETIES — A CLARIFICATION

In tropical America *Desmodium axillare* is widespread and well known. It extends from southern Mexico through Central America, the West Indies, and at least the northern half of South America. The confusion which has surrounded the definition of its varieties is largely the result of insufficient knowledge of the types.

Desmodium axillare (Sw.) DC. Prodr. **2**: 333. 1825.

Var. **axillare**

Hedysarum axillare Sw. Prodr. 107. 1788; Fl. Ind. Occ. 1274. 1806. Holotype, Jamaica, *Swartz* (S; GH, negative no. 8189); isotype (? BM; GH, negative nos. 7794 a, b, c).

Meibomia axillaris (Sw.) O. Ktze. Rev. Gen. Pl. **1**: 195. 1891.

D. axillare (Sw.) DC. var. *α. genuinum* Urb. Symb. Antill. **2**: 303. 1900.

Nephromeria axillaris (Sw.) Schindl. Repert. Sp. Nov. **20**: 284. 1924.

Meibomia axillaris (Sw.) O. Ktze. var. *α. obtusifoliola* O. Ktze. *loc. cit.* Holotype, Cayey, 2000′, Portorico, Mar. 1874, *Kuntze* (NY; GH, negative no. 4022).

D. axillare (Sw.) DC. var. *α. obtusifoliola* (O. Ktze.) Urb. *op. cit.* **4**: 291. 1905.

Nephromeria axillaris (Sw.) Schindl. var. *α. obtusifoliola* (O. Ktze.) Schindl. *loc. cit.*

Hedysarum reptans Poir. in Lam. Encyc. Méth. Bot. **6**: 422. 1804. Holotype, Santo Domingo, *Desportes* (P–JU, no. 15,543; GH, negative no. 8190).

Meibomia reptans (Poir.) O. Ktze. *ibid.* 198.

D. radicans Macfad. Fl. Jam. **1**: 269. 1837, based on *Hedysarum axillare* Sw.

Meibomia andina Rusby, Mem. Torrey Club **3**: 21. 1893, *pro parte*, as to isotypes (GH, MO, US), not as to holotype (NY), Yungas, Bolivia, *Bang 650.*

The typical variety of *Desmodium axillare*, based on *Hedysarum axillare* Sw., has been recognized by authors under various epithets. It should now properly be called var. *axillare* "without citation of an author's name."[2] It was possible to study the holotype of *Hedysarum axillare* Sw. at the Regnellska Typherbariet of the Botanical Department, Naturhistoriska Riksmuseum, Stockholm, and a photograph of this specimen is reproduced here (FIG. 1). A specimen in the British Museum (Nat. Hist.) annotated by Schindler as "probably the type specimen of Hedysarum axillare Sw." may be an isotype (GH, negative no. 7794), but the specimen from Swartz's herbarium should be accepted as the holotype. Schindler came to the same conclusion after he had annotated the sheet in the British Museum (probably in 1922), for in his bibliographic study on *Desmodium* [Schindler, 1928, p. 5, entry (356)] he noted "Or. in H. Stockh. [var. *obtusifoliola*]."

From a study of material in Paris the conclusion in my earlier paper (Schubert, 1941) to place *Hedysarum reptans* in the synonymy of this variety, is confirmed. The holotype of *H. reptans* Poir., a specimen collected by Desportes, is in the Herbier Jussieu (P–JU) of the Muséum National d'Histoire Naturelle. Another specimen, in the Herbier Générale (P) of the same museum, also determined as *H. reptans*, is var. *stoloniferum* (var. *sintenisii*). A photograph of Poiret's type is reproduced here (FIG. 2).

Var. **acutifolium** (O. Ktze.) Urb.

D. axillare (Sw.) DC. var. *β. acutifolium* (O. Ktze.) Urban, Symb. Antill. **4**: 292. 1905. Holotype, Panama, Colón, June 1874, *Kuntze* (NY; GH, negative no. 6273).

Meibomia axillaris (Sw.) O. Ktze. var. *β. acutifolia* O. Ktze. Rev. Gen. Pl. **1**: 195. 1891.

Nephromeria axillaris (Sw.) Schindl. var. *β. acutifolia* [as "acutifoliola"] (Urb.) Schindl. Repert. Sp. Nov. **20**: 284. 1924.

D. axillare (Sw.) DC. var. *β. angustatum* Urb. *op. cit.* **2**: 303. 1900.

D. axillare (Sw.) DC. var. *β. angustatum* Urb. f. *robustius* Urb. *loc. cit.* Isotype, Sierra de Luquillo, Portorico, *Sintenis 1689* (GH).

D. axillare (Sw.) DC. var. *β. acutifolium* (O. Ktze.) Urb. f. *robustius* (Urb.) Urb. *op. cit.* **4**: 292. 1905, based on *D. axillare* var. *β. angustatum* f. *robustius*.

Nephromeria axillaris (Sw.) Schindl. var. *β. acutifolia* (Urb.) Schindl. f. *robustior* (Urb.) Schindl. *loc. cit.*

Hedysarum oblongifolium Bertero ex DC. Prodr. **2**: 332. 1825, *pro syn.*

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[2] Int. Code of Bot. Nomenclature, 1961. Article 26.

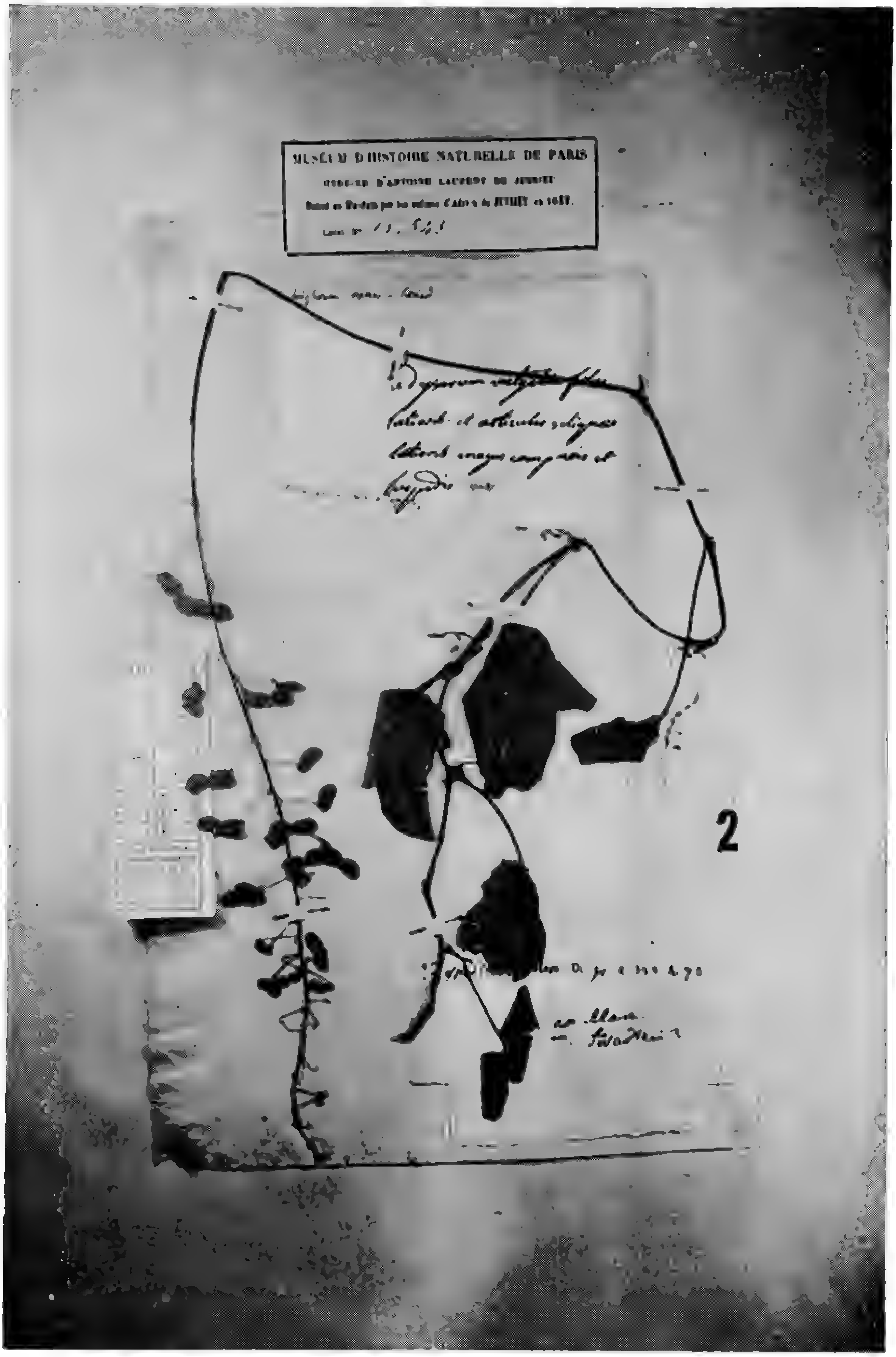


FIG. 2. Holotype of *Hedysarum reptans* Poir., × ½.

D. oblongifolium Bertero ex DC. *loc. cit.*

Meibomia umbrosa Britt. Bull. Torrey Club **37**: 353. 1910. Holotype, Troy, Jamaica, Sept. 13–18, 1906, *Britton 444* (NY; GH, negative no. 6303).

Meibomia prorepens Blake, Contr. U. S. Nat. Herb. **24**: 6. 1922. Holotype, Los Amates, Dept. Izabal, Guatemala, May 29, 1919, *S. F. Blake 7718* (US; GH, fragment and negative no. 4046).

In my earlier treatment (p. 79) I placed (with some doubt) the names *Hedysarum stoloniferum* Rich. ex Poir. and *Desmodium stoloniferum* (Rich. ex Poir.) Steud. in the synonymy of var. *acutifolium*, following Schindler, who treated *Desmodium axillare* as a *Nephromeria* and made the required combinations. Examination of the type shows that in this instance Schindler was in error and that the epithet *stoloniferum* must be taken up for var. *sintenisii.* The question will be discussed under that variety. I also noted in my earlier study (Schubert, 1941, p. 86) that Schindler placed DeCandolle's name, *D. spirale* (Sw.) DC., var. *β. stoloniferum* (Rich. ex Poir.) DC. in the synonymy of *D. wydlerianum* Urb. DeCandolle's material in Herbier DeCandolle of the Conservatoire et Jardin Botaniques, Geneva, is *D. wydlerianum,* but it is the Richard material in Herbier Jussieu, Paris, which must be taken as the type.

Var. **stoloniferum** (Rich. ex Poir.) comb. nov.

Hedysarum stoloniferum Rich. ex Poir. in Lam. Encyc. Méth. Bot. **6**: 421. 1804. Holotype, Antilles, *Richard* (P–JU, no. 15,570; GH, negative nos. 8191 a, b, c, d).

D. spirale β. stoloniferum (Rich. ex Poir.) DC. Prodr. **2**: 333. 1825.

D. stoloniferum (Rich. ex Poir.) Steud. Nomencl. ed. 2, **1**: 496. 1840.

D. axillare var. *γ. Sintenisii* Urb. Symb. Antill. **2**: 303. 1900. Lectotype, Sierra de Yabucoa in sylva primaeva montis Cerro Gordo, *Sintenis 2781* (GH).

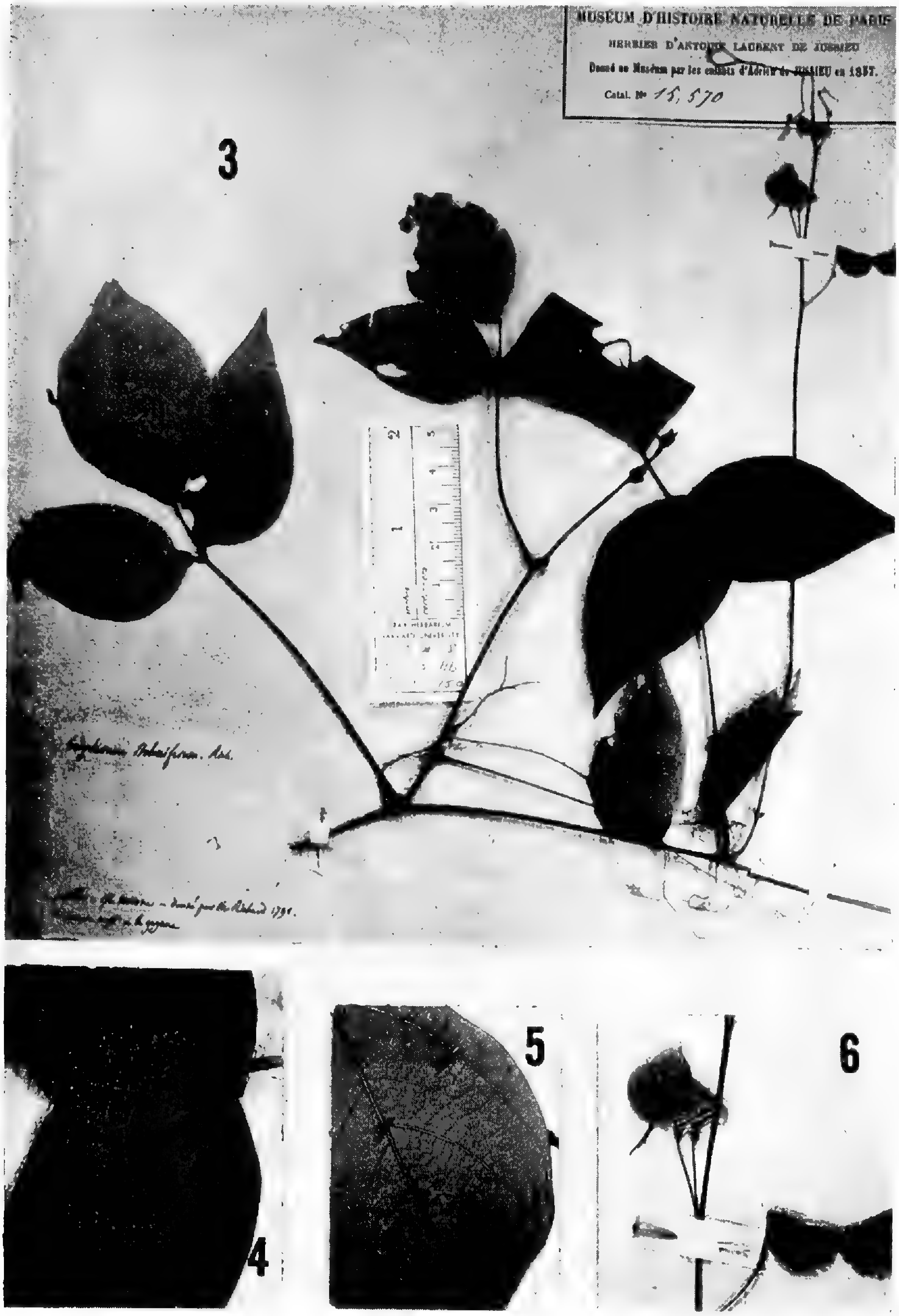
Meibomia Sintenisii (Urb.) Britt. in Britton & Wilson, Sci. Surv. Porto Rico & Virgin Isl. **5**: 402. 1924.

Nephromeria axillaris (Sw.) Schindl. var. *γ. Sintenisii* (Urb.) Schindl. Repert. Sp. Nov. **20**: 284. 1924.

D. axillare var. *Sintenisii* sensu Schubert, Contr. Gray Herb. **135**: 84–86, *pl. 1., figs. A1–7.* 1941.

Meibomia albida Blake, Contr. U. S. Nat. Herb. **24**: 5. 1922. Holotype, Quebradas, Dept. Izabal, Guatemala, *Blake 7510* (US; GH, isotype and negative no. 7510).

As noted under var. *acutifolium* the epithet *stoloniferum* must be taken up for var. *sintenisii,* not as earlier supposed for var. *acutifolium.* The type material of *Hedysarum stoloniferum* in Herbier Jussieu does not have long, spreading pilosity on the stems, nor leaflets velutinous beneath, characters of var. *acutifolium,* but does have the characters of var. *sintenisii.* Therefore, *stoloniferum,* a much earlier epithet, should be taken up for the taxon in place of *sintenisii.* A photograph of the holotype and enlargements of significant details are reproduced here (FIGS. 3–6).



FIGS. 3–6. *Hedysarum stoloniferum* Rich. ex Poir. 3, Holotype, × ½; 4, portion of upper surface of leaflets, × 1; 5, portion of lower surface of leaflet, × 1; 6, loments, × 1.

COMMENTS ON JUNGHANS' LIST OF THONNING'S AND ISERT'S COLLECTIONS

A valuable addition to the many recent studies of African plants has been made by Dr. Jens Junghans (1961, 1962) in his paper on Danish collections in West Tropical Africa, in which he emphasizes the collections of Thonning and Isert, and the extensive publication of Schumacher with its descriptions based on them. The purpose of the study was to locate the type-specimens and give the pertinent bibliographic references. This has been carefully done and the paper should be a most useful tool in work treating African plants. It should be kept in mind however, that although new descriptions were formulated for many species based on the collections of the Danish botanists, Schumacher himself did not consider all the species new, and, as a result, although the specimens are the basis of his descriptions, they are types only when they represent new species. An unfortunate omission in the paper, from the bibliographic point of view, is that page references for descriptions of species are made only to the "preprint" edition of Schumacher's paper. Junghans notes in his bibliography that Schumacher's paper, originally published in 1827, was republished in 1828 and 1829 (Schumacher 1827, 1828, 1829). He neglects to note however, that the preprint was differently paged and that as a result authors may cite different page references for the same names, depending on which copy of the publication they have. The table below will show how great the discrepancy may be. The first column lists the species of *Hedysarum* in Junghans' paper, the second column the page reference from Junghans and/or *Index Kewensis*, and the third column the page reference from Schindler (1928).

Hedysarum	Reference to Schumacher from Junghans and/or IK	Reference to Schumacher from Schindler
deltoideum	361	135
fruticulosum	363	137
granulatum	362	136
lanceolatum	360	134
ovalifolium	359	133
pictum	364	138
rugosum	358	132
umbrosum [3]	362	136

During my stay in Copenhagen I was able to study and photograph some of the *Hedysarum* collections described by Schumacher, and it seems appropriate to equate the names under *Hedysarum* in Junghans' list with the names in current use. Eight species of *Hedysarum* were listed (pp. 350, 351), all of which are now maintained in other genera or relegated to synonymy of species in other genera. I list here the names from Junghans with their equivalents and in the following pages add some relevant synonymy and discussion.

[3] Not in *Index Kewensis*; not cited by Schindler.

1. HEDYSARUM DELTOIDEUM Schum. & Thonn. in Schum. in Beskr. Guin. Pl. 361. 1827,[4] Danske Vid. Selsk. Naturv. Afhdl. **4**: 135. 1829;[5] Junghans, Bot. Tidsskr. **57**: 350. 1961 = **Desmodium velutinum** (Willd.) DC.

2. HEDYSARUM FRUTICULOSUM Schum. & Thonn. in Schum. BGP. 363. 1827, DVS. 137. 1829; Junghans, *ibid.* 350 = **Desmodium ramosissimum** G. Don.

3. HEDYSARUM GRANULATUM Schum. & Thonn. in Schum. BGP. 362. 1827, DVS. 136. 1829; Junghans, *ibid.* 351 = **Desmodium triflorum** (L.) DC.

4. HEDYSARUM LANCEOLATUM Schum. & Thonn. in Schum. BGP. 360. 1827, DVS. 134. 1829; Junghans, *ibid.* 351 = **Desmodium gangeticum** (L.) DC.

5. HEDYSARUM OVALIFOLIUM Schum. & Thonn. in Schum. BGP. 359. 1827, DVS. 133. 1829; Junghans, *ibid.* 351 = **Alysicarpus ovalifolius** (Schum.) Léonard.

6. HEDYSARUM PICTUM Jacq. Collect. 2: 262. 1788, Icones 3: *pl. 567.* 1792; Willd. 3(2): 1204. 1802; Hornem. De Ind. Pl. Guin. 23. 1819; Schum. BGP. 364. 1827, DVS. 138. 1829; Junghans, *ibid.* 351 = **Uraria picta** (Jacq.) Desv.

7. HEDYSARUM RUGOSUM Willd. Sp. Pl. 3(2): 1172. 1802; Hornem. De Ind. Pl. Guin. 23. 1819; Schum. BGP. 358. 1827, DVS. 132. 1829; Junghans, *ibid.* 351 = **Alysicarpus rugosus** (Willd.) DC.

8. HEDYSARUM UMBROSUM Isert ex Schum. BGP. 362. 1827, DVS. 136. 1829 (*nomen nudum*); Junghans, *ibid.* 351 = **Desmodium velutinum** [?].

The species of this list are, in general, either of wide natural distribution, or introduced by various means throughout tropical areas of the world. Since, therefore, they have been much collected and several have been redescribed and renamed many times from different regions, it seems worthwhile to include what synonymy I have been able to check and to add other available pertinent information in an effort toward eventual completeness.

Desmodium velutinum (Willd.) DC. Prodr. **2**: 328. 1825.

Hedysarum velutinum Willd. Sp. Pl. 3(2): 1174. 1802. Holotype, *hb. Willd. 13763* (B; GH, negative no. 8194).

Hedysarum lasiocarpum P. Beauv. Fl. Oware & Benin 1: 32. *pl. 18.* 1806. Lectotype, *Palisot de Beauvois* [in fruit] (G; A, photo. G no. 635; isotype [in flower] G; A, photo. G no. 633).

Desmodium lasiocarpum (P. Beauv.) DC. *ibid.*

Hedysarum latifolium Roxb. Hort. Bengal. (Cat. Calc.) ed. Carey 57. 1814, *nomen nudum*, but based on *Hardwicke*, 1801; Ker, Bot. Reg. **5**: *pl. 355* and descr. 1819.

Desmodium latifolium (Roxb. ex Ker) DC. *ibid.*

Hedysarum deltoides Poir. in Lam. Encyc. Suppl. **5**: 15. 1817.

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[4] This reference will be abbreviated as BGP when it occurs again in this paper.

[5] Additional references to this work will be abbreviated as DVS.

Hedysarum deltoideum DC. Prodr. 2: 328. 1825 *pro syn.* Reference to Poiret's species was made here, with a query, in the synonymy of *Desmodium lasiocarpum* as "Hedys. deltoideum."

Hedysarum deltoideum Schum. & Thonn. in Schum. BGP. 361. 1827, DVS. 135. 1829, based on Guinea: Aquapim [or Akwapim], *Thonning* [2 collections, one in fl., one in fr.] (C; GH, negative nos. 8192a, b, c, d). This seems to be a redescription of *Hedysarum deltoides* Poir. presumably based on a specimen "misit Vahl, 1804 e Guinea," labeled *Hedysarum deltoideum* (P–JU, no. 15,578; GH, negative no. 8193).

Anarthrosyne cordata Klotzsch in Peters, Reise Mossamb. Bot. 1: 39, *pl. 7.* 1862.

Pseudarthria cordata (Klotzsch) C. Muell. in Walp. Ann. Bot. Syst. 7: 765. 1868. There is no doubt about the plant concerned here, but the validity of the combination is somewhat questionable.

Additional references to and synonyms of *D. velutinum* may be found in the following papers: Schindler, A. K., [1925, p. 6; 1928, p. 28 entries (499) and (692)]. Schubert, B. G. (1952, p. 294; 1954, p. 194). M. S. Knaap-van Meeuwen, *Desmodium* in Malaysia, in Reinwardtia 6(3): 264. 1962. [It should be noted throughout this last cited paper that references to "Léon., Fl. Congo Belge 5: . . ." should be attributed to B. G. Schubert rather than Léonard.]

Desmodium ramosissimum G. Don, Gen. Syst. 2: 294. 1832, non Arechav. 1901; B. G. Schubert, Bull. Jard. Bot. Bruxelles 22: 293. 1952. Holotype, W. Trop. Afr.: St. Thomas, *G. Don* (BM; GH, negative no. 7799).

Hedysarum mauritianum Willd. Sp. Pl. 3(2): 1185. 1802. Holotype, *hb. Willd. 13794* (B; GH, negative no. 8201) [= *D. canum* (Gmel.) Schinz & Thellung].

Desmodium mauritianum (Willd.) DC. Prodr. 2: 334. 1825, based on *H. mauritianum* Willd., as to name but not as to plant.

Aeschinomene arborea Sieb. ex DC. *ibid.*, *pro syn.*, based on *Sieber, Fl. Maurit. exs. 155* (dupl. A); presumably not *Aeschynomene arborea* L.

Hedysarum fruticulosum Schum. & Thonn. in Schum. BGP. 363. 1827, DVS. 137. 1829, non Desv. 1826; Junghans, *ibid.* 350. Holotype, Guinea: Aquapim, *Thonning* [with mss. no. 203, fl. & fr.] (C; GH, negative nos. 8202 a, b); another sheet, in fruit, coll. *Thonning* (C; GH, negative no. 8202 c) is a probable isotype; a presumable isotype is in Paris "misit D. Vahl 1804 e Guinea" (P–JU 15,580; GH, negative no. 8203). An *Isert* collection cited by Junghans I have not seen.

Desmodium fruticulosum (Schum.) Walp. Repert. 1: 737. 1842, based on the preceding. The name *Hedysarum fruticulosum* Schum. & Thonn. in Schum. is preoccupied by *H. fruticulosum* Desv. It is very frustrating not to know the basis of the latter name. Desvaux said his plant came from Madagascar, but the name seems neither to have been taken up by any later author nor considered by Schindler who examined all the Desvaux material available.

Desmodium triflorum (L.) DC. Prodr. 2: 334. 1825.

Hedysarum triflorum L. Sp. Pl. 749. 1753. Holotype, *Hedysarum* no. 45 "Hedysarum 3-foliatum repens . . ." coll. *Burmann* (LINN; A, photo.).

Hedysarum granulatum Schum. & Thonn. in Schum. BGP. 362. 1827, DVS. 136. 1829; Junghans, *ibid.* 351. Holotype, Guinea: *Thonning* (C; GH, negative nos. 8204 a, b). A presumable isotype is a sheet in Paris, sent by Vahl in 1804 "e Guinea" (P–JU 15,576; GH, negative no. 8204 c).

It is interesting that both the collection at Copenhagen and that at Paris are annotated *Hedysarum granuliferum* in Schumacher's hand, but the epithet under which the species was published is *granulatum.* Junghans (p. 351) noted also that two sheets of Isert are this species. A very curious fact overlooked by both Junghans and Schindler, and perhaps by Schumacher, is that Biehler (p. 32, 1807) described *Hedysarum granuliferum* in a doctoral dissertation in 1807, based on a Thonning collection from Guinea. The dissertation was republished by Sprengel in the *Mantissa Prima* of *Florae Halensis* (Sprengel, p. 48, 1807), and the species *H. granuliferum* was attributed to him in *Index Kewensis.* (For notes concerning these two papers and the dates of publication see Fernald, 1945.) What plant Biehler had from Sprengel's herbarium, however, it is hard to say, for he described it as having "pedunculis axillaribus unifloris, leguminibus monospermis." Schumacher described his plant with "Racemus laterifolius, 4–6 florus. . . . Lomentum 2–7 articulatum, . . ." It is possible that Schumacher knew of Biehler's publication and for that reason changed the epithet of his species.

Desmodium gangeticum (L.) DC. Prodr. 2: 327. 1825.

Hedysarum gangeticum L. Sp. Pl. 746. 1753. Holotype, *Hedysarum* no. 13 "**gangeticum** 5" (LINN; A, photo.).

Aeschinomene gangetica (L.) Poir. in Lam. Encyc. Méth. Bot. **4**: 453. 1798 [?], based on specimen in Lamarck herbarium (P–LA; GH, negative no. 8200).

Pleurolobus gangeticus (L.) J. St. Hil. Nouv. Bull. Soc. Philom. **3**: 192. 1812, Jour. Bot. **1**: 61. 1813.

Meibomia gangetica (L.) O. Ktze. Rev. Gen. Pl. **1**: 196. 1891.

Hedysarum ochroleucum Moench, Meth. 118. 1794, based on "*Hedysarum gangeticum L. Icon. Burmann. Zeyl. Tab. 49. fig. 2.*" This seems to be a simple renaming of the Linnaean *Hedysarum gangeticum.* It has nothing to do with the later (1864) *Desmodium ochroleucum* M. A. Curtis ex Canby, of eastern North America. Moench's name was properly placed in synonymy by DeCandolle (p. 327, 1825).

Hedysarum maculatum L. Sp. Pl. 746. 1753. Holotype, *Hedysarum* no. 14 "**maculatum** 4 // Hedysarum capparidis folio" (LINN; A, photo.).

Aeschinomene maculata (L.) Poir. in Lam. Encyc. Méth. Bot. **4**: 452. 1798 [?], based on specimen in Lamarck herbarium (P–LA; GH, negative no. 8199).

Pleurolobus maculatus (L.) J. St. Hil. in Nouv. Bull. Soc. Philom. **3**: 192. 1812, Jour. Bot. **1**: 61. 1813.

Desmodium gangeticum var. *maculatum* (L.) Baker in Hook. f. Fl. Brit. Ind. **2**: 168. 1876; Hepper in Keay, Hutch. & Dalz. Fl. West Trop. Afr. ed. 2. **1**(2): 584. 1958.

Hedysarum colinum Roxb. Hort. Bengal. (Cat. Calc.) ed. Carey 57. 1814, *nomen nudum* but based on *Nalla-mandu*, 1802.

Hedysarum collinum Roxb. Fl. Ind. 3: 349. 1832; Wight, Icon. 1: *pl. 272.* 1840.

Hedysarum lanceolatum Schum. & Thonn. in Schum. BGP. 360. 1827, DVS. 134. 1829; Junghans, *ibid.* 351. Holotype, Guinea: *Thonning* [with mss. no. 201, in fr.] (C; GH, negative no. 8196 a, b); probable isotype "e Guinea" sent in 1804 by Vahl (P–JU 15,577; GH, negative no. 8198).

Desmodium lanceolatum (Schum.) Walp. Repert. 1: 737. 1842, non Schindl. ex Gagnep. 1920.

Desmodium polygonoides Welw. ex Bak. in Oliv. Fl. Trop. Afr. 2: 161. 1871. Holotype, Angola: highlands of Pungo Andongo, *Welwitsch 2160* (BM; GH, negative nos. 7802 a, b).

Meibomia polygonoides (Welw.) O. Ktze. Rev. Gen. Pl. 1: 198. 1891, as "polygonodes."

Desmodium cavalerieri Léveillé, Fl. Kouy-Tchéou 232. 1914. Holotype, *J. Cavalerie 3274* (E; A, photo.).

Desmodium gangeticum is a widespread polymorphic species varying considerably in habit and leaflet shape but not in its more significant characteristics. I have cited above only those species for which I have seen authentic material or a photograph, or purely nomenclatural synonyms for which the basis is known. Additional synonymy which I have not yet checked or of species from areas not yet studied may be found in Schindler (1928) and Knaap-van Meeuwen (pp. 249, 250, 1962).

Alysicarpus ovalifolius (Schum.) Léonard, Bull. Jard. Bot. Bruxelles 24: 88. *fig. 11.* 1954.

Hedysarum ovalifolium Schum. & Thonn. in Schum. BGP. 359. 1827, DVS. 133. 1829; Junghans, *ibid.* 351. Holotype, Guinea: *Thonning* (C; BRUX, photo.).

Léonard illustrated his full discussion of this species with a photograph of the holotype and cited full synonymy, *op. cit.* The species has been taken up in *Desmodium* as *D. ovalifolium* (Schum.) Walp. Repert. 1: 737. 1842 (which is a later homonym) and also as *D. thonningianum* Dietr. Synop. Pl. 4: 1147. 1847.

Uraria picta (Jacq.) Desv. Jour. Bot. 1: 123. *pl. 5, fig. 19.* 1813; Léonard, Fl. Congo Belge et du Ruanda Urundi 5(2): 232. *fig. 14.* 1954.

Hedysarum pictum Jacq. Collect. 2: 262. 1788, Icon. 3: *pl. 567.* 1792; Willd. Sp. Pl. 3(2): 1204. 1802; Hornem. De Ind. Pl. Guin. 23. 1819; Schum. BGP. 364. 1827, DVS. 138. 1829; Junghans, *ibid.* 351. Holotype, Guinea: *Isert* (W [fide Schindler]); isotype, *Isert* (C [fide Junghans]). Junghans also cited a Thonning collection (C).

This species, illustrated by a handsome plate in Jacquin's *Icones, loc. cit.*, seems to have had a remarkably uncluttered nomenclatural history.

Alysicarpus rugosus (Willd.) DC. Prodr. 2: 353. 1825; Léonard, Bull. Jard. Bot. Bruxelles **24**: 92. *fig. 12*. 1954.

Hedysarum rugosum Willd. Sp. Pl. 3(2): 1172. 1802; Hornem. De Ind. Pl. Guin. 23. 1819; Schum. BGP. 358. 1827, DVS. 132. 1829; Junghans, *ibid.* 351. Holotype, Guinea: *Isert, hb. Willd.* (B; BRUX, photo.). A presumable isotype was sent to Paris by Vahl in 1804 (P–JU 15,575; GH, negative no. 8195).

This species was not considered new by Schumacher who cited the reference to Willdenow and included a transcription of Willdenow's diagnosis. The species, with its synonymy is amply treated by Léonard, *ibid.*

HEDYSARUM UMBROSUM Isert ex Schum. BGP. 362. 1827, DVS. 136. 1829, *nomen nudum in nota*; Junghans, *ibid.* 351.

Schumacher wrote, under *Hedysarum deltoideum* that a sheet in Isert's collection bears the name *Hedysarum umbrosum*, and that it might be a variety of *H. deltoideum* or the same thing. Schindler did not cite this name, nor is it listed in *Index Kewensis*. It is based on a collection of Isert (C) which I have not seen.

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THE MORPHOLOGY AND RELATIONSHIPS OF CIRCAEASTER

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THE PRESENT MORPHOLOGICAL STUDY of *Circaeaster agrestis* Maxim. was initiated because this plant is another example, in addition to *Kingdonia*, of an angiosperm with open dichotomous venation. This type of foliar vasculature is extremely rare in the dicotyledons and its taxonomic and phylogenetic significance raises very difficult problems which have recently been discussed in detail (Foster 1959, 1961a, 1961b; Foster & Arnott 1960). Throughout the long and vexed taxonomic history of *Circaeaster,* little attention has been given to its dichotomous venation and no attempt has been made to study possible fluctuations in the details of this pattern or to determine the existence of anastomoses or blind vein-endings. It is believed that the present study, based on the comparison of a wide range of leaf material, gives a fairly accurate picture of the trends of variation and demonstrates the often remarkable symmetry of the dichotomous pattern of venation.

In addition to the study of foliar vasculature, an effort was made to gain an accurate idea of the organization of the inflorescence and the morphology of the flower. This aspect of my investigation, supplemented by the embryological data provided by Junell (1931), has made it possible to review critically the various ideas which have been advanced regarding the systematic relationships of *Circaeaster.* It is my hope that the present article may serve to stimulate renewed interest in such relic genera as *Kingdonia* and *Circaeaster* and to demonstrate the fascinating evolutionary and taxonomic problems illustrated by the morphology of these herbaceous representatives of the Ranales.

DISTRIBUTION

The accompanying map (FIG. 1) reveals the extensive pattern of distribution of *Circaeaster* in Asia. Its present "range," to judge from the herbarium collections which I have examined, lies roughly along a curve extending from Kumaun through the Himalayas, southeastern Tibet, and northwestern Yunnan to the mountains of Kansu[1] and Shensi in north-

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[1] This portion of China corresponds approximately to the "country" formerly called

FIG. 1. The distribution of *Circaeaster* and *Kingdonia* in Asia. Each solid dot (*Circaeaster*) or solid triangle (*Kingdonia*) indicates an approximate locality from which herbarium specimens were studied.

western China. The extremely few collections from Nepal, Sikkim, Szechuan, Kansu and Shensi do not necessarily indicate the infrequency of the genus in these areas. Further botanical surveys will very probably indicate a much wider and more continuous distributional pattern than is shown on the present map. Throughout its area of distribution, *Circaeaster* consistently occurs at relatively high altitudes which range from 8000–9000 feet in Shensi, Szechuan, and Sikang to 11,000–12,000 feet in Yunnan and Tibet. The highest altitude represented in any of the collections studied was 14,000 feet in Bhutan.

The data included on many herbarium labels gives some idea of the ecology of *Circaeaster* and the plants with which it is associated. It evidently prefers moist, shaded environments and has been found growing in habitats described as wet leaf mold under Rhododendrons; in the shade of a damp cave associated with bryophytes, *Circaea alpina* and other plants; forming large colonies on damp soil under *Hippophaë*; in open fir forest, etc. Despite its small size, *Circaeaster* must have considerable charm and attractiveness in nature, as illustrated by notes from a collection of *Polunin, Sykes, & Williams* in Nepal: "Growing in shallow soil on damp rock ledge. Stems pink. Leaves pale green. Filaments pale green, anthers brown. Ovaries green, with white hairs, stigma brown."

"Tangut" by the Mongols, a fact which explains Maximowicz's (1881, p. 557) reference to *Circaeaster* as "herbula *tangutica*" (see Prejevalsky 1876, 2: 301–302).

The map also indicates the much more restricted pattern of distribution of *Kingdonia*, a genus which Diels (1932) and Janchen (1949) assumed is closely related to *Circaeaster*. According to my limited information, both genera grow under very similar ecological conditions and it is interesting, and perhaps taxonomically significant, that their distribution coincides so exactly in northwestern Yunnan and in the mountains of Shensi and Kansu provinces (see map, FIG. 1). Future botanical explorations may result in the discovery of other localities for *Kingdonia* and thus remove the puzzle of its present apparent restriction to only two widely separated regions in China.

TAXONOMIC HISTORY

Specimens of the same kind of plant, later described and published as the genus *Circaeaster*[2] by Maximowicz in 1881, were discovered and collected about 1854 in Kumaun by the British botanists Strachey and Winterbotham. Their collections were sent to J. D. Hooker at Kew who prepared a drawing and an analysis of the plant for the Linnean Society. Unfortunately his data and the specimens were lost and in 1882 Hooker wrote to Mr. Duthie, who was to collect plants in the Himalayas, asking him to make an effort to find *Circaeaster* and emphasizing that "the plant is worth a pilgrimage, for I know nothing in the least like it" (see Huxley, 1918, p. 248). Duthie was successful in his search and his copious material, collected in Kumaun, enabled Oliver (1895) to prepare the detailed description and illustrations of *Circaeaster* which appeared in Hooker's *Icones Plantarum*.

During this early period of discovery and description, efforts were made to assign *Circaeaster* as an "anomalous genus" to some existing family in the dicotyledons. Maximowicz (1881), who based his description of the genus on specimens collected in 1880 in Kansu by Przewalski, was the first to suggest the possible affinities of *Circaeaster* with the Chloranthaceae. However, he confessed that its divergence in several respects might justify segregating it in a new family near the Chloranthaceae. Oliver (1895), on the other hand, expressed serious doubt as to Maximowicz's proposals and regarded *Circaeaster* "as a degraded form, allied perhaps to Anemoneae (Ranunculaceae)."

The disagreements as to the relationships of *Circaeaster* became intensified in subsequent taxonomic works and unfortunately were not always accompanied by additional studies on the actual morphology of the plant. On the one hand, Bentham and Hooker (1883) and Hooker (1890) followed Maximowicz and classified *Circaeaster* under the Chloranthaceae. Bentham regarded *Circaeaster* as "a very distinct genus but, it seems to us, with essential characters relating it to *Chloranthus* and indeed in its

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[2] Maximowicz (1881) devised the name "*Circaeaster*" on the basis of the resemblance of its fruits with those of *Circaea* and because of the stellate disposition of the leaves. It is interesting to note that the vernacular Chinese name for *Circaeaster* is "Hsin Yeh Shu," literally "star-leaf herb" (How, 1958).

habit to some specimens of *C. japonica* Sieb." On the other hand, the affinities of *Circaeaster* with the Ranunculaceae were re-emphasized by Diels (1932) who based his decision upon the assumption that a close relationship exists between this genus and *Kingdonia*. The latter had previously been assigned to the Ranunculaceae by Balfour and Smith (1914). Diels's conclusions were later adopted without reservation by Janchen (1949) who segregated *Circaeaster* and *Kingdonia* as the two genera comprising the subtribe Kingdoniinae under the tribe Clematidae, subfamily Ranunculoideae of the Ranunculaceae.

These attempts to assign *Circaeaster* to either the Chloranthaceae or Ranunculaceae were in strong contrast with the efforts of other authors to segregate the genus in a new, independent family, the Circaeasteraceae. Post and Kuntze (1904) appear to have initiated this taxonomic treatment by suggesting that *Circaeaster* is either to be regarded as the sole genus in the subfamily "Circaeastereae" of the Chloranthaceae or as the representative of a distinct family, the Circaeasteraceae. Hutchinson, in both the 1926 and 1959 editions of his *Families of Flowering Plants* placed *Circaeaster* in the monotypic family Circaeasteraceae under the order Berberidales. Several other authors also accepted the family Circaeasteraceae. Hallier (1903), in his preliminary conspectus of flowering plants, included *Circaeaster* in the Ranunculaceae but later (1912) he grouped it under the family "Circaeastracées" in the order Ranales. Handel-Mazzetti (1931) located the family between the Ranunculaceae and Berberidaceae and Johansen (1950), following Hutchinson, classified it as a family under the Berberidales. Gundersen (1950), however, was less certain of the ordinal position of the family and apparently regarded *Circaeaster* as a possible genus to be included in the Berberidaceae.

Without question the detailed and meticulous investigations of Junell (1931) represent the most comprehensive morphological study of the past on *Circaeaster*. The living colony [3] of this plant which had been maintained for some years in the Botanical Garden at Upsala, Sweden, provided Junell with abundant material for his research on floral ontogeny, micro- and megasporogenesis, and the development of the gametophytes, endosperm, and embryo. Despite his expectations that an embryological study would shed new light on the vexed relationships of *Circaeaster*, this hope was not realized. In his skeptical opinion, "the systematic position of the plant is, on the contrary, about as uncertain as before." He correctly emphasizes that one of the inherent difficulties is the fact that the "life history" of those plants with which *Circaeaster* might be compared, is far too little known. This is certainly true with reference to *Kingdonia*, the embryology of which will continue to remain unknown until adequate preserved material can be obtained from China (see Foster, 1961a, p. 408).

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[3] According to Junell, the plants grown at Upsala were obtained from the Botanic Garden at Edinburgh. That material originated, in turn, from collections of *Circaeaster* made in Sikkim in 1910 by W. W. Smith.

MATERIALS AND METHODS

The material used as the basis for the present investigation was obtained from the following herbaria, the abbreviations for which are taken from Lanjouw and Stafleu's *Index Herbariorum*, Ed. 4, pt. 1. (Regnum Vegetabile **15.** 1959): Arnold Arboretum of Harvard University, Cambridge (A), British Museum (Natural History), London (BM), Indian Botanic Garden, Calcutta (CAL), Royal Botanic Garden, Edinburgh (E), Conservatoire et Jardin botaniques, Genève, Switzerland (G), Herbarium, Royal Botanic Garden, Kew (K), Botanical Museum and Herbarium, Lund, Sweden (LD), Muséum National d'Histoire Naturelle, Paris (P), Naturhistoriska Riksmuseum, Stockholm (S), U. S. National Museum, Smithsonian Institution, Washington (US), and Botanical Research Station of Academia Sinica, Shensi, China (WUK). Grateful acknowledgement is made to the directors and curators of these herbaria for allowing me to remove leaf specimens, and in some cases entire plants, for my morphological studies.

The complete citations of the localities in China, Tibet and the Himalayas (see map, Fig. 1) where the specimens were collected are as follows: **China.** KANSU: *G. N. Potanin, s.n.* (P). SHENSI: Hsiang Sui Precipice, alt. 2800 m., *Liu 10678* (WUK). SIKANG: Kangting (Tachienlu) district, Chetola, alt. 3500 m., *Harry Smith 16936* (S); Chi-na-tung, Tsa-wa-rung, *Wang 65301, 65390* (A); Sacred Mountain, Kar-war-kar-loo, alt. 3400 m., *Wang 66252* (A). SZECHUAN: Karlang, alt. 3400 m., *Harry Smith 4141* (LD, S). YUNNAN: Western flank of the Lichiang Range, alt. 12,000 ft., *Forrest 6416* (E, K); moist rocky situations on the Chung-Tien plateau near Hsia-chung-Tien, alt. 12,000–13,000 ft., *Forrest 118* (E, K); *Handel-Mazzetti 8035* (US); "ad confines Tibeticas subjugo Dokerla," *Handel-Mazzetti 8035* (G); Anougu (Ngantschang), alt. 3550 m., *Handel-Mazzetti 7679* (P). **Tibet.** Tongolo, *Soulié 585* (G, P); Tongolo (Prin. de Kiala), *Soulié 355* (G, K); Kongbo Province, Sang La, Tsangpo Valley, alt. 12,000 ft., *Ludlow, Sherriff & Taylor 5033* (E); Kongbo Province, Hunket, Tumbatse, Rong Chu, alt. 11,600 ft., *Ludlow, Sherriff & Taylor 5033A* (E). **Bhutan.** Padima Tso near Thampe La, alt. 14,000 ft., *Ludlow, Sheriff & Hicks 17179* (E). **Sikkim.** Nuighil, alt. 13,000 ft., *W. W. Smith 4124* (CAL). **Nepal.** Bhurchula Lekh, near Jumia, alt. 12,000 ft., *Polunin, Sykes & Williams 4653* (BM); Suli Gad, between Rohagaon and Lulo Khola, alt. 10,000 ft., *Polunin, Sykes & Williams 3412* (BM); Langtang Valley, alt. 12,000 ft., *Polunin 1506* (BM); Rambrong, Lamjung, alt. 13,000 ft., *Stainton, Sykes & Williams, 6182* (BM). **Kumaun.** Amongst rocks under shade of trees near Saba Udigar in the Ralam Valley, alt. 8,000–9,000 ft., *J. F. Duthie 3354* (G); amongst rocks in the Ritum Valley, August 21, 1884, *J. F. Duthie, s.n.* (US 40004).

The descriptions and illustrations of foliar venation in this paper are based on material cleared with the aid of 2.5% NaOH and concentrated chloral hydrate, and stained with safranin. For the study and illustrations of the organography of the inflorescence and the structure and vasculature of the flowers, two methods were employed: (1) the outer portions of the leaves of a number of plants were first removed and the partly defoliated specimens then cleared and stained by the same techniques used for studying leaf venation; and (2) some of the defoliated plants (including the upper part of the hypocotyl) were cleared and then dehydrated by the tertiary butyl alcohol method, infiltrated with "Histowax," sectioned transversely at 7–8μ in thickness, and stained with a combination of safranin and light green. Because of the very small size and crowded arrangement of the numerous flowers, serial transections proved indispensable in the reconstruction of the morphology and vasculature of the remarkable inflorescence of *Circaeaster* (see FIG. 30a–d).

Thanks are due to Mr. Nels Lersten for his assistance with the processing, sectioning and staining of some of the inflorescence material and to Miss Charlotte Mentges who prepared the outline map represented in FIG. 1. The photomicrographs of leaf venation and the transections of the inflorescence were made by Mr. Victor Duran and the line drawings prepared by Mrs. Emily R. Reid. Appreciation is also due to Dr. Shiu-ying Hu, of the Arnold Arboretum, Harvard University, for translating into English the descriptions of *Circaeaster* and *Kingdonia* found in the recent treatise on Chinese plants by How (1958), to Dr. Rimo Bacigalupi and Professor Arthur E. Gordon for their assistance with the Latin description in Maximowicz's (1881) article, and to my wife for her help in proofreading the manuscript.

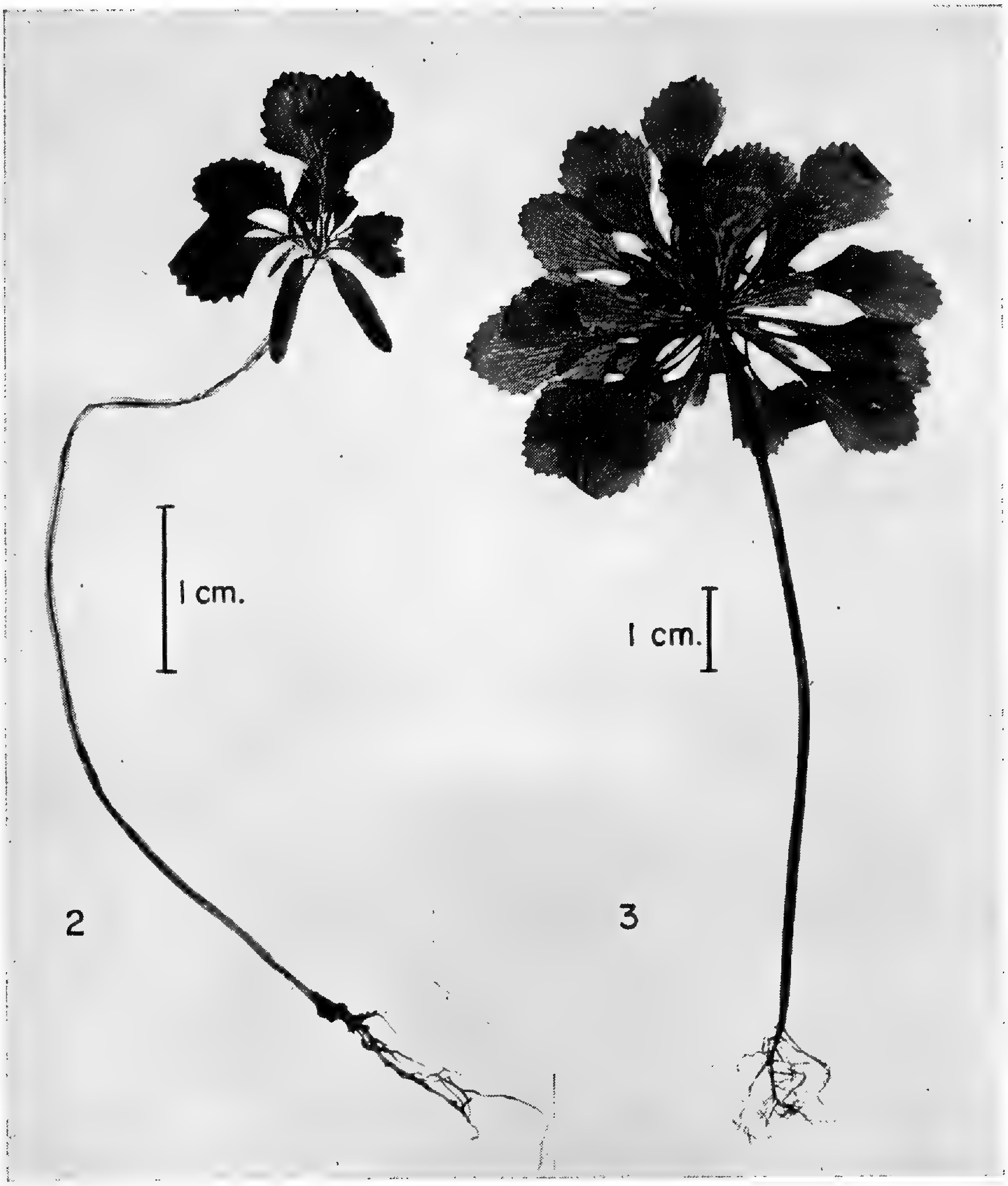
This paper was written during my appointment as Miller Research Professor at the University of California for the academic year 1962–63. It is a pleasure to express my thanks for the opportunity for study provided by this appointment.

GENERAL ORGANOGRAPHY

Plants of *Circaeaster* are annual herbs with a very distinctive and unusual habit of growth. The elongated axis is the result of the exaggerated development of the hypocotyl which bears at its summit, below the rosette of crowded leaves, a pair of linear and persistent cotyledons (FIGS. 2–3). Junell (1931) studied the early phases of germination and his Figure 7e shows clearly the early and conspicuous elongation of the hypocotyl of the young seedling. Troll (1938, p. 1093 footnote) compared the growth-form of *Circaeaster* with the "little-tree rosette" ("Bäumschenrosetten") habit of certain species of *Biophytum* (Oxalidaceae). In *B. sensitivum,* for example, the general organography of a flowering specimen, as depicted by Troll (1937, p. 222, Abb. 141) is remarkably similar to a mature specimen of *Circaeaster,* despite the obvious differences in leaf form.

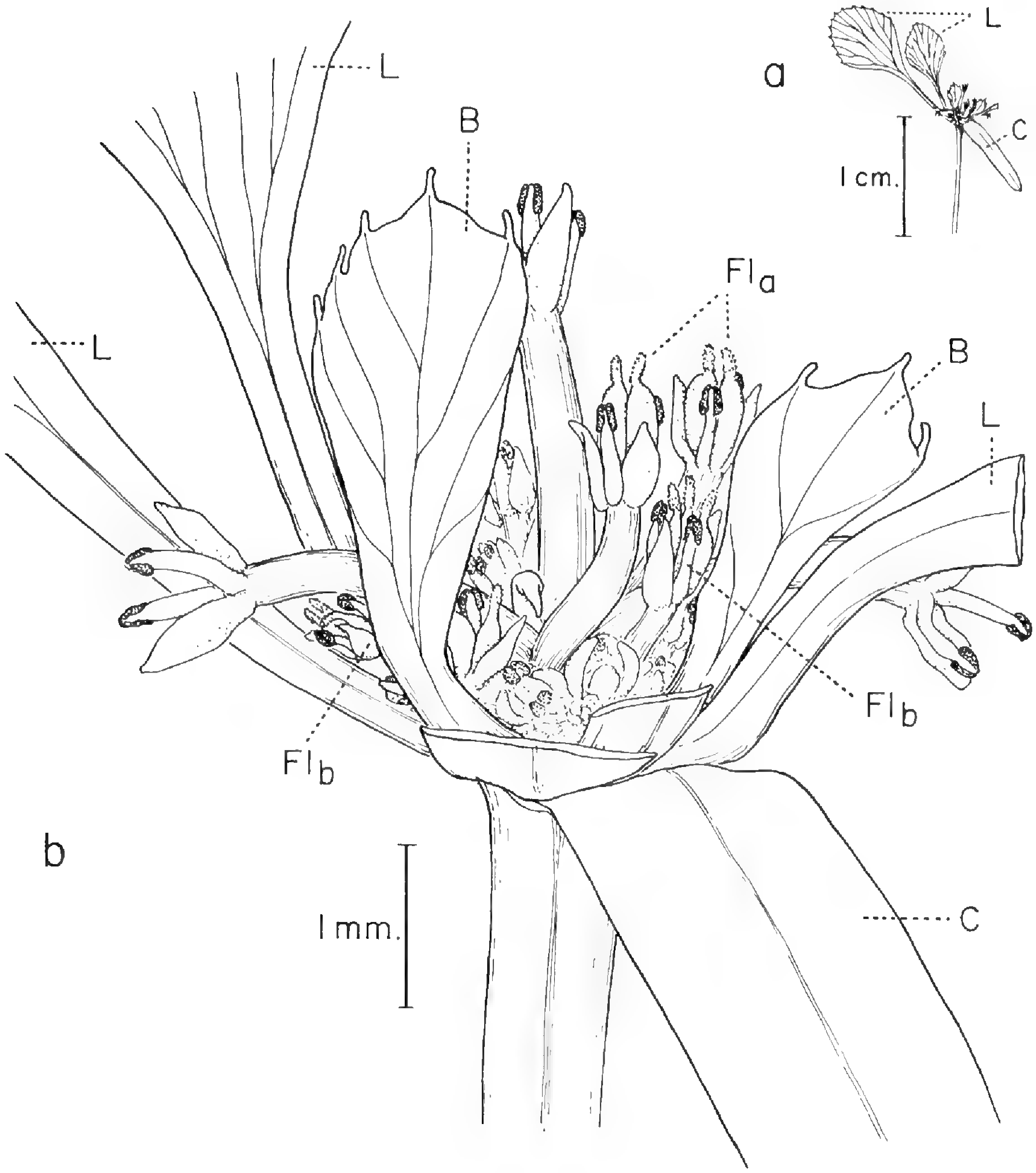
Although the hypocotyl of *Circaeaster* may reach a length of 8 cm. or more in vigorous specimens, it is difficult to determine from the vague statements in the literature whether the rosette of leaves, is borne in an upright or a prostrate position in nature. Junell (1931), with an opportunity to study living plants in cultivation, merely states that the plant has "an upright, unbranched, smooth stem." It seems possible, however, that in some cases the hypocotyl may remain buried in the moss or the leaf mold in which the plant frequently grows in its natural habitat.

The development of an individual plant of *Circaeaster* is terminated by



FIGS. 2 and 3. General organography and habit of *Circaeaster*. 2, specimen showing the typical elongated hypocotyl, the pair of persistent cotyledons and, just above the left cotyledon, a maturing hairy fruit (*Wang 65930*, A). 3, a very robust plant from the living collection at Upsala (*Junell s.n.*, P). Note the cotyledons, primary leaves, and the conspicuous pattern of open dichotomous venation.

the formation, in the center of the rosette of leaves, of a condensed terminal inflorescence composed of numerous minute flowers (FIG. 4). Flowers, in the most varied stages of development, may occur at the same time in a given individual. Following pollination, the very slender pedicels of many of the flowers elongate and bear at their tips one or more fruits (with their characteristic uncinate hairs), together with the persistent tepals and the remains of the stamens (FIGS. 34–35).



FIGS. 4a and b. Cleared and partially defoliated specimen showing the fasciculate arrangement of the flowers in the terminal inflorescence. (*Stainton, Sykes & Williams 6182*, BM). 4a, low power view, emphasizing minute size of flowers; 4b, greatly enlarged view of same. Note elongated pedicels of flowers in center of inflorescence and the occurrence of both bi- and tricarpellate flowers. B, bract; C, cotyledon; Fl$_a$, bicarpellate flower; Fl$_b$, tricarpellate flower; L, foliage leaf.

MORPHOLOGY AND VASCULATURE OF LEAVES

Phyllotaxis. The foliar organs of a mature specimen of *Circaeaster* consist of two linear cotyledons, a variable number of small petiolate foliage leaves and the bracts which subtend the peripheral fascicles of flowers of the abbreviated inflorescence (FIGS. 30a–b). These appendages, however, are so crowded in their attachment to the stem that it is very difficult, without an ontogenetic study, to determine whether the phyllotaxis is decussate, whorled, or spiral. Junell (1931) examined the sequence of leaf-primordia formation in four seedlings but encountered such variability that he reached no firm conclusion. FIG. 30a supports his observation that the two cotyledons do not lie in the same plane; it also shows that the position of the six leaves and five bracts might be interpreted as the result of a slightly "distorted" pattern of decussate phyllotaxis.

Nodal Anatomy. Serial transections reveal that the vascular system of the upper end of the hypocotyl is a diarch primary xylem plate flanked on each side by two well-developed collateral strands of secondary phloem and secondary xylem. At the level of attachment of the cotyledons, each of these appendages is vascularized by a trace which diverges from a corresponding protoxylem pole. The xylem portion of each cotyledonary trace is often composed of two closely spaced strands of tracheary elements while the phloem appears as a continuous strip of tissue. Two similar traces, derived from the remainder of the primary xylem plate, extend into the bases of the first "pair" of foliage leaves, which lie approximately at right angles to the plane of the cotyledons.

At this level of section, a division of the collateral strands of secondary vascular tissue occurs and produces four large bundles; the center of the axis is now represented by a parenchymatous pith. The single traces of the remaining foliage leaves seem to originate as branches of these four major components of the highly condensed "eustele." FIG. 30a–d shows that the xylem of each leaf trace is often conspicuously double at various levels in its extension through the petiole.

The accurate reconstruction of the vasculature of the axis is complicated by the common origin of leaf and bract traces or bract and pedicel traces from the same major bundle of the stele. Moreover, it has not been possible, with the very limited study of "revived" herbarium material to discover the origin and the basal interconnections of the vascular systems of the central flowers. Unfortunately Junell (1931), with abundant fresh material at his disposal, apparently made no attempt to reconstruct the remarkable vasculature of the shoot or inflorescence of *Circaeaster*.

Form and Venation of Cotyledons. The cotyledons of *Circaeaster* are linear or strap-shaped appendages and vary in size from 7–10 mm. in length and 1.5–3 mm. in maximum width. In contrast with the dichotomously veined lamina of the foliage leaves, the entire cotyledon is traversed by an unbranched midvein which represents the upward extension of its single trace (FIGS. 2, 6). Careful study of cleared preparations indicates that the xylem of the midvein, at various levels or throughout its course, consists of two closely approximated strands of tracheids which may separate as two very short endings below the blunt apex of the cotyledon (FIG. 6). Serial transections confirm the fluctuation in the degree of doubleness of the xylem at various levels (FIGS. 30a–d, cotyledon at left).

Form and Venation of Foliage Leaves. The foliage leaves are clearly demarcated into petiole and lamina; the latter varies from broadly spatulate to rhomboidal in form and is provided with small mucronate dentations at its distal margin (FIGS. 5, 7–13, 15–29). Considerable fluctuation was observed in the size of the leaf, not only between plants from different collections but also between the successive leaves in a single rosette. The largest leaves studied measured about 30 mm. in length with a maximum lamina diameter of 16–17 mm. (*Liu 10678*, WUK). At the opposite extreme, the very small leaves shown in FIGS. 7–11 are all less than 7 mm. in length and measure only 2.25–3.5 mm. in lamina width. Leaves from other collections were somewhat intermediate in their dimensions between these two extremes.

Although the distinctive pattern of open dichotomous venation is superficially evident even in dry herbarium specimens, the few descriptions of the foliar vasculature in the literature are very brief and in part inaccurate. The first specific description of dichotomous venation in *Circaeaster* was given by Oliver (1895) who stated: "The petioles, like the hypocotyledonary axis, are traversed by a solitary vascular bundle which repeatedly forks in the lamina giving off a branch to each serrature." Junell's (1931) description is similar but slightly more detailed. He found that the petiolar bundle divides into two or three branches, the median one of which often does not divide further. "Finer lateral veins are not present" and in the colony of *Circaeaster* grown at Upsala, the leaves had on the average 14 teeth with a corresponding number of vein endings. No additional information on leaf venation is found in Diels's (1932) paper and Troll (1938) merely attempted, on purely theoretical grounds, to argue that the dichotomous venation of *Circaeaster* represents a secondary "modification" of pinnate venation. In none of these descriptions is reference made either to blind vein-endings or to anastomoses, examples of which were encountered in the present survey (FIGS. 23–29). The descriptions and illustrations given in the present paper indicate a wide variation in the *details* of the venation pattern in *Circaeaster* and are based on the study of 97 cleared leaves derived from a total of 24 different herbarium collections.

In many of the plants studied, the cotyledons are followed by a series of 2 or more small leaves with extremely simple patterns of dichotomous venation (FIGS. 7–9, 12, 13, 15, 16). For convenience, these leaves will be designated as "primary" or "juvenile leaves" although it is recognized that there is no clear morphological demarcation between them and the succeeding more highly vascularized foliage leaves. A striking example of a gradual progressive elaboration of dichotomous venation is shown in the leaf series represented in FIGS. 7–11. Each of the three very small "primary leaves" is vascularized by a trace with double xylem, which extends through the short petiole and dichotomizes near the base of the lamina (FIGS. 7–9). The dichotomous branching of the two basal veins in the first leaf occurs at about the same level and yields four vein-endings which terminate below corresponding marginal teeth (FIG. 7). In the second leaf with five vein-endings, dichotomy of the basal veins occurs at different levels producing a "midvein" and two dichotomized lateral veins; the branch of one lateral, however, terminates blindly without a corresponding marginal tooth (FIG. 8). In the third primary leaf, three symmetrical pairs of vein-endings have been produced by the dichotomy, at nearly the same level, of the central and the two basal lateral veins (FIG. 9). This leaf is followed by two larger appendages, with eight and nine vein-endings respectively, terminating below corresponding teeth (FIGS. 10–11). The increase in number of veins in these organs has resulted from further symmetrical or asymmetrical branching of the lateral vein-systems.

The primary leaves of other collections are notable because of the prominence of an unbranched "midvein" which traverses the central region of the lamina (FIGS. 12–13, 23). Appendages of this type tend to develop an odd rather than an even number of vein-endings. Most commonly, the midvein originates as the inner of the two veins formed by the dichotomy of one of the main xylem strands of the petiolar bundles. In a few cases, however, the midvein is formed by the union of the two central bundles produced by the dichotomy — at different levels — of each of the two xylem strands in the upper region of the petiole (FIG. 14). From a broad comparative viewpoint it is interesting to note that both of the types of midvein origin found in the primary leaves of *Circaeaster* also occur in the dichotomously veined tepals of the flower of *Kingdonia* (Foster 1961a, plate 1).

The increasing complexity of the venation in successive "primary leaves" of a plant reaches its culmination in the elaborate patterns of dichotomous venation found in well-developed foliage leaves (FIGS. 5, 17–29). Profuse and often very regular dichotomous branching of the veins imparts an elegance and a symmetry to the various patterns which may now be examined in some detail.

The *degree* of symmetry of the venation pattern appears closely associated with (1) variations in the number of main veins in the lamina base and (2) the patterns and levels of successive dichotomous branching in each of the principal systems of veins. Very commonly a central and two main lateral veins diverge at nearly the same level in the lamina base; as in the primary leaves, the central vein is produced by the division of one of the two main xylem strands of the petiolar bundle. In leaves with this type of basal vasculature, the successive dichotomous branching of the central and both lateral veins may be extremely regular, resulting in an even number of vein-endings (FIGS. 5, 19). Essentially similar patterns, but with an odd number of vein-endings are formed if certain of the distal veins fail to dichotomize before terminating at the margin (FIGS. 20, 24, 27).

Transitions to a more isotomous type of basal vein-dichotomy were also encountered in the present survey. In these cases, *each* of the two xylem strands of the petiolar bundle tends to dichotomize at a low level in the lamina base yielding four or sometimes five main veins. The pattern of dichotomous branching of these veins is variable, however, and produces either an odd (FIGS. 18, 21) or an even (FIG. 22) number of marginal vein-endings. A distinctive feature of the leaf shown in FIG. 18 is the divergence, from one of the basal vein-dichotomies, of a long unbranched central vein which resembles the "midvein" in primary leaves (cf. FIGS. 12, 13, 18 and 23). This venation pattern was observed in a few of the foliage leaves from a cultivated specimen of *Circaeaster* (*Junell s.n.*, P). Usually the "central vein" in foliage leaves branches dichotomously at some level in the lamina (FIGS. 5, 19–22, 24).

The only examples of a strictly isotomous pattern of basal venation were found in the leaves of a specimen from the Shensi collections (*Liu 10678*, WUK). In these appendages a central vein system is not formed and the vasculature of the two halves of the lamina is derived from the pair of veins produced by the *equal division* of the petiolar bundle (FIGS. 15–17). In the larger primary leaf and the foliage leaf which follows it, the isotomous branching is repeated at the same level by each of the two main veins (FIGS. 16, 17). The venation of the smaller primary leaf (FIG. 15) is the simplest pattern encountered in the present study and is highly suggestive of a "transition" between cotyledonary and foliage-leaf venation (cf. FIGS. 6 and 15).

In the majority of the leaves examined, *all* the vein-endings terminate in corresponding marginal teeth. This type of one-to-one correlation seems to predominate regardless of the degree of symmetry of the venation pattern or the form or size of the lamina.[4] Careful study, however, has revealed that in addition to this normal pattern of marginal venation, the leaves of a few collections possess blind vein-endings, i.e., veins which terminate in various positions distal to the lamina margin (FIGS. 8, 22–26). Usually only one or two leaves of a given plant form veins of this type and their occurrence in either primary leaves or the larger foliage leaves is sporadic and unpredictable. Frequently only a single blind vein-ending may develop in an otherwise regular pattern of dichotomous venation. In these instances it is usually obvious that such a vein represents the shorter of the two branches derived from a dichotomy (FIGS. 22, 24). The most consistent and profuse development of blind vein-endings was observed in a series of plants from one of the collections from Nepal (*Stainton, Sykes & Williams 6182*, BM). Out of a total of 24 leaves examined, 16 showed blind endings located at various points in the venation (FIGS. 25, 26). In one of these leaves (FIG. 25) there are three blind terminations, each of which clearly represents an "overtopped" branch of a dichotomized system of veins. A similar morphological interpretation seems valid for the four delicate and much shorter vein-endings shown in FIG. 26.

Possibly the apparent infrequency of blind vein-endings observed in *Circaeaster* is merely the result of insufficient sampling. But it is interest-

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[4] In a few of the leaves examined, one of the marginal teeth (usually the outermost one in the series) is vascularized by a strand of xylem which is unconnected with the xylem of the adjacent vein. Discontinuous strands of this type raise interesting ontogenetic questions which, however, could not be solved by the study of cleared leaves of herbarium specimens.

ing that in the much larger dichotomously veined leaves of *Kingdonia*, blind endings are relatively numerous and occur in all the specimens which were studied (Foster & Arnott 1960, p. 695, Table I). Until ontogenetic studies have been made on the leaves of the two genera, however, the full morphological significance of blind vein-endings in the open dichotomous venation patterns must remain a question.

Throughout the present investigation a very careful search was made for vein anastomoses. They proved to be extremely infrequent and only four examples were encountered in my survey of nearly 100 leaves. Only a single anastomosis occurs in each case and its position in the venation pattern varies from leaf to leaf (Figs. 28, 29). As in *Kingdonia* the anastomoses represent fundamentally the union between the adjacent branches of two vein-dichotomies. Fig. 27 shows an interesting example of the close approximation, without fusion, between the inner and nearly equal branches of two veins which have dichotomized at about the same level. In another leaf from a different collection (*Soulié 585*, P) a similar pattern was observed except that the two veins were anatomically joined for a very short distance before their divergence as two separate strands. In each of the anastomoses shown in Figs. 28, 29, however, the two inner branches which unite are conspicuously unequal in length and degree of development. The shorter and more slender branch (consisting of a single file of tracheids) joins its neighbor either near the level of a vein-dichotomy (Fig. 28) or at a much higher point (Fig. 29). In both cases, the areoles which result are characteristically elongated and closely resemble those produced by similar vein-unions in *Kingdonia* (Foster 1959, pl. 2).

INFLORESCENCE

The minute and numerous flowers of *Circaeaster* are aggregated in a compact terminal inflorescence which occupies the center of the "rosette" of leaves (Figs. 4, 30). Although cleared and partly defoliated specimens are useful in showing the fasciculate arrangement of the flowers and the small dichotomously veined bracts, the complex organization of the inflorescence is fully revealed only by the study of microtomed serial transections. These are difficult to secure because the short epicotylar axis is frequently bent or excessively compressed in herbarium specimens. The description which follows is based on the study of the relatively few satisfactory transectional series which were obtained.

Figures 30a–d represent a series of transections of an inflorescence composed of 28 flowers. The majority of the flowers are disposed in five peripheral fascicles and each fascicle is subtended by a small bract (Figs. 30a and b, flower-groups subtended by bracts B1–B5). The fascicles are numbered according to the length of their associated bracts, number 1 having the longest bract (661μ) and number 5 the shortest (152μ). It is uncertain whether this sequence indicates an ontogenetic succession but it should be noted that each bract and its subtended fascicle occurs *between* the bases of two adjacent foliage leaves. Most of the flowers in the peripheral fascicles are in very early stages of development but in three fascicles the largest flower was sufficiently mature to have ripe pollen or primary sporogenous tissue in the anthers (FIG. 30c, flowers subtended by bracts B1, B3, B4). In some fascicles, the flowers are collaterally arranged and basally joined to form a very short stalk or "peduncle" adnate to the bract (FIG. 30a, B4).

The five largest and best developed flowers in this inflorescence are devoid of bracts and collectively represent a central fascicle. Beginning at the base of this fascicle, the elongated pedicels of flowers V, IV, III and II progressively become free, and flower I (with the longest pedicel and most highly developed carpel) morphologically represents the terminal flower of the entire inflorescence (FIGS. 30a–d).

Transections of the inflorescence of several other specimens revealed a similar general type of morphology but showed that the number of flowers in the peripheral fascicles may consistently be reduced to two. In a plant collected in Yunnan (*Forrest 6416*, E) each bract subtends a pair of basally united flowers, one pedicellate and well developed, the other small and rudimentary. It seems possible that only the larger flower in each of these fascicles may be functional. Similar examples of two-flowered fascicles were found in studying serial transections of the inflorescence shown in FIG. 4. The possible significance of this divergence from the many-flowered fascicles illustrated in FIGS. 30a and b can only be determined by the comparison of a much wider range of material than I have been able to assemble.

Very few efforts have been made in the past to interpret or to classify the peculiar and distinctive inflorescence of *Circaeaster*. Maximowicz (1881) observed the association of small hyaline bracts with the bases of the flower pedicels and stated that the "very minute flowers are fascicled in the upper axils forming a many-flowered terminal inflorescence." Bentham and Hooker (1883) were more explicit; they regarded the inflorescence as a small raceme "reduced to a fascicle with the common rachis scarcely or not at all developed." Oliver (1895) characterized the arrangement of the floral pedicels as "umbellate-fasciculate." In the modern period the morphological and taxonomic significance of the inflorescence has been entirely ignored by Diels (1932), Janchen (1949), and Hutchinson (1959). As far as I can discover, Junell (1931) is the only investigator to propose an interpretation of the inflorescence based upon its methods of development. Using longitudinal sections he found that the order of flowering is centrifugal and concluded that "*Circaeaster* apparently has a cymose inflorescence."

In the light of the present study it is difficult to decide whether the inflorescence of *Circaeaster* is morphologically equivalent to either a reduced cyme or to a raceme. From a speculative viewpoint it is possible to imagine that excessive phylogenetic reduction of an orginally cymose or racemose terminal inflorescence has occurred, resulting in the elimination of all bracts except those which subtend the peripheral fascicles of flowers. But until the taxonomic affinities of *Circaeaster* have been fully clarified, the evolution of its peculiar inflorescence will continue to remain an intriguing but unsolved problem.

MORPHOLOGY AND VASCULATURE OF FLOWERS

The minute apetalous hermaphroditic flowers of *Circaeaster* are highly variable with respect to the number of tepals (T), stamens (S), and carpels (C) which they develop and the total range in variation observed in this study may be summarized by the formula T^{2-3}, S^{1-3}, C^{1-3}. Variation is extensive not only between flowers of different collections but even among the flowers of the same inflorescence. For example, in both of the collections from Tibet (*Soulié 355*, P, G), the majority of the flowers in the inflorescence consist of 3 tepals, 1 stamen and 1 carpel (FIG. 30c, peripheral flowers of bracts B1, B3, B4; FIG. 30d, central flower IV); one of the central flowers in each inflorescence, however, has 2 tepals, 2 stamens, and 1 carpel (FIG. 30d, flower V). This latter pattern, which was apparently regarded as "typical" for the genus by Maximowicz (1881) and Hutchinson (1959) is infrequent in my material and I have only observed it, in addition to the cases just noted, in the flowers of the peripheral fascicles of the inflorescence of a collection by Forrest (*6416*, E). In some collections, bi- and tricarpellate flowers appear to predominate and both types occur in the same inflorescence (FIG. 4, fl_a, fl_b). The most unusual flower encountered consists of 3 tepals, 3 stamens, and 3 carpels (FIG. 33). This flower, which appears perfectly "normal" in structure, occurs in an inflorescence largely composed of flowers with 2 tepals, 2 stamens and 2 carpels.

The vascular system of the flower pedicel consists of one or two strands of narrow tracheids flanked by two bundles of phloem; in many cases, the phloem appears to surround the xylem giving the appearance of a typical "protostele." Near the level of attachment of the floral organs, two important structural changes are evident: (1) an active cambial zone develops beneath the phloem tissue and (2) the previously slender strand of xylem abruptly dilates and now consists of a mass of short tracheids with enlarged lumina. Each of the single traces of the tepals, stamens and carpels diverges from this central "nest" of tracheids but "revived" herbarium material was too poor in quality to permit an accurate reconstruction of the vasculature of the floral receptacle (see semidiagrammatic representations in FIGS. 31–35).

In cleared material, the persistent scale-like tepals often appear devoid of vasculature and serial transections reveal that the single weak trace may end below or at the base of these appendages. In more robust specimens, however, the upward extension of the trace forms a midvein containing a very delicate unbranched strand of xylem.

The stamens of *Circaeaster* are distinctive in structure because only one pair of introrse microsporangia is developed. Dehiscence is longitudinal and very small tricolpate pollen grains have frequently been observed adhering to the elaborate papillae of the stigma (FIG. 31). Each stamen is vascularized by a single median vein which terminates below the narrow connective separating the pair of microsporangia (FIGS. 31–35).

Each of the carpels is vascularized by a well-developed amphicribral trace which divides near the base of the ovary into a dorsal and a ventral vein (FIGS. 32–34). These two strands constitute the total vasculature of the carpel and no additional venation is developed as the carpel matures into a fruit. The dorsal bundle extends up the convex abaxial side of the carpel and ends below the base of the papillate stigma. The ventral vein traverses the adaxial side of the carpel and according to Junell (1931) passes through the massive funiculus of the single functional ovule and terminates at the chalazal end of the embryo sac.

The enlargement of a carpel into a fruit is accompanied by the profuse development of unicellular hairs which are conspicuously hooked at maturity (FIGS. 34, 35). These trichomes are progressively initiated in a basipetal sequence from the ovary wall and first appear in an area well below the terminal stigma (FIGS. 32, 33). As a result, the upper end of the mature fruit remains entirely glabrous (FIGS. 34, 35). I have never observed any example of the completely or partially glabrous fruits which Handel-Mazzetti (1931) and Junell (1931) noted in certain collections. Hooker (1890) emphasized the possible role of the uncinate hairs in the dispersal of the fruits and believed that they are "such aids to dispersion that it [i.e., *Circaeaster*] may be supposed to be common though so inconspicuous as to be overlooked."

DISCUSSION

In the more than 80 years that have elapsed since the establishment of the genus *Circaeaster* by Maximowicz (1881), no general agreement has been reached as to the systematic affinities of this peculiar genus. A considerable part of the controversy has been due to the exploitation of a very few selected morphological features for *direct* comparison with presumably homologous characters in members of such families as the Chloranthaceae, Ranunculaceae and Berberidaceae. Unfortunately this practice has been based to some extent on an inaccurate, or at the very least, an inadequate understanding of the floral morphology of *Circaeaster*. Furthermore, when the *combination* of highly remarkable morphological and embryological characters of *Circaeaster* is fully appreciated and compared with the situation in the suggested relatives of *Circaeaster*, the "anomalous" position of the genus is emphasized and justification is provided for its segregation in the monotypic family Circaeasteraceae. In the light of the present investigation, supplemented by the embryological data provided by Junell (1931), the various proposals for classifying *Circaeaster* may now be critically examined.

The possible relationship of *Circaeaster* to the family Chloranthaceae in the Piperales was first suggested by Maximowicz (1881) and his viewpoint was later adopted for the Bentham and Hooker (1883) system of classification. As far as I can determine, this taxonomic treatment was fundamentally based on the assumption that the flower of *Circaeaster,* like that of members of the Chloranthaceae, is unicarpellate and that the ovary contains a single, pendulous orthotropous ovule. While it is true that unicarpellate flowers commonly occur in *Circaeaster*, there is considerable variation even between flowers of the same inflorescence and gynoecia composed of 2 or 3 carpels have been encountered frequently in the present investigation (FIGS. 4, 31–33). But in addition to the divergence in carpel number, the presumed relationship between *Circaeaster* and the Chloranthaceae is negated by the following additional contrasts: (1) *pollen*, tricolpate in *Circaeaster* (Erdtman 1952), monocolpate, acolpate or polycolpate in the Chloranthaceae (Swamy 1953); (2) "*ethereal* oil cells" (i.e., secretory idioblasts) absent in *Circaeaster* (Schulze 1900, Solereder 1908, Metcalfe & Chalk 1950), present in all genera of the Chloranthaceae (Swamy 1953); (3) *vessel members,* with simple perforations in *Circaeaster* (Cheadle 1953, p. 34), with scalariform perforations in all members of the Chloranthaceae (Swamy 1953); (4) *foliar venation*, open dichotomous in *Circaeaster*, pinnate-reticulate in the Chloranthaceae (Swamy 1953); (5) *pollen tube*, mesogamous in *Circaeaster* (Junell 1931), porogamous in the Chloranthaceae (Schnarf 1931); (6) *endosperm*, cellular and of the *Adoxa*-type in *Circaeaster* (Junell 1931), cellular, the first walls predominantly transverse in *Hedyosmum* of the Chloranthaceae (Swamy 1953). In connection with these contrasts, it is interesting to note that Junell (1931) found two points of resemblance between *Circaeaster* and the Saururaceae, a family included with the Chloranthaceae and Piperaceae in the order Piperales (Hutchinson 1959). According to Junell, the genus *Saururus*, which usually has 3–4 free or basally joined carpels, shows "great similarity" to *Circaeaster* in that in both genera, *two* orthotropous ovules begin development from the inner surface of the carpel but only one of them becomes fertilized and forms the single seed. However, as Junell admits, an important difference between the two genera is the development of a massive perisperm in the seeds of *Saururus*. A further divergence, in my opinion, is the unusual formation of the *Adoxa*-type of endosperm in *Circaeaster.*

With reference to the Ranales (*sensu lato*), the possible affinity of *Circaeaster* with the Ranunculaceae was originally suggested by Oliver (1895) but he gave no morphological evidence to support his conjecture. Diels (1932), however, strongly insisted that *Circaeaster* should be regarded as the most extremely reduced member of the Ranunculaceae and that its closest affinities are with *Kingdonia* which had already been classified as a new genus in this family by Balfour and Smith (1914). The two main points of resemblance between *Circaeaster* and *Kingdonia* used by Diels to support his argument are the presence of a solitary, orthotropous, pendulous ovule and the dichotomous venation of the leaves. In the light of our present knowledge, these points of agreement are clearly not decisive in the determination of the correct systematic position of *either* genus (Foster 1959, 1961a). To judge from the recent studies of Bersier

(1960), Vijayaraghavan (1962) and Bhandari (1962), the ovule in a variety of genera of Ranunculaceae is typically anatropous, and there is no evidence that the orthotropous pendulous ovule of either *Circaeaster* or *Kingdonia* has arisen as a "modification" of this feature. As Swamy (1953) pointed out in discussing the relationships of the Chloranthaceae, "the very fact that orthotropous ovules occur in many unrelated families suggests that its development may as well be due to parallel evolutionary trends." The use by Diels (1932) of dichotomous venation as indicating the affinity between *Circaeaster* and *Kingdonia* and hence justifying the assignment of these genera to the Ranunculaceae, seems particularly unconvincing. As I have discussed in detail in several recent papers, the unilacunar node, the four leaf traces and the palmate open dichotomous venation of the leaf of *Kingdonia* are not duplicated, as far as I can determine, in any of the generally recognized genera of the Ranunculaceae (Foster 1959, 1961a). A similar objection arises to the use of the unifasciculate leaf trace and open dichotomous venation of *Circaeaster* in supporting the family relationships of this genus with the Ranunculaceae (Figs. 5, 7–13, 15–29). In this connection it should be emphasized that the investigations of Sterkx (1900) revealed that even the cotyledons of a wide range of ranunculaceous genera develop relatively complex net venation. In place of a *divergent* and open dichotomous pattern of branching, the main lateral veins *converge* towards the leaf apex and join the well-defined midvein (see also Höster & Zimmerman 1960 and Höster 1962).

It is a curious fact that although Janchen (1949) fully agreed with Diels's taxonomic conclusions, he made no reference to the highly distinctive venation of *Kingdonia* and *Circaeaster*. His precise assignment of these two genera to the tribe Clematideae in the Ranunculaceae was based on the absence of nectariferous leaves, the uniovulate carpels, and the pendulous ovule. Janchen concluded that because of the form of their leaves (simple or palmately divided) and the herbaceous character of the plants, the subtribe Kingdoniinae comprising *Circaeaster* and *Kingdonia* must be regarded as "a secondarily simplified group, derived from Anemoninae-like ancestors." This speculation, however, is not supported by several of the "unique" features revealed by Junell's (1931) embryological study of *Circaeaster*: (1) the mesogamous course of the pollen tube and (2) the *Adoxa*-type of endosperm development. Although cellular endosperm is characteristic of a number of woody ranalian families (Swamy 1953, Swamy & Bailey 1949), the endosperm in all investigated members of the Ranunculaceae is nuclear in type (Schnarf 1931). In this connection, it should be mentioned that Swamy and Ganapathy (1957) concluded that the "Nuclear-type endosperm is in all probability more advanced than Cellular-type endosperm." If this idea is valid, it is difficult to imagine that the distinctive and very rare *Adoxa*-type of endosperm of *Circaeaster* is the result of phylogenetic derivation from the nuclear type characteristic of the Ranunculaceae as a whole.

When the *totality* of evidence from foliar vasculature, anatomy, inflorescence and flower, and the embryology is weighed and compared, there appears to be no convincing evidence for retaining *Circaeaster* as an "anomalous" genus in any of the families which have just been discussed. On the contrary, I fully agree with Huchinson's (1959) placement of the genus in an independent monotypic family, the Circaeasteraceae, although I cannot accept the major characters he employs to classify this family under the order Berberidales. In his key to the six families which he includes in this order, Hutchinson separates the Circaeasteraceae on the basis of the "single" carpel and the "solitary, axillary" flower. It is difficult to understand why these characters were used and emphasized even in the family description because (1) the number of carpels in *Circaeaster*, as shown by the previous descriptions of Hooker (1890), Oliver (1895), Junell (1931), and Janchen (1949), varies from 1–4 and (2) the flowers of *Circaeaster* are not "solitary in the upper leaf-axils," but are clearly united in fascicles which collectively form a condensed inflorescence. Maximowicz (1881), Bentham and Hooker (1883), and Oliver (1895) all drew attention to the fasciculate arrangement of the flowers of *Circaeaster*. In the material which I have studied, the peripheral fascicles consist of 2–many basally united flowers, each group subtended by a bract while the central fascicle consists of a united group of flowers which are clearly devoid of bracts (FIGS. 30a–d). Thus on the basis of fluctuation in carpel number and the peculiar morphology of the inflorescence, I am forced to disagree with Hutchinson's description and with his suggestion that *Circaeaster* is "a very reduced relative of the Podophyllaceae or Berberidaceae." The systematic affinities of the Circaeasteraceae appear rather to lie within the Ranales (*sensu lato*). But as is true of a number of monotypic ranalian families recently segregated by Bailey and his associates, positive assertions regarding the evolutionary derivation of the Circaeasteraceae from any existing ranalian family would appear premature and highly speculative at present.

In certain morphological respects, *Circaeaster* seems obviously highly reduced and specialized. Its annual and peculiar rosette-habit of growth, markedly condensed stem and inflorescence and its minute flowers all appear to be strongly derivative characters. But the open and often very symmetrical dichotomous venation is a very puzzling character from a phylogenetic standpoint. Is this distinctive and unusual venation "primitive," or is it the result of "reversion" or "reduction" from a more complex type of foliar vasculature? These are difficult questions, comparable to those which have been raised in discussing the significance of open dichotomous venation in *Kingdonia* (Foster 1959, 1961a, 1961b; Foster & Arnott 1960). But if phylogenetic "reduction" is invoked to "explain" the dichotomous venation of *Circaeaster*, it is difficult to understand why this type of vasculature is not frequently encountered in the small leaves of other specialized dicotyledonous herbs. From a brief survey, using clearing techniques, it is evident on the contrary that relatively complex reticulate venation is characteristic of the small leaves of such genera as *Anagallis* (Primulaceae), *Stellaria* (Caryophyllaceae), *Helxine* (Urticaceae), *Oxalis* (Oxalidaceae), and *Dichondra* (Convolvulaceae). Moreover, in the highly specialized genus *Raoulia* (Compositae) in which Solbrig (1960) studied the results of reduction on reticulate venation patterns, the "open" venation found in a few species is highly irregular in type and quite unlike the dichotomous venation of *Circaeaster*.

In conclusion, it must be emphasized that remarkably few examples of vein anastomoses were found in the present survey of *Circaeaster* (FIGS. 28, 29). Their sporadic occurrence and elemental nature throw no light on the problem of the phylogenetic origin of the dichotomous venation. Likewise, the blind vein endings which were discovered, clearly seem to represent the incompletely developed branches of dichotomized veins and hence do not appear to be "vestiges" of a former reticulate venation pattern (FIGS. 23–26). Possibly the striking resemblances between the dichotomous venation patterns of *Circaeaster* and *Kingdonia* are the result of parallel evolution from an ancient and primitive type of angiospermic vasculature. At any event, it is interesting — and perhaps more than coincidental — that the only known authentic examples of open dichotomous venation in the angiosperms occur in two relic genera which grow in comparable environments in the high montane areas of western and southwestern China (see map, FIG. 1). The future comparative study of other herbaceous ranalian dicotyledons in this part of Asia may well yield results of considerable taxonomic and morphological significance.

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EXPLANATION OF PLATES

PLATE I

FIG. 5. *Wang 65301* (A). Cleared leaf, photographed with dark-field illumination, showing the very symmetrical type of open dichotomous venation which frequently occurs in *Circaeaster.* Note especially the gradual separation of the two xylem strands below the dichotomy of the central vein.

PLATE II

FIGS. 6–14. Venation of the cotyledon and various types of primary leaves in *Circaeaster.* 6–11, *Polunin, Sykes & Williams 3412* (BM), foliar sequence in one plant beginning with the univeined cotyledon (FIG. 6) and showing progressive elaboration of dichotomous venation in the primary leaves (FIGS. 7–9) and successive adult leaf types (FIGS. 10 and 11); 12 and 13, *Wang 66252* (A), primary leaves from same plant showing derivation of mid-vein from basal vein dichotomy. 14, *Wang 65301* (A), details of petiolar vasculature of a primary leaf showing origin of mid-vein from union of central branches of two dichotomized xylem strands. Drawing made from cleared leaf photographed with dark-field illumination.

PLATE III

FIGS. 15–22. Examples of very symmetrical patterns of dichotomous venation in *Circaeaster*, arranged in the order of increasing number of marginal vein-endings. The scale indicates the wide range in size of these leaves. 15–17, *Liu 10678* (WUK), three successive leaves from same plant, illustrating marked regularity of all basal vein-dichotomies. 18, *Junell s.n.* (P), a leaf with 13 vein-endings, from the plant shown in FIG. 3. 19, *Liu 10678* (WUK), a leaf with 14 vein-endings. 20, *Harry Smith 4141* (S), a leaf with 17 vein-endings. 21 and 22, *Soulié 355* (K), two leaves from same plant with respectively 19 and 20 marginal vein-endings. Note short central blind vein-ending in FIG. 22.

PLATE IV

FIGS. 23–29. Leaves with blind vein-endings or anastomoses. 23, *Stainton, Sykes & Williams 6182* (BM), primary leaf with single lateral blind vein-ending. 24, *Liu 10678* (WUK), leaf with symmetrical dichotomous venation and a single central blind vein-ending. 25, *Stainton, Sykes, & Williams 6182* (BM), leaf with two lateral and one central blind vein-endings. 26, *The same*, leaf with four blind vein-endings; 27, *The same*, leaf showing close approximation of two adjacent veins. 28, *The same*, leaf with anastomosis at left. 29, *Forrest 118* (K), leaf with anastomosis connecting two veins at right.

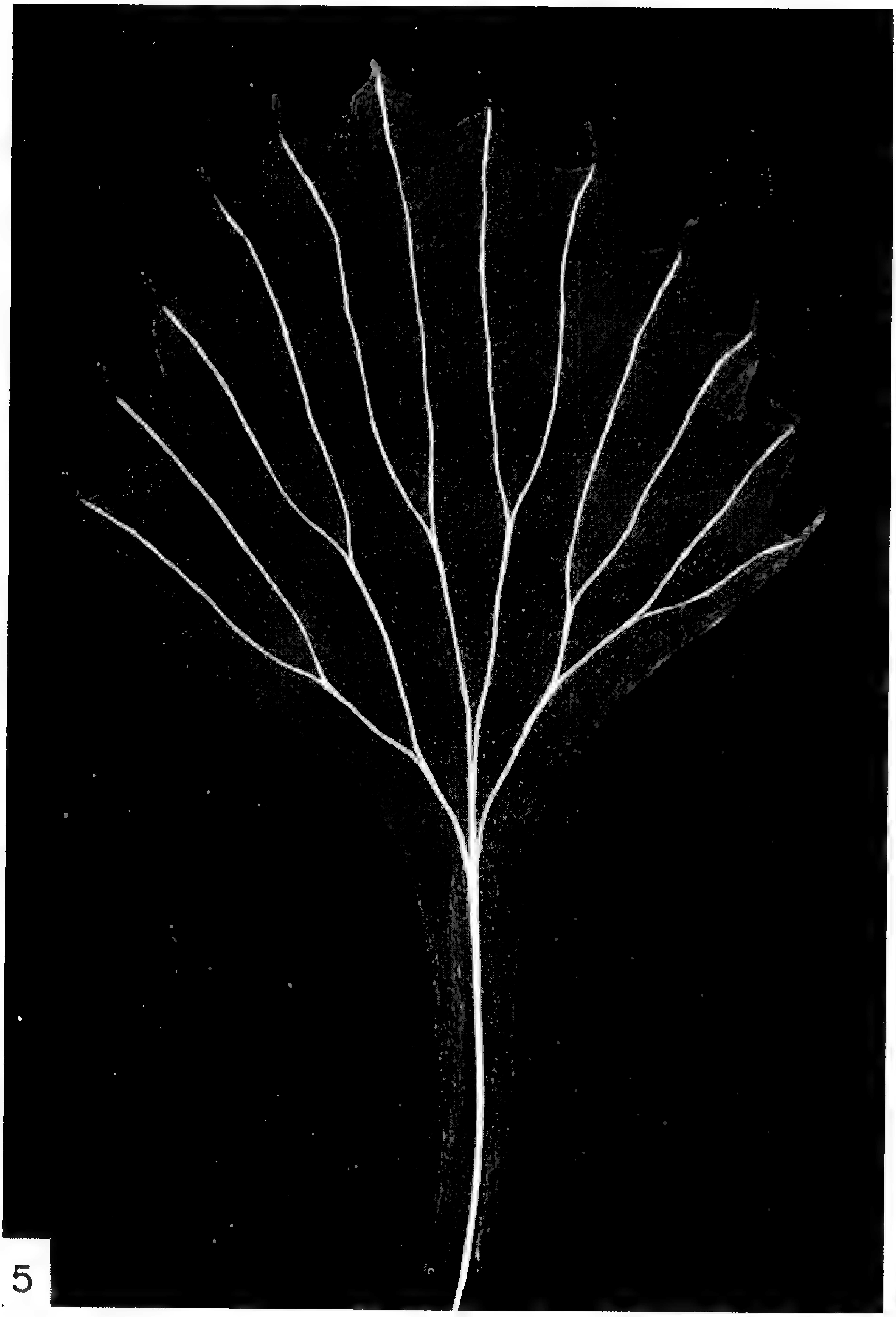
PLATE V

FIGS. 30 a–d. Semidiagrammatic transections of a flowering specimen of *Circaeaster* (*Soulié 355*, P) showing the cotyledons, leaves (L) and the inflorescence. The intervals between FIGURES a and b, b and c, and c and d are respectively 16 μ, 144 μ and 248 μ. The flowers in each of the five peripheral fascicles are designated by arabic numerals corresponding to the numbers of their subtending bracts (B1–B5). The five central ebracteate flowers are indicated by roman numerals (I–V). Note that the xylem (shown in black) in the petiolar bundles usually consists of two closely spaced strands.

Abbreviations for the organs of individual flowers shown in c and d: T, tepal; S, stamen; C, carpel.

PLATE VI

FIGS. 31–35. Morphology of the flower and fruit of *Circaeaster*. Vasculature in all figures shown diagrammatically by broken lines. 31, *Wang 65930* (A), at right a fascicle of 3 flowers, the largest consisting of an elongated pedicel, 2 tepals, 2 stamens, and 2 young glabrous carpels; the arrow indicates an enlarged view of the sessile, papillate stigma of one of the carpels. 32, *The same*, older stage of a bicarpellate flower showing the dorsal (left) and ventral (right) veins of the larger carpel and the initiation of hairs. 33, *Polunin, Sykes & Williams 4653* (BM), a trimerous flower consisting of 3 tepals, 3 stamens, and 3 carpels; note young hairs. 34–35, *Wang 65930* (A), young fruits showing the typical and profuse uncinate hairs; note persistence of stamens with dehiscent anthers. C, carpel; H, hair, P, pollen grain; S, stamen; T, tepal.



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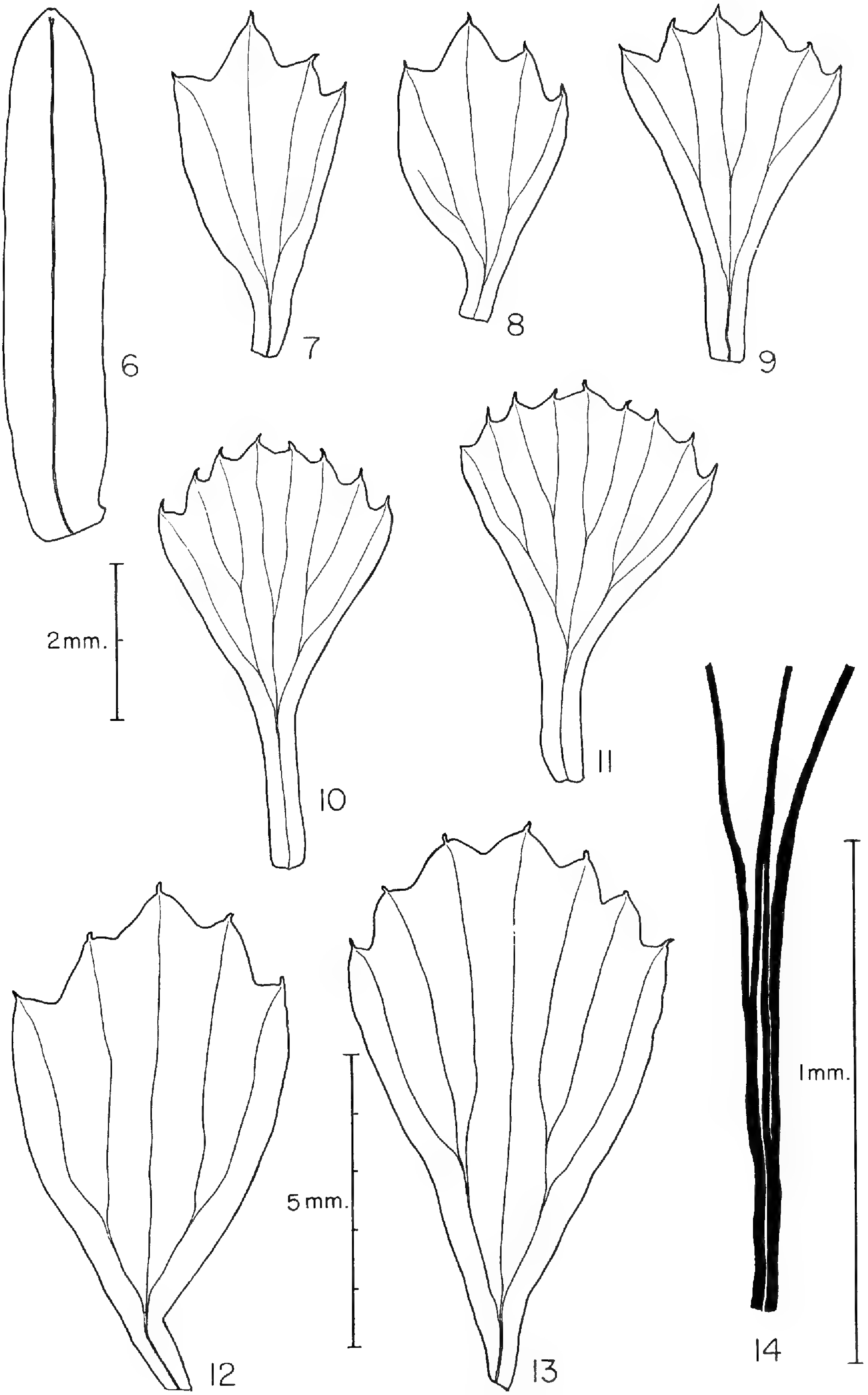
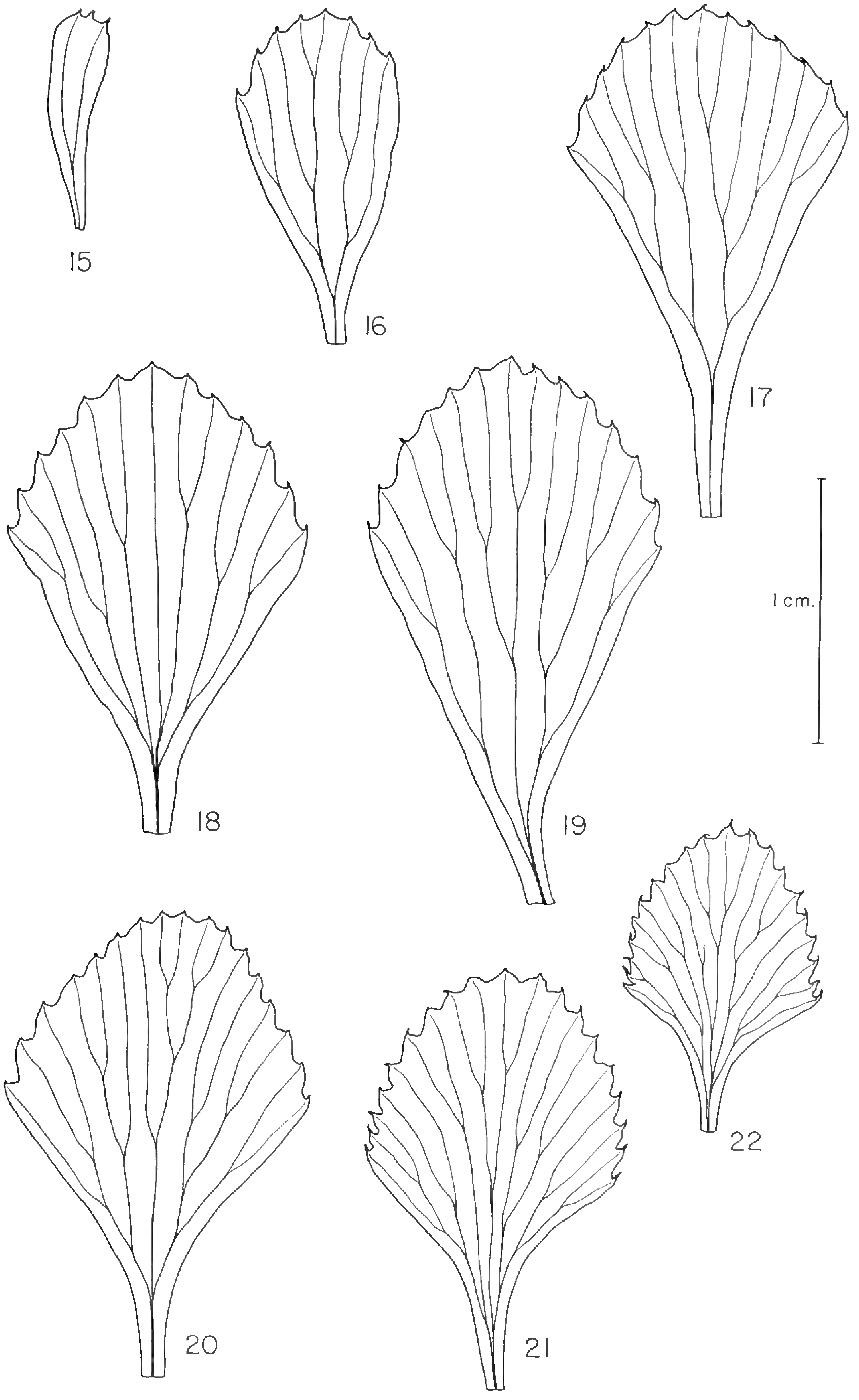
Foster, Circaeaster



FOSTER, CIRCAEASTER

PLATE III



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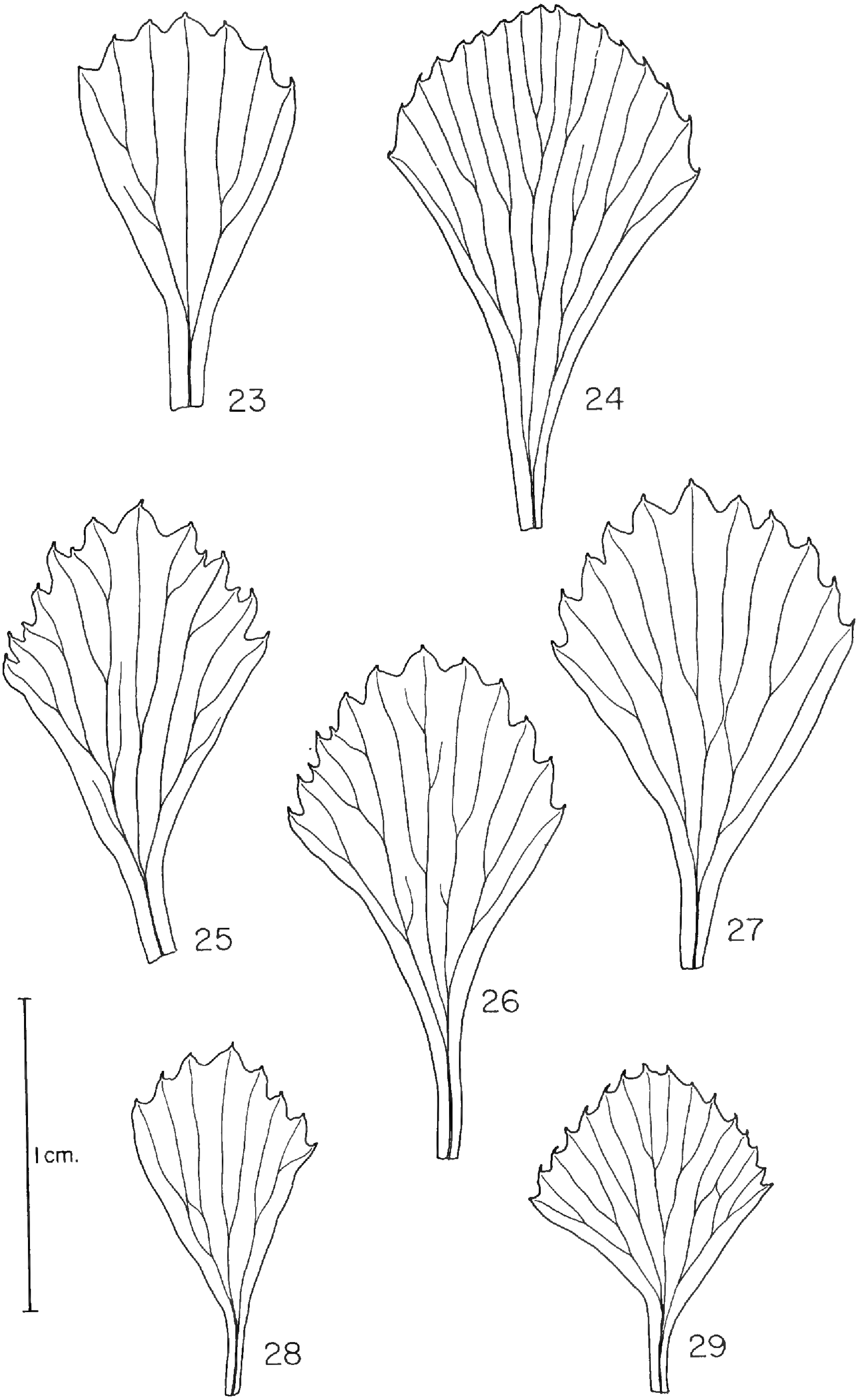

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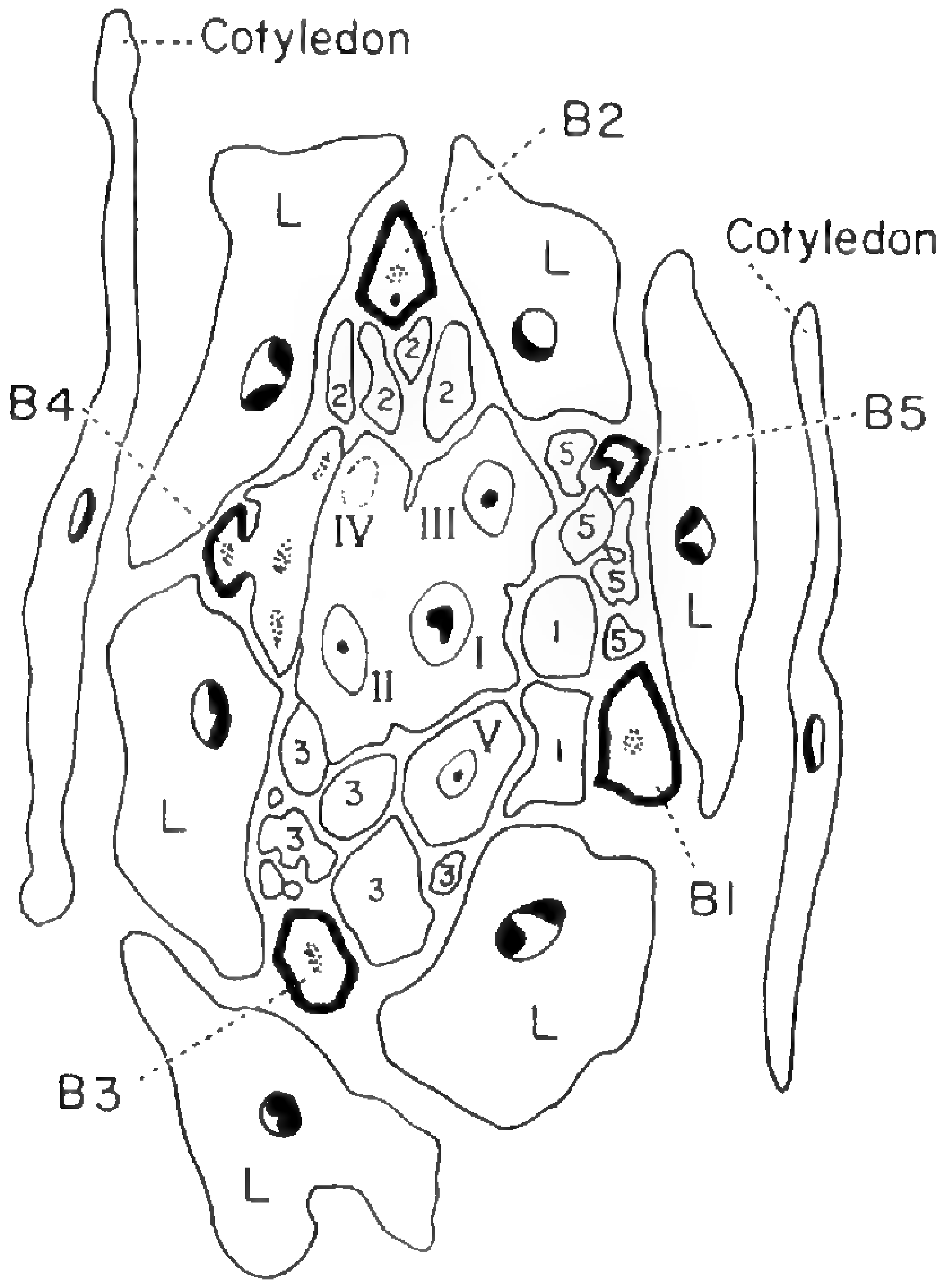

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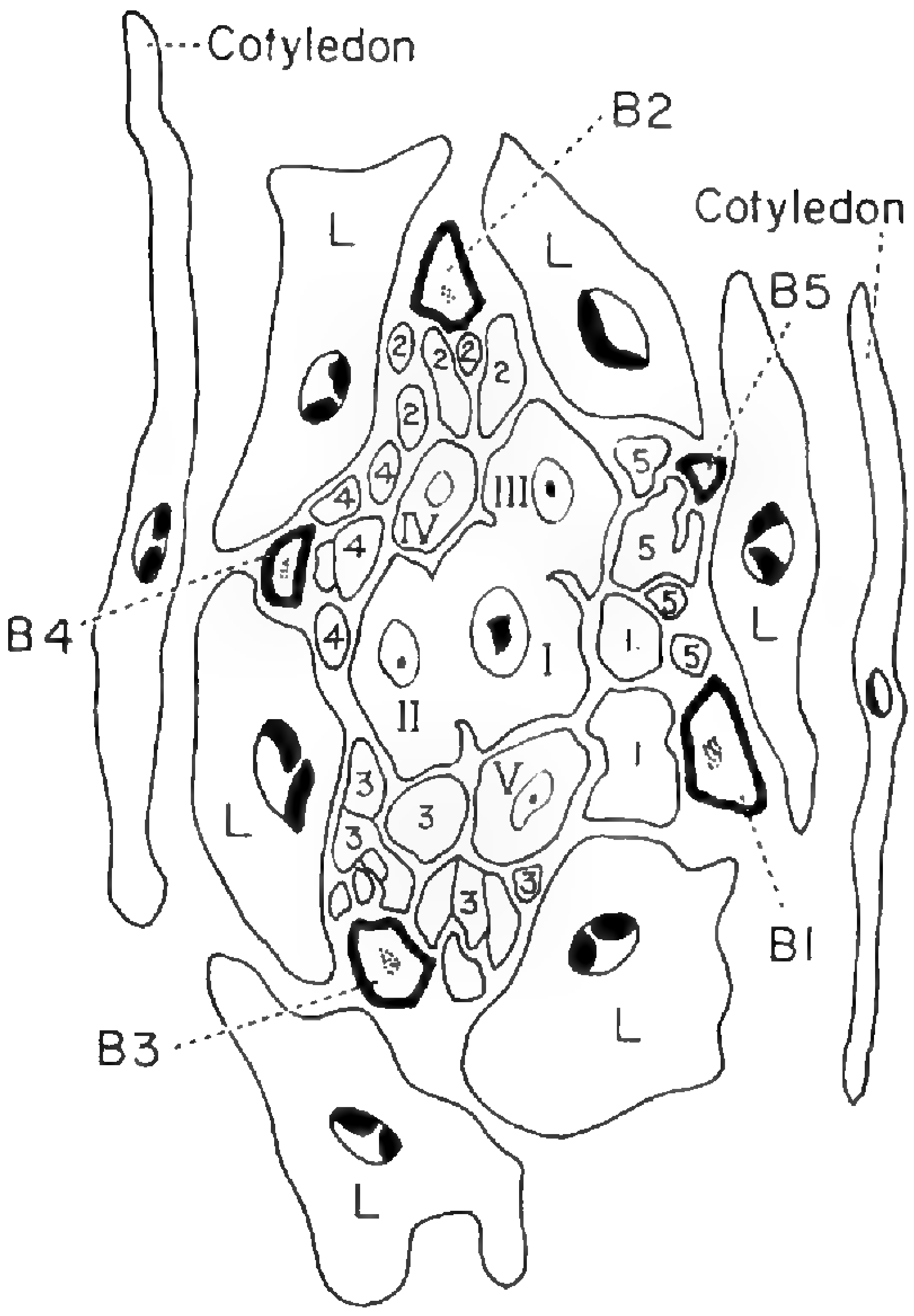

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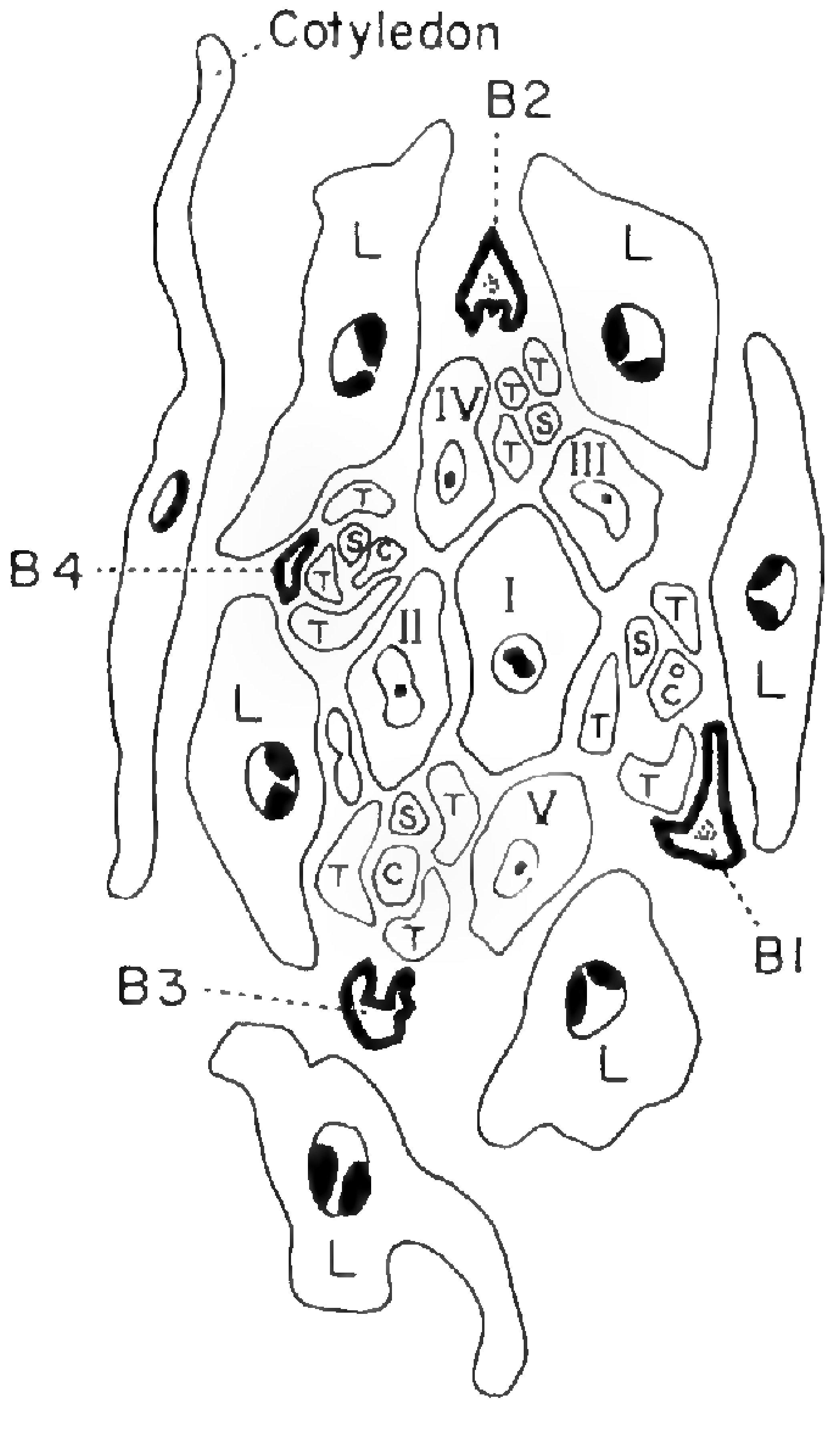

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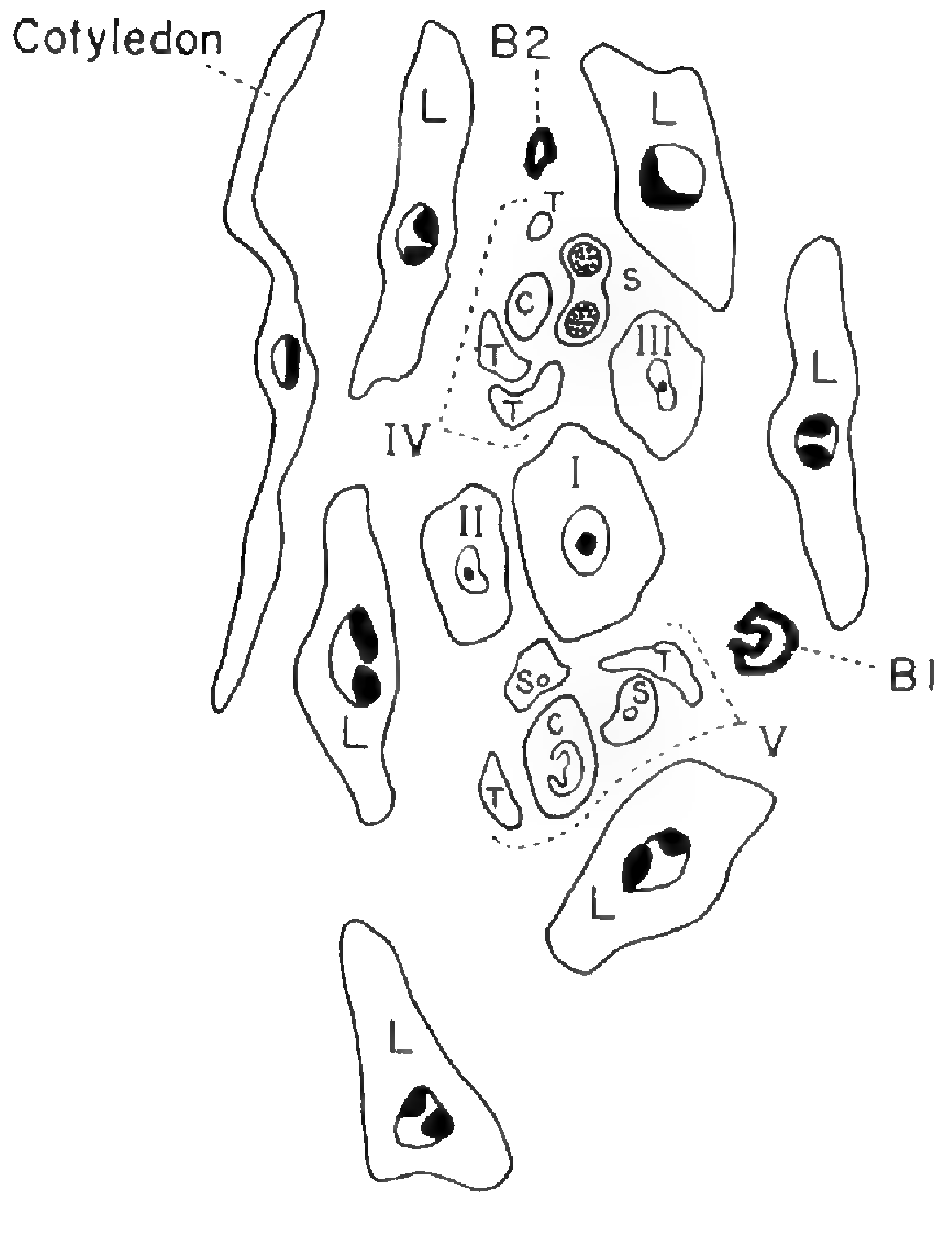

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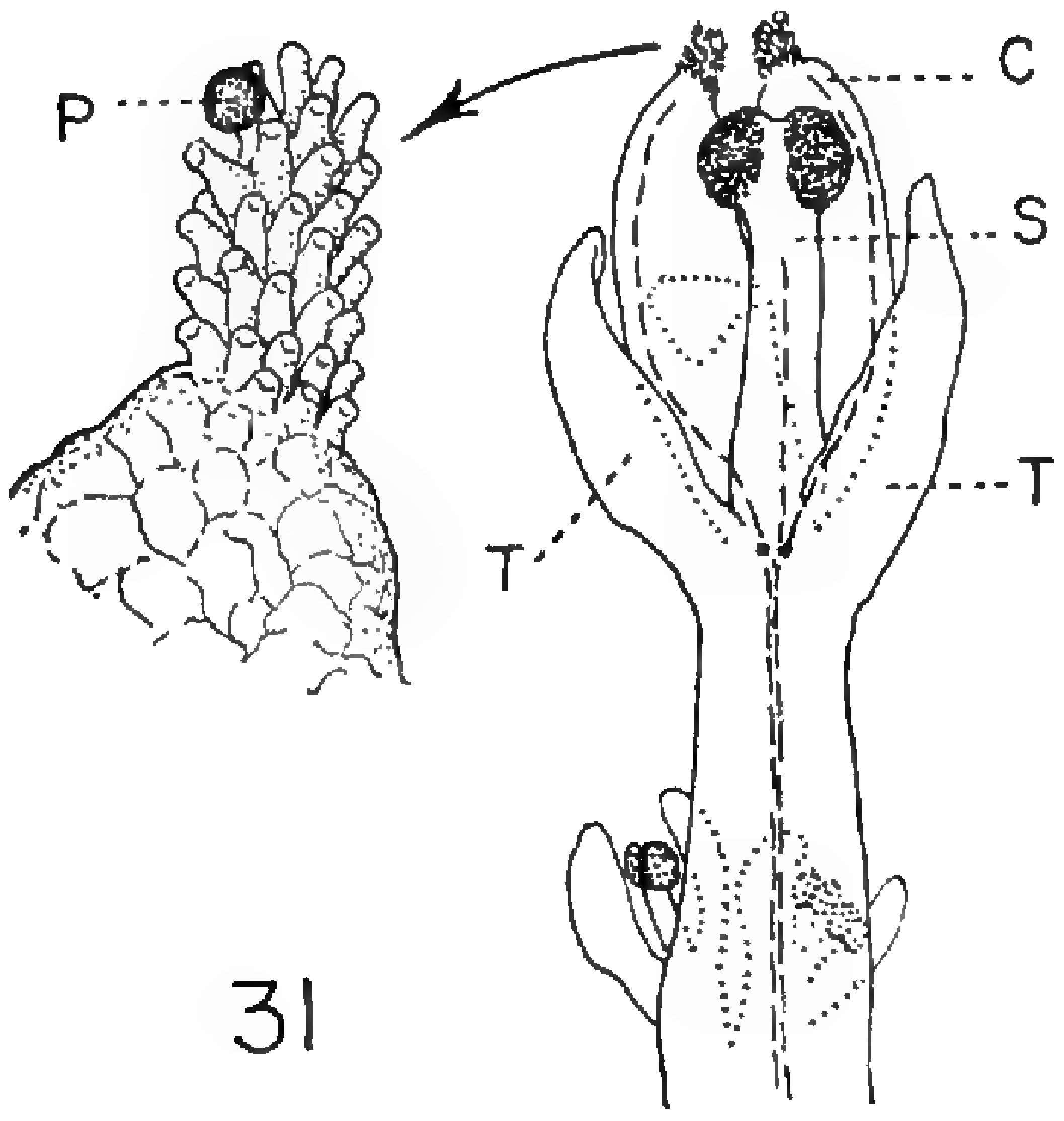
Foster, Circaeaster



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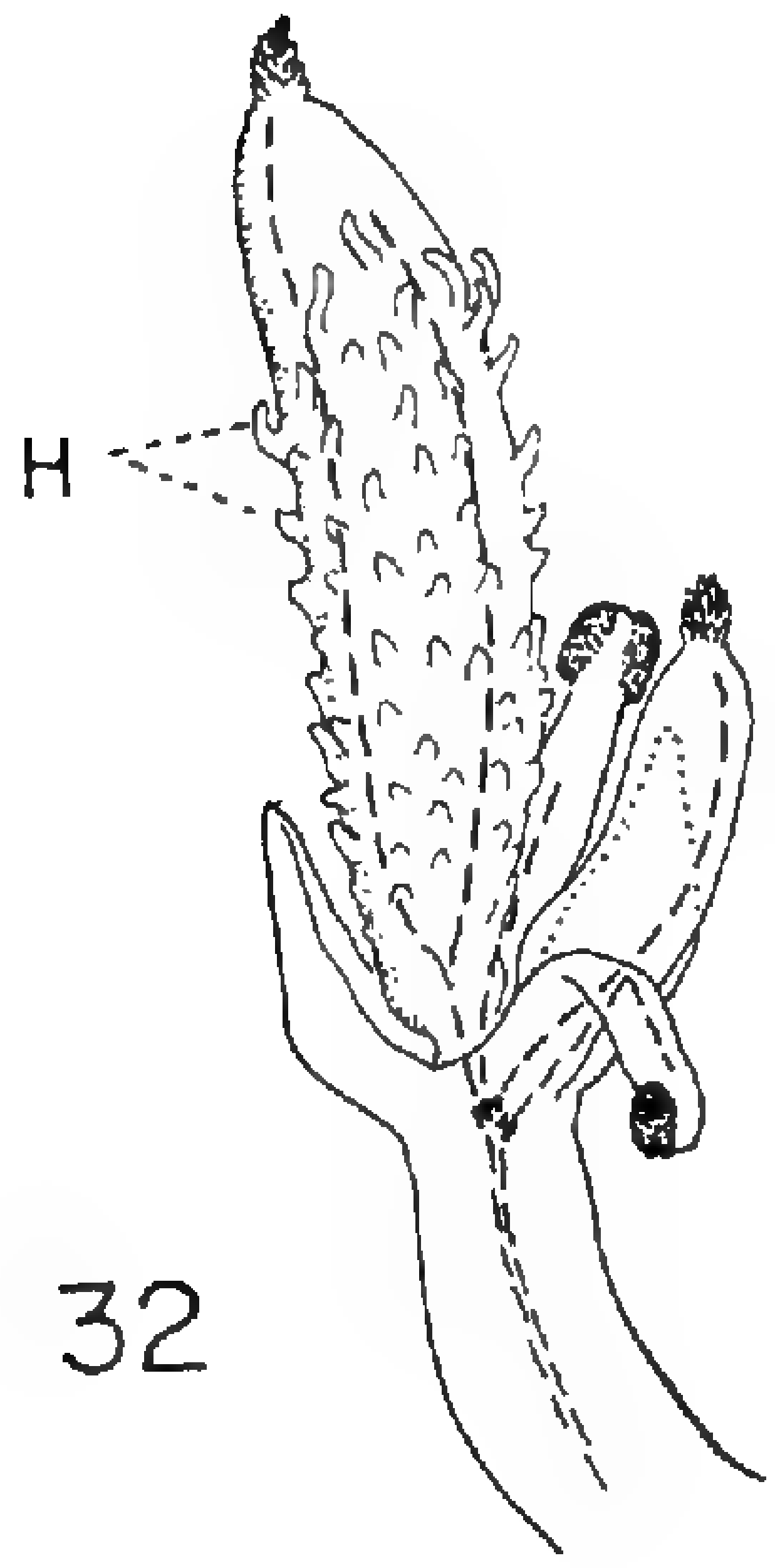

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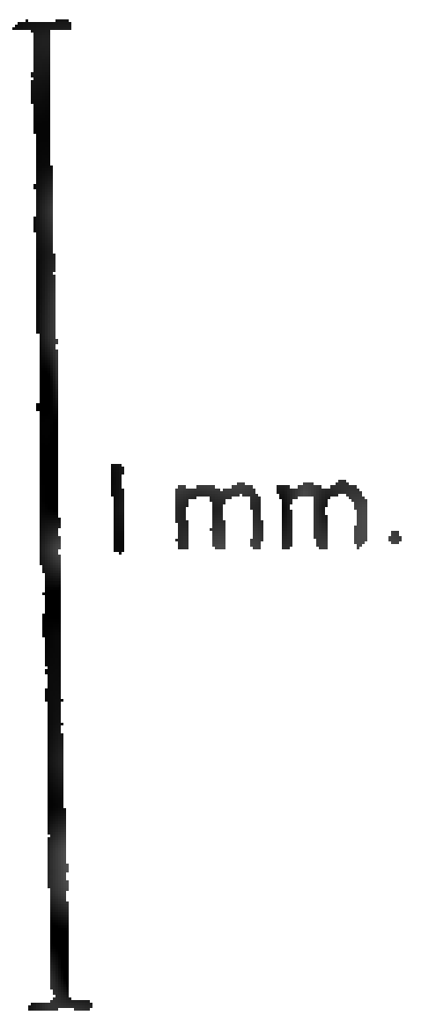

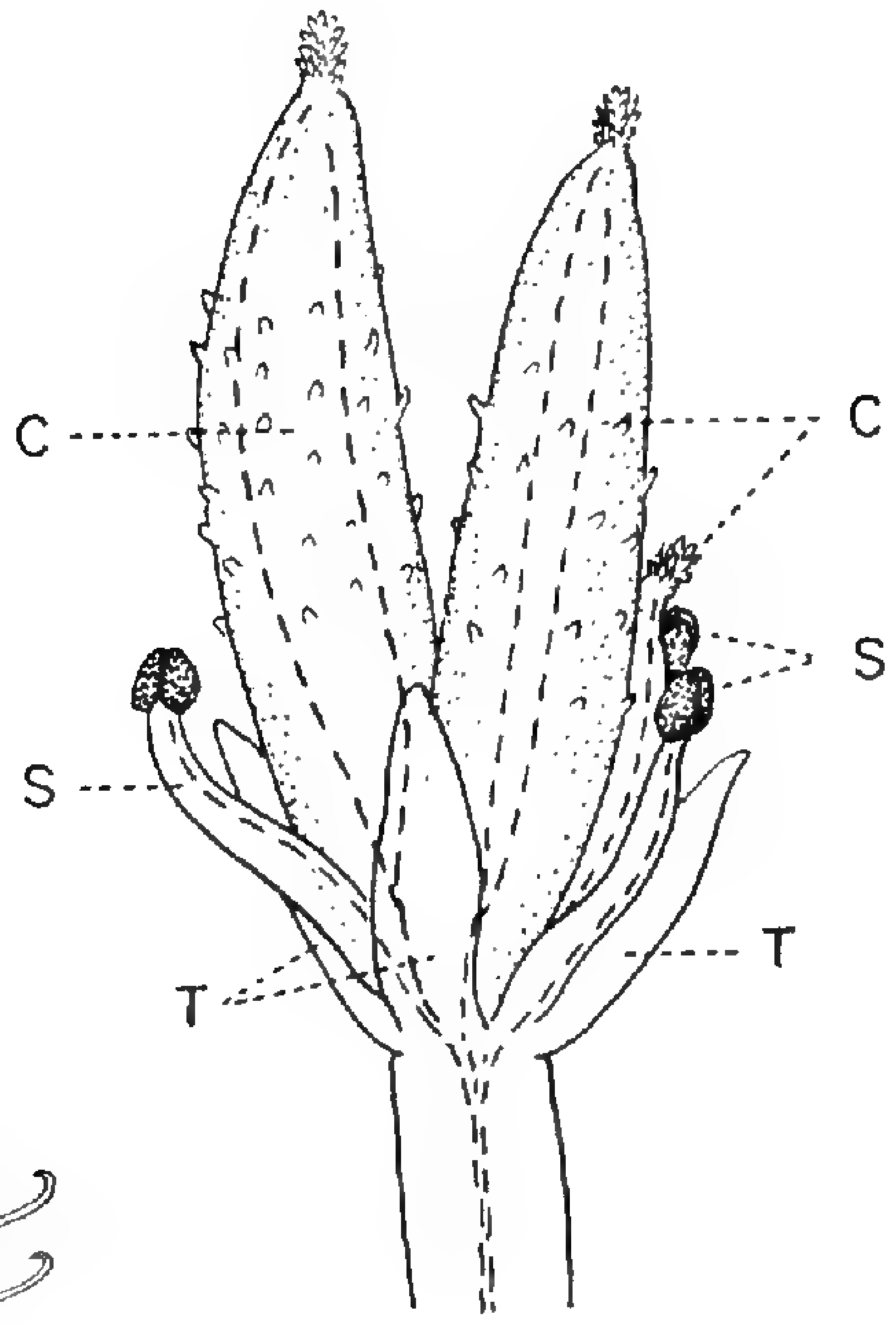

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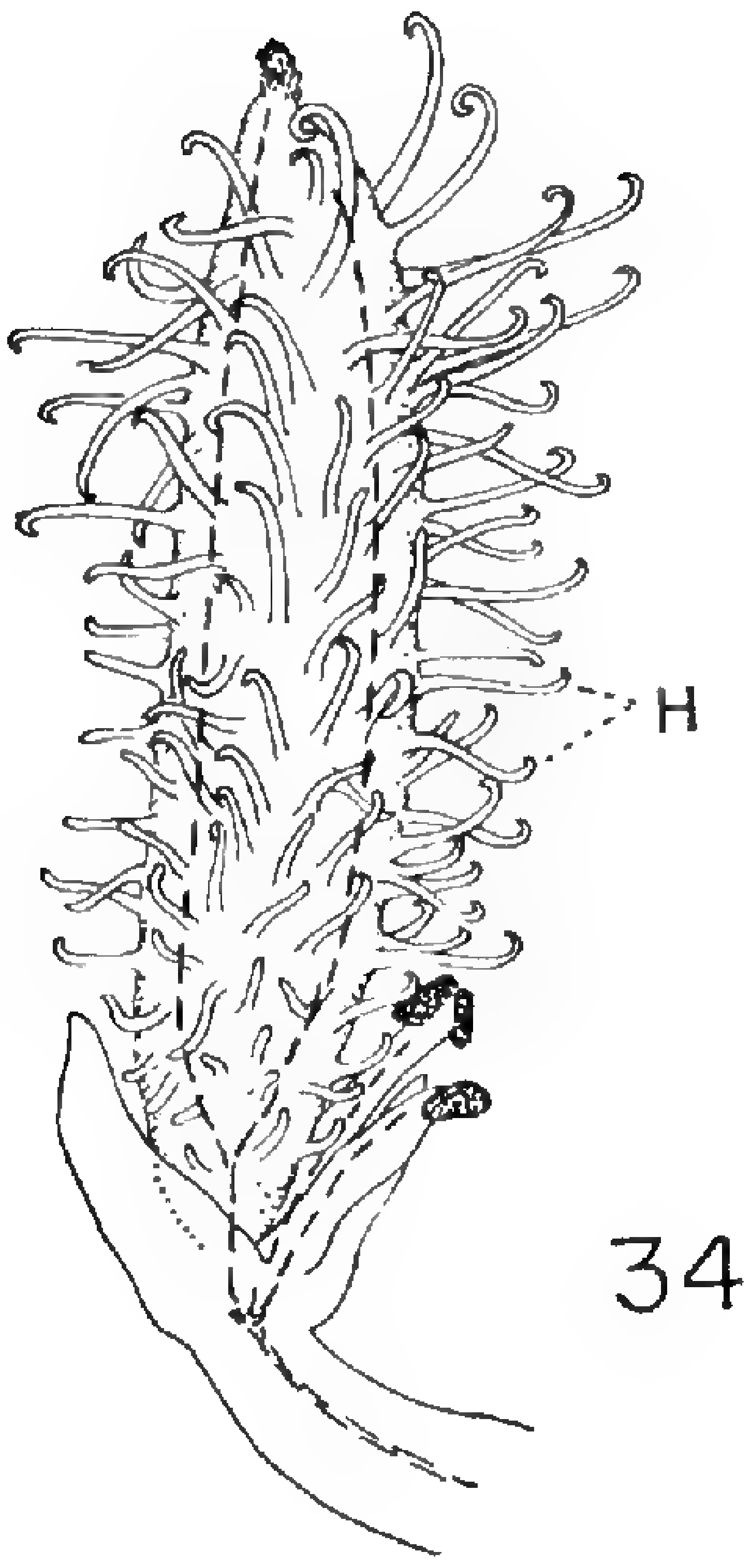

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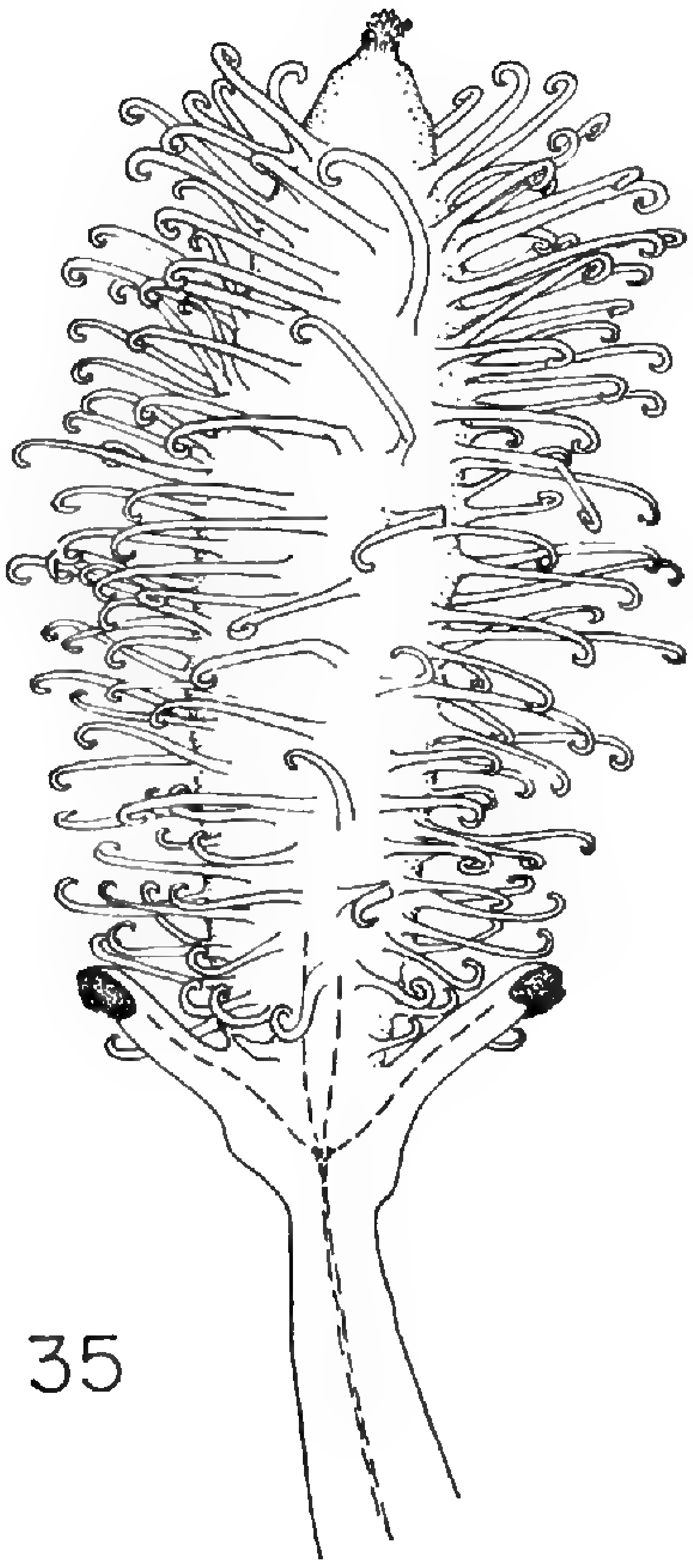

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Foster, Circaeaster

MORPHOLOGICAL AND PALEOBOTANICAL STUDIES OF THE NYSSACEAE, II

THE FOSSIL RECORD

RICHARD H. EYDE AND ELSO S. BARGHOORN

AN EARLIER PAPER by the first author (Eyde, 1963) dealt with the distribution and the distinguishing characteristics of modern species of Nyssaceae and placed special emphasis on the comparative morphology of nyssaceous fruits. In the present paper, we shall take up the fossil record of the family, applying critical comments based on our studies of modern Nyssaceae whenever possible. Although in our own research we have been primarily concerned with structural features of the fruits, we have also included here a review of reports of other fossil remains — leaves, pollen, and wood — that have appeared in recent years. It is hoped that the present work will serve as a useful supplement to Kirchheimer's detailed monograph (1938) on fossil Nyssaceae.

Convincing nyssaceous fossils are not presently known from horizons below the Tertiary. The Jurassic "pollen" designated as "cf. *Nyssa*" by Reissinger (1950, Pl. XIII, figs. 11 a & b) is probably a tetrad of spores; in any case, the comparison with *Nyssa* cannot be taken seriously. Cretaceous leaf impressions that were assigned to *Nyssa* in some of the older works (Kirchheimer, 1938, pp. 119–123) are mostly poorly preserved specimens, and in view of the lack of striking identifying features in the leaves of modern *Nyssa*, these fossils can hardly be considered as evidence for the occurrence of the genus. The same comment may be made regarding a single incomplete leaf impression from the Cretaceous of Texas described by MacNeal (1958) as *N. woodbinensis*. Dorf (1942, pp. 29 & 78) compared the Cretaceous "seeds" *Carpites walcottii* with *Nyssa aquatica*. Judging from Dorf's illustrations (Pl. 19, figs. 1 & 2), however, the resemblance is very remote. *Carpites walcottii* apparently lacks a germination valve, and the apical projections found on this fossil have no counterpart in bona fide remains of *Nyssa*. Recently Samylina (1961) compared some ribbed fruits (?) from the Lower Cretaceous of the Maritime Territory, U. S. S. R., with fruits of *Nyssa*, applying the names *Nyssidium orientale* and *Nyssidium* sp. to her fossils. Samylina's comparison is based on a fancied resemblance between the nyssaceous germination valve and an unsculptured region at one end of each *Nyssidium* specimen. In fruits of Nyssaceae, however, major external ridges and grooves pass over the entire stone, including the germination valve. The fact remains that we have no knowledge of the Mesozoic antecedents of *Nyssa*.

TERTIARY LEAVES

All of the supposedly nyssaceous leaf remains found in Tertiary deposits have been compared to *Nyssa* with one exception: Johnson (1937) described several impressions taken from Eocene beds of the Isle of Mull as *Davidioidea hebridica* because of their resemblance to leaves of modern *Davidia*. The first author recently saw some of these fossils on display in the British Museum (Nat. Hist.), London, and will confirm the general similarity to *Davidia*. However, as Kirchheimer noted (1938, p. 117), comparable leaves are also found in *Tilia*; therefore, these fragments can hardly be taken as proof that an ancient davidioid tree once grew in Scotland.

The name *Nyssa* has been applied to numerous Tertiary leaf impressions collected in the northern hemisphere during the past hundred years. In many cases the impressions are incomplete and details are not preserved. Even when preservation is good, it is difficult to establish the occurrence of the genus from the leaves alone, for most *Nyssa* foliage is without conspicuous identifying features. Kirchheimer has observed that leaves and leaflets resembling entire-margined leaves of *Nyssa* may be found in genera of Annonaceae, Moraceae, Juglandaceae, Fagaceae, Magnoliaceae, Lauraceae, Sapindaceae, Ebenaceae and Apocynaceae (1938, p. 78). On the other hand, some of the reports of *Nyssa* currently appearing in paleobotanical literature not only are based on well-preserved leaf impressions but also are supported by associated nyssoid pollen or fruits and by the remains of other plants that would be found today associated in a *Nyssa-Taxodium* swamp.

Kirchheimer catalogued very meticulously the fossil leaves attributed to *Nyssa* in literature published prior to 1938; therefore, we shall mention only those that have been reported since that date. The name *N. europaea*, originally published by Unger in 1845, has been applied during the past decade to leaf remains from the Miocene of Poland (Kownas, 1955) and to Pliocene impressions from Georgian S. S. R. (Kolakovskiy, 1957) and from the Vienna Basin (Berger, 1952). A new name, *N. rottensis*, was applied by Weyland (1941) to leaves collected in Oligocene beds of Germany; subsequently this name was treated as a synonym of *N. europaea* Ung. by Kownas (1955). Other new names that have been assigned to supposedly nyssoid leaf impressions by European authors are *N. zaisanica* Grubov (*in* Krishtofovich, 1956), based on Oligocene material collected near Lake Zaysan in Kazakhstan, and *N. hungarica* Andreánszky (1959), based on a specimen from the Sarmatian beds of northern Hungary. Andreánszky's fossil has been compared with the foliage of modern *N. aquatica* because of its size and its coarsely serrated margin. Johnson (1941) used the name *N. elliptica* in describing a leaf imprint from presumably Oligocene sediments of County Tyrone, Northern Ireland, but the very brief description is unaccompanied by an illustration; consequently, Johnson's name has no validity under the International Code of Botanical Nomenclature. Krishtofovich and Baykovskaya referred to a leaf imprint

(1951, Pl. VI, fig. 2) found in Miocene deposits of the Donets Basin simply as "*Nyssa* sp.", and Pantić (1956) listed *Nyssa* as a constituent of a lower Miocene leaf-florule in Yugoslavia.

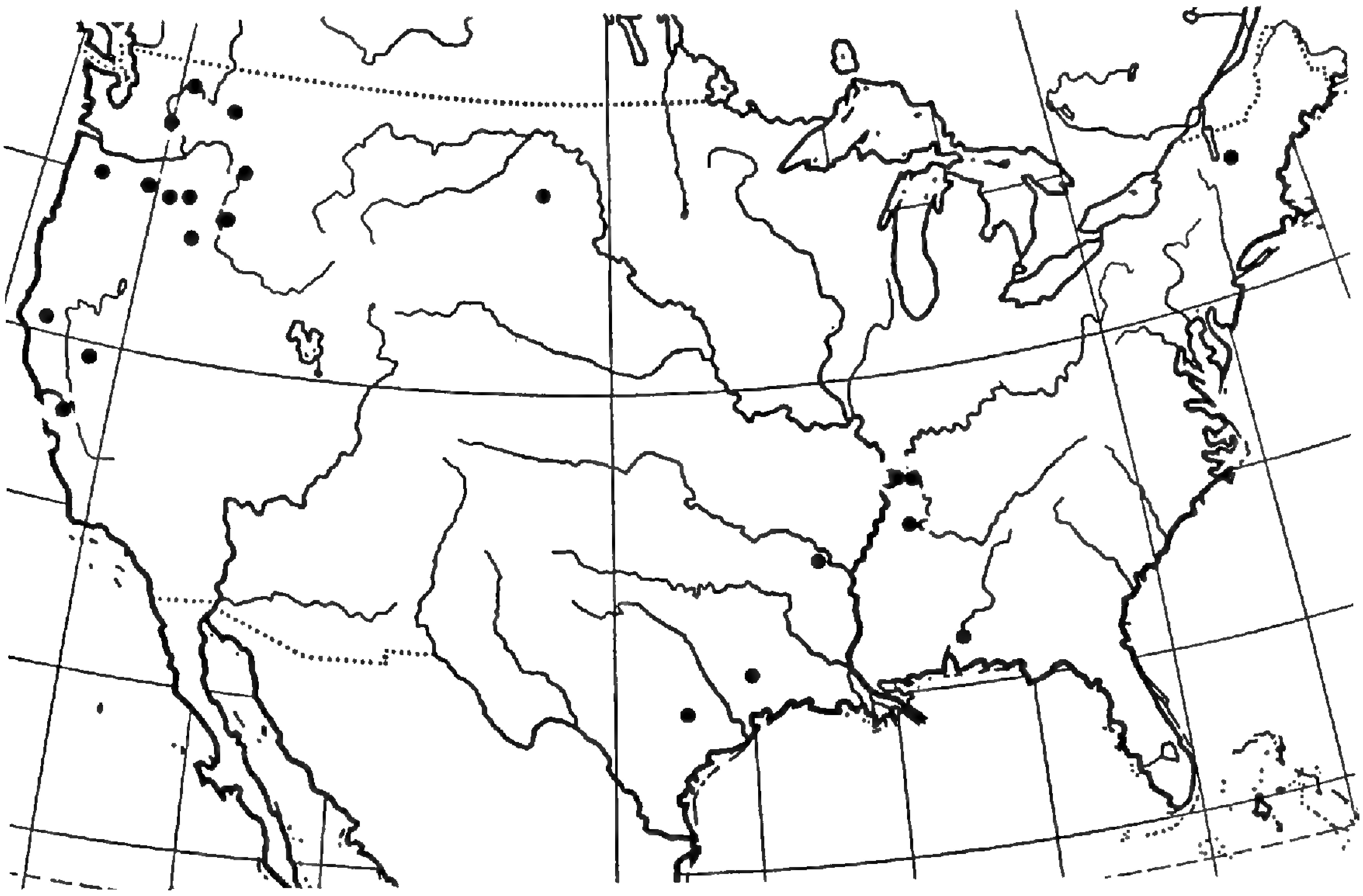
Probably the most reliable of all the European reports is that of Kräusel and Weyland (1954), who based their identification on a microscopic comparison between epidermal cells of modern *Nyssa* leaves and leaves obtained from Oligocene beds of East Germany.

Leaf impressions that are presumably referable to *Nyssa* have been reported frequently from Tertiary deposits of the western United States. Chaney and Axelrod (1959) simplified the treatment of these remains by combining many specimens from different horizons and localities into two fossil species, *N. copeana* (Lesq.) Chaney & Axelrod and *N. hesperia* Berry. The first of these species includes leaves formerly referred to *N. elaenoides* Lesq. (Condit, 1944; Axelrod, 1944), *N. oregonensis* Smith (1938), and to other genera as well. The closest modern equivalent is said to be *N. sylvatica*. The name *N. hesperia* was originally applied by Berry (1931) to fruits preserved as casts in the Latah formation at Spokane, Washington. Chaney and Axelrod follow the broadened usage begun by Brown (1937b, 1946) in assigning many of the leaves previously called *N. knowltonii* to *N. hesperia*. According to these authors, the fruits resemble markedly those of modern *N. aquatica*.

We find that the similarity between *Nyssa hesperia* and *N. aquatica* has been overstated. The fossil fruits from Spokane are in fact morphologically similar to fruits of the *N. sylvatica* alliance, a point which will be taken up in another section of this paper. Admittedly, the venation of the fossil leaves figured by Brown (1937a, Pl. 62, figs. 1–3; especially fig. 3) is matched in leaves of *N. aquatica*. However, the coarse, subapical teeth that Brown took to indicate a relationship with *N. aquatica* are not comparable in position to the more basally situated teeth sometimes found on the leaf-margins of this species. (Teeth are occasionally present on leaves of *N. ogeche* and *N. sylvatica* as well, but we have never seen a leaf of any species of *Nyssa* on which the teeth were located only near the apex.)

Other American leaf impressions were described by MacGinitie (1941, p. 152) as *Nyssa californica*. These leaves were found in the Eocene Chalk Bluffs flora of California along with nyssoid fruits. MacGinitie compared the leaves with modern *N. sylvatica* and included both organs under one specific name, citing a fruit as the holotype (Pl. 40, fig. 4). More recently, Becker (1961) designated leaf impressions from the Oligocene Ruby River flora as *N. crenata*, a name originally coined by Chaney (1920). Smiley (1961, p. 177) mentions *Nyssa* as a member of the Mio-Pliocene Ellensburg flora; however, his systematic treatment has not been published at the time of this writing.

Brown's posthumous work on the Paleocene flora of the Rocky Mountains and Great Plains (1962) includes the new combination *Nyssa alata* (Ward) Brown and a new species, *N. borealis*. The names are applied to fossils resembling modern leaves of *N. sylvatica* and *N. aquatica*, respectively.



MAP. 1. Reports of Tertiary Nyssaceae in North America (fruits, pollen, wood). Copyright, Rand McNally Co.

TABLE I and the distribution maps (MAPS 1–3) do not include records based only on leaf impressions, because such records are often doubtful or completely worthless. However, when leaves resembling *Nyssa* have been reported in association with nyssoid pollen or fruits, this fact has been noted in TABLE I.

TERTIARY POLLEN

The tricolporate pollen grains of modern Nyssaceae have been described by Wodehouse (1935, 1942), Erdtman (1952), and Chao (1954), and by a number of other workers who have had occasion to examine modern pollen in connection with their fossil studies. Among the latter are Ingwersen, who presented a very detailed description (1954, pp. 58–60), and Traverse (1955), who offered observations on the Asiatic nyssas, which are not included in most works. The pollen of *Camptotheca* is said to be very similar to that of *Nyssa*, and the two would not be readily separable in the fossil condition. According to Erdtman (1952), *Davidia* pollen differs morphologically from the pollen of other nyssaceous species; according to Chao (1954, p. 99), however, there are no significant morphological differences between nyssoid and davidioid pollen.

Pollen grains of modern *Nyssa sylvatica* measured by Macko (1959) were 29 μ and 31 μ in diameter; the average polar diameter obtained by Chao (1954) from this same species was 45.9 μ. Almost all of the published measurements obtained from any modern nyssaceous species would fall between these two extremes; however, *Davidia* pollen is said to be somewhat smaller (Erdtman, 1952), and the diameter of *N. ogeche* pollen has been reported as 51 μ (Wodehouse, 1942). The latter report is of interest because large fossil forms have been reported by several authors, e.g., *Nyssa ingentipollinia* Traverse (1955), *Nyssoidites rodderensis* Thiergart (Potonié, 1960), and *Nyssa* f. *magna* (Doktorowicz-Hrebnicka, 1957a). This suggests that a careful comparative study of fossil and modern *Nyssa* pollen might enable one to infer affinities below the generic level. It should be added in passing that some of the fossil pollen that has been assigned to Nyssaceae is smaller than pollen of the modern species. Pokrovskaya (1956b, pp. 200, 201) figures grains as small as 16.5 μ in diameter.

Nomenclatural treatment of fossil pollen grains differs widely from author to author, some workers favoring a natural system, others a "half-natural" system, still others a completely artificial system. Thus, nyssoid pollen grains have been recorded as *Nyssa*, as *Nyssapollenites*, and *Nyssoidites* (Potonié, 1960), and as *Tricolporopollenites* (Thomson & Pflug, 1953). Many authors elect not to coin specific epithets for fossil pollen and simply report "*Nyssa* sp.," appending numerical subscripts (Pokrovskaya, 1956a, p. 351) or letters, etc., when the nyssoid pollen can be subdivided on the basis of size or of minor morphological features. Other authors treat the microfossils in the same manner as macroscopic remains, assigning binomials according to the International Code of Botanical Nomenclature. For instance, the names *Nyssa neshobensis*, *N. thompsoniana*, and *N. ingentipollinia* were given by Traverse (1955) to exines found in the Brandon lignite. In the system originated by Thomson and Pflug, the binomial *Tricolporopollenites kruschii* R. Pot. is applied to exines with the same morphological characteristics as modern nyssaceous pollen, and variants in size and minor features are indicated as "subspecies": *T. kruschii* subsp. *analepticus* R. Pot., *T. kruschii* subsp. *triangularis* Stanley, etc.

As a result of the rapid world-wide increase in palynological research during the past two decades, nyssaceous pollen has been collected from a great many localities in Europe, Asia, and North America and from all Tertiary horizons, Paleocene through Pliocene. Some localities have yielded only a single questionable exine, but in others (e.g., Raukopf, 1959, p. 17) the nyssoid grains constitute more than 10 per cent of the arboreal pollen.[1] Localities from which nyssaceous pollen has been recorded are listed in TABLE I. We have not attempted a critical evaluation of each report, because in many cases there is no accompanying illustration. Most of the European records are supported by associated fruit-remains, by paleoecological evidence, and by the opinions of distinguished palynologists. On the other hand, Kirchheimer (1938, p. 133) and Thomson (1954, p. 337) have mentioned the possibility of confusing the smaller nyssoid

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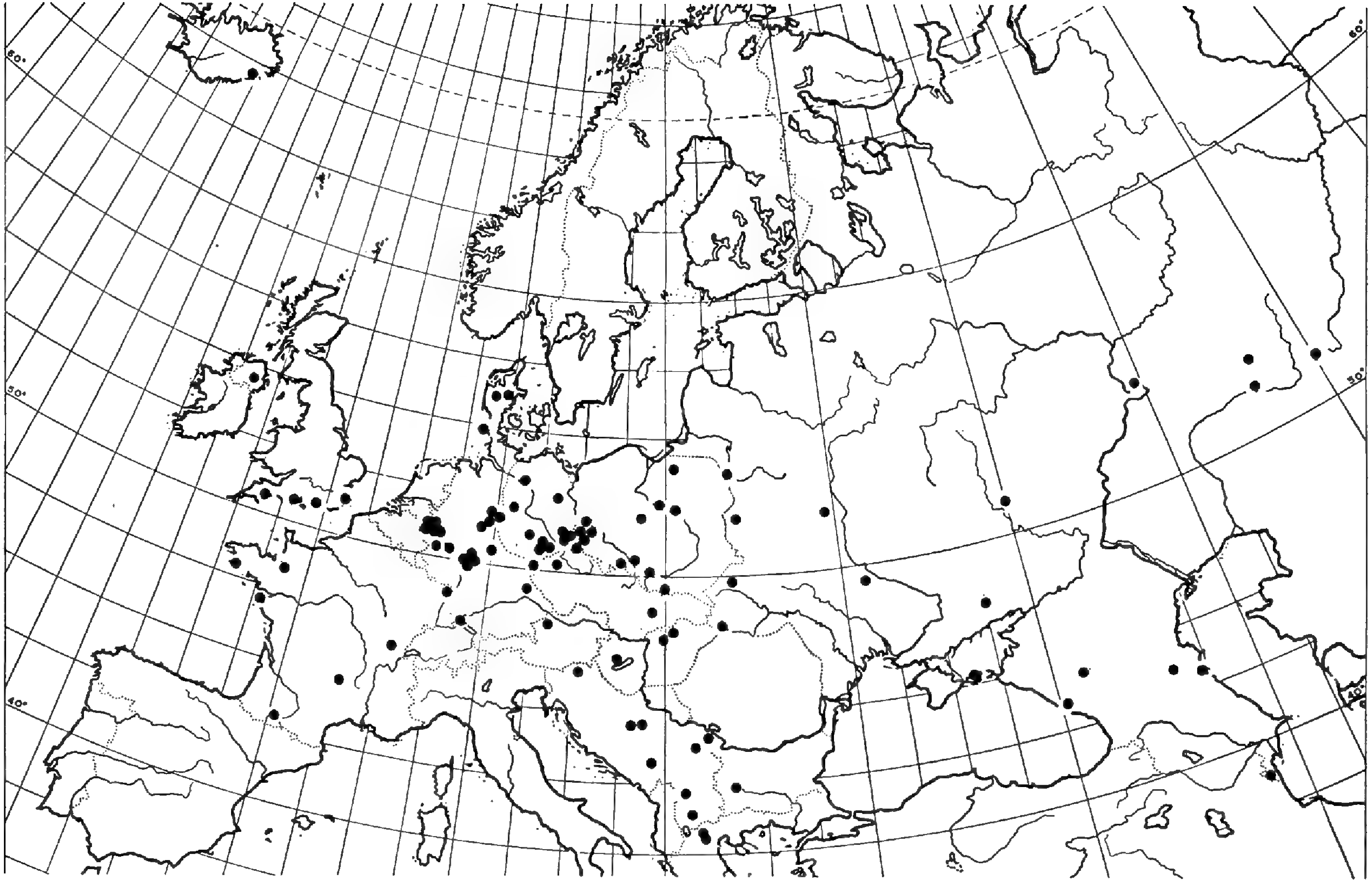
[1] Lewis and Cocke (1929) found that the pollen of *Nyssa* reaches a maximum of 40 per cent of the total pollen a foot below the soil-surface of the Dismal Swamp, a locality where trees of *Nyssa* are very abundant today.



Map 2. Reports of Tertiary Nyssaceae in Europe (fruits and pollen). Copyright, Rand McNally Co.

exines with pollen of Rhamnaceae and Vitaceae, and a number of authors have stated their belief that the so-called *Nyssa* pollen collected from early Tertiary beds was produced by ancient mastixioid trees as well as by nyssaceous trees (see, for instance, Thiergart, 1945, pp. 63–65).

In compiling TABLE I, we have attempted to be thorough; undoubtedly, however, some localities have been overlooked. A truly complete compilation would be very difficult in view of the great diversity of works in which palynological reports now appear. Some of these works, especially those in Slavic languages, are not obtainable even in our major libraries. Furthermore, we have not intentionally included reports based on a single pollen grain or reports regarded by their authors as questionable, with one exception: the recording of pollen resembling *Nyssa* from the early Tertiary of Kotel'nyy Island in the Arctic Ocean (Kuprianova, 1960, Pl. V, fig. 2). This locality is particularly interesting because it is by far the most northern site from which *Nyssa* has been reported in recent years. (All of the older records of Arctic *Nyssa* were based on poorly preserved leaves and misidentified fruits.) The same deposits yielded pollen of *Liquidambar*, Taxodiaceae, and other temperate plants.

TABLE I. **Localities From Which Fossil Nyssaceae Have Been Reported**

LOCALITY	AGE *	KIND OF FOSSIL †	REFERENCE
UNITED STATES			
Harding Co., S. D.	Paleo	P	Stanley, 1960
Nevada Co., Calif. (Chalk Bluffs flora)	M Eo	Fr, L	MacGinitie, 1941
Wheeler Co., Calif. (Clarno flora)	U Eo	Fr	Scott, 1954
Trinity Co., Calif. (Weaverville flora)	M Oligo	Fr, L	MacGinitie, 1937
Vantage, Wash.	Mio	W	Prakash & Barghoorn, 1961
Spokane, Wash.	M Mio	Fr, L	Berry, 1929
Grand Coulee, Wash.	M Mio	Fr, L	Berry, 1931
Whitebird, Ida.; Washington Co., Ida.	M Mio	Fr, L	Berry, 1934
Mascall flora near Dayville, Ore.	Mio	Fr, P, L	Chaney & Axelrod, 1959; Gray, 1958
Stinking Water flora near Drewsey, Ore.	Mio	P	Gray, 1958
Blue Mt. flora near Bates, Ore.	Mio	P, L	Gray, 1958; Chaney & Axelrod, 1959

* Paleo = Paleocene; L Eo = lower Eocene; M Oligo = middle Oligocene; U Mio = upper Miocene; etc. In most cases we have simply repeated the age suggested by the cited author. Some of these stratigraphic opinions, notably Kirchheimer's (see Quitzow, 1952), have been disputed.

† Fr = fruit; P = pollen; W = wood; L = leaf.

TABLE I. (*Continued*)

LOCALITY	AGE *	KIND OF FOSSIL †	REFERENCE
UNITED STATES (*continued*)			
Northern Cascade Mts., Ore.	Mio	P	Wolfe, 1962
San Pablo, Calif.	U Mio	Fr, L	Condit, 1938
Benton, Ark.	L Eo	P	Jones, 1960
Chester Co., Tenn.	L Eo	Fr	Berry, 1930
Puryear, Tenn.	M Eo	Fr	Berry, 1916a
Bell City, Ky.	M Eo	Fr	Berry, 1930
Hardeman Co., Tenn.	M Eo	Fr	Berry, 1930
Smithville, Tex.	M Eo	Fr	Berry, 1924
Lufkin, Tex.	M Eo	Fr	Berry, 1924
Claiborne Bluffs, Ala.	M Eo	P	Gray, 1960
Trinity Co., Tex.	Oligo	Fr	Berry, 1924, and present paper
Columbus, Ky.	Oligo	Fr	Present paper
Karnes Co., Tex.	Oligo	Fr	Present paper
Brandon, Vt.	Early Tertiary	Fr, P	Present paper; Traverse, 1955
ICELAND			
Hoffell on the Hornafjord	Mio or Plio	P	Schwarzbach & Pflug, 1957
NORTHERN IRELAND			
Lough Neagh Clays	L or M Oligo?	P	Watts, 1962
GREAT BRITAIN			
London Clay localities: Sheppey; Herne Bay; Bognor	L Eo	Fr, P	Chandler, 1961; Macko, 1961
Bournemouth Beds and Bagshot Beds	M Eo	Fr	Chandler, 1962
Bovey Tracey, Devon.	M Oligo	Fr	Chandler, 1957
FRANCE			
St. Tudy (Finistère)	M Eo	Fr	Reid, 1927
La Sennetièrre (L.A.)	Eo	P	Durand, 1960
Landéan (I.-et-V.)	Oligo	P	Durand, 1959
Orignac (H.-P.)	Mio	P	Sittler, 1958
Joursac & Sainte-Reine (Cantal)	Mio	P	Sittler, 1958
Allèriot (S.-et-L.)	Oldest Plio	P	Sittler, 1958
Soufflenheim (B.-R.)	U Plio	Fr	Kirchheimer, 1957
NETHERLANDS			
Heerlen	L Mio?	P	Weyland & Takahashi, 1961
Haanrade	M Mio	P	Manten, 1958
Swalmen; Reuver	Plio	Fr, P	Reid & Reid, 1915; Kirchheimer, 1957; Altehenger, 1959, p. 35

TABLE I. (*Continued*)

LOCALITY	AGE *	KIND OF FOSSIL †	REFERENCE
DENMARK			
Salten; Silkeborg	U Oligo?	Fr	Kirchheimer, 1957
Bjerregårde; Studsgård	Mio	P	Ingwersen, 1954
GERMANY			
Antweiler	Paleo & Eo	P	Thomson & Pflug, 1953
Helmstedt	Paleo & Eo	P	Thomson & Pflug, 1953
Geiseltal near Merseburg	M Eo	P	Thomson & Pflug, 1953
Messel near Darmstadt	M & U Eo	P	Thomson & Pflug, 1953
Kassel	U Eo to L Oligo	P	Thomson & Pflug, 1953
Herzogenrath near Aachen	M or U Oligo	Fr	Kirchheimer, 1957
Rur Valley near Düren	M or U Oligo	Fr	Kirchheimer, 1938; Thomson, 1958
Rott near Bonn	U Oligo?	P, L	Thiergart, 1958; Weyland, 1941
Niederpleis near Siegburg	M or U Oligo	Fr	Kirchheimer, 1957
Offenbach on the Main	M or U Oligo	Fr	Kirchheimer, 1938
Sieblos (Rhön Mts.)	M Oligo	Fr	Kirchheimer, 1957
Regis near Altenburg, Saxony	Oligo	L (cuticle)	Kräusel & Weyland, 1954
Vicinity of Mittweida & Grimma, Saxony	M or U Oligo	Fr, P	Kirchheimer, 1938 & 1957; Hunger, 1952
Klettwitz near Senftenberg	M or U Oligo	Fr	Kirchheimer, 1957
Wiesa near Kamenz	M or U Oligo	Fr	Kirchheimer, 1957
Marxheim in the Lower Main region	U Oligo	P	Mürriger & Pflug, 1952
Schacht Houtgen near Krefeld	M Mio	P	Brelie, von der, 1958
Ville near Köln	Mio	Fr, P, L (cuticle)	Thomson, 1958; Neuy-Stolz, 1958; Kräusel & Weyland, 1954
Salzhausen near Nidda	U Mio	Fr	Kirchheimer, 1957
Öhningen on the Boden See	U Mio	Fr	Kirchheimer, 1955
Berlin; Malliss in Mecklenburg; Jahmen in the Lausitz	Mio	P	Raukopf, 1959
Haidhof near Ponholz, Bavaria	U Mio	Fr	Kirchheimer, 1938
Wackersdorf, Bavaria	Mio	P	Meyer, 1956
Icksberg near Kaldenkirchen	Reuverian Plio	Fr	Kirchheimer, 1957
Weilerswist, North Rhine-Westphalia	Plio	P	Altehenger, 1959
Lower Main Valley: Höchst; Niederursel; Niederrad	Reuverian Plio	Fr	Kirchheimer, 1957
Wetter Valley near Friedberg	Reuverian Plio	Fr, P	Kirchheimer, 1957; Leschik, 1956

TABLE I. (*Continued*)

LOCALITY	AGE *	KIND OF FOSSIL †	REFERENCE
GERMANY (*continued*)			
Sylt, North Frisian Is.	Reuverian Plio	P	Weyl, Rein, & Teichmüller, 1955
Brunswick: Wallensen; Willershausen; Solling near Uslar	Plio	P	Altehenger, 1959
AUSTRIA			
Ampflwang in Hausruck	L Plio?	P	Meyer, 1956
POLAND			
Zittau Valley	L Mio	Fr	Czeczott, Zalėwska, & Skirgiello, 1959
Miroslawice Gorne	L Mio	P	Doktorowicz-Hrebnicka, 1957b
Kłodnica Valley near Gliwice	L Mio	P	Macko, 1957
Konin on the Warta	Mio	P	Kremp, 1949
Dobrzyń on the Vistula	Mio	Fr, L	Kownas, 1955
Nowa Wies near Opole; Laçzi near Nysa; Węgliniec Basin	Mio	P	Macko, 1959
Sites near Nielona Góra (Grünberg), Głogów, and Bolesławiec (Bunzlau), all in Lower Silesia	U Mio	Fr	Kirchheimer, 1957
Poznań clays: vicinity of Olsztyn and NW of Warsaw	L or M Plio	P	Doktorowicz-Hrebnicka, 1957a
Krościenko; Huba; Mizerna	Reuverian Plio	Fr, P	Szafer, 1946, 1954
HUNGARY			
Halimba	L Eo	P	Kedves, 1961
Petöfi-bánya near Hatvan	Plio	P	Nagy, 1959
Eger	Helvetian Mio	Fr	Zeller-Igali, 1955
CZECHOSLOVAKIA			
Vrsovice near Louny (Laun)	L Mio	Fr	Kirchheimer, 1957
Handlová	U Mio	P	Pacltová, 1958
Vonšov (Fonsau) near Cheb	Plio	P	Rudolph, 1935
YUGOSLAVIA			
Ugljevik in NE Bosnia	Late Oligo-early Mio	P	Weyland, Pflug, & Pantić, 1958
Pljevlja in Montenegro	M Mio	P	Weyland, Pflug, & Pantić, 1958

TABLE I. *(Continued)*

LOCALITY	AGE *	KIND OF FOSSIL †	REFERENCE
YUGOSLAVIA *(continued)*			
Despotovac in Serbia	U Mio	P	Weyland, Pflug, & Pantić, 1958
Jabukovac in Serbia	Sarmatian Mio	Fr	Pantić, 1957
Kreka near Tuzla	Pontian (Mio-Plio)	P	Weyland, Pflug, & Pantić, 1958
Oslomey Mine near Kičevo	Plio	P	Pantić & Nicolić, 1956
Velenje in Slovenia	Reuverian Plio	P	Weyland, Pflug, & Pantić, 1958
GREECE			
Vévi	Plio	P	Weyland, Pflug, & Pantić, 1958
Ptolemaïs	Plio	P	Weyland, Pflug, & Müller, 1960
BULGARIA			
Dospey near Samokov	Oligo	Fr	Palamarev, 1961
U.S.S.R.			
White Russia: northwestern part	U Eo	P	Manykin, 1958b
White Russia: southern part	Oligo-Mio	P	Manykin, 1958a
L'vov, Ukrainian SSR	Tortonian Mio	P	Shchekina, 1956, 1957
Vinogradov, Trans-Carpathian Ukraine	Tortonian Mio	P	Shchekina, 1958a
Cherkassy Region, Ukrainian SSR	M Eo	P	Shchekina, 1958b
Environs of Kiev	Poltavian Mio	P	Shchekina, 1962
Novotroitskoye near Volnovakha, Ukrainian SSR	Oligo	P	Karlov, 1956
Kerch Peninsula, Crimea	Plio	P	Maslova, 1961
Voronezh Region	Early Tertiary	P	Zaklinskaya, 1953a
Solenovskaya near the Lower Don	Mio	P	Pokrovskaya, 1956b
Cherkessk on the Kuban	Oligo	P	Kozyar, 1957
Duab River, western Caucasus	Plio	Fr, P	Kolakovskiy, 1958
Karabudakhent; other localities in Dagestan & Checheno-Ingush	Oligo & Mio	P	Grossgeym & Gladkova, 1951; Gladkova, 1953; Pokrovskaya, 1956a, 1956b
Talysh Mts., Azerbaijan SSR	Oligo-Mio	P	Dzhabarova & Kasumova, 1961
Zhiguli Mts., Volga Valley	M Plio	P	Grishchenko & Glushchenko, 1956

TABLE I. (*Continued*)

LOCALITY	AGE *	KIND OF FOSSIL †	REFERENCE
U.S.S.R. (*continued*)			
Southern Urals near Yumaguzino & Chernyy Otrog	Oligo	P	Pokrovskaya, 1956b
Urals: Kolchin near Bredy; Bilimbay near Chelyabinsk	Mio	P	Pokrovskaya, 1956a
Turgay Depression; Zhilanchik Basin; NW Kazakhstan & Kurgan Region	Eo, Oligo, & Mio	P	Pokrovskaya, 1954, 1956a, 1956b; Abuzyarova, 1955, 1958; Boytsova & Pokrovskaya, 1954; Kornilova, 1955; Zaklinskaya, 1955; Rzhanikova, 1956
Pavlodar on the Irtysh & vicinity	Eo, Oligo, & Mio	P	Zaklinskaya, 1953b
Ashutas Mt. near Lake Zaysan	Oligo	Fr, P, L	Krishtofovich, 1956; Il'inskaya, 1957; Rzhanikova, 1958
Antropovo on the Tavda	Oligo	Fr	Dorofeyev, 1961
Uvat; Lar'yak; other sites on the W. Siberian Lowland	L Oligo	P	Pokrovskaya, 1956b
Tara on the Irtysh	Mio	Fr	Krishtofovich & Borsuk, 1939
Tebisskaya Station near Barabinsk	Mio	P	Pokrovskaya, 1956a
Rezhenka near Tomsk	Oligo	Fr	Dorofeyev, 1958
Kireyev Ravine near Tomsk	Early Mio?	Fr	Dorofeyev, 1960b
Zaobsky Ravine near Tomsk	Mio?	Fr	Kolesnikova, 1961
Dunayevsky Ravine on the Tym	Oligo	Fr	Dorofeyev, 1960a
Kotel'nyy Island	Paleo?	P	Kuprianova, 1960
Lower Aldan R. near Ust' Tatta	?	P	Khoreva & Giterman, 1961
Smirnovka on the Amur	Oligo	P	Fin'ko & Zaklinskaya, 1958
Maykhe R.; Suputinka R.; other sites in southern Maritime Territory	Oligo & Mio	P	Pokrovskaya, 1956a, 1956b; Sedova, 1957

TABLE I. (*Continued*)

LOCALITY	AGE *	KIND OF FOSSIL †	REFERENCE
JAPAN			
Kushiro coalfield, Hokkaidō	Mio	P	Okazaki, 1952
Ombetsu R., Hokkaidō	?	W	Mädel, 1959
Aomori Pref., Honshū	Plio	P	Sohma, 1958c
Sendai, Honshū	Mio & Plio	P	Sohma, 1956, 1957a, 1957b, 1958a
Nagoya, Honshū	Plio	P	Sohma, 1958b
NE Shikoku	U Plio	P	Sohma, 1960
Nahari, Shikoku	Plio	P	Jimbō, 1958
Ca. 25 sites in northern & central Honshū; one site in Kyūshū	Plio	Fr	Miki, 1956

TERTIARY WOODS

Fossil woods of Nyssaceae are extremely rare. Apparently none were described in the scientific literature until Beck (1945) reported a collection of two dozen specimens gathered in Idaho, Oregon, and central Washington. Beck did not attempt a formal systematic and descriptive treatment of his woods, but he did section the fossils, and he compared them with sections of woods of three modern *Nyssa* species — *N. sylvatica, N. aquatica,* and *N. ogeche.* He found that all of the modern woods used for reference could be matched by one or more of his fossils. Beck concluded that we have the choice of "one extremely variable Miocene species or as many or more species as represented in eastern America today."

Subsequently, Prakash and Barghoorn (1961) discovered a single specimen of silicified *Nyssa* wood among material collected from the Miocene Columbia Basalts near Vantage, Washington, the same area from which Beck obtained most of his *Nyssa* fossils. This wood was described in detail and designated as a new fossil species, *N. eydei.* The authors stated (p. 354) that "a survey of the structural features of the fossil indicates that the nearest affinity of the fossil is with *Nyssa ogeche.*"

The comparison of *Nyssa eydei* with modern *N. ogeche* was stated rather emphatically, because the imperforate tracheary elements of the fossil wood have exceptionally thin walls and large lumina, features that are characteristic of *N. ogeche* specimens in the reference collection of the Arnold Arboretum. While preparing the present paper, however, we had occasion to re-examine the reference slides in association with Dr. Prakash, and we found that this collection also contains some specimens of *N. aquatica* wood in which the fibers have thin walls and large lumina. Possibly these thinner-walled specimens of *N. aquatica* were taken from the lower portions of trees: Penfound (1934) reported that the wall thickness of all wood components in trees of this species is less at the base of the trunk than at higher levels. (It is well-known that the spongy root-wood was formerly used to make surgeon's tents. See, for instance, *Merck's 1907 Index,* p. 450.) Gradation in wall thickness in wood of *N. aquatica* is apparently related to the swamp habitat, and it seems not unlikely that a similar gradation would also be found in stems of other aquatic nyssas. At any rate, thin-walled structure is not confined to wood of *N. ogeche*; therefore, the presence of this character in the fossil *N. eydei* cannot be taken as proof that *N. ogeche* is its nearest living equivalent.[2]

So far there has been only one other nyssaceous wood described in the paleobotanical literature. The specimen was found as a pebble in the Ombetsu River near Kushiro, Japan, and its stratigraphic source is not known. Mädel (1959) described the fine structure of this fossil and assigned it to *Nyssoxylon,* a form-genus created to include fossil woods showing features in common with modern *Nyssa* and *Davidia.* The Japanese fossil was named *Nyssoxylon japonicum* Mädel and this species was designated as the type of the new genus.

Mention of a fossil *Nyssa* wood is made in the unpublished doctoral dissertation of Dukes (1961). The exact source of the silicified specimen that Dukes believes to be a *Nyssa* remnant is unknown; the wood was acquired from a collector in Louisiana, and it may be of Wilcox (lower Eocene) age.

TERTIARY FRUITS

Paleobotanists of the 19th century frequently compared any longitudinally ridged or striated fruit with *Nyssa.* As a result, a map presented by Berry (1923, p. 245), which purported to show the ancient distribution of *Nyssa,* contained a number of Arctic localities. These represented, at least in part, records of "*Nyssidium*" fruits, which Heer (1870) had erroneously compared with modern *Nyssa.* Subsequently, Brown (1939) transferred Heer's *Nyssidium* species, along with leaves formerly known as *Nyssa arctica* Heer and *Nyssa reticulata* Heer, to *Cercidiphyllum.* The fossil fruits *Nyssa denveriana* Knowlton and *Nyssa? racemosa* Knowlton were transferred to *Cercidiphyllum* at the same time. Many of these same fossils have since been assigned to *Trochodendrocarpus* by Khrishtofovich (1958).

The characteristic germination valve of the *Nyssa* stone was discovered[3]

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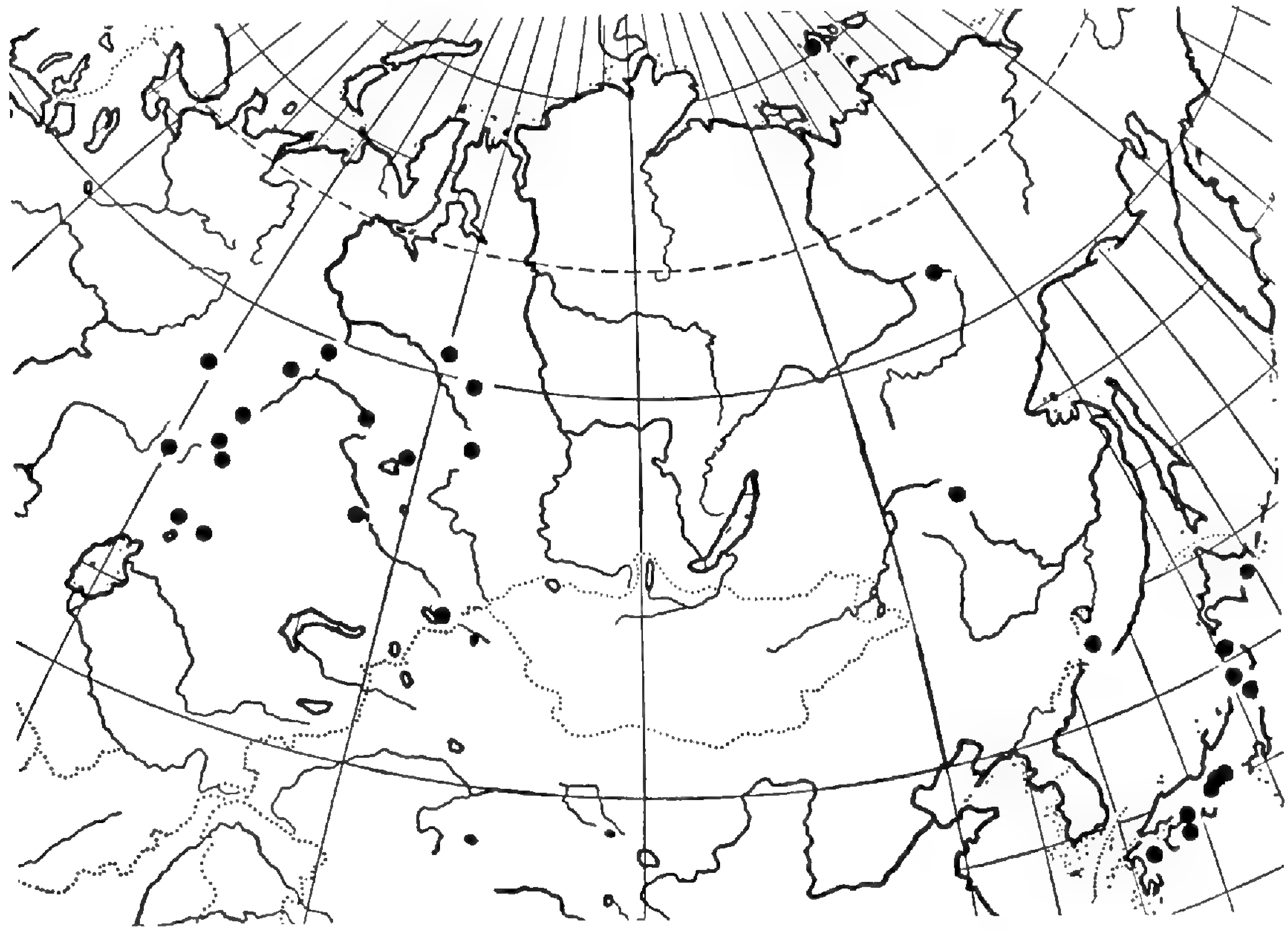
[2] Sudworth and Mell, in their key for distinguishing American "gumwoods," (1911, pp. 13, 14) listed thin-walled fibers as an identifying characteristic of *N. ogeche,* but later workers have not found this key to be of value. Wood anatomists of the Forest Products Research Laboratory, Great Britain, have expressed doubt that woods of American *Nyssa* species can be separated (Brazier and Franklin, 1961, p. 30), and Dr. B. F. Kukachka, wood anatomist of the U. S. Forest Products Laboratory, has written, "So far as I am concerned, the normal stem wood of the various species is so similar as to preclude the possibility of specific determination with any degree of certainty." (Letter to Eyde dated October 20, 1961).

[3] Actually, the method of germination was known to Mark Catesby, who published the earliest botanical description of a *Nyssa* tree and to Peter Collinson, who first introduced the genus into England. The phenomenon is mentioned in a posthumous work of Catesby's (1763, p. 11) and in a letter written by Collinson to John Bartram in 1741 (Darlington, 1849, p. 147).

by C. and E. M. Reid during their paleobotanical researches (1915) and later reported by Hill (1933). The detection of this structure made possible the easy recognition of most well-preserved *Nyssa* fruits and the rejection or transfer of many fossils that had been mistakenly referred to Nyssaceae. Thus, forms previously known as *Nyssa obovata* Weber, *Nyssites* Geyler & Kinkelin, and *Pseudonyssa* Kinkelin have been placed in *Styrax* (see Kirchheimer, 1957, pp. 315, 316), and several of the "*Nyssa*" species found in the Bovey Tracey lignite have turned out to be *Symplocos* (Chandler, 1957).



MAP. 3. Reports of Tertiary Nyssaceae in Asia (fruits, pollen, wood). Copyright, Rand McNally Co.

During the past 30 years, the various revisionary treatments by Chandler, Kirchheimer, and Miki have established sound taxonomic order in the European and Japanese collections of fossil *Nyssa* fruits. Since these authors have not had access to American specimens, however, the record in this hemisphere has remained in confusion. This is especially true of the abundant and excellently preserved *Nyssa* fruits of the Brandon, Vermont, brown coal deposit, for these remains had been very poorly investigated, in spite of the fact that they excited considerable botanical interest, from time to time, for more than a century.

Historical details regarding the Brandon lignite have been presented elsewhere (see Barghoorn and Spackman, 1950; Traverse, 1955) and need not be reviewed here except where the fossil *Nyssa* fruits are concerned. The first scientific paper dealing with the lignite, written by Edward Hitchcock and published in the *American Journal of Science* (1853), included 20 sketches of fossil fruits and seeds, some of them exhibiting the characteristic nyssoid germination valve. This paper was also published in 1853 as pp. 22–34 of House Document 39, Commonwealth of Massachusetts. Hitchcock presented preliminary descriptive comments on the fossils, but he assigned no names to them; instead he sent a set of specimens to Leo Lesquereux, at that time America's foremost authority on fossil plants, who published further descriptive remarks and assigned binomials. Meanwhile, Hitchcock prepared a modified version of his 1853 paper — with additional drawings — and published this in his *Report on the Geology of Vermont* (1861). Lesquereux's paper containing the names of the fossils was duplicated in the second volume of the *Report.* Nomenclaturally, this is an unusual situation: Lesquereux's names are validated by illustrations that appeared earlier in Hitchcock's paper. Moreover, both papers were presented twice in the scientific literature — first in the *American Journal of Science,* then in the *Geology of Vermont.*

Since the pioneer work of Hitchcock and Lesquereux, there has been only one attempt at a general systematic treatment of the Brandon fruit remains, that of G. H. Perkins, State Geologist of Vermont. Perhaps the kindest thing that can be said for Perkins's work (1904, 1905, 1906) is that it introduced photographs of the Brandon fruits and seeds into the scientific literature and thereby brought renewed attention to an important fossil locality. From the botanical viewpoint, the venture was virtually valueless. Almost every minor variation in size, shape, and preservation was named as a "new species," and descriptions embodied little more than a statement regarding the dimensions and outline of each specimen. Hardly any new suggestions were made regarding the modern affinities of the fossils; instead, most of the "species" were placed in poorly defined form-genera. The largest nyssoid fruits were designated as *Glossocarpellites,* and others were classified as *Monocarpellites, Bicarpellites,* or *Tricarpellites,* depending upon the apparent number of carpels. As a result of this procedure, fruits that might very well have been borne on the same plant were assigned to different form-genera. Following Lesquereux, Perkins designated some of the smaller Brandon fruits as *Nyssa* — indeed, he listed 19 "species" of *Nyssa* — but we have found only a part of these to be nyssoid during our investigation.

For our own studies, we have had available a larger collection of specimens than Perkins possessed. Moreover, most of our material is better preserved than Perkins's material, for it has not been allowed to dry since its removal from the lignite. Whole fruits were collected by breaking chunks of lignite in the hands and keeping them moist until their transferral to the laboratory, where they were soaked for a few days in hydrofluoric acid or brushed vigorously to remove adhering quartz particles. (Physical and chemical characteristics of the lignite were discussed by Barghoorn and Spackman, 1950.) After prolonged washing in running water to remove the acid, the specimens were transferred to a solution of glycerine, ethanol, and water, in which they have been kept for several years.

We found it convenient to immerse individual specimens in a dish of water while examining them with the dissecting microscope. When dry specimens were desired for photographic or display purposes, we placed wet fruits under an inverted beaker and allowed them to dry out very gradually, for rapid desiccation produces cracks and other distortions. Internal structure was studied by means of microtome sections, some of the specimens being embedded in celloidin before cutting. The fossils were much softer and more easily sectioned than their modern counterparts.

In the systematic revision of the Brandon nyssas that follows, we have recognized four major morphological groups and have designated them as fossil species, making new nomenclatural combinations where necessary. In addition, we are assigning a new epithet to the Japanese fossil fruit previously called *Nyssa rugosa* by Miki (1956). We are very grateful to Professor Miki for sending specimens of this fossil and of other fossil nyssas from Japan so that we could compare them with our Brandon material.

Nomenclatural treatment of the Brandon fruits has been very much simplified by the location of the original specimens figured by Edward Hitchcock in 1853 and 1861 and by C. H. Hitchcock in 1862. This material was formerly housed in the American Museum of Natural History (see Perkins, 1904, p. 171) and was transferred to the U. S. National Museum in 1955. Through the cooperation of Drs. S. Mamay and J. A. Wolfe of the U. S. Geological Survey the specimens were examined several times during our investigation and some of them were photographed for inclusion in this paper. The fossils are carefully labelled with the numbers of the figures in Hitchcock's 1861 publication, and a comparison of the more distinctive specimens with Hitchcock's illustrations shows that they are indeed the figured fruits.

TAXONOMIC TREATMENT

1. **Nyssa brandoniana** (Lesq.) Eyde & Barghoorn, comb. nov.

FIGS. 1, 6, 7.

Unnamed fruit, E. Hitchcock, Am. Jour. Sci. II. **15**: 97. *fig. 1.* 1853, Geol. Vt. **1**: 229. *figs. 111–116.* 1861.

Carpolithes brandoniana Lesquereux, Am. Jour. Sci. II. **32**: 356. 1861, in Hitchcock, Geol. Vt. **2**: 713. 1861; Knowlton, Bull. Torrey Club **29**: 640. *pl. 25, figs. 1, 2, 11, 12.* 1902; Perkins, Rep. Vt. State Geol. **4**: 175. *pl. 75, figs. 10, 11, 20.* 1904.

Carpolithes elongatus Perkins, Rep. Vt. State Geol. **4**: 176. *pl. 75, figs. 1–3.* 1904.

Carpolithes emarginatus Perkins, *ibid.* 177. *pl. 75, fig. 4.*

Carpolithes grandis Perkins, *ibid.* 178.

Carpolithes Hitchcockii Perkins, *ibid.* 179. *pl. 75, fig. 19.*

Carpolithes mucronatus Perkins, *ibid.* 179. *pl. 75, figs. 15, 17.*

Carpolithes obtusus Perkins, *ibid.* 177. *pl. 75, figs. 5–8, 14.*

Carpolithes ovatus Perkins, *ibid.* 178. *pl. 75, fig. 9.*

Carpolithes parvus Perkins, *ibid.* 179.

Carpolithes simplex Perkins, *ibid.* 178. *pl. 75, fig. 12.*

Carpolithes solidus Perkins, *ibid.* 179. *pl. 75, fig. 18.*
Carpolithes vermontanus Perkins, *ibid.* 179. *pl. 75, fig. 13.*
Glossocarpellites elongatus Perkins, Bull. Geol. Soc. Am. **16:** 511. *pl. 87, fig. 17.* 1905, Rep. Vt. State Geol. **5:** *pl. 53, fig. 17.* 1906.
Glossocarpellites obtusus Perkins, Bull. Geol. Soc. Am. **16:** 511. *pl. 87, fig. 16.* 1905, Rep. Vt. State Geol. **5:** *pl. 53, fig. 16.* 1906.
Glossocarpellites parvus Perkins, Bull. Geol. Soc. Am. **16:** 510. *pl. 86, fig. 15.* 1905, Rep. Vt. State Geol. **5:** 207. *pl. 52, fig. 15.* 1906.
Glossocarpellites grandis Perkins, Rep. Vt. State Geol. **5:** 206. *pl. 54, figs. 1–3.* 1906.

Description. — Endocarps 25–45 mm. long, 18–30 mm. broad; rounded, elliptical, or obovate in outline; compressed in dorso-ventral direction. Unilocular, with conspicuous outline of germination valve usually extending slightly more than half the length of endocarp; valve narrower at base, wider above, tapering to acuminate apex. Surface of endocarp relatively smooth (sometimes warty in places) with occasional bits of leathery skin adhering to best-preserved specimens. Prominent mid-dorsal ridge present on upper half of valve, pits on both sides of dorsal ridge and at center of valve base indicating points where minor vascular strands passed from dorsal carpellary bundle into endocarp wall. Several longitudinal grooves at base of stone indicate former position of major peripheral bundles, and six or more pairs of grooves arching from sides of stone to placental region on flattened ventral surface indicate former position of ovular supply. Endocarp wall thinnest (about 2 mm.) near apex, thickest (more than 4 mm.) near base, composed of thick-walled fibers, as in modern *Nyssa.*

Material. — There are about 50 fruits and numerous fragments in the Paleobotanical Collections of the Botanical Museum, Harvard University (*No. 56599*). Most of these specimens have been kept in preservative, and some of them show remarkable retention of external details. Rapid drying evidently causes gaping of the valve and longitudinal splitting of the endocarp wall at the base of the dehiscence line, for such distortions are frequently encountered in material collected by earlier workers. Specimens figured by Hitchcock (1861) as figs. 111–117 and named *Carpolithes brandoniana* by Lesquereux are in the U. S. National Museum; all of these fruits are of the same kind except the one corresponding to fig. 117, which is a *Nyssa fissilis.* The specimens for Hitchcock's figs. 111–113 bear *U. S. N. M. nos. 42066–42068.* We have chosen *U. S. N. M. 42067* as the lectotype.

Affinities. — The relatively smooth surface, the conspicuous valve margins, and the vascular pattern of *Nyssa brandoniana* are duplicated so closely in fruits of modern *N. javanica* that a close alliance of the two cannot be doubted. The fossils are much larger, to be sure, but the occurrence of the unusually large-fruited form "*N. megacarpa*" (the status of this plant is discussed by Eyde, 1963) proves that modern *Nyssa* has not completely lost the genetic capacity for producing endocarps of exceptional size. The fossil differs from its modern counterpart in the possession of more massive ventral valve margins and in the greater number of placental strands visible on the ventral surface. Furthermore, marks of minor branches of the dorsal bundle are not commonly noticeable on the valve of *N. javanica* fruits. It is interesting that members of this alliance had already become unilocular in the early Tertiary; most other nyssas at that time produced fruits in which two or more locules were common.

The Miocene Latah formation has yielded an impression of a large fruit resembling modern *Nyssa javanica* in observable surficial features. A germination valve is not discernible with certainty, but the shape of the fruit, undulations of the relatively smooth surface, and imprints of transverse fibers are very suggestive of *N. javanica*. The specimen, *U. S. N. M. 37012*, was collected in Spokane, Washington, and figured and described by Knowlton (1926) as *Carpites magnifica*; Berry (1929) renamed it *Nyssa magnifica*. If this is indeed a *Nyssa* fruit, it is the closest fossil ally of *N. brandoniana*.

The fossil fruits *Palaeonyssa multilocularis* (Reid & Chandler, 1933; Chandler, 1961), and *P. spatulata* (Scott, 1954), from Eocene deposits of England and Oregon, respectively, share an important feature with *Nyssa brandoniana* and *N. javanica*, i.e., relative smoothness of the external surface. Other *Nyssa* fruits, fossil or modern, bear prominent ridges and grooves that have developed in association with vascular bundles supplying superior parts of the flower. In *N. brandoniana* marks of these peripheral bundles may be found on the basal part of the fruit, but at higher levels any sculpturing is associated with carpellary vasculature only. The "broad gently rounded ribs" mentioned by Reid and Chandler in their description of *P. multilocularis* (1933, p. 432) occur only opposite the septa and are associated with ventral carpellaries, rather than peripheral bundles; Scott's specimens were described as "at most slightly ridged." A possible phylogenetic relationship between *Palaeonyssa*, *N. brandoniana*, and *N. javanica* will be discussed along with the affinities of *N. fissilis*.

2. **Nyssa fissilis** (Lesq.) Eyde & Barghoorn, comb. nov.

FIGS. 2, 12–14, 23–25.

Unnamed fruit, E. Hitchcock, Am. Jour. Sci. II. **15**: 98. *figs. 2, 3, 6, 12.* 1853, Geol. Vt. **1**: 229. *figs. 117–128.* 1861.

Carpolithes fissilis Lesquereux, Am. Jour. Sci. II. **32**: 356. 1861, in Hitchcock, Geol. Vt. **2**: 713. 1861.

Carpolithes Grayana Lesquereux, Am. Jour. Sci. II. **32**: 356. 1861, in Hitchcock, Geol. Vt. **2**: 714. 1861.

Carpolithes irregularis Lesquereux, Am. Jour. Sci. II. **32**: 356. 1861, in Hitchcock, Geol. Vt. **2**: 714. 1861.

Fagus Hitchcockii Lesquereux, Am. Jour. Sci. II. **32**: 357. 1861; in Hitchcock, Geol. Vt. **2**: 714. 1861.

Tricarpellites fissilis Knowlton, Bull. Torrey Club **29**: 641. *pl. 25, figs. 7, 8.* 1902; Perkins, Rep. Vt. State Geol. **4**: 188. *pl. 77, figs. 61–64.* 1904, Bull. Geol. Soc. Am. **16**: 512. *pl. 87, fig. 19.* 1905.

Aristolochites apicalis Perkins, Rep. Vt. State Geol. **4**: 203. *pl. 80, fig. 144.* 1904.

Bicarpellites Grayana Perkins, *ibid.* 190. *pl. 78, fig. 69.*

Bicarpellites Knowltonii Perkins, Rep. Vt. State Geol. **4**: 191. *pl. 78, figs. 71, 72.* 1904, Bull. Geol. Soc. Am. **16**: 510. *pl. 86, fig. 14.* 1905, Rep. Vt. State Geol. **5**: *pl. 52, fig. 13.* 1906.

Bicarpellites obesus Perkins, Rep. Vt. State Geol. **4**: 191. *pl. 78, fig. 75.* 1904.

Bicarpellites rotundus Perkins, *ibid.* 191. *pl. 78, fig. 76.*

Bicarpellites rugosus Perkins, *ibid.* 191. *pl. 78, fig. 70.*

Bicarpellites vermontanus Perkins, *ibid.* 192. *pl. 78, figs. 88, 89.*

Hicoria biacuminata Perkins, *ibid.* 193. *pl. 78, figs. 77, 81,* Bull. Geol. Soc. Am. **16**: 512. *pl. 87, fig. 22.* 1905, Rep. Vt. State Geol. **5**: *pl. 53, fig. 22.* 1906.

Hicoroides angulata Perkins, *ibid.* **4**: 183. *pl. 76, figs. 28, 32, 33.* 1904, Bull. Geol. Soc. Am. **16**: 513. *pl. 87, fig. 27.* 1905, Rep. Vt. State Geol. **5**: *pl. 53, fig. 27.* 1906.

Hicoroides ellipsoidea Perkins, Rep. Vt. State Geol. **4**: 184. *pl. 76, fig. 41.* 1904, Bull. Geol. Soc. Am. **16**: 513. *pl. 87, fig. 26.* 1905, Rep. Vt. State Geol. **5**: *pl. 53, fig. 26.* 1906.

Hicoroides globulus Perkins, *ibid.* **4**: 184. *pl. 76, figs. 42, 43.* 1904.

Hicoroides parva Perkins, *ibid.* 184. *pl. 81, fig. 172.*

Hicoroides triangularis Perkins, *ibid.* 183. *pl. 76, fig. 40.*

Juglans brandonianus Perkins, *ibid.* 182. *pl. 76, fig. 36,* Bull. Geol. Soc. Am. **16**: 511. *pl. 87, fig. 21.* 1905, Rep. Vt. State Geol. **5**: *pl. 53. fig. 21.* 1906.

Monocarpellites elegans Perkins, Rep. Vt. State Geol. **4**: 181. *pl. 76, figs. 25, 30.* 1904.

Monocarpellites gibbosus Perkins, *ibid.* 181. *pl. 76, fig. 26,* Bull. Geol. Soc. Am. **16**: 512. *pl. 87, fig. 18.* 1905, Rep. Vt. State Geol. **5**: *pl. 53, fig. 18.* 1906.

Monocarpellites Hitchcockii Perkins, *ibid.* **4**: 182. *pl. 76, fig. 29.* 1904.

Monocarpellites irregularis Perkins, *ibid.* 181. *pl. 76, fig. 27.*

Monocarpellites medius Perkins, *ibid.* 182. *pl. 76, fig. 34.*

Monocarpellites orbicularis Perkins, *ibid.* 181. *pl. 76, fig. 24.*

Monocarpellites ovalis Perkins, *ibid.* 182. *pl. 76, fig. 35.*

Monocarpellites pyramidalis Perkins, *ibid.* 180. *pl. 76, fig. 22.*

Monocarpellites sulcatus Perkins, *ibid.* 180. *pl. 76, fig. 23,* Bull. Geol. Soc. Am. **16**: 512. *pl. 87, fig. 20.* 1905, Rep. Vt. State Geol. **5**: *pl. 53, fig. 20.* 1906.

Monocarpellites vermontanus Perkins, *ibid.* **4**: 182. *pl. 76, fig. 35.* 1904.

Monocarpellites Whitfieldii Perkins, *ibid.* 180. *pl. 76, fig. 21.*

Tricarpellites acuminatus Perkins, *ibid.* 190. *pl. 78, fig. 83.*

Tricarpellites amygdaloideus Perkins, *ibid.* 188. *pl. 77, fig. 58.*

Tricarpellites angularis Perkins, *ibid.* 187. *pl. 77, fig. 57.*

Tricarpellites carinatus Perkins, *ibid.* 186. *pl. 77, fig. 47.*

Tricarpellites castanoides Perkins, *ibid.* 187. *pl. 77, fig. 54.*

Tricarpellites contractus Perkins, *ibid.* 189. *pl. 77, fig. 67.*

Tricarpellites Dalei Perkins, *ibid.* 186. *pl. 77, fig. 48.*

Tricarpellites elongatus Perkins, *ibid.* 186. *pl. 77, fig. 45.*

Tricarpellites fagoides Perkins, *ibid.* 188. *pl. 77, fig. 59.*

Tricarpellites hemiovalis Perkins, *ibid.* 190. *pl. 81, fig. 171.*

Tricarpellites inequalis Perkins, *ibid.* 186. *pl. 77, fig. 44.*

Tricarpellites lignitus Perkins, *ibid.* 186. *pl. 77, fig. 46.*

Tricarpellites major Perkins, *ibid.* 189. *pl. 77, fig. 66.*

Tricarpellites obesus Perkins, *ibid.* 188. *pl. 77, fig. 60.*

Tricarpellites ovalis Perkins, *ibid.* 187. *pl. 77, fig. 53.*
Tricarpellites Pringlei Perkins, *ibid.* 189. *pl. 77, fig. 68.*
Tricarpellites rostratus Perkins, *ibid.* 187. *pl. 77, fig. 52.*
Tricarpellites rugosus Perkins, *ibid.* 187. *pl. 77, fig. 55.*
Tricarpellites Seelyi Perkins, *ibid.* 189. *pl. 77, fig. 65.*
Bicarpellites abbreviatus Perkins, *ibid.* 5: 209. *pl. 56, fig. 1.* 1906.
Bicarpellites attenuatus Perkins, *ibid.* 210. *pl. 54, fig. 9.*
Bicarpellites bicarinatus Perkins, *ibid.* 210. *pl. 54, fig. 10.*
Bicarpellites brevis Perkins, *ibid.* 213. *pl. 55, fig. 13.*
Bicarpellites carinatus Perkins, *ibid.* 210. *pl. 54, fig. 11.*
Bicarpellites crassus Perkins, *ibid.* 211. *pl. 55, figs. 2, 3.*
Bicarpellites crateriformis Perkins, *ibid.* 211. *pl. 55, fig. 1.*
Bicarpellites inequalis Perkins, *ibid.* 211. *pl. 55, fig. 4.*
Bicarpellites lanceolatus Perkins, *ibid.* 211. *pl. 55, fig. 5.*
Bicarpellites latus Perkins, *ibid.* 212. *pl. 55, figs. 6, 7.*
Bicarpellites major Perkins, *ibid.* 212. *pl. 55, figs. 8, 11, 12.*
Bicarpellites medius Perkins, *ibid.* 212. *pl. 55, figs. 9, 10.*
Bicarpellites ovatus Perkins, *ibid.* 213. *pl. 55, fig. 14.*
Bicarpellites papillosus Perkins, *ibid.* 213. *pl. 55, fig. 15.*
Bicarpellites parvus Perkins, *ibid.* 214. *pl. 55, fig. 16.*
Bicarpellites quadrangulatus Perkins, *ibid.* 214. *pl. 56, fig. 2.*
Bicarpellites quadratus Perkins, *ibid.* 214. *pl. 56, fig. 3.*
Bicarpellites solidus Perkins, *ibid.* 215. *pl. 56, fig. 4.*
Bicarpellites sulcatus Perkins, *ibid.* 215. *pl. 56, figs. 5, 6.*
Hicoroides levis Perkins, *ibid.* 217. *pl. 56, fig. 15.*
Monocarpellites amygdaloidus Perkins, *ibid.* 208. *pl. 54, fig. 4.*
Monocarpellites multicostatus Perkins, *ibid.* 208. *pl. 54, figs. 5–7.*
Monocarpellites pruniformis Perkins, *ibid.* 208. *pl. 54, fig. 8.*
Tricarpellites alatus Perkins, *ibid.* 216. *pl. 56, figs. 11, 12.*
Tricarpellites brandonianus Perkins, *ibid.* 217. *pl. 56, figs. 13, 14.*
Tricarpellites curtus Perkins, *ibid.* 216. *pl. 56, figs. 7, 8.*
Tricarpellites triangularis Perkins, *ibid.* 216. *pl. 56, figs. 9, 10.*

Description. — Endocarps 17–44 mm. long, 13–28 mm. broad, 5–15 mm. thick across inflated base; rounded, elliptical, ovate, or obovate in outline; flattened, elliptical, concavo-convex, or triangular in cross section; bearing a short apical mucro when well-preserved. Mostly bilocular, occasionally trilocular, perhaps also unilocular; triangular germination valves usually occupying somewhat less than half the length of endocarp. Surface divided into 10–15 prominent longitudinal ridges (sometimes obscured by compression or abrasion) and intervening grooves, with remnants of heavy vascular strands visible in places along crests of ridges. Fibrous endocarp wall up to 5 mm. thick.

Material. — There are about 750 fruits of this species among the Paleobotanical Collections of the Botanical Museum, Harvard University (*No. 56600*), exhibiting a very wide range of variability in size and shape. The dimensions given above include the largest and smallest specimens obtained from the lignite.

In addition, we have found two specimens of *Nyssa fissilis* (*No. 56601*) among fruits taken from the silt that overlies the lignite (see Barghoorn & Spackman, 1950, for a description of this deposit). One of these silt fruits (FIGS. 23, 24) is the smallest *N. fissilis* we have seen, measuring 13 mm. in length and 9 mm. in breadth. The other (FIG. 25) has a very narrow outline — measuring 21 mm. in length and 7.5 mm. in diameter — and unusually sharp ridges. The silt specimens are of special interest, for they illustrate the differences in form that can be brought about by differences in compressional conditions. Apparently the fruit called *Aristolochites apicalis* by Perkins (1904, fig. 144) is also a *Nyssa fissilis* from the Brandon silt. We have found the figured fossil, bearing Perkins's label, among material sent to us by the Vermont State Museum, and it is similar to our smaller silt specimen.

We have chosen *U. S. N. M. 42071*, the specimen shown as fig. 118 in Hitchcock's 1861 report, as the lectotype for this species.

Affinities. — The most distinctive feature of the fruit of *Nyssa fissilis* is the position of its peripheral vascular bundles on the crests of the ridges. Since compression and abrasion frequently obscure this feature, it is fortunate that we were able to examine such a large collection of specimens. Apparently Perkins had observed the marks of the peripheral strands when, in a rare moment of descriptive zeal, he mentioned "rows of papillae" along the ridges of his "*Bicarpellites papillosus*" (1906, p. 213). Since the only modern *Nyssa* fruit in which ridges and bundles are similarly associated is that of *N. aquatica*, it is not unreasonable to infer an affinity between *N. aquatica* and *N. fissilis*.

One finds in *Nyssa fissilis* just those differences that might reasonably be expected if this fossil really is ancestrally related to the unilocular fruit of *N. aquatica*: both locules and peripheral bundles are more plentiful. (It follows that the appendages supplied by peripheral bundles were also more numerous in the flower from which the *N. fissilis* fruit developed than in the modern counterparts.) We are not sure whether any of the fossils are unilocular. Many of them appear to be unilocular when cut in half (hence Perkins's designation *Monocarpellites*), but whenever we have examined microtome sections of such specimens, we have found a tightly closed abortive locule in addition to a fertile one. The *N. fissilis* population was evidently one in which the ovary was undergoing reduction from a trilocular to a bilocular condition: distinctly three-sided fruits are common, but many of these completely lack a third locule.

Past attempts by various authors to compare fossil *Nyssa* fruits with fruits of *N. aquatica* have had no morphological basis. Impressions and coalified fruits combined under the name *N. hesperia* (Chaney & Axelrod, 1959) have been examined during our investigation; and we find that they bear broad rounded ridges with vascular bundles in intervening grooves, as in the modern *N. sylvatica* complex. These features are very well preserved in specimens collected from the Latah formation (*U. S. N. M. 38653, 38654*, and some specimens without numbers) and in material from the Mascall and Weaverville floras that was sent to us for inspection through the courtesy of Dr. Wayne L. Fry of the University of California Museum of Paleontology (*U. C. M. P. 1071, 3231, & 1275*). A fruit from the Citronelle formation in southern Alabama was designated as *N. aquaticaformis* by Berry (1916b, pp. 203, 204; Pl. 47, fig. 8) because of a supposed resemblance to *N. aquatica*. An inspection of Berry's figured specimen has shown, however, that the fruit is in all observable features — size, shape, and papery wings — identical with fruits of modern *N. ogeche*. Berry believed the fossil to be of Pliocene age, but geological opinion has more recently favored a Pleistocene age for the Citronelle formation (Fisk, 1945; Doering, 1958). Since "*N. aquaticaformis*" was collected within or almost within the western limits of the present *N. ogeche* range, the finding is of little importance.

On the other hand, a Miocene fruit found in the Zittau Valley of central Europe and compared by Czeczott and Skirgiello (in Czeczott, Zalewska, & Skirgiello, 1959) with modern *Nyssa ogeche* looks much more like *N. aquatica*. The better of two specimens, which the Polish authors show in Pl. 7, fig. 20, of their work, bears three prominent ridges on the side of the fruit where the vague outline of a valve can be seen; these ridges occupy the same positions with respect to the valve as would the dorsal ridge and two flanking ridges of a modern *N. aquatica* stone. The Zittau Valley fossil is not well-preserved and the authors cautiously call it "?*Nyssa* sp.". If the suggested identification is correct, this fruit is probably an intermediate between *N. fissilis* and *N. aquatica*.

Many of the three-sided specimens of *Nyssa fissilis* resemble *Palaeonyssa* in size and shape, but the valves of the Brandon fossils are generally triangular in outline, while those of *Palaeonyssa* are oval. Moreover, *Palaeonyssa* fruits do not have 10–15 ridges such as one finds on the surface of *N. fissilis*. It seems unlikely that the relative smoothness of all known *Palaeonyssa* specimens is due to abrasion alone. We prefer to view the three- or four-locular *Palaeonyssa* as representing a primitive smooth-surfaced condition from which the ridged and furrowed *N. fissilis* fruit has evolved. This change could have come about through increasing fusion of peripheral bundles with carpellaries in the ancient flowers that produced these fruits, and a consequent greater influence of the peripherals on the development of the woody endocarp. Evidence for such change has been found in flowers of modern Nyssaceae.

In the first author's previous paper it was concluded that the modern species *Nyssa javanica* and *N. aquatica* are more closely related to each other than either one is to members of the *N. sylvatica* complex. This relationship between *N. javanica* and *N. aquatica* could be explained by assuming that *Palaeonyssa* is ancestral to both. In this view, *N. brandoniana* and *N. fissilis* would be regarded as intermediates in the divergence, *N. fissilis* representing a stage about halfway between *Palaeonyssa* and *N. aquatica* and *N. brandoniana* being much more like its modern counterpart, *N. javanica*. This view would require a more rapid reduction in the number of locules along the line that produced *N. javanica* and a slower reduction in the number of locules along the line that produced *N. aquatica*, ultimately resulting in a unilocular ovary in each.

3. **Nyssa complanata** Lesquereux FIGS. 5, 15–19.

Unnamed fruit, E. Hitchcock, Am. Jour. Sci. II. **15**: 100. *figs. 13, 14.* 1853, Geol. Vt. **1**: 231. *figs. 153, 154.* 1861.
Nyssa complanata Lesquereux, Am. Jour. Sci. II. **32**: 361. 1861, in Hitchcock, Geol. Vt. **2**: 717. 1861; Perkins, Rep. Vt. State Geol. **4**: 198. *pl. 79, fig. 112.* 1904, *ibid.* **5**: 219. *pl. 57, figs. 3, 5.* 1906.
Nyssa microcarpa Lesquereux, Am. Jour. Sci. II. **32**: 361. 1861, in Hitchcock, Geol. Vt. **2**: 717. 1861; Perkins, Rep. Vt. State Geol. **4**: 194. *pl. 79, fig. 90.* 1904.
Bicarpellites minimus Perkins, *ibid.* 192. *pl. 78, fig. 79.*
Nyssa curta Perkins, *ibid.* 199. *pl. 79, fig. 111. ibid.* **5**: 219. *pl. 57, figs. 4, 6.* 1906; Berry, U. S. Geol. Surv. Prof. Paper **92**: 125. *pl. 19, fig. 10.* 1930.
Lescuria attenuata Perkins, Rep. Vt. State Geol. **5**: 220. *pl. 57, figs. 7–10.* 1906.

Description. — Endocarp 5.6–11.8 mm. long, 3.2–8.8 mm. broad; mostly ovate or elliptical in outline. Locules two to four, with triangular valves confined to upper half of endocarp. Surface bears 10–15 rounded longitudinal ridges with remains of vascular bundles in intervening grooves. Internal vascular pattern visible in cross sections, conforming to pattern in modern *Nyssa sylvatica* complex except for presence of additional strands in axis at base. Endocarp wall up to 800μ thick, composed of single inner layer of longitudinal fibers surrounded by narrow zone of circumlocular fibers and outer region where aggregates of fibers run in many directions.

Material. — More than 250 specimens of *Nyssa complanata* in the Paleobotanical Collections of the Botanical Museum, Harvard University (*No. 56602*) were inspected and measured in the course of our work, many of which were extremely fragile and, consequently, crumbled when handled. This fragility is partly due to evaporation of the preserving fluid on the museum shelf, followed by fungus attack, and partly due to the structure of the endocarp wall itself. Splitting of the dorsal wall along the mid-dorsal groove is quite common, and transverse sections show that in most specimens the septa are ruptured. The deformation that accompanies septal collapse frequently makes it impossible to ascertain by external examination the number of locules in a fruit. There are flattened fruits in our collection that appear beyond doubt to be unilocular, but whenever we have sectioned one of these, we have found a second or even a third locule. A few specimens have a five-faced appearance, but sectioning has shown this condition to be a compressional distortion of a four-celled fruit. As a matter of curiosity, however, we have separated our collection on the basis of external appearance and found 118 (46 per cent) "trilocular," and 101 (39 per cent) "bilocular," and 39 (15 per cent) "four-locular."

The holotype for *Nyssa complanata* (*U. S. N. M. 42074*) is the fruit shown as fig. 153 in Hitchcock's 1861 work. Our FIG. 5 is a photograph of this specimen and another to which Lesquereux assigned the name "*N. microcarpa*" (*U. S. N. M. 42073*).

Affinities. — The nearest living equivalents of *Nyssa complanata* are members of the modern *N. sylvatica* complex. The fossils differ from their modern counterparts in those respects which might be anticipated in an ancestral member of this alliance: they are multilocular and have more numerous peripheral vascular bundles. The internal vascular supply appears as dark spots in thick sections taken from the better specimens, with the same pattern as that found in the modern fruits except for the occurrence of a few extra strands in some of the fossils. These strands run longitudinally in the basal part of the axis along which the septa are united, and they diminish and disappear after a short distance. They can best be interpreted as remnants of a receptacle tip extending slightly beyond the bases of the carpels. We have not found similar strands in modern nyssas. Another interesting feature of the fossils is the lobed appearance of sections taken from the basal part of some of the three- or four-locular fruits (FIG. 18). In such sections the carpels seem to retain their distinctness more than in sections taken at higher levels in the fruit. Histologically, the fossils are somewhat more comparable to bilocular fruits of *N. sinensis* than to fruits of *N. sylvatica*, for the thick ventral wall of unilocular *N. sylvatica* has no exact counterpart among the fossils. Except for the greater breadth of some compressed specimens, the size of the fossils falls within the range of variation found in the modern *N. sylvatica* complex.

Fossils morphologically similar to *Nyssa complanata* have been collected in many countries of the northern hemisphere from horizons that range from lower Eocene to upper Pliocene in age. The small lignitized *Nyssa* stone from the Eocene Wilcox flora that Berry (1930) assigned to Perkins's *N. curta* is indistinguishable from the smaller Brandon specimens; therefore, we have transferred it to *N. complanata.* The name *N. wilcoxiana* Berry (1916a, 1930, 1941) has been applied to a number of other Eocene fossils from the southeastern United States, some of which, though poorly preserved, resemble *N. complanata* in gross features. Two impressions figured by Berry (1930, Pl. 19, figs. 7 & 8) and entered in the collections of the National Museum as *U. S. N. M. 39920* are possibly related to the Brandon species; however, there is insufficient retention of detail in these specimens even for certain identification as *Nyssa.* A more convincing impression (*U. S. N. M. 36361*), collected at "Station 20, Wilcox group" and identified by Berry as *N. wilcoxiana*, measures 13 mm. in length, 8 mm. in breadth, and shows the outline of a germination valve and a ribbed surface; it is likely that an impression of *N. complanata* would be very similar in appearance. The fossil fruits collected in the western United States and known as *N. hesperia* (previously discussed in this article) and *N. californica* MacGinitie (1941) are very much like *N. complanata* except for their somewhat greater size. The specimens of *N. hesperia* that we have inspected range from 10–18 mm. in length.

Fossil *Nyssa* fruits have been found in a great many localities on the European continent (TABLE I), particularly in brown coal deposits. With the exception of the rare form from the Zittau Valley that we have discussed under the affinities of *N. fissilis*, all of these fossils are allied to the modern *N. sylvatica* complex. In the older literature a variety of names were assigned to these remains, but Kirchheimer, who has been the principal investigator of European Tertiary fruits and seeds, was unable to find specific distinctions; therefore he combined all of these fossils into one fossil species, *N. disseminata* (Kirchheimer, 1938). In recent years, the name *N. disseminata* (Ludwig) Kirchheimer has been applied to almost all fossil *Nyssa* fruits found in continental Europe. The name has also been applied to all similar remains found in Asiatic U. S. S. R. (TABLE I), except for a recent finding from Oligocene deposits along the Tavda River, which Dorofeyev (1961) has designated as *N. macrocarpa*. Unfortunately, Dorofeyev's announcement of this finding includes only the new name and some illustrations (Pl. I, figs. 29–32) without an accompanying description of size and distinguishing features. It is not clear from the figures how the Tavda River fossil is to be separated from *N. disseminata*. Even if the proposed new species does differ in some important respect, it will have no status under the rules of nomenclature until some sort of description has been published.

Kirchheimer, in 1938 and again in 1957 (pp. 572, 573), has discussed variation in *Nyssa disseminata*. Fossils from the Oligocene and Miocene are usually larger (up to 22 mm. long) than Pliocene specimens (as little as 5 mm. in length). Furthermore, only the unilocular condition has been reported for Pliocene fruits, whereas a minority of the older fruits are bilocular and occasionally trilocular. *Nyssa* fruits with four locules have not yet been noted among the continental European collections. Thus, the *N. complanata* population differs from *N. disseminata* by virtue of its greater average number of locules. There are also differences in average size between early Tertiary specimens of *N. disseminata* and the Brandon population. In other respects, however, the two are quite similar and isolated fruits of *N. complanata* would surely be called *N. disseminata* if they had been collected in a European brown coal.

British authors have preferred to maintain separate names for fossil fruits of the *Nyssa sylvatica* alliance rather than to unite them with the brown coal species. E. M. Reid (1927) described as *N. oviformis* two silicified fruits collected from a presumably Eocene locality in Brittany. The excellently preserved specimen shown in Pl. I, fig. 4, of Mrs. Reid's paper bears a marked resemblance in thickness and outline to a large bilocular stone of modern *N. sinensis*. There are apparently no notable differences between these French fossils and the London Clay fruits described as *Protonyssa bilocularis* by Reid and Chandler in 1933 (changed to *Nyssa bilocularis* by Chandler, 1961). Miss Chandler (1957) used the name *N. boveyana* for lignitized endocarps found in the Oligocene Bovey Tracey lignite, material that is similar in size and general features to modern *N. sylvatica* and to *N. disseminata*. The small pyritized fruit described by Miss Chandler as *N. cooperi* in her recent revision of the London Clay flora (1961) seems also to belong with this alliance, since its major vascular bundles, wherever visible, are seen to lie in longitudinal grooves. This fossil bears an interesting resemblance to *N. complanata* in size (9.5 mm. long and 6.25 mm. broad) and in the possession of three locules. Unfortunately, only one specimen of *N. cooperi* is presently known.

Pliocene fruits allied with the *Nyssa sylvatica* complex collected at a number of localities in Japan were thoroughly reviewed by Miki (1956). These fruits are so similar to *N. sylvatica* that Miki has used that name in describing them. It is peculiar that all of these fossils are unilocular, since the modern *Nyssa* population geographically closest is the frequently bilocular *N. sinensis* of China.

In view of the general similarity of all of the fossils discussed in this section and their dissimilarity to those discussed in preceding sections, it seems we are dealing here with a natural group — an evolutionary alliance established in the early Tertiary (*Nyssa cooperi, N. complanata*) from which the closely related modern species (*N. sinensis, N. sylvatica*, and *N. biflora*) have evolved. It can hardly be expected that all members of this alliance would fall into a direct line of descent. Indeed, there must have been numerous instances of divergence, speciation, and extinction during the course of the Tertiary, and a part of the variation in size and minor features found in the fossil record of this group may be attributed to such events. Considering the variation encountered in fruits collected from modern members of the alliance, however, it is unlikely that we can detect any evolutionary changes save the broader ones such as reduction in number of locules.

The newly described *Nyssoidea eocenica* (Chandler, 1962), found in middle Eocene strata of southern England, may possibly be related to this same general alliance, since it has a similar arrangement of ridges and vascular bundles and bears a superficial resemblance to members of the modern *Nyssa sylvatica* complex. However, *Nyssoidea eocenica* is characterized by a short germination valve and by an internal dorsal ridge on the endocarp wall, a feature unknown in *Nyssa* species.

4. **Nyssa lescurii** (C. H. Hitchcock) Perkins FIGS. 3, 4, 8, 27, 28.

Carpolithes Lescurii C. H. Hitchcock, Proc. Portland Soc. Nat. Hist. **1:** 95. *pl. 1, fig. 5.* 1862.
Nyssa ascoidea Perkins, Rep. Vt. State Geol. **4:** 196. *pl. 79, fig. 96.* 1904.
Nyssa Clarkii Perkins, *ibid.* 199. *pl. 81, fig. 167.*
Nyssa crassicostata Perkins, *ibid.* 196. *pl. 79, fig. 97*, Bull. Geol. Soc. Am. **16:** 509. *pl. 86, fig. 11.* 1905, Rep. Vt. State Geol. **5:** *pl. 52, fig. 11.* 1906.
Nyssa elongata Perkins, Rep. Vt. State Geol. **4:** 197. *pl. 79, fig. 102.* 1904.
Nyssa equicostata Perkins, *ibid.* 198. *pl. 79, fig. 110.*
Nyssa excavata Perkins, *ibid.* 199. *pl. 81, fig. 166.*
Nyssa Jonesii Perkins, *ibid.* 197. *pl. 79, fig. 101*, Bull. Geol. Soc. Am. **16:** 509. *pl. 86, fig. 8.* 1905.

Nyssa lescurii Perkins, Rep. Vt. State Geol. **4:** 197. *pl. 79, fig. 100.* 1904, Bull. Geol. Soc. Am. **16:** 509. *pl. 86, fig. 9.* 1905, Rep. Vt. State Geol. **5:** 218. *pl. 52, fig. 9; pl. 57, fig. 2.* 1906.

Nyssa multicostata Perkins, *ibid.* **4:** 197. *pl. 79, fig. 103.* 1904.

Nyssa ovata Perkins, *ibid.* 196. *pl. 79, fig. 98.*

Nyssa acuticostata Perkins, *ibid.* **5:** 218. *pl. 56, figs. 16, 17.* 1906.

Nyssa rugosa sensu Kräusel, Jahrb. Preuss. Geol. Landesanstalt **39:** 387. 1918, in part, not Weber, Palaeontographica **2:** 185. *pl. 20, fig. 10.* 1852.

Description. — Endocarp 13.5–24 mm. long, 7–13.5 mm. broad; elliptical or ovate in outline; often almost rounded in cross section. Short conical projection at apex is encircled by irregular line of detachment of perianth lobes. Unilocular or bilocular (both conditions common); germination valves confined to apical half, not usually visible externally. Surface divided into 10–15 (occasionally more) mostly rounded ribs with vascular strands traversing intervening grooves. Transverse fibrous elements composing outer part of endocarp wall visible on surface of broadest ribs. Endocarp wall up to 3 mm. thick (often thickest along dorsal midline of valve); fibrous internal tissues greatly compressed. Only the thick outer cell walls of the outermost integumentary cell layer remain in the tightly shut locules.

Material. — The Paleobotanical Collections of the Botanical Museum, Harvard University, contain almost 50 specimens (all catalogued as *No. 56603*), many of them broken. Fruits of this kind have been collected only from the Brandon silt; i.e., they have not been found in the lignite body itself. Conversely, other fossil species of *Nyssa* have not been encountered in the silt, except for the two examples of *N. fissilis* mentioned earlier. This is a rather peculiar circumstance, since deposition of the Brandon silt is believed to have followed deposition of the lignite without any great intervening lapse of time (Traverse, 1955, p. 34).

It is evident that these fruits have been compressed in a different manner from the nyssas found in the lignite. Most specimens are flattened little or not at all, and there is no concavity of the dorsal region to mark the position of the germination valve. The fibrous tissue has a very dense appearance in cross section, all or most of the lumina in the elements having been obliterated.

Apparently there were no fruits of this kind among Edward Hitchcock's original collections. The first description is that of C. H. Hitchcock (1862), who was geologist for the state of Maine. The holotype (*U. S. N. M. 42072*) is the specimen figured with this description; it is one of the largest examples of *Nyssa lescurii* that we have seen (FIG. 4).

Affinities. — These fossils have features in common with fossil and modern members of the *Nyssa sylvatica* alliance, a fact which led Kräusel (1918) to unite them with the nyssas of the German brown coal as a single fossil species. *Nyssa lescurii* is distinguishable from members of that alliance, however, by means of its thick endocarp wall, its conical apical projection, and its greater size. Specimens of *N. complanata*, for instance, are not nearly so long nor so massive as those of *N. lescurii*, and it is impossible to confuse the two.

A further difference between *Nyssa lescurii* and *N. complanata* can be seen when cross sections are compared under the microscope. The locule in *N. complanata* is lined by a single layer of longitudinal fibers, surrounded by a zone of transverse fibers arranged circumferentially around the locule, but sections taken from *N. lescurii* show several layers of longitudinal fibers between the locule and the zone of circumlocular fibers. The latter arrangement seems to prevail in *N. fissilis* and *N. brandoniana* also; whereas the fruits of modern *Nyssa* species all seem to have a layer of longitudinal fibers that is only one cell thick at most places in the endocarp.

The apical region of these fruits is distinctive. Remains of the disk and of the rim along which calyx and corolla lobes were situated are not seen in other Brandon nyssas. The conical projection is suggestive of a similar structure to be found in flowers and fruits of *N. ogeche* and possibly indicates a relationship between *N. lescurii* and this modern species. The only other fossil *Nyssa* fruit that we have seen on which the vestige of a conical disk is present is *N. pachycarpa* Miki (1956), a thick-walled bilocular fruit from the Japanese Pliocene (FIG. 26). Specimens of *N. pachycarpa* tend to be more flattened than those of *N. lescurii*, but otherwise the two fossils are very much alike. The fruit shown in cross section as item N(a) of Miki's fig. 5 seems to be compressed in the same manner as the fossils from the Brandon silt, the thickness of the endocarp wall being exaggerated along the center of the valve. Item N(b) of this same figure shows a contrasting cross section from another fruit in which the valve is much thinner.

A number of fossils having points in common with *Nyssa lescurii* have been acquired from early Tertiary beds of the southern United States. Some of these have been reported in the literature as *N. wilcoxiana* Berry, a name that has been applied to an assortment of remains that differ considerably in their observable features. An impression (*U. S. N. M. 39922*) taken from the Eocene Holly Springs sand and figured by Berry in 1930 (Pl. 39, figs. 8, 9) resembles *N. lescurii* in size and shape, as also does a coalified fruit from the Claiborne flora of Smithville, Texas (mentioned by Berry in 1924, p. 89). The latter specimen is shown in our FIGS. 21 and 22. Another fossil with similar characteristics is the impression (*U. S. N. M. 35979*) from the Wilcox flora that Berry called *N. eolignitica* (1916a, Pl. 99, fig. 8). The Claiborne and Jackson floras include molds known as *N. texana* Berry that may appropriately be discussed here because of their resemblance in ellipsoidal shape and broad ribbing to *N. lescurii*. During our comparative review we have examined the material originally figured by Berry (1924, Pl. 22, fig. 5 & Pl. 39, fig. 3) and now in the National Museum as *U. S. N. M. 38332* and *38387*, and some additional collections, not previously reported, have been made available to us through the courtesy of Dr. Jack Wolfe of the U. S. Geological Survey. The latter material includes fruit molds from the vicinity of Columbus, Kentucky, and from Trinity County and Karnes County in Texas; according to Dr. Wolfe, the strata from which these collections were made are of Oligocene age. All of the molds are very much alike except for slight variations in size: Berry's figured specimens are about 30 mm. long; those from Kentucky and Trinity County are 22–27 mm. long; and the better of two molds from Karnes County is 19 mm. long (FIG. 20). Identification as *Nyssa* is secure, because casts of the locules are nicely preserved in the Trinity County material, and the outline of the germination valve is occasionally quite clear (FIG. 10). The great abundance with which the molds occur in the sandstone matrix is impressive, especially at the Trinity County locality, where molds of mastixioid fruits as well as nyssoid fruits are present (FIG. 9). The molds are larger than the lignitized *N. lescurii* fruits, and there is no evidence of an apical projection or of a second locule. Moreover, the marks of the vascular bundles in the 12–15 longitudinal grooves are thicker in the molds — perhaps owing to the former presence of multiple strands in each groove — than they are in *N. lescurii.* Some of these differences could be due to differences in preservation, however. For instance, molds would not be expected to reveal the bilocular condition if a second locule were abortive and tightly shut by compression.

Although all of the fossils mentioned in this discussion might conveniently be combined into one morphological category on the basis of superficial similarities in size and general appearance, it is doubtful whether they constitute a natural group. Judging by the relationship between ridges and vascular bundles, each of these forms is more closely related to the *Nyssa sylvatica* alliance than to *Palaeonyssa, N. brandoniana, N. fissilis,* etc. It is probable, however, that none of these forms is as closely allied to *N. sylvatica* and its antecedents as are the forms discussed under the affinities of *N. complanata.* Possibly *N. lescurii* or one of the other fossils that we have discussed here is ancestrally related to the puzzling modern species *N. ogeche*; it is also possible that all of these forms belong to evolutionary lines that have terminated in extinction.

5. **Nyssa aspratilis** Eyde & Barghoorn, nom. nov. FIG. 11.

Nyssa rugosa Miki, Jour. Inst. Polytech. Osaka Univ. D. 7: 287. *text-fig. 5, A–F; pl. 1, fig. D.* 1956, not Weber, Palaeontographica 2: 185. *pl. 20, fig. 10.* 1852.

Remarks. — The new name is applied to larger (20–24 mm. long) bilocular endocarps from the Japanese Pliocene that differ from *Nyssa pachycarpa* in the extreme rugosity of their surfaces. The name *Nyssa rugosa* cannot be used for these fruits, because this combination was validly published more than a century ago by Weber as a designation for certain fossils of the German brown coal (see Kirchheimer, 1938, for discussion and references). When we brought this point to the attention of Professor Miki during his visit to Harvard in 1959, he requested that we make the necessary nomenclatural change in our review.

The affinities of *Nyssa aspratilis* are difficult to ascertain, because the roughness of the surface obscures the marks of major vascular bundles. One specimen shows evidence of a median dorsal ridge (FIG. 11), indicating a relationship with *N. aquatica* and *N. javanica*. The ridge is not visible in other specimens that we have seen, however.

REJECTED AND DOUBTFUL FORMS

Nyssa cylindrica Perkins, Rep. Vt. State Geol. **4**: 195. *pl. 79, fig. 91.* 1904.
Nyssa gracilis Berry, Jour. Geol. **17**: 29. *fig. 10.* 1909.
Nyssa jacksoniana Berry, U. S. Geol. Surv. Prof. Paper **92**: 192. *pl. 65, fig. 7.* 1924; Ball, Bull. Agr. Mechan. Coll. Tex. IV. **2**: 168. *pl. 24, fig. 7.* 1931.
Nyssa laevigata Lesquereux, Am. Jour. Sci. II. **32**: 361. 1861, in Hitchcock, Geol. Vt. **2**: 717. 1861.
Nyssa lamellosa Perkins, Rep. Vt. State Geol. **4**: 195. *pl. 79, figs. 93, 94.* 1904.
Nyssa solea Perkins, *ibid.* 194. *pl. 78, fig. 78.*

The fossils listed by Perkins as *Nyssa cylindrica, N. lamellosa, N. laevigata*, and *N. solea* have not been disposed of in the foregoing nomenclatural treatment. *Nyssa cylindrica* Perkins is a fragmentary specimen of doubtful affinity, and *N. laevigata* Lesquereux is apparently a fossil *Symplocos*. These names were applied to fossils figured by Hitchcock in 1861 (as figs. 155 and 156, respectively); the original specimens are in the National Museum. We have not seen the original fruits figured by Perkins as *N. solea* and *N. lamellosa*, but Perkins's photographs are matched by fruits in our own collections; hence we have been able to establish the identity of both. *Nyssa solea* may confidently be referred to *Symplocos*, a genus that is well represented at Brandon by pollen as well as fruit remains. Perkins compared *N. lamellosa*, a large fruit with very thick longitudinal wings, to modern *N. ogeche*, and Reid and Chandler accepted the supposed affinity of this fossil to *Nyssa* "without hesitation" (1933, p. 431). We had not investigated the internal structure at the time Professor Miki visited the Harvard laboratory and suggested a comparison with *Melliodendron*, a styracaceous genus that is encountered in the Japanese lignites. Subsequently we prepared some microtome sections from one of two examples of *N. lamellosa* in our collection and found that the internal structure is very unlike that of *Nyssa*. A preliminary comparison with sections taken from a *Melliodendron* fruit suggests that *N. lamellosa* is indeed a close relative of modern *Melliodendron*.

In the course of our review, we have also examined two fossils from the southern United States that have been referred to *Nyssa* without adequate evidence. The Miocene impression from Virginia described and figured by Berry as *N. gracilis* is not at all convincing, and the same may be said for the single specimen of *N. jacksoniana* Berry that we were able to examine. The latter, bearing *no. 1345*, Collection of the A. & M. College of Texas, was kindly sent on loan by Dr. F. W. Gould of that institution; it is one of the fossils from the Fayette formation of Texas that Ball described as *N. jacksoniana* Berry. The eight to ten impressions seen on this specimen bear ridges that are much finer and more numerous than those of a *Nyssa* stone, and there is no sign of a germination valve. We have not been able to locate the fossils originally figured as *N. jacksoniana* by Berry.

It is unfortunate that remains of fruits of *Camptotheca* or *Davidia* have not yet been correctly identified in the fossil record. The thick walled bi- or trilocular fruit called *Camptotheca crassa* by C. and E. M. Reid (1915, Pl. 14, figs. 1, 3, 4) is not at all like the thin-walled unilocular endocarp of modern *Camptotheca*. Moreover, the hard bony wings mentioned by the Reids in their description of the fossil can hardly be compared with the "wings" of *Camptotheca*, which are the dried outer fleshy tissues of the fruit wall. According to Kirchheimer (1957, p. 184), "*Camptotheca crassa*" is a fossil *Halesia*. Pliocene beds of Japan have yielded fruits designated as *Paleodavidia multipterium* (Miki, 1956), but Professor Miki has informed us in conversation that these remains were incorrectly identified and that they will subsequently be transferred to Styracaceae.

THE PLEISTOCENE RECORD

Pollen of Nyssaceae is not often reported from Pleistocene localities that are beyond the present distributional limits of the family. European palynologists have observed that deposits of Reuverian age (accepted as upper Pliocene by most palynologists) characteristically contain pollen of *Fagus*, *Nyssa*, *Sciadopitys*, *Liquidambar*, *Carya*, *Pterocarya*, and *Tsuga*, as well as pollen of the *Taxodium* type and the *Sequoia* type; of this list, only *Carya*, *Pterocarya*, and *Tsuga* continue into overlying beds of Teglian (lower Pleistocene) age (Rein, 1955; Florschütz, 1956; Zagwijn, 1960). Similar observations have been made in Japan, and strata of uncertain age are frequently classified on this basis, those containing pollen of *Nyssa*, Taxodiaceae, and *Liquidambar* being assigned to the Tertiary, and higher strata lacking these groups being assigned to the Pleistocene.

Notwithstanding, there are a few records of nyssaceous pollen in European deposits presumed to be Pleistocene. For instance, Szafer (1954), while investigating Pliocene and Pleistocene plant remains in southern Poland, found *Nyssa* pollen in horizon "Mizerna III," which he considers a part of the oldest interglacial interval. Nyssaceous pollen has also been recorded from interglacial strata of Italy (Paganelli, 1960) and of White Russia (Makhnach, 1957; Tsapenko & Makhnach, 1959, pp. 101, 118). The possibility of redeposition of Tertiary sediments is often acknowledged by workers who encounter a limited amount of typically Tertiary pollen in a Pleistocene horizon; on the other hand, it does not seem necessary to assume that *Nyssa* was completely exterminated in Europe during the first glaciation. The argument for the continuation of *Nyssa* in Europe — at least locally — during a part of the Pleistocene would be strengthened considerably by the discovery of fruit remains in sediments known to have been deposited after the first glaciation. As far as we are aware, however, the only findings of Pleistocene endocarps have been made in the southeastern United States (Berry, 1952), where *Nyssa* trees are plentiful today.

Although the fossil record does not yet reveal the pattern of Pleistocene extermination that resulted in the present disjunct distribution of the Nyssaceae, the evidence is abundant that the family was widely distributed on the northern continents from the beginning of the Tertiary until the advent of the Ice Age. To judge from the variety of forms found in the London Clay, in the Brandon deposits, and in the Japanese Pliocene beds, the number of well-marked species has commonly been as great or greater in past epochs than it is today. We may look forward to additional paleobotanical findings — hopefully in strata of Cretaceous age — that will extend our knowledge of this interesting family deeper into the past and increase our understanding of the relationships between the Nyssaceae and other groups of angiosperms.

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EXPLANATION OF PLATES

PLATE I

Figs. 1–5. Fossil *Nyssa* stones from Brandon. Fig. 1. *N. brandoniana*, specimens figured by Hitchcock in 1861; center specimen is holotype (*U. S. N. M. 42067*). Fig. 2. *N. fissilis* from type collection, mounted on card and bearing original label; holotype on left above (*U. S. N. M. 42071*). Fig. 3. *N. lescurii*, Brandon lignite, showing variation in size and shape. Fig. 4. *N. lescurii*, holotype (*U. S. N. M. 42072*). Fig. 5. *N. complanata* from Hitchcock's collection; holotype (*U. S. N. M. 42074*) on left; fruit on right is original "*N. microcarpa*" of Lesquereux. Figs. 1–3, natural size; Figs. 4 & 5, × 2.

PLATE II

Figs. 6–12. Figs. 6 & 7. *Nyssa brandoniana*, × 2.7, Brandon lignite — note median ridge and marks of minor vascular strands on valves. Fig. 8. *N. lescurii*, × 5, from Brandon, cut to show exaggerated thickness of endocarp wall at center of valve. Fig. 9. Molds of nyssoid and mastixioid endocarps in sandstone matrix, × ½; Oligocene, Trinity Co., Tex. Fig. 10. Smaller specimen, × 1, same locality, showing locule cast of *Nyssa* fruit. Fig. 11. *N. aspratilis*, × 2.4, from Japan — note rough surface and median dorsal ridge. Fig. 12. Apical view, × 2, of three-sided *N. fissilis* (Brandon lignite), showing two open valves; third locule is often lacking in such stones.

PLATE III

Fig. 13. *Nyssa fissilis*, natural size, from Brandon lignite, showing great variation in shape and dimensions.

PLATE IV

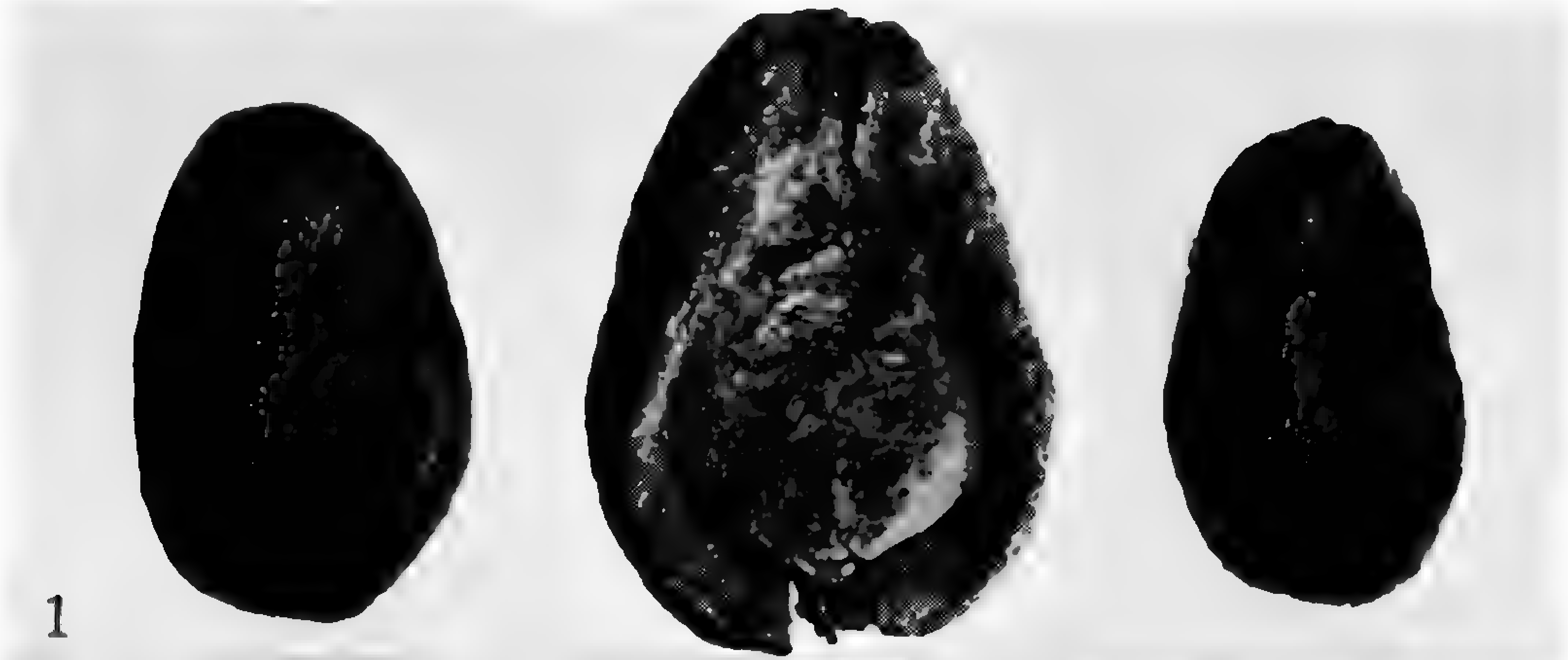
Fig. 14. Transections of bilocular *Nyssa fissilis*, × 5, from Brandon, showing thickness and fibrous composition of endocarp wall — note remains of seed in upper section.

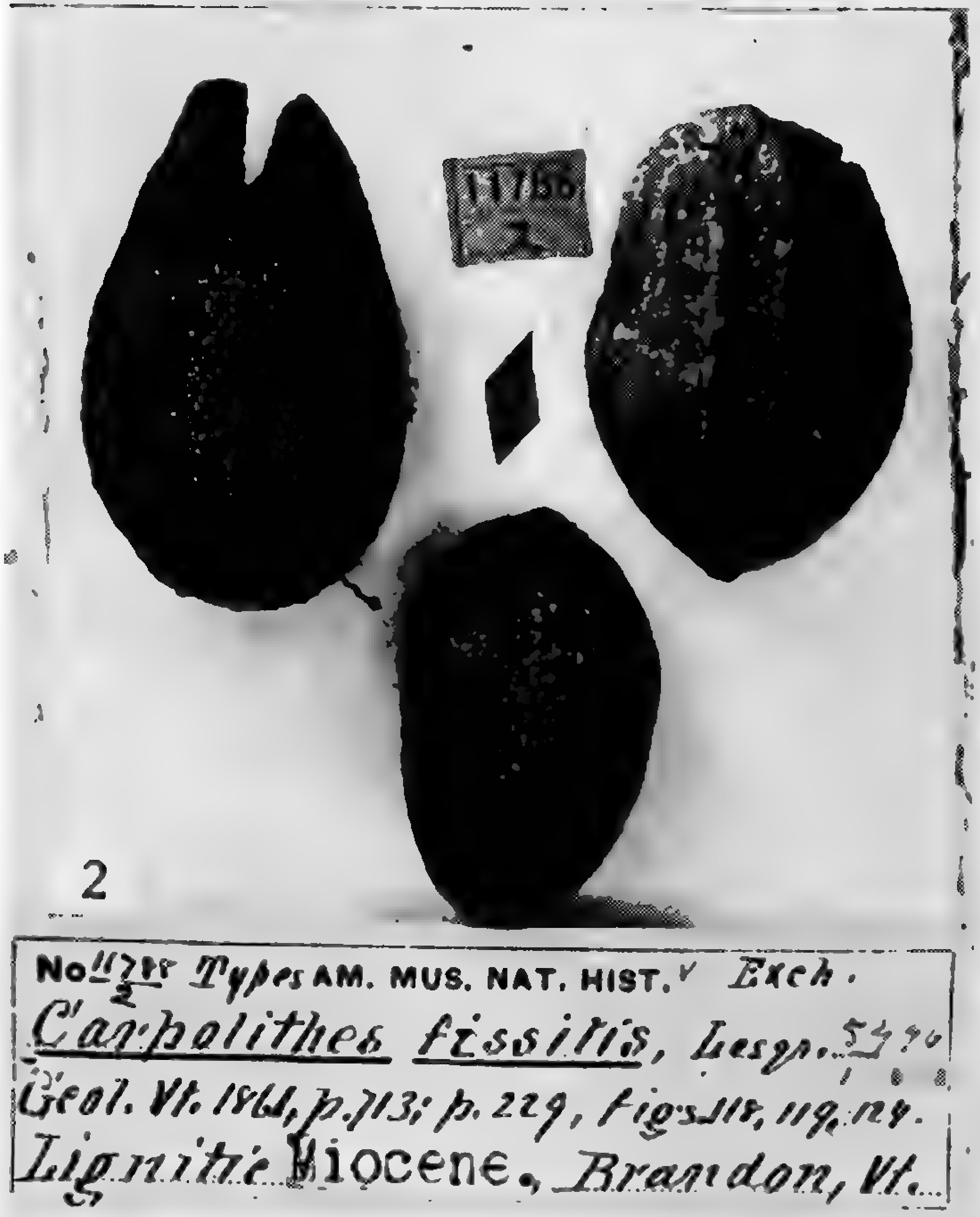
PLATE V

Figs. 15–19. *Nyssa complanata*, Brandon lignite. Figs. 15 & 16, × 2.6, show variation in size; fossils in Fig. 16 were photographed under water — note that peripheral bundles are more numerous in specimens on right than in modern *N. sylvatica*. Figs. 17–19. Transections, × 10. Fig. 17 is from a four-locular stone with a five-sided appearance owing to splitting along mid-dorsal line opposite one of the locules — note rupture and displacement of septa. Figs. 18 & 19 show basal sections of two trilocular stones; individual carpels are recognizable here.

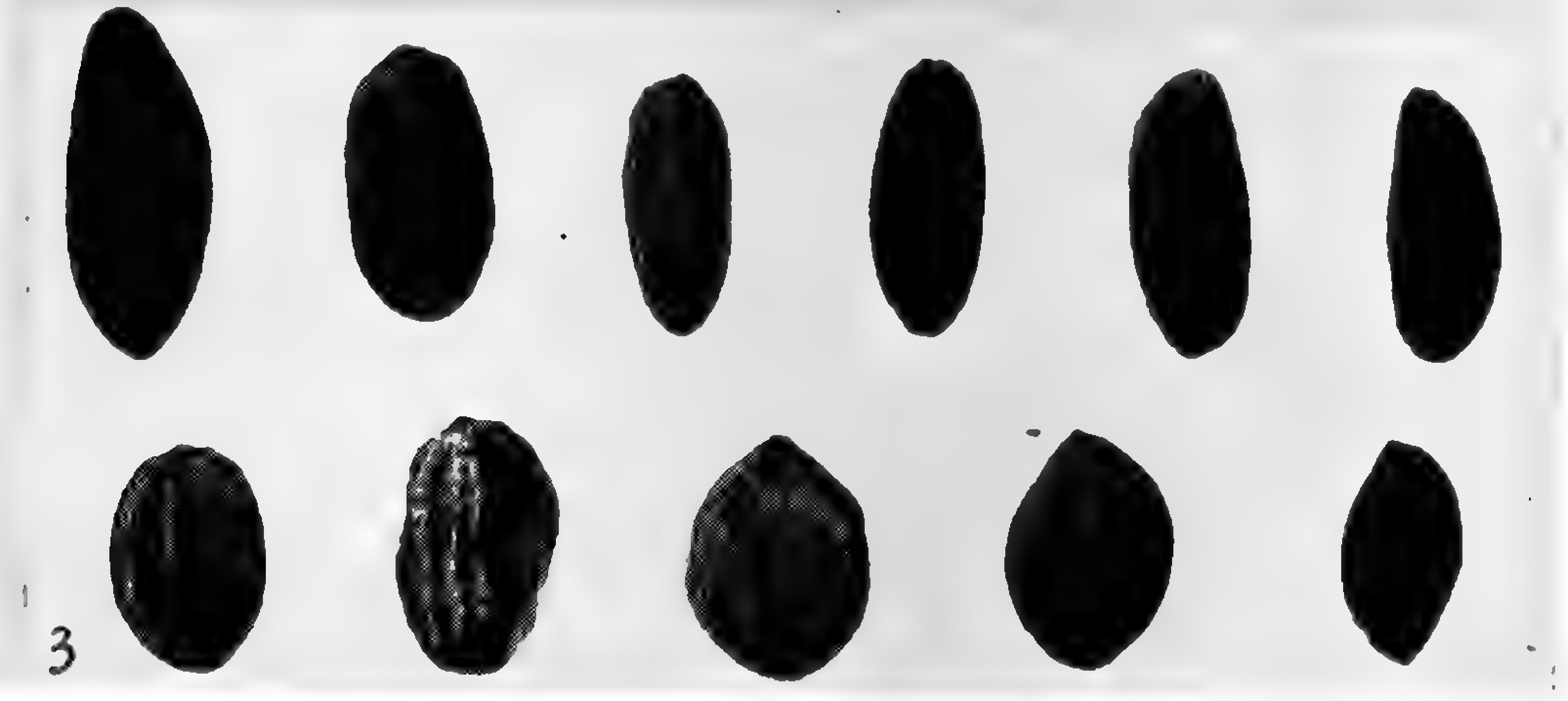
PLATE VI

FIGS. 20–28. FIG. 20. Oligocene fruit (half mold), × 2, from Karnes Co., Tex., which resembles *Nyssa lescurii* in size and shape. FIG. 21. Eocene stone, × 2, from Smithville, Tex., with similar features. FIG. 22. *The same* — opposite side. FIGS. 23–25. *N. fissilis* collected from Brandon silt (Paleobotanical Collections, Bot. Mus., Harvard *No. 56601*); these stones have undergone more intensive compression than the lignite specimens shown in FIG. 13. FIG. 23. Smallest example of *N. fissilis* known, × 2.8. FIG. 24. *The same*, apical view. FIG. 25. Another stone, × 3 — note prominence of dorsal ridges, narrow valve. FIG. 26. *N. pachycarpa*, × 2.7; Japanese Pliocene. FIG. 27. *N. lescurii*, apical end × 5, showing conical disk and rim along which perianth lobes were located. FIG. 28. *N. lescurii*, transection × 10; both from Brandon.





No. 11788/2 Types AM. MUS. NAT. HIST. ✓ Exch.
Carpolithes fissilis, Lesqx. 5490
Geol. Vt. 1861, p. 713; p. 229, figs. 118, 119, 124.
Lignitic Miocene, Brandon, Vt.



Eyde & Barghoorn, Studies of Nyssaceae, II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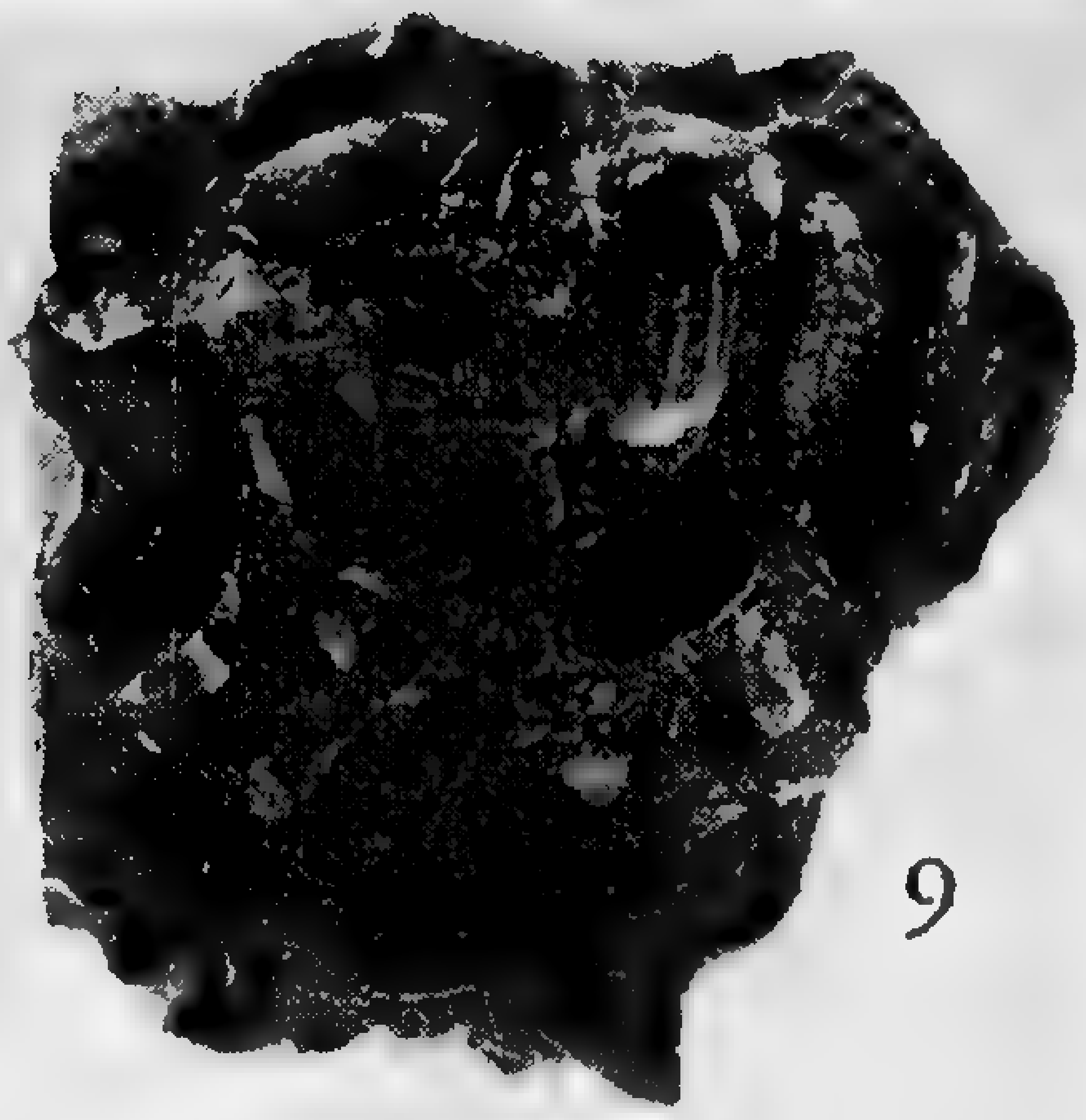
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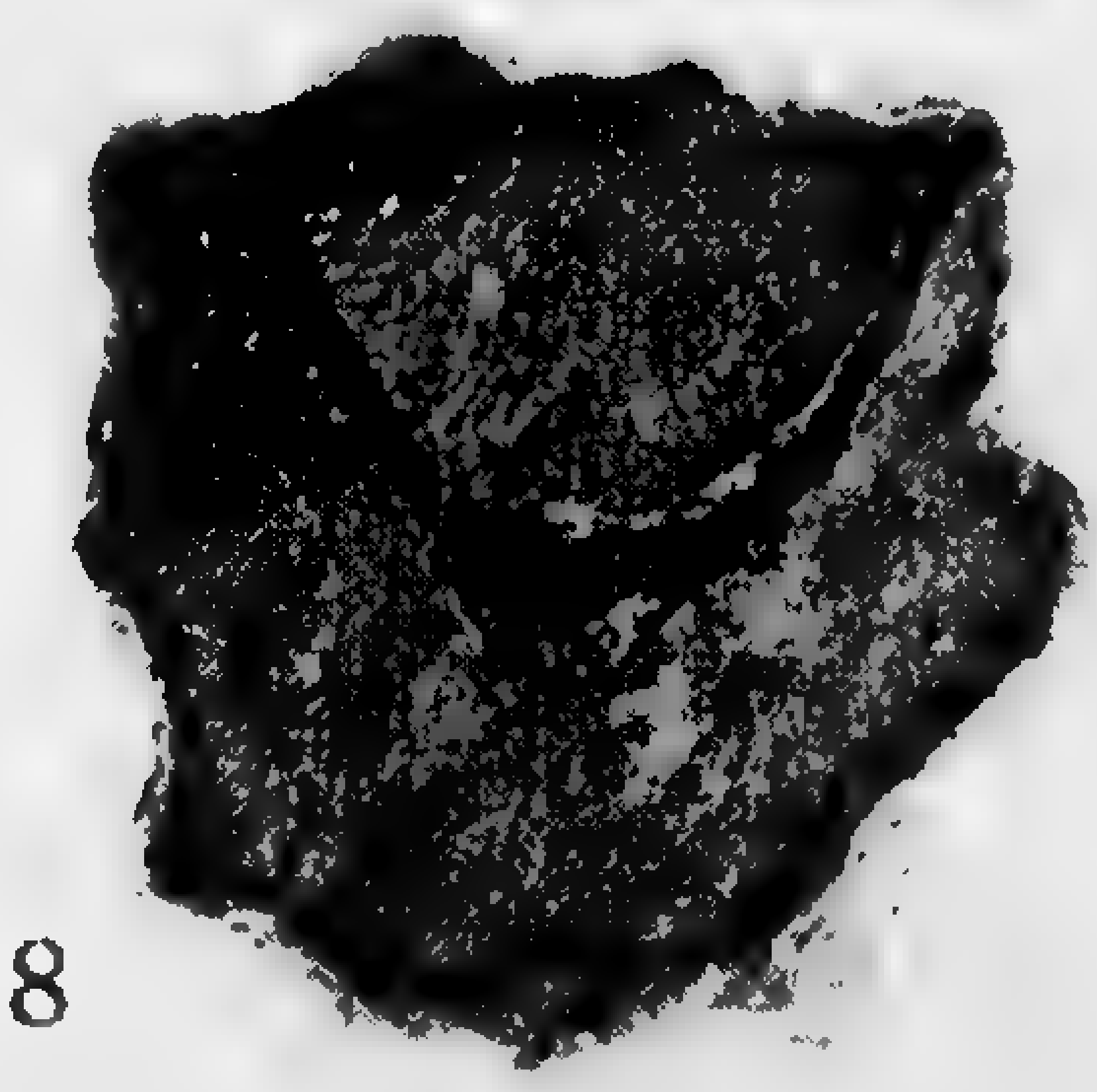
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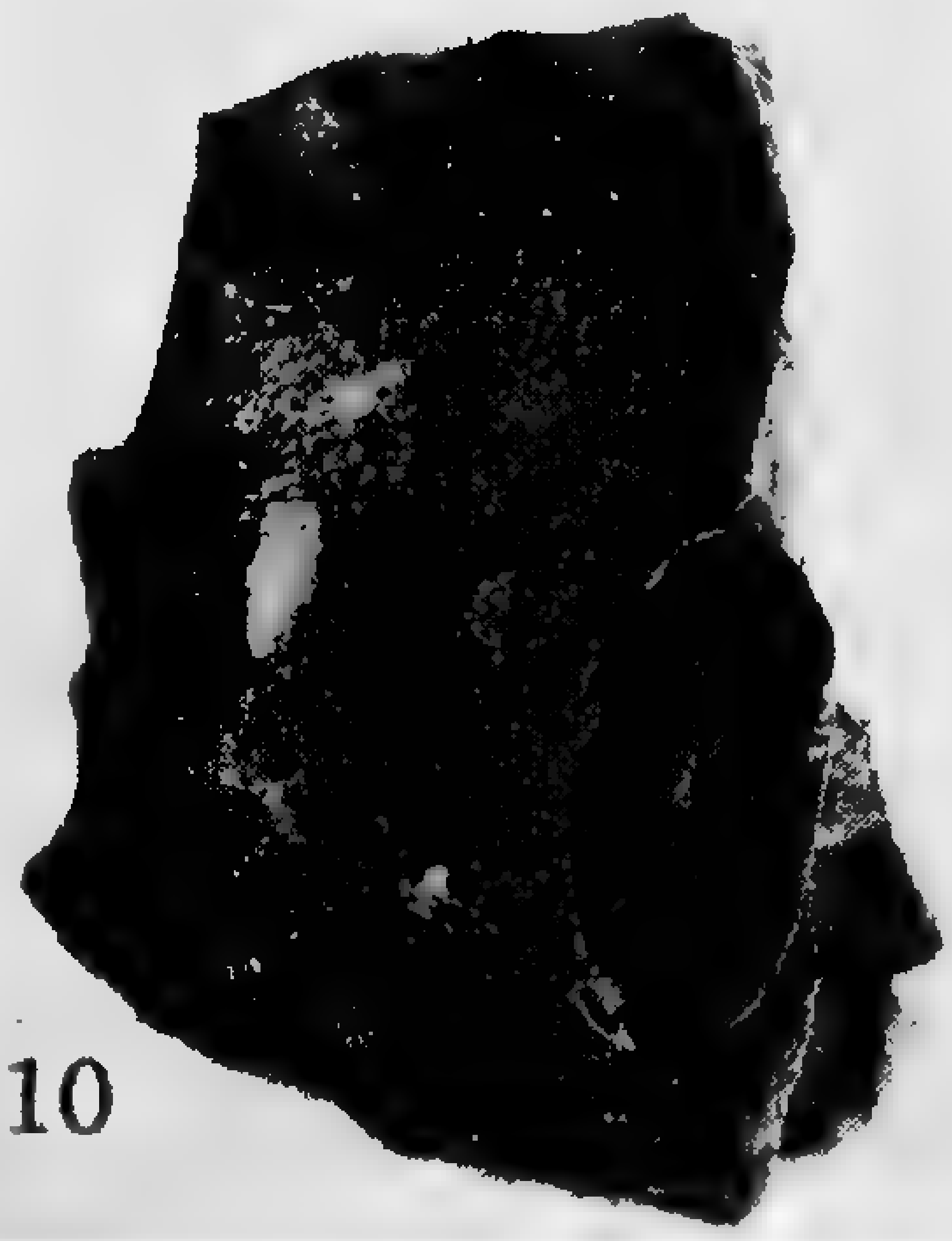
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Eyde & Barghoorn, Studies of Nyssaceae, II


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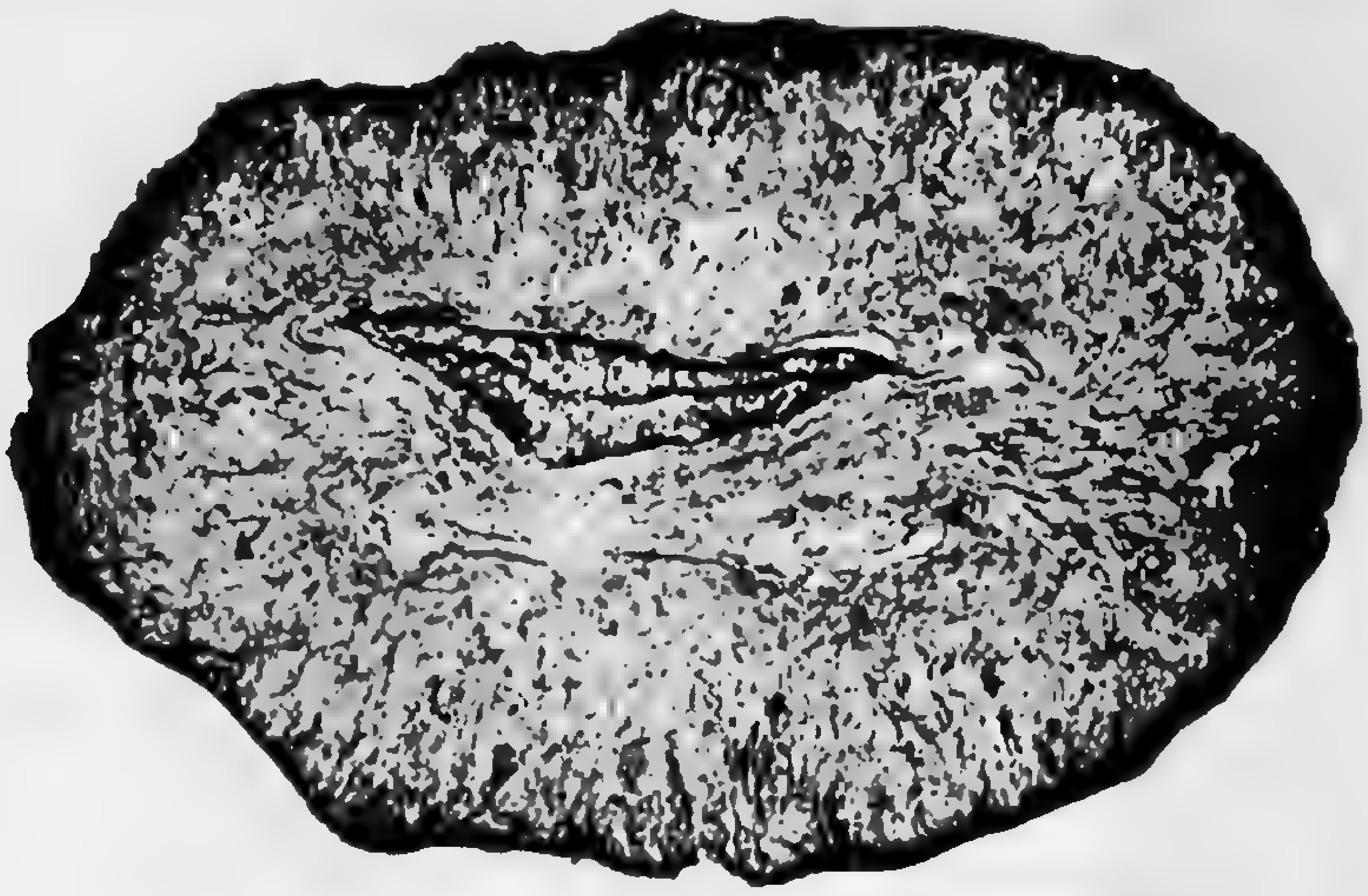

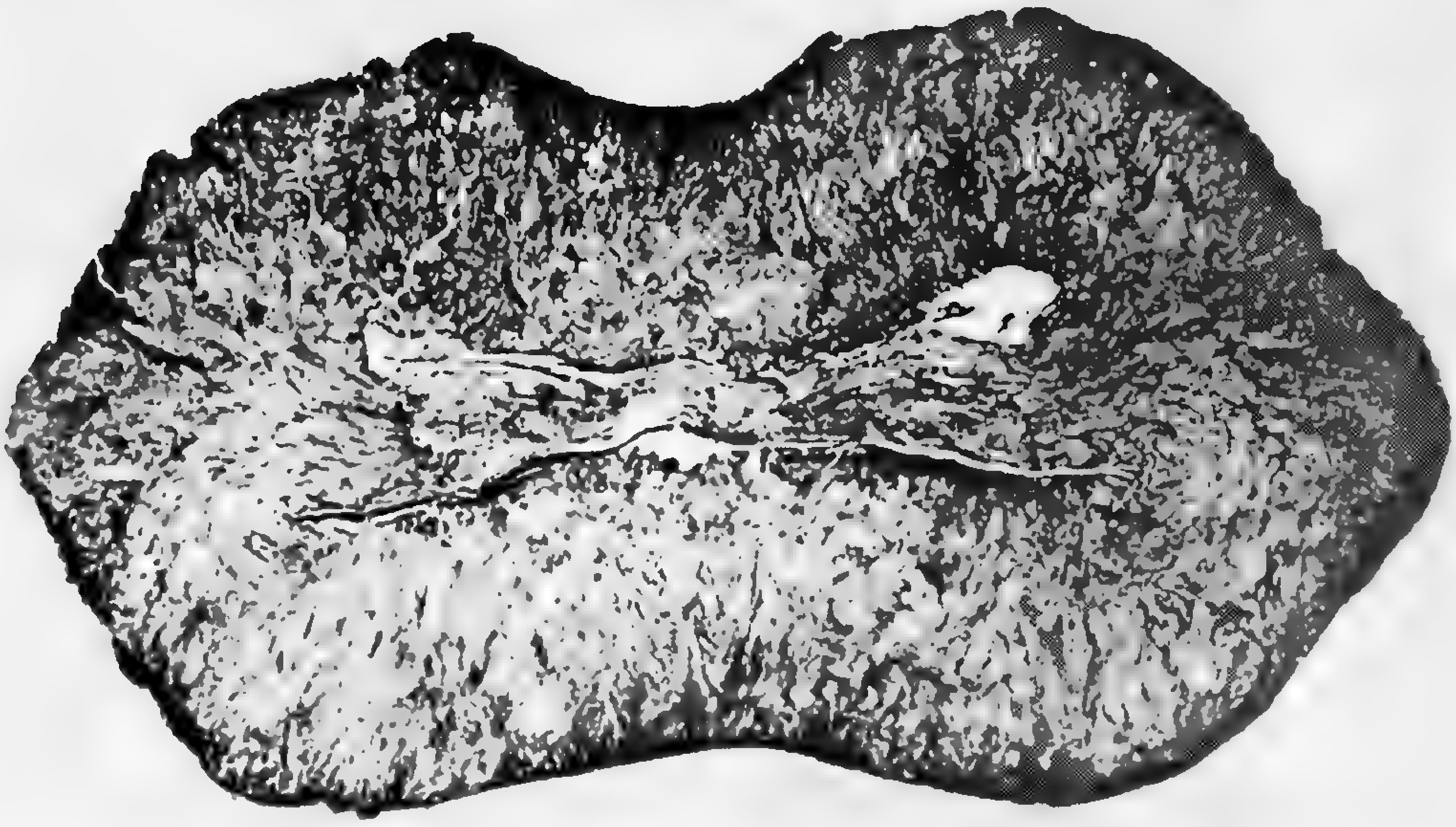

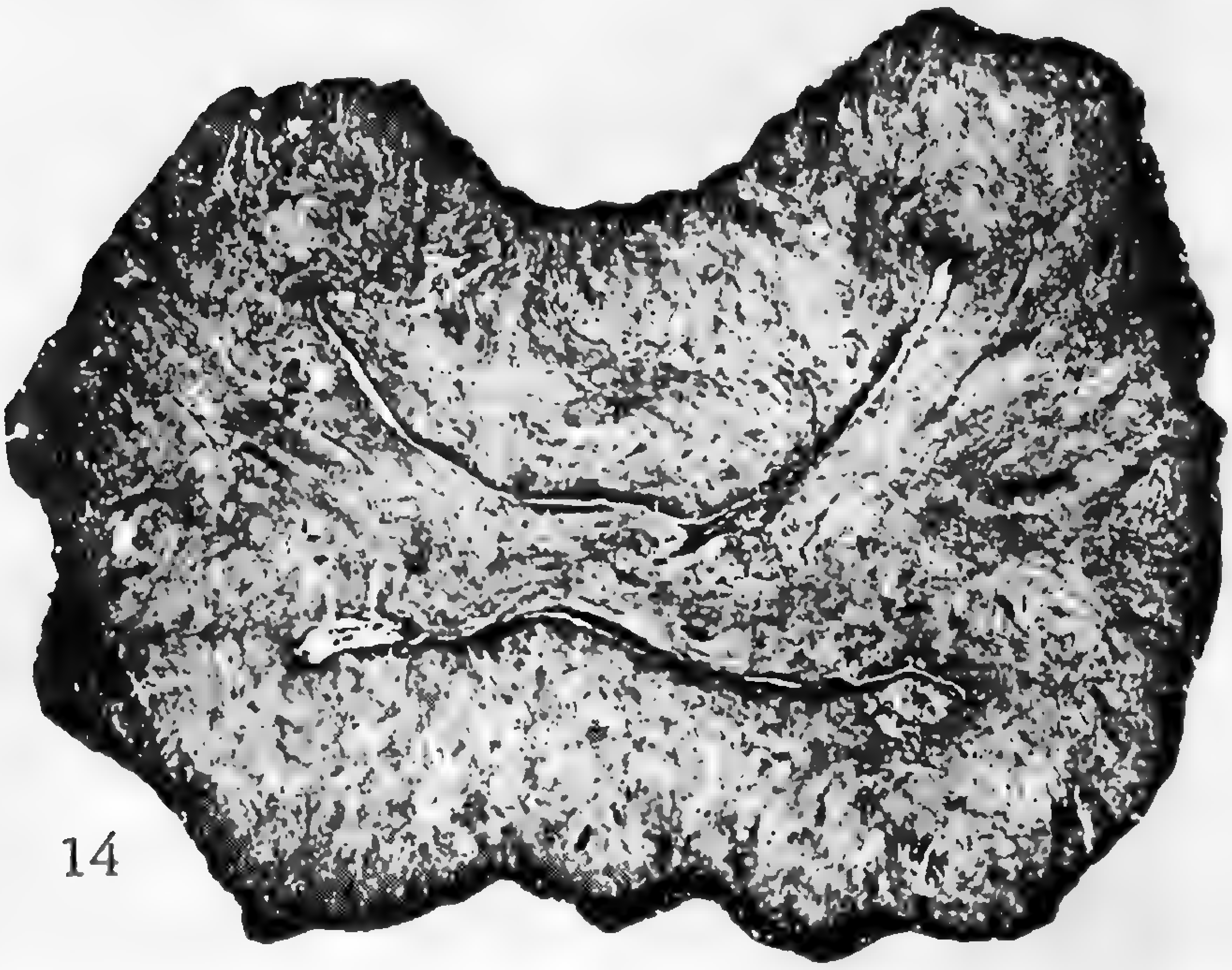

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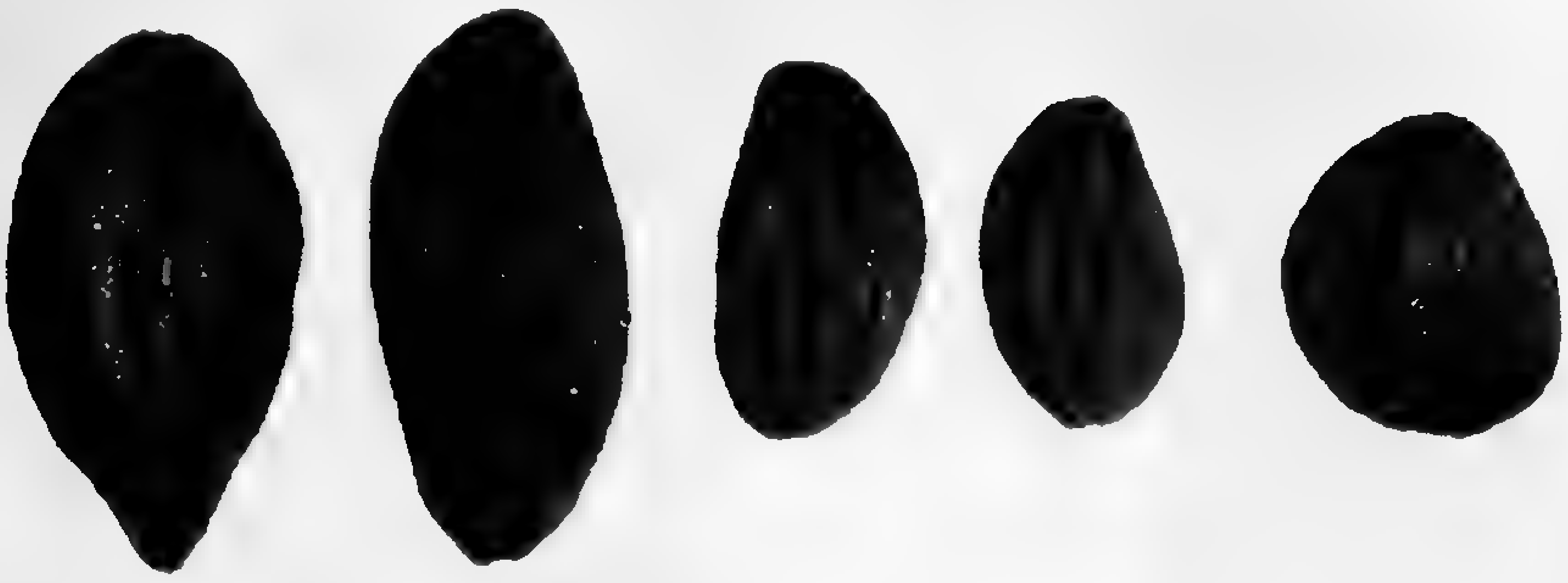
Eyde & Barghoorn, Studies of Nyssaceae, II



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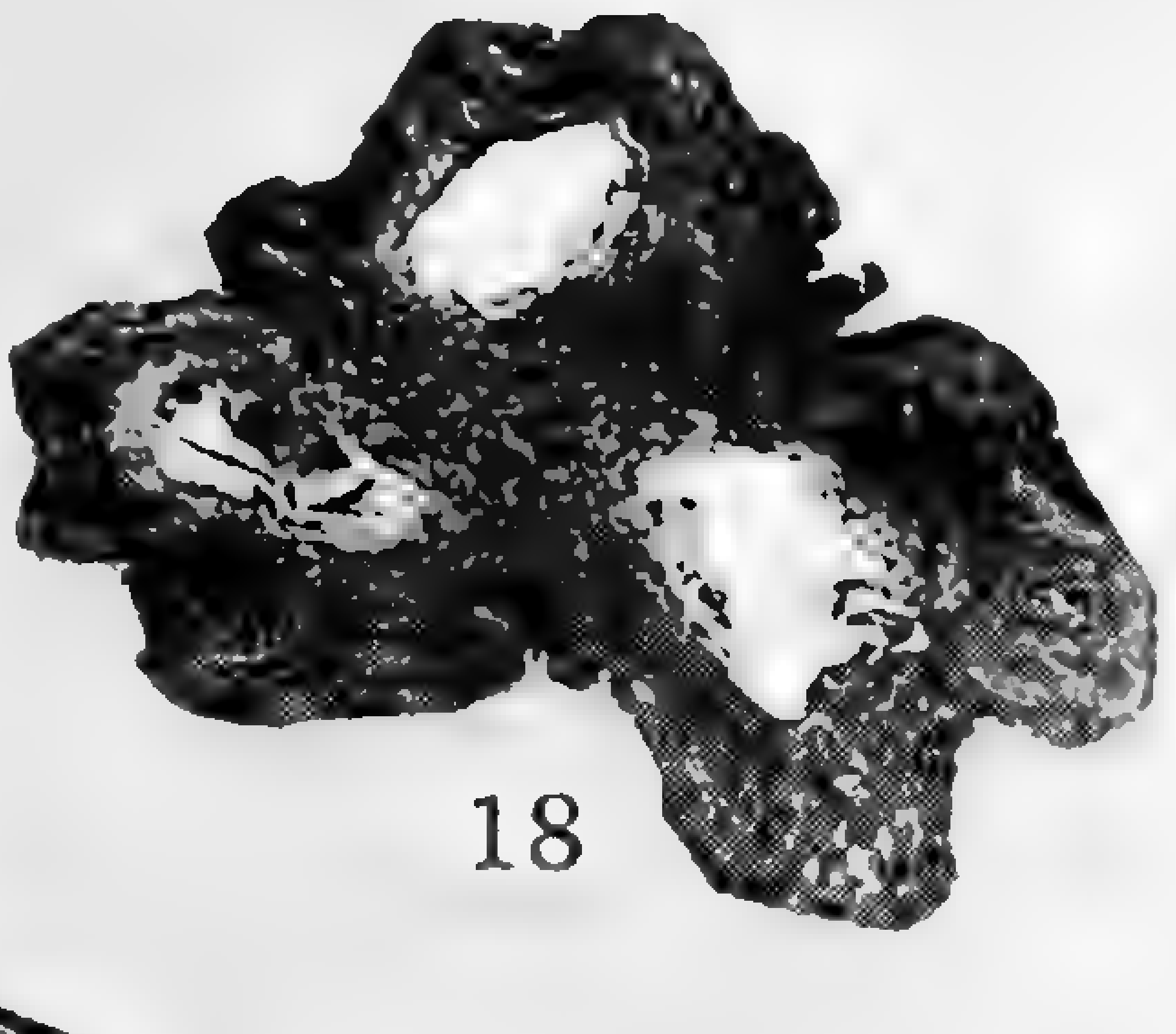

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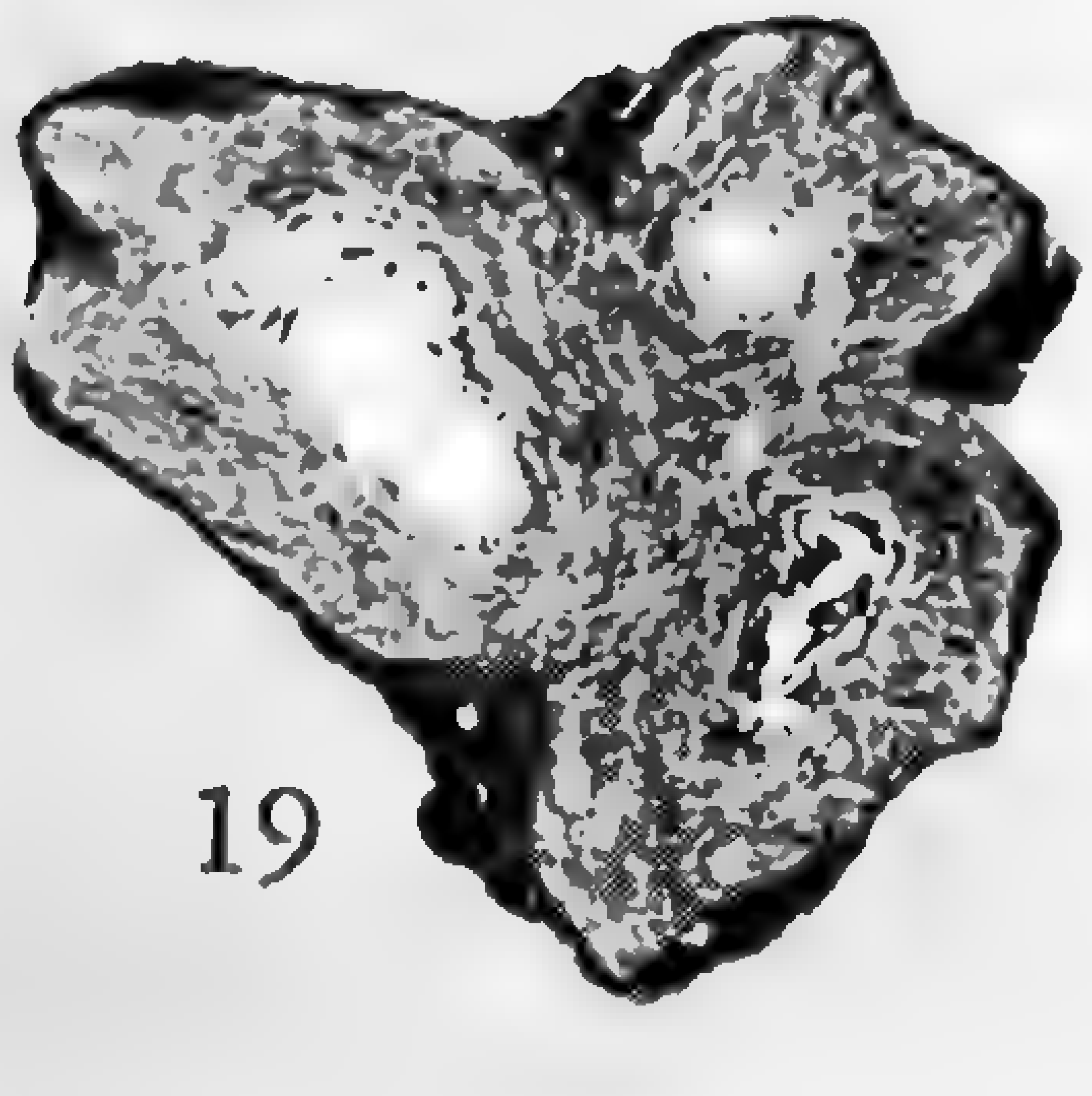

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Eyde & Barghoorn, Studies of Nyssaceae, II


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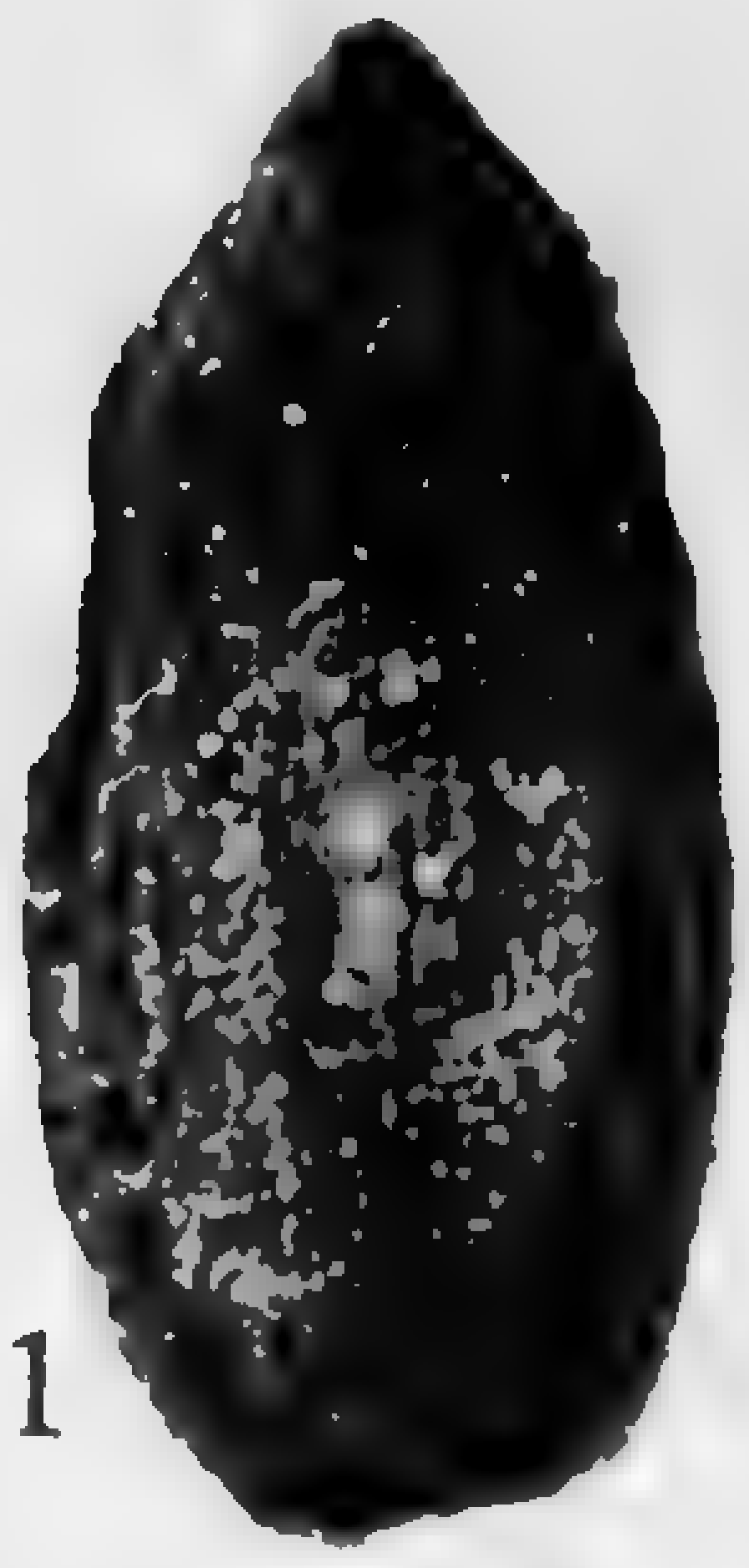
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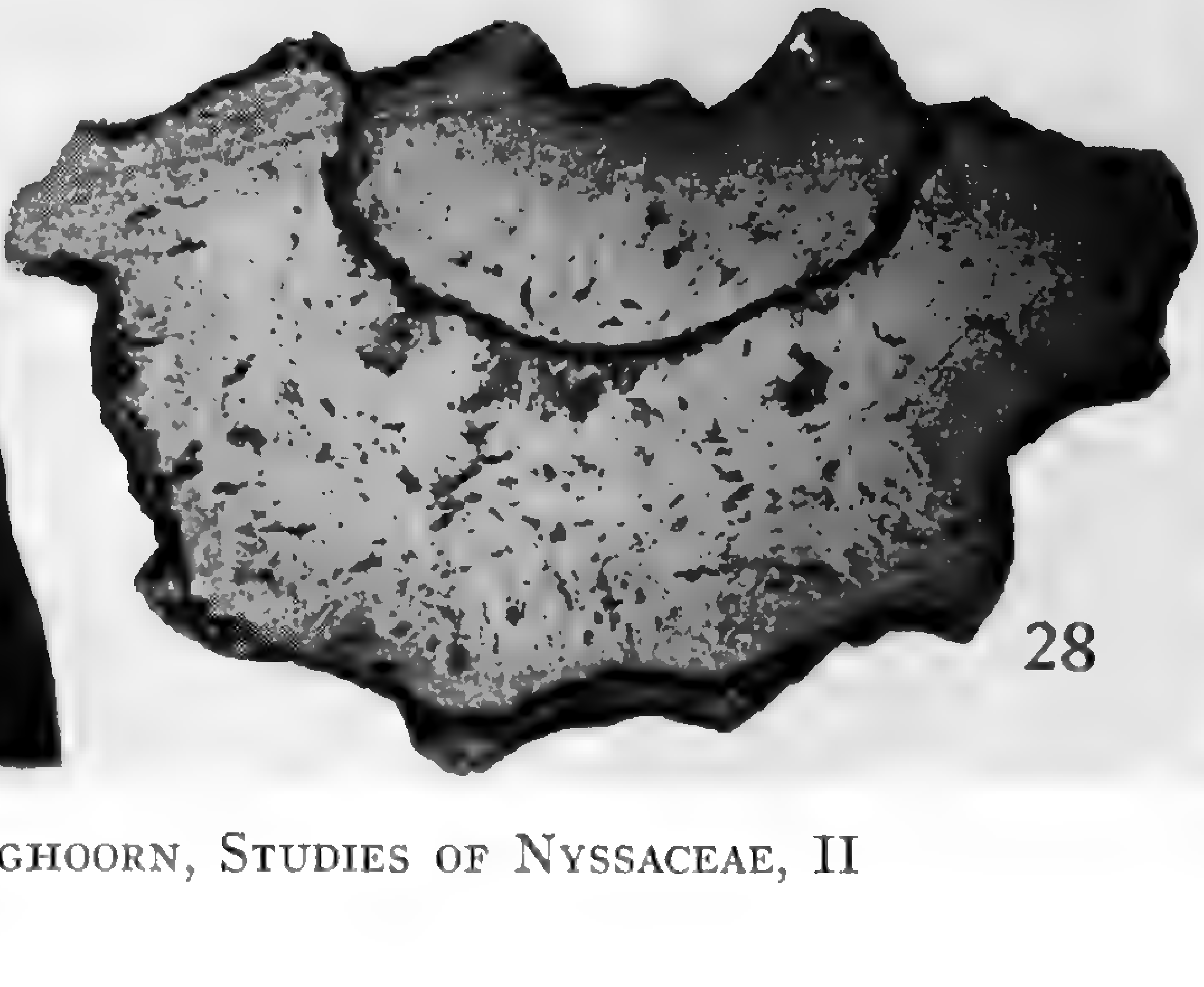
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EYDE & BARGHOORN, STUDIES OF NYSSACEAE, II

THE GENUS NESTEGIS FROM NEW ZEALAND

P. S. Green

The four representatives of the Oleaceae native to New Zealand form a closely related group which is characterized, in particular, by the lack of a corolla. Endlicher (Prodr. Fl. Norfolk. 56. 1833), when publishing a description of the first known species, under Vahl's name *Olea apetala*, proposed a separate section, *Gymnelaea*, to accommodate it, and Spach (Hist. Nat. Vég. Phan. **8**: 258. 1839) raised the section to generic rank. However Rafinesque, scoffing at the idea of an apetalous *Olea*, had proposed generic separation a year earlier than this, and validly, if sketchily, published the name *Nestegis* (Sylva Tellur. 10. 1838). Nevertheless this apetalous condition is not unique in the family for it is also found in two Asiatic species of *Olea*, in the New World *Forestiera*, and in many members of the predominantly temperate genus *Fraxinus*.

After being ignored for over a century the genus was recently revived by Johnson (as *Gymnelaea*, Contr. New S. Wales Nat. Herb. **2**: 411. 1957 and as *Nestegis* in Degener, New Ill. Fl. Hawaiian Is. 300. Nestegis. 1958). There is no doubt that the New Zealand species are not members of *Olea* in the strict sense, although until 1957 this had been their traditional classification. On the other hand the exact delimitation of *Nestegis* is not clear. The affinity of the New Zealand species lies with plants from New Caledonia which I have recently, if conservatively, treated in the genus *Osmanthus* (Jour. Arnold Arb. **44**: 268–283. 1963), with Australian plants belonging to *Notelaea*, and I believe, with members of the predominantly Malaysian genus *Linociera*. Lack of petals makes it difficult to assess affinities with these other genera whose diagnostic characters are primarily features of the corolla. Furthermore, since the four New Zealand species form, amongst themselves, a compact natural group it seems best, for the present, at least, to treat them in a separate genus, for which *Nestegis* is the oldest name.

The species included in this revision are usually described as dioecious but the situation cannot be so simply defined. From an examination of the specimens cited in the accounts which follow, it became apparent that monoecism also occurs and, in addition, flowers may be unisexual or hermaphrodite, even on the same inflorescence or branch. Most flowers were found to be unisexual, either female with nonfunctional stamens or male with abortive ovaries, but hermaphrodite flowers with a fully developed ovary or with one which is diminutive yet apparently functional have also been seen. The unisexual flowers are not uniform either. Female flowers with no stamens, with small abortive stamens, or with fully developed yet apparently empty stamens have been found, as have male flowers with ovaries of different sizes. Nor does the sexual expression appear to be constant from year to year, for in one gathering of *Nestegis cunninghamii* (*Healy 52/46*) bearing male flowers only (each with an abortive ovary) fruits from the previous year were still carried on the same shoots. Clearly, observations on the variability in sex expression are needed on living plants, carried out over a period of years, between different trees as well as between different branches and inflorescences of the same tree. The number of stamens in each flower is also variable. Two is the characteristic number, but except for *N. cunninghamii*, three and four have been seen in each species, and in *N. lanceolata* some flowers with six have been found. Nor is this variation confined to functional stamens alone for two, three, or four abortive ones may be developed in female flowers.

Like many woody plants of New Zealand the species of *Nestegis* have juvenile leaves which are quite dissimilar from those of the adult plant, leading to difficulties in identification when immature specimens are taken. There is need for more careful collecting to illustrate the authentic juvenile foliage of each species. It appears, however, that when immature, *Nestegis apetala* differs markedly from the other species in possessing leaves which may be broader than the adult and are certainly broader in proportion to their length, whereas the other species have juvenile leaves which are usually much narrower than the adult, and in proportion to their breadth, clearly narrower. Even *N. montana*, which shows the least difference between adult and juvenile foliage has immature leaves which are no broader than the adult and may be longer.

Affinities between these four New Zealand species are conjectural. *Nestegis montana* and, especially, *N. cunninghamii* both possess distinct calyx tubes which may indicate some relationship, but the latter species has inflorescences and young shoots densely hairy, often almost tomentose, with distinctive hairs broadest at the base, and more or less appressed. *N. montana* possesses a scattered puberulence in these same parts but with more slender, erect hairs different in aspect. A puberulence similar to this is exhibited by *N. lanceolata* and the New Zealand material of *N. apetala*, in which, however, the calyces lack a distinct tube. In leaf type each species is distinctive and there are few morphological characters which can be used to assess affinities.

I should like to express my grateful thanks and appreciation to the directors and curators of the cited herbaria for the loan of material or facilities for study. All the material cited has been examined, and the respective herbaria are indicated by the abbreviations published in the *Index Herbariorum*, Ed. 4, 1959. I should particularly like to thank Dr. Lucy B. Moore of New Zealand for information and helpful criticism based upon her knowledge of the species in the field, and Miss Judith Kroll for the drawing of the figures.

KEY TO THE SPECIES

1. Adult leaves up to 3 times as long as broad, elliptic to broadly elliptic, occasionally slightly ovate or lanceolate; juvenile leaves broadly elliptic to rotund, about twice as long as broad or less, broader in proportion than the

adult; primary veins of leaf, where visible, 5–7(–8) per side; shoots glabrous even when young. Norfolk Island and northern parts of North Island, New Zealand. . . . . 1. *N. apetala.*

1. Adult leaves 4 or more times as long as broad, usually narrowly lanceolate to linear, at the most (and rarely) lanceolate or elliptic; juvenile leaves narrowly lanceolate to linear, at least 6 times as long as broad, narrower in proportion than the adult; primary veins of leaf, where visible, 4–12 or more per side; shoot glabrescent or pubescent, at least when young, sometimes minutely so. New Zealand.
   2. Leaves when adult 1 cm. or more broad, lanceolate, narrowly lanceolate or elliptic, primary veins usually more or less visible; petiole (3–)4–17 mm. long.
      3. Midrib above, and primary veins, flush or slightly raised above surface of lamina, glabrous or glabrate, rarely pubescent, 4–6(–7) per side (more or less obscure in juvenile leaves); inflorescence only puberulous, sometimes sparingly so towards the top; calyx divided almost to the base, tube (where developed) less than 1 mm. long. . . . . 2. *N. lanceolata.*
      3. Midrib above, and primary veins to some extent, impressed below surface of lamina, pubescent when young, 8–10 per side (–12, or obscure in juvenile leaves); inflorescence densely pubescent, almost tomentose, at least before fruiting; calyx more or less campanulate with distinct tube 1–2 mm. long (FIG. 3). . . . . . . 3. *N. cunninghamii.*
   2. Leaves when adult less than 1 cm. broad; linear or very narrowly lanceolate, primary veins completely obscure or only barely visible; petiole 3 mm. long or less. . . . . 4. *N. montana.*

1. **Nestegis apetala** (Vahl) L. Johnson in Degener, New Ill. Fl. Hawaiian Is. 300. Nestegis. 1958.

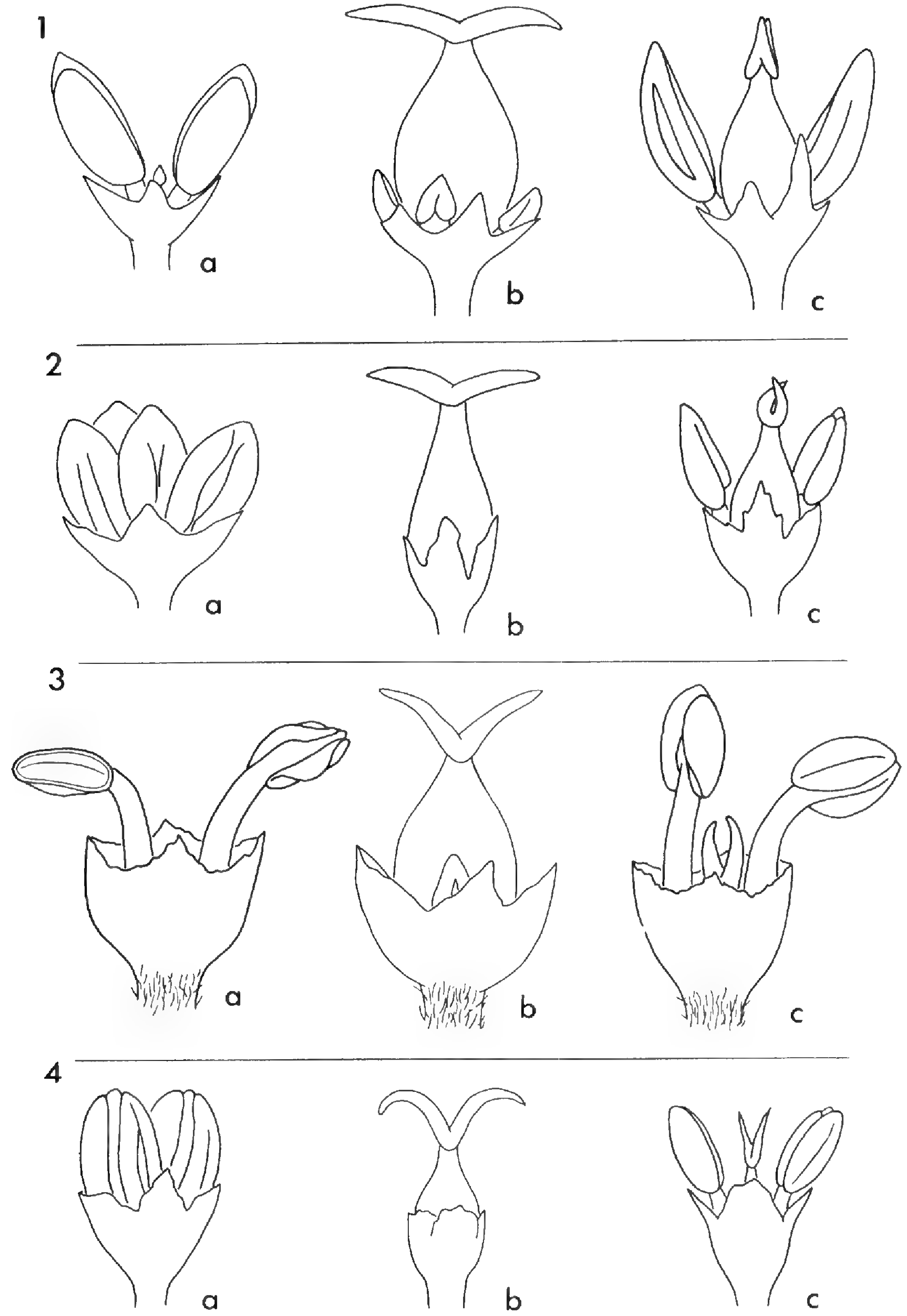
Olea apetala Vahl, Symb. Bot. **3**: 3. 1794 et Enum. Pl. **1**: 42. 1804; Willdenow, Linn. Sp. Pl. ed. 4. **1**: 46. 1797; Martyn in Miller, Gard. Dict. ed. 9. **2**: Olea, no. 5. 1807; Roemer & Schultes, Syst. Veg. **1**: 71. 1817; Endlicher, Prodr. Fl. Norfolk. 56. 1833 et Ic. Gen. Pl. *pl. 54.* 1838; G. Don, Gen. Syst. **4**: 48. 1837; A. Cunningham, Ann. Nat. Hist. **2**: 46. 1839; De Candolle, Prodr. **8**: 284. 1844; Kirk, Trans. New Zealand Inst. **3**: 165. 1871; F. Mueller, Fragmenta Phytogr. Austral. **8**: 43. 1873, *ibid.* **9**: 169. 1875; Kirk, Trans. New Zealand Inst. **14**: 375. 1882 et Forest Fl. New Zealand, 37, 38, *pls. 27, 28.* 1889; Cheeseman, Man. New Zealand Fl. 437. 1906 et ed. 2. 718. 1925; Allan, New Zealand Trees & Shrubs, 132. 1928; Cockayne & Turner, Trees of New Zealand, 139. 1928; Cranwell & Moore, Rec. Auck. Inst. Mus. **1**: 308, 309. 1935; Allan, Fl. New Zealand, **1**: 545. 1961.

Nestegis elliptica Rafinesque, Sylva Tellur. 10. 1838, *nom. illegit.*

Olea endlicheri F. Mueller, Fragmenta Phytogr. Austral. **8**: 43. 1873 et Jour. Bot. **23**: 354. 1885.

Gymnelaea apetala (Vahl) L. Johnson, Contr. New S. Wales Natl. Herb. **2**: 412. 1957; Allan, Fl. New Zealand **1**: 1025. 1961.

Shrub or small tree, 3–6 m. tall, monoecious or dioecious, branches glabrous, spreading, often tortuous (*fide* Kirk), bark grayish brown, thick and furrowed (*fide* Kirk). *Leaves* glabrous, petiole 6–14(–20) mm. long,



FIGS. 1–4, all × 7. A selection of individual flowers (a, male; b, female; c, hermaphrodite) of: 1, *Nestegis apetala*; 2, *N. lanceolata*; 3, *N. cunninghamii*; 4, *N. montana*. (1a & c drawn from *Robinson 232*; 1b, *Kirk 54*; 2a, *Kirk 203*; 2b, *Kirk s.n.* (A); 2c, *Zotov* (CHR *48665*); 3a, *Poole* (CHR *69138*); 3b, *Kirk s.n.* (GH); 3c, *Healy 53/870*; 4a, *Druce* (CHR *82400*); 4b & c *Mason 2546*).

glabrous; lamina coriaceous, elliptic to broadly elliptic, occasionally slightly ovate or lanceolate, or even rotund when juvenile, (4.5–)5–11(–12.5) cm. long by (1.5–)1.8–4(–6) cm. broad (up to 14 cm. by 8.5 cm. when juvenile); margin entire, slightly thickened, more or less undulate; apex acute or subacuminate, occasionally subapiculate, often slightly recurved; base attenuate or acute (or rounded in juvenile leaves), slightly decurrent onto the petiole; venation usually obscure, only primary veins sometimes barely visible, 5–7(–8) per side; midrib above usually flush with the lamina surface. *Inflorescence* axillary, decussate, opposite-flowered (occasionally subopposite) often borne below the leaves, 1–3 per axil, 1.5–5 cm. long, 11–21-flowered (rarely 4 flowers per node), glabrous or with minute scattered puberulence (in New Zealand plants only); bracts concave, ovate or lanceolate, 2–3 mm. long, early deciduous. Flowers unisexual or hermaphrodite (FIG. 1), pedicels 1–5 mm. long. *Calyx* glabrous with 4, unequal, often irregularly shaped or deeply erose teeth, (0.2–)0.5–1.5 mm. long. *Corolla* absent. *Stamens* 2, occasionally to 4, in hermaphrodite or male flowers, anthers 1.8–2.2 mm. long on broad filaments 0.2–0.5 mm. long; in female flowers nonfunctional 0.5–1 mm. long. *Ovary* in hermaphrodite or female flowers 1.5–3 mm. long with 2 stigmatic lobes 0.5–1.5 mm. long; in male flowers abortive, 0.5 mm. long with undeveloped stigmatic lobes. *Drupe* oblong-ovoid, slightly asymmetrical, 10–15 mm. long by 6–7 mm. broad, red (*fide* Cheeseman); endocarp hard, 0.3 mm. thick.

HOLOTYPE: New Zealand, without locality, *ex Herb. Vahl* (O).

Norfolk Island. *Ferd. Bauer* (ex. Herb. Endlicher, W); *A. Cunningham 1* (K); Nov. 1898, *Robinson 153* (NSW); 1902, *Robinson 232* (NSW); May 1904, *Robinson s.n.* (K); Nov. 1902, *Maiden & Boorman s.n.* (NSW); 11 Oct. 1962, *Ralston* (CHR *130986–130991*); *Metcalfe s.n.* (NSW).

New Zealand. NORTH ISLAND: Bay of Islands, near Motuaroa, Dec. 1769, *Banks & Solander s.n.* (E); Bay of Islands, near Oke Bay, Dec. 1956, *Atkinson* (CHR *97054A & B*); Aorangi Island, Poor Knights Islands, 24 Apr. 1961, *Newhook* (CHR *97311 A & B*); Big Chicken, Hen and Chicken Islands, coastal forest, 18 Feb. 1962, *Reynolds* (CHR *12908 A & B*); Taranga Island, *Kirk 517* (GH), March 1869, *Kirk 166* (K), 1875, *Hector s.n.* (GH, P) and *Cheeseman s.n.* (NSW, NY); Great Barrier Island, *Kirk s.n.* (GH) and Jan. 1868, *Kirk 54* p.p. (K); Nelson Island, May 1868, *Kirk 54* p.p. (K). Without definite locality, *ex Herb. Vahl* (holotype, O).

Since, at the time of its first description, the most distinctive feature of this species was its lack of corolla, the epithet *apetala* seemed most appropriate. However, when later collections from New Zealand revealed other species without petals a certain amount of confusion arose which also involved the type locality. Allan (Fl. New Zealand, 1: 545. 1961) gives this locality as Norfolk Island, but Vahl's holotype is labelled "Nova Zelandia" and there is no reason to doubt that this is correct and that the specimen was collected on either Captain Cook's first or second voyage. However, the first full description and illustration were published by Endlicher and based on the plant from Norfolk Island. Mueller, without indicating how they may be distinguished, separated the Norfolk Island plant as a species, *Olea endlicheri*, but on the basis of geographical distribution alone this action is not justified. The fact that all the species from New Zealand are apetalous misled several early workers, a point further discussed under *Nestegis cunninghamii*, the species with which there seems to have been the most confusion.

To judge from the material of *Nestegis apetala* available for this investigation there is one minor character by which the Norfolk Island plant may be distinguished from the New Zealand material. The inflorescences in all the material from the former area have proved to be completely glabrous whereas every specimen examined from New Zealand has a minute and scattered puberulence on the inflorescence rachis. It would be interesting if this difference could be checked on an even wider range of material.

Nestegis apetala has an inflorescence and flowers similar to *N. lanceolata*, although the inflorescence is more robust. Of all four species *N. apetala* is distinct in having leaves which are the broadest in proportion to their length, a character especially evident in the juvenile foliage, which, as has been pointed out above, is unique within this group. Although occurring in Norfolk Island, *N. apetala* is the least widely distributed of the species in New Zealand, occurring only in the northern parts of North Island as far south as Great Barrier Island and now, I am informed by Dr. Lucy B. Moore, known almost exclusively from islands off the Auckland east coast where it is, in places, locally dominant in low coastal forest.

2. **Nestegis lanceolata** (Hooker f.) L. Johnson in Degener, New Ill. Fl. Hawaiian Is. 300. Nestegis. 1958.

Olea lanceolata Hooker f. Fl. Nov.-Zeland. **1**: 176. 1852 et Handbook New Zealand Fl. 186. 1864; Kirk, Trans. New Zealand Inst. **14**: 377. 1882 et Forest Fl. New Zealand, 107, 108, *pls. 60, 61.* 1889; Laing & Blackwell, Plants New Zealand, 334. 1906 et ed. 5. 355. 1950; Cheeseman, Man. New Zealand Fl. 438. 1906 et ed. 2, 719. 1925, et Ill. New Zealand Fl. **2**: *pl. 134.* 1914; Allan, New Zealand Trees & Shrubs, 132. 1928; Cockayne & Turner, Trees of New Zealand, 93. 1928; Bailey & Bailey, Hortus, 423. 1930, et Hortus Second, 507. 1941; Gudex, Trans. Roy. Soc. New Zealand, **85**: 58. 1957; Allan, Fl. New Zealand **1**: 546. 1961.

Gymnelaea lanceolata (Hooker f.) L. Johnson, Contr. New S. Wales Natl. Herb. **2**: 412. 1957; Allan Fl. New Zealand, **1**: 1025. 1961.

Tree to about 15 m. tall (*fide* Kirk) with trunk to about 1 m. in diameter (*fide* Kirk), monoecious or dioecious, branches puberulous. *Leaves* glabrous, petioles (3–)4.5–11 mm. long, puberulous, at least when young; lamina thickish or coriaceous, (narrowly ovate to) lanceolate or narrowly lanceolate (to very narrowly lanceolate or almost linear in juvenile leaves), (3.5–)5–9(–11) cm. long by (0.7–)1–2.5(–3.5) cm. broad (6–13 cm. long or more by 0.4–0.8 cm. broad in juvenile leaves); margin entire, scarcely thickened; apex acute; base attenuate, acute, slightly decurrent onto the petiole; venation with primary veins usually visible, 4–6(–7) per side (more or less obscure in juvenile leaves), sometimes obscurely reticulate, midrib above flush or slightly raised above lamina surface. *Inflorescence* axillary, decussate, 1–3 per axil, 1–3 cm. long, 11–17-flowered, somewhat slender, puberulous, sometimes sparingly so towards the apex; bracts ovate to lanceolate, slightly concave, 1–2 mm. long, early deciduous. Flowers unisexual or hermaphrodite (FIG. 2), pedicels 0.5–3 mm. long. *Calyx* glabrous, deeply divided almost to the base into 4 unequal, irregular, often somewhat erose teeth, 0.5–1.5 mm. long, or with a tube at the most 0.5 mm. long, often smaller in the male than the female. *Corolla* absent. *Stamens*, in male flowers 2–4(–6), anthers 1–2 mm. long with a scarcely discernible blunt appendage; filament broad 0.3–0.5 mm. long; in female flowers a scarcely discernible subtriangular stump 0.1 mm. high or 2(–4) non-functional anthers 1.5–2 mm. long, acute, filament broad 0.5–1 mm. long. *Ovary* in female flowers 1.5–3 mm. long with 2 stigmatic lobes 1–1.5 mm. long; in male flowers abortive, more or less conical, 0.3–1 mm. high. *Drupe* ellipsoid or oblong-ellipsoid, 8–11 mm. long by 4–5 mm. broad, crimson (*fide* Hooker), red, or orange (*fide* Cheeseman); endocarp hard 0.3–0.6 mm. thick.

LECTOTYPE: New Zealand, without locality, *Colenso? or Sinclair? s.n.* (K — see below).

New Zealand. NORTH ISLAND: "Radar" bush, Te Paki Station, Far North, forest, 31 Dec. 1953, *Moore* (CHR *83637*); Kaiaka, Dec. 1902, *Carse s.n.* (CHR *11046*, O); 3 m. W. of Broadwood, Hokianga Co., 10 Nov. 1961, *Melville 5284* (CHR *130633*); Waipoua Forest, forest with high canopy, 7 Nov. 1961, *Moore* (CHR *129162–3*); Waipoua, kauri forest, 7 Nov. 1961, *Melville* (*5210*) *& Moore* (CHR *130563*); Warkworth, without collector (CHR *7842*); Warkworth, N. Auckland, Jan. 1930, *Moore* (CHR *40594*); Mahurangi, *Kirk s.n.* (A); Simpson's Bush, Warkworth, 3 Jan. 1946, *Moore* (CHR *52896*); Cowan's Bay Road, Rodney County, bush edge, 4 Jan. 1962, *Moore* (CHR *125571–2*); Little Barrier Island, 19 Feb. 1905, *Cockayne 9144* (E); Great Barrier Island, *Kirk 83 & s.n.* (K); Cape Colville, Stony Bay, 193–, *Moore* (CHR *40604*); Auckland, May 1947, *Gibbs* (CHR *118760*); Swanson, rain forest, April 1933, *Mason* (CHR *22016*); Huia River, Manukau, April 1871, *Cheeseman s.n.* (E, NY); Thames range, *Tryon s.n.* (BRI); Thames Gold Field, *Kirk s.n.* (GH); Tairua, Thames, *Adams s.n.* (K); Tolago Bay, Aug. 1929, *Meebold 4960* (NY); Ohakune Track, Mt. Ruapehu, 22 Oct. 1945, *Mason* (CHR *54046*); Tarawera, Hawke's Bay, 2 Feb. 1909, *Petrie* (CHR *118759*); Ruahine-Cook botanical district, Merry Hill, Feilding, in rain forest, March 1926, *Allan* (CHR *11040*, GH); Feilding, without collector, (CHR *11059*); forest near Feilding, Dec. 1924, *Allan s.n.* (NY); Mauriceville, near Mt. Bruce, 5 Feb. 1945, *Zotov* (CHR *48665*, *77632*, *& 112476*); Western Lake Reserve, Wairarapa, 4 May 1958, *Moore* (CHR *129157*); Lake Pounui, S. W. Wairarapa, forest remnant, 3 Sept. 1960, *Macmillan* (CHR *129160*); Featherston, Wairarapa, Dec. 1959, *Moore* (CHR *129156*) and 20 May 1960, *Taylor* (CHR *129287*); Featherston, Wairarapa, Abbott's Creek, forest remnant, 17 March 1953, *Healy 53/520* (CHR *83229*); Maidstone Park, Upper Hutt, 17 Dec. 1952, *Healy 52/469* (CHR *84664*), Dec. 1952, *Healy 52/46* (CHR *88458 A–D*), 31 Dec. 1952, *Healy 52/521* (CHR *84661 A–C*), and 10 Jan. 1953, *Healy 53/71* (CHR *84662 A–E*); near Upper Hutt, beech forest remnant, 3 Feb. 1953, *Healy 53/245* (CHR *83228 A–D*); back of racecourse, Trentham, forest remnant, stony flats, 7 Jan. 1953, *Healy 53/32* (CHR *84660 A & B*); Animal Research Station, Wallaceville, forest remnant on stony flats, 2 Apr. 1953, *Healy S/53/680* (CHR

82995 & 88442 A & B) and 18 Dec. 1952, *Healy 52/476* (CHR *84663 A–C*); Wellington, in bush, 600 m., rare, March 1909, *Travers s.n.* (P). Without locality: 1826 *A. Cunningham 65 & s.n.* (K); *Sinclair s.n.* (BRI, E).

SOUTH ISLAND: Maitai Valley, Nelson, *Kirk s.n.* (BRI); Northern Wairoa River, *Cheeseman s.n.* (K).

When describing *Nestegis lanceolata* for the first time Hooker distinguished two varieties without naming them: "var. α, foliis ovato-lanceolatis 3-uncialibus" and "var. β, foliis anguste lineari-ellipticis 2-uncialibus." Kirk (Trans. New Zealand Inst. **14**: 377. 1882) gives additional characters for the two varieties, which he calls primary forms: "*a*. Bark of twigs whitish, prominently warted, leaves ovate, lanceolate, acuminate, segments of calyx linear," and "*b*. Bark of twigs dark, scarcely warted, leaves linear-lanceolate, racemes more slender than in var. *a*, segments of perianth broader." Certainly some of the specimens I have examined do have larger leaves than others, but two distinctly different leaf sizes do not seem evident and Allan in his recent *Flora* states that the distinction between the forms is not at all clear cut. In fact, when the length of leaves was measured on all the gatherings examined and cited above, it was found that there was continuous variation in this character and no disjunction into two groups whether the largest, smallest, or a typical leaf was chosen from each specimen; nor was any geographical pattern evident in the localities from which the larger leaved specimens had been collected. An examination of the inflorescences and calyces did not reveal any characters for the separation of two distinct entities either. However, observations in the field are required and one possibility which calls for investigation is the chance that the larger leaved plants are the result of hybridization between this species and another. According to Cockayne and Allen (Ann. Bot. **48**: 38. 1934) "hybrids [with *Nestegis cunninghamii*] appear to be not uncommon in damaged forest" in the south of North Island where the two species are said to be common. Since no obvious hybrid material either of this or any other parentage has been seen in this investigation, it would be valuable to know whether these hybrids are sterile or fertile and, if the latter, to what degree. Any hybrid with *N. cunninghamii* might be expected to exhibit the characteristic prominent golden (at least in dried material) hairs of this species but these have not been seen in the variable material of *N. lanceolata*.

According to Allan (Fl. New Zealand **1**: 546. 1961) the fruit of *Nestegis lanceolata* usually has two seeds per locule but in all the fruiting specimens I have seen there has been only a single seed, which is characteristic of all the genera closely allied to *Olea*.

The distribution of *Nestegis lanceolata* is wide in the North Island and in the South Island it has been recorded from the Wairoa Valley and from Kaituna and the Rai Valley (Cheeseman, Man. Fl. New Zealand, ed. 2. 719, 1925). The native names are Maire and White Maire.

In the herbarium at Kew there are two sheets named *Olea lanceolata* by Hooker from which the lectotype may be selected. These bear eight specimens representing a mixture of gatherings, with four or possibly six entities between them; one sheet is annotated "var. α" (although this was later deleted) and the other "var. β." In his diagnosis Hooker describes only the flower and not the fruit; in fact, the fruit is hardly mentioned at all in the protologue, so I have excluded the fruiting specimens from consideration in the choice of lectotype. There then remain four specimens, two with the larger leaves which would correspond to Hooker's var. α and two with the smaller leaves of var. β. In light of the reference by Cockayne and Allan (mentioned above) to hybridization, I have excluded the larger leaved specimens because of the nomenclatural confusion that would result should they be shown to represent plants of hybrid origin. Two specimens remain, both on the sheet labelled "var. α." One, a mere scrap, is contained in a paper capsule labelled "Flowers of 2424" (a Colenso number?) the other, a slightly more adequate specimen in the bottom left-hand corner, is the one I have selected as lectotype. It is not individually labelled and may possibly be further material of no. *2424* or, alternatively, it may be the Sinclair material cited by Hooker in his protologue. There appears to be no material labelled as Sinclair's at Kew but this specimen certainly matches very closely sheets of Sinclair in the Edinburgh and Brisbane herbaria. Whoever collected it, it represents var. β and bears leaves 4 to 6 cm. long and a few male flowers with dehisced anthers.

3. **Nestegis cunninghamii** (Hooker f.) L. Johnson in Degener, New Ill. Fl. Hawaiian Is. 300. Nestegis. 1958.

Olea cunninghamii Hooker f. Fl. Nov.-Zeland. **1**: 175. 1852 et Handbook New Zealand Fl. 186. 1864; Buchanan, Trans. New Zealand Inst. **6**: 221. 1874; Kirk, Trans. New Zealand Inst. **14**: 376. 1882 et Forest Fl. New Zealand, 103–105. *pl. 59 & 59B.* 1889; Laing & Blackwell, Plants New Zealand, 334, 335. 1906 et ed. 5. 355. 1950; Cheeseman, Man. New Zealand Fl. 437. 1906 et ed. 2. 718. 1925; Allan, New Zealand Trees & Shrubs, 132. 1928; Cockayne & Turner, Trees of New Zealand, 92, 154. 1928; Bailey & Bailey, Hortus, 423. 1930 et Hortus Second, 507. 1941; Gudex, Trans. Roy. Soc. New Zealand, **85**: 58. 1957; Allan, Fl. New Zealand, **1**: 545. 1961.

Gymnelaea cunninghamii (Hooker f.) L. Johnson, Contr. New S. Wales Natl. Herb. **2**: 412. 1957; Allan, Fl. New Zealand, **1**: 1025. 1961.

Tree to 20 m. tall (*fide* Kirk) with trunk to 1.5 m. in diameter (*fide* Kirk), monoecious or dioecious, branches pubescent or becoming glabrous with age. *Leaves* glabrous, petiole (4–)7–14(–17) mm. long, pubescent, at least when young; lamina coriaceous, narrowly lanceolate or sometimes narrowly ovate or elliptic (more or less linear-lanceolate when juvenile), (5.5–)7–12(–21) cm. long by (1.2–)1.5–3(–4.5) cm. broad (7–23 cm. long by (0.4–)0.7–1.6 cm. broad when juvenile); margin entire, slightly thickened; apex acute or occasionally almost obtuse, tip often blunt; base acute (narrowly cuneate in juvenile leaves); venation obscure, primary veins only just visible, 8–10 pairs (to 12 pairs in juvenile leaves or obscure); midrib sunk, pubescent at least when young. *Inflorescence* axillary, decussate, frequently borne below the leaves, 1 or occasionally 2 per axil, 1.5–4 cm. long, 9–19-flowered, stout, densely pubescent; bracts concave, ovate or lanceolate, 2.5–4 mm. long, early deciduous, glabrous or occasionally pubescent on the midrib toward the tip, especially the upper ones. Flowers unisexual or occasionally hermaphrodite (FIG. 3), pedicels 1–2.5 mm. long. *Calyx* glabrous, more or less campanulate, 2–3 mm. long, with 4 irregular, unequal, often more or less erose teeth, 0.5–1 mm. long, tube 1–2 mm. long. *Corolla* absent. *Stamens* 2, in male and hermaphrodite flowers, anthers 1.5–2 mm. long, with a barely discernible terminal appendage, filaments 1.5–3 mm. long; in female nonfunctional, anthers 0.5–2 mm. long, acute, on broad filaments 0.4–1.3 mm. long. *Ovary*, in female flowers 2–3.5 mm. long (in hermaphrodite (?) ca. 1 mm. long) with 2 stigmatic lobes 1–1.5 mm. long; in male flowers abortive, more or less conical 0.5–0.8 mm. long, somewhat bluntly bifid at the apex. *Drupe* ovoid or oblong-ovoid, slightly asymmetrical, 10–15 mm. long by 7–10 mm. broad, red (*fide* Cheeseman); endocarp hard, 0.3 mm. thick.

LECTOTYPE: New Zealand, without locality, *Colenso s.n.* (K, ? isolectotype P).

New Zealand. NORTH ISLAND: Purua, Whangarei, Sept. 1899, *A.T.* (CHR *11047*); Kaitaia, North Auckland, Sept. 1902, *Carse s.n.* (O); Upper Waihaha River, West Taupo, edge of mixed podocarp forest, 27 July 1950, *Poole* (CHR *79236*); Volcanic Plateau, Hauhangatahi, 9 Jan. 1933, *Allan* (CHR *6578 & 6579 p.p.*); N. W. slopes of Pureora, King Country, 820 m., 21 Jan. 1947, *Rawson* (CHR *56465*); Maungapohatu, 18 March 1930, *Moore* (CHR *40774*); Egmont, forest, ca. 400 m., Feb. 1960, *Druce* (CHR *86726–7*); Scenic Reserve, Rongokaupo, near Ohakune, 16 March 1962, *Melville 6736* (CHR *130982–3*); Makapoua Valley, Ruahine foothills, near Taihape, *Spiers* (CHR *129161*); Ruahine–Cook district, Ruahine mountains above Table-Flat, 18 Nov. 1928, *Zotov* (CHR *360*); Dress Circle, 5 Nov. 1928, *Zotov* (CHR *22673*); Mauriceville, near Mt. Bruce, 5 Feb. 1945, *Zotov* (CHR *48666*); Wairarapa, *Kirk s.n.* (BRI, GH); Dry River, Wairarapa, *Kirk* (CHR *118758*); Ruamahanga, Wairarapa, May 1879, *Kirk 894* and *s.n.* (K); Ruamahanga Basin, *Kirk s.n.* (A); Eastern Wairarapa, near "Pahaoa Pinnacles," Pahaoa River, 25 Oct. 1953, *Mason 2537* (CHR *81796*); S. W. Wairarapa, Lake Pounui, forest remnant, 3 Sept. 1960, *Macmillan* (CHR *129159*); S. W. Wairarapa, Western Lake Reserve, forest edge, 3 Sept. 1960, *Moore* (CHR *129158 A & B*); Upper Hutt, remnant tree enclosed in shrubby area, 14 Jan. 1953, *Healy 53/870* (CHR *80796a–e*); near railway station, Silverstream, Hutt Valley, remnant tree by creek, 6 Dec. 1953, *Healy* (CHR *85913A & B*); Pakuratahi, *Kirk 614* (K) and 1 Nov. 1941, *Moore* (CHR *11038, 50035, & 50037*); Barton's Bush, Lower Hutt, 10 Oct. 1950, *Poole* (CHR *69138*); Wallaceville, Research Station grounds, Sept. 1943, *Sinclair* (CHR *69387*); behind Wallaceville laboratories, Wellington, 18 Sept. 1943, *Moore* (CHR *40121–2*); Korokoro Domain, 7 Sept. 1952, *Hutson* (CHR *83395*); Ohakune, near Wellington, taxad forest, 9 Oct. 1929, *Sledge 172* (K); Garden of B. C. Aston, Wellington, 20 Sept. 1948, *Poole* (CHR *61878*); Cape Palliser, *Kirk s.n.* (NSW). Without locality: *Colenso 712, 1798,* and *2036* (K), and *s.n.* (K, lectotype, P, ?isolectotype); without collector (CHR *11037A & B*).

Cultivated. U.S.A.: Golden Gate Park, San Francisco, California, spring 1931, *Walther s.n.* (A).

From each of the other New Zealand species *Nestegis cunninghamii* may be distinguished by its relatively stout, hairy inflorescence axes and pedicels, and its somewhat campanulate calyx. At least on dried material the hairs usually appear golden in color and although to a lesser or greater extent the other species bear scattered hairs on the axes they are never almost tomentose. *Nestegis montana* approaches this species in possessing a distinct calyx tube but it is smaller (less than 1 mm. long) and surrounds the androecium and gynoecium less than in *N. cunninghamii.* Another feature which may be used to distinguish material of this species is the way in which the midrib on the upper side of the leaf is sunk below the surface of the lamina. This is evident even in juvenile foliage which is also identifiable by the possession of at least a few characteristic hairs on the petioles or in their axils.

This species was early confused with *Nestegis apetala* because of its apetalous condition, but from my examination of the specimens cited above I do not believe it is the *Olea apetala* of Allan Cunningham as first suggested by Hooker in his *Flora Novae-Zelandiae,* a suggestion subsequently copied by others. Hooker was under the impression that *N. apetala* was confined to Norfolk Island and did not include it in either of his Floras, while the reference to *N. apetala* by Cunningham in his *Florae Insularum Novae Zelandiae Precursor* (Ann. Nat. Hist. 2: 46. 1839) cites two gatherings, one by Sir Joseph Banks in 1769 and the other his own, in 1826. Despite the citation of what is presumably these same two gatherings by Hooker in his protologue of this species, a duplicate of the Banks specimen in the Edinburgh herbarium shows it to be *N. apetala,* and although I have seen Cunningham material of this same species from Kew I have seen none of *N. cunninghamii.* It appears that Kirk was the first to draw attention to the fact that Vahl's species is, in fact, a native of New Zealand in his paper "*Notes on certain New Zealand plants not included in the Handbook of the New Zealand Flora*" (Trans. New Zealand Inst. 3: 165. 1871) and, as mentioned under *N. apetala,* Mueller went so far as to distinguish the Norfolk Island plant as a different species, *Olea endlicheri.*

Widely distributed in the North Island of New Zealand, this species is also recorded from the northernmost parts of South Island: according to Cheeseman (Man. New Zealand Fl. ed. 2. 718. 1925) from Marlborough, "extremely rare," Pelorus Sound, Kaikoura and Conway River, but I have seen no material from these localities. The native names given by Cheeseman are Maire, Mairerau-rui and Black Maire.

According to a note by Kirk attached to his specimen *894* at Kew, this species also has been confused with *Mida salicifolia* A. Cunn. of the Santalaceae (as *Santalum cunninghamii*). On the note he states that *Notelaea cunninghamii* "is the *Santalum cunninghamii* of Buchanan's List of Wellington Plants" (Trans. New Zealand Inst. 6: 223. 1874) and further that wood specimens of this species were distributed under this name. Unfortunately, as will be seen under *N. montana,* that species has also been confused with *Mida salicifolia.*

In selecting a lectotype, of the four sheets at Kew named *Olea cunning-*

hamii in Hooker's hand, I have chosen the Colenso sheet without a number, it is the only one bearing both flowers and fruit and it also carries a drawing of a male flower, all of which are described in the protologue. Unfortunately, however, the male flower is not that of this species but of *Nestegis apetala* and reference to its characteristics in the diagnosis and description of Hooker should be ignored.

4. **Nestegis montana** (Hooker f.) L. Johnson in Degener, New Ill. Fl. Hawaiian Is. 300. Nestegis. 1958.

Olea montana Hooker f. Fl. Nov.-Zeland. **1:** 176. *pl. 46A & B.* 1852 et Handbook New Zealand Fl. 187. 1864; Kirk, Trans. New Zealand Inst. **14:** 377. 1882 et Forest Fl. New Zealand, 39, 40. *pls. 29, 30.* 1889; Schimper, Pflanzen-Geogr. 506. 1898; Cheeseman, Man. New Zealand Fl. 438. 1906 et ed. 2. 719. 1925; Allan, New Zealand Trees & Shrubs, 133, 145. 1928; Cockayne & Turner, Trees of New Zealand, 94. 1928; Bailey & Bailey, Hortus, 423. 1930 et Hortus Second, 507. 1941; Gudex, Trans. Roy. Soc. New Zealand, **85:** 58. 1957; Allan, New Zealand Fl. **1:** 546. 1961.

Gymnelaea montana (Hooker f.) L. Johnson, Contr. New S. Wales Natl. Herb. **2:** 413. 1957; Allan, Fl. New Zealand, **1:** 1025. 1961.

Tree to 10 m. or more tall (to 16 m. *fide* Kirk), trunk to 60 cm. in diameter (*fide* Kirk), monoecious or dioecious, branches slender, glabrate or puberulous when young. *Leaves* glabrous, petioles 1.5–3 mm. long, glabrous, or minutely puberulous when young, usually dark green, more glossy than those of other species (*fide* Moore); lamina coriaceous, linear to very narrowly lanceolate, (2.5–)4–7(–8.5) cm. long by (0.2–)0.5–0.6(–0.7) cm. broad (juvenile leaves 5–13 cm. long by 0.2–0.7 mm. broad); margin entire, scarcely thickened; apex acute; base attenuate into the petiole; venation obscure, only the midrib visible above and below. *Inflorescence* axillary, decussate, often borne below the leaves, 1 (or 2) per axil, 1.5–3(–4) cm. long, (5–)7–17-flowered, scattered puberulous to glabrate, slender; bracts ovate-lanceolate, acute to acuminate, 1.5–3 mm. long, early deciduous. Flowers unisexual or hermaphrodite (FIG. 4), pedicels 1.5–3 mm. long. *Calyx* glabrous, somewhat campanulate, 1–1.5 mm. long with 4 irregular, unequal, somewhat erose teeth about 0.5–1 mm. long, and a distinct tube about 0.5 mm. long. *Corolla* absent. *Stamens,* in male and hermaphrodite (?) flowers 2–4 with anthers oblong-ovate, 1.3–2 mm. long on filaments 0.3–0.8 mm. long, absent in female flowers. *Ovary* in female or hermaphrodite (?) flowers 1–2 mm. long with 2 stigmatic lobes 0.7–1.5 mm. long, in male flowers abortive, more or less conical, ca. 0.2 mm. high. *Drupe* narrowly ovoid, about 6–9 mm. long, red (*fide* Cheeseman).

LECTOTYPE: New Zealand, without locality, *Colenso 711* (K).

New Zealand. NORTH ISLAND: Wangaroa, 1834, *R. Cunningham 563* p.p. (K) and *Kirk 121* (K); Cowan's Bay Road, Rodney County, 5 Jan. 1962, *Moore* (CHR *125570*); Kokohuia, Pukepoto, North Auckland, ca. 300 m., Oct. 1915, *Carse s.n.* (O); Waitakerei, Auckland, Nov. 1881, *Cheeseman s.n.* (NY); Titirangi Range, *Cheeseman 95* (K), Oct. 1870, *Cheeseman s.n.* (E, NSW) and Sept. 1872, *Cheeseman s.n.* (NY); Swanson, rain forest, *Mason* (CHR *22124*); Rangitoto, without collector, (CHR *8192*); Oratia, near Auckland, Sept. 1929, *Meebold 5337* (NY); Maraeroa-Mangapehi Road, King Country, cut-over bush, ca. 600 m., 27 Jan. 1947, *Rawson* (CHR *56513*); Tokaanu-Taumarunui Road, near Kuratau Stream, 20 Jan. 1950, *Hamlin* (CHR *69844*); Ruahine-Cook district, near Mt. Matthews, ca. 300 m., 25 Dec. 1932, *Zotov* (CHR *6492*); Foxton, Kahikatea, forest remnant between high consolidated dunes, April 1940, *Poole* (CHR *23756*); Mt. Wainui, near Wellington, forest margin, ca. 200 m., 17 Jan. 1942, without collector (CHR *95349*); Makara, *Kirk s.n.* (A); Hurunuiorangi village, Wairarapa valley, 1849, *Colenso 1119* (K); Turanganui valley, Wairarapa, Feb. 1947, *Druce* (CHR *82176*); Turanganui River, Haurangi Mountains, Wairarapa, 20 Feb. 1947, *Zotov* (CHR *59307*); Dry River, Wairarapa, *Kirk s.n.* (GH); Ruamahanga, Wairarapa, *Kirk* (CHR *118757*); Wainuioru River, Eastern Wairarapa, ca. 1½ miles above junction with Pahaoa River, 26 Nov. 1953, *Mason 2546* (CHR *84707*); E. Wairarapa, 7 miles N. E. of Hinakura, forest, ca. 150 m., 25 Oct. 1953, *Druce* (CHR *82400*); Cascades, without collector (CHR *8180*). Without locality: *A. Cunningham s.n.* (K), *1797*, *2032*, *&* *2033* (K) and 1847, *Colenso 711* (K, lectotype).

SOUTH ISLAND: Snowden's Bush, Nelson, *Gibbs* (CHR *118756*).

The distribution of this species is very similar to that of *Nestegis lanceolata*. It occurs widely in the North Island and has also been recorded from south of the Cook Strait: from the Rai Valley and from near Brightwater (Cheeseman, Man. Fl. New Zealand, ed. 2. 719. 1925), although I have only seen the one gathering cited above. The native names are Orooro and Narrowleaved Maire.

Of all the New Zealand species *Nestegis montana* possesses the narrowest foliage and in this is distinct from each of the others. Its juvenile leaves are also narrow, and partly for this reason the species has been confused with *Mida salicifolia* A. Cunn. of the Santalaceae (as has *N. cunninghamii*, see above under that species). At Kew one of the specimens of *N. montana* exhibiting juvenile leaves originally bore the name *Metrosideros ? salicifolia* A. Cunn. This was collected at Wangaroa by Richard Cunningham (number *563*), the type locality and number of *M. salicifolia* (Ann. Nat. Hist. 3: 114. 1839). Furthermore Hooker, along with his original description and plate, illustrated (as his fig. C) a pair of leaves of this same species saying he now suspected they were *Mida salicifolia*. The specimen from which this figure was taken is attached to one of the sheets named by Hooker.

There are six sheets at Kew bearing the name *Olea montana* in Hooker's hand, which, therefore, have to be taken into consideration in choosing a lectotype. Three of them are Colenso gatherings in fruit only, so I have selected another sheet which bears material exhibiting the greatest number of the characteristics mentioned by Hooker in his protologue. This is *Colenso 711* with juvenile and adult shoots, flowering material, and the original pencil drawings which became figures 1 to 5, and illustrate male flowers and their parts (although originally published as female). The fruit (figures 6 to 9) was illustrated from *Colenso 2032* which bears the original pencil sketch but, apart from showing adult foliage and fruiting inflorescences, does not exhibit as wide a range of characteristics as *Colenso 711*.

COMPARATIVE ANATOMY OF THE LEAF-BEARING CACTACEAE, X

THE XYLEM OF PERESKIA COLOMBIANA, PERESKIA GUAMACHO, PERESKIA CUBENSIS, AND PERESKIA PORTULACIFOLIA

I. W. BAILEY [1]

OF THE FOUR SPECIES under consideration in this paper the one with the greatest stature is probably *Pereskia colombiana* Britt. & Rose, said to be a tree which attains a height of eleven meters (Backeberg, 1958), but in some localities has a smaller, shrub-like form (Britton & Rose, 1919). The largest section of a stem collected for me by Romero Castañeda, in the type locality of the species in Colombia, is approximately 30 centimeters in diameter.

On the other hand, *Pereskia guamacho* Web. is described as a shrub one to three meters high, but may become a tree ten meters high with a trunk up to 40 centimeters in diameter (Britton & Rose, 1919). The largest stem collected for me by Steyermark in Venezuela is four centimeters in diameter.

Of the other two species considered in this paper, *Pereskia cubensis* Britt. & Rose is commonly a tree up to four meters high (Backeberg, 1958), but under favorable conditions may attain a height of seven meters and a stem diameter of 30 centimeters (Boke, 1954). The largest stem available to me from the Atkins Garden in Cuba is six centimeters in diameter.

The fourth species, *Pereskia portulacifolia* (L.) Haw., is a tree which may attain a height of somewhat more than six meters and stem diameters of as much as 16 centimeters (R. A. Howard, personal communication). The largest stem collected for me by Jiménez at Jimani, Dominican Republic, is four centimeters in diameter.

A number of taxonomists who have studied *Pereskia colombiana* and *P. guamacho* in their native habitats consider them to be conspecific. Therefore, it is desirable to determine whether they are geographical races of a single species or whether their variations in habit of growth and in the form and venation of their leaves are due solely to environmental rather than genetic influences. The structure of the xylem, as of the phloem (Bailey, 1961), and the form and vasculature of the leaves (Bailey, 1960) is remarkably similar in the two putative species. The earlier-formed secondary xylem of stems resembles that of *P. sacharosa* Griseb. and other pereskias discussed in preceding papers of this series. The vessels tend to

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[1] This investigation was financed by a grant from the National Science Foundation. I am indebted to the American Philosophical Society for the loan of a Wild microscope.

be diffusely distributed in a matrix of dense libriform fibers (FIGS. 1 and 5). The wood parenchyma tends to be scanty paratracheal and the fully lignified multiseriate rays are comparatively narrow. In subsequently formed secondary xylem, there are more or less precocious transitions to a form of structure that does not occur in stems of *P. sacharosa*, *P. grandifolia* Haw., *P. bleo* DC. (Bailey, 1963c) and such pereskias of Peru and Bolivia as *P. humboldtii* Britt. & Rose, *P. weberiana* K. Schum., and *P. diaz-romeroana* Cárd. (Bailey, 1963a), but which appears to be an accentuation of structural changes that occur in the outer secondary xylem of large stems of *P. conzattii* Britt. & Rose, *P. autumnalis* (Eichlam) Rose, and *P. nicoyana* Web. (Bailey, 1963b). The paratracheal parenchyma becomes increasingly abundant forming concentric zones which alternate with zones of greater density, i.e., having fewer vessels and a higher proportion of libriform fibers (FIGS. 2 and 6). The alternating zones vary markedly in width in the transverse section of a large stem, with more or less abrupt transitions from dense to softer tissue (compare FIGS. 2, 3, and 6). Such zonation may prove to be an indication of successive seasonal changes in cambial activity and in the maturation of cambial derivatives.

In stems of *Pereskia colombiana* and *P. guamacho*, as in those of other pereskias, the vessels vary considerably in diameter, in number per unit area, and in their degree of aggregation into clusters and zonal arrangements in different parts of a single mature plant (FIGS. 1–6). The multiseriate rays similarly vary markedly in height, width, form, and spacing; and their constituent cells exhibit conspicuous differences in size, form, and orientation. The most obvious differences occur in passing radially from the first-formed secondary xylem to the outermost wood of enlarged stems. As in other pereskias and in many dicotyledonous trees of normal form, the first-formed multiseriate rays tend to be vertically extensive. During radial extension of these rays they become dissected into lower and wider parts of fusiform outline as seen in tangential longitudinal sections (FIG. 11). These fusiform parts subsequently become laterally displaced during increase in circumference of the cambium (FIGS. 7 and 9). During such transitional changes in the multiseriate rays their successively formed parts exhibit more or less precocious differences in form and orientation of their constituent cells, i.e. from "erect" to nearly isodiametric to "procumbent." At times rays in the outer secondary xylem which are composed largely of slender procumbent cells may be jacketed by broader erect cells (FIG. 7), as in *P. sacharosa* (Bailey, 1962) and *P. conzattii* (Bailey, 1963b).

In the limited number of roots of *Pereskia colombiana* and *P. guamacho* available to me at present, there are more precocious changes in structure than in stems of equivalent diameter. In passing from the first-formed secondary xylem outward, there tends to be an abrupt increase in the diameter of vessels and in their number per unit area, likewise in the amount of paratracheal parenchyma and in the length of procumbent ray cells (FIG. 4). On the contrary, the multiseriate rays tend to retain a vertically extensive form (FIGS. 10 and 12). The inner part of the first-formed multiseriate rays is composed largely of unlignified cells, some of which contain druses and others large single crystals of calcium oxalate. In the outward extension of the rays, patches of unlignified cells alternate with fully lignified parts of the multiseriate rays. Furthermore, more or less extensive arcs of unlignified wood parenchyma occur at times in the roots of these pereskias.

The secondary xylem in stems of *Pereskia cubensis* is of a relatively dense form. The vessels which are diffusely distributed in the inner secondary xylem (FIG. 13) exhibit more or less conspicuous aggregations into concentric patterns in subsequently formed tissue (FIG. 14). The lignified wood parenchyma is scanty paratracheal and the lignified multiseriate rays, which vary considerably in width and in number per unit area, are composed of varying mixtures of slightly erect, isodiametric and slightly procumbent cells (FIGS. 13–15). As in the fully lignified rays in stems of *P. colombiana* and *P. guamacho* crystals of calcium oxalate occur in the form of single large ones or a few independent ones; aggregations into typical druses being absent. The first-formed multiseriate rays are vertically extensive. They become dissected in their outward extension into lower rays of more or less fusiform outline (as seen in tangential longitudinal sections) which become laterally displaced during increase in the circumference of the cambium (FIG. 15). As in other pereskias, in immature stems of largest diameter broadening of the parenchymatous interfascicular gaps of the eustele may occur during later stages of development of the primary body. In such stems (FIG. 13) the innermost part of the first-formed multiseriate rays may be composed of tangentially, rather than vertically or radially, elongated cells. In the outermost secondary xylem of the largest available stem of *P. cubensis* there is no conspicuous occurrence of broad concentric zones of wood parenchyma, such as occur so characteristically in the case of *P. colombiana* and *P. guamacho* in stems of comparable diameters. Unfortunately specimens are not available at present for determining whether such parenchymatous zonations ever occur in the outermost secondary xylem of stems which attain a diameter of 30 centimeters.

The structure of the xylem in roots of *Pereskia cubensis* closely resembles that which occurs in roots of *P. colombiana* and *P. guamacho*. There is a similar tendency for precocious increase in diameter of the vessels, for the occurrence of alternating parts of unlignified and fully lignified cells in the rays, and for the development of more or less extensive arcs of unlignified wood parenchyma (compare FIGS. 4 and 16). Druses as well as single large crystals tend to be present in unlignified parts of the rays. Furthermore, there is a similar tendency for the multiseriate rays to retain a vertically extensive form (compare FIGS. 8, 10, and 12).

The xylem in the largest available stem of *Pereskia portulacifolia* resembles that of *P. cubensis*. The vessels (FIG. 17) are of similar size and distributional patterns, the wood parenchyma is scanty paratracheal and the lignified rays are of comparable variations in form and internal cellular organization (FIGS. 17 and 19). The wood retains its density (i.e. high proportion of libriform fibers) throughout, and even in its outermost part differs conspicuously from that in stems of equivalent diameter of *P. colombiana* and *P. guamacho*, i.e. in the absence of broad concentric zones of wood parenchyma. However, the form and cellular composition of the lignified multiseriate rays in the outermost secondary xylem is fundamentally similar in the four putative species (compare FIGS. 9, 11, and 19).

The xylem in roots of *Pereskia portulacifolia* resembles that which occurs in roots of *P. cubensis, P. guamacho* and *P. colombiana* (FIGS. 18 and 20). In all four of the putative species there is an obvious phylogenetic tendency toward elimination of secondary walls and lignification in parts of the multiseriate rays, and toward the occurrence of more or less numerous and extensive arcs of unlignified wood parenchyma (FIGS. 16, 18, and 20). In the limited number of roots available to me this phylogenetic trend toward increasing succulence appears to be more highly accentuated in roots of *P. cubensis* and *P. portulacifolia* than in those of *P. colombiana* and *P. guamacho*, but such a conclusion needs to be verified by examination of much additional material from many plants of the four species.

CONCLUSIONS

The secondary xylem in stems of *Pereskia cubensis* and *P. portulacifolia* resembles that which occurs in *P. sacharosa, P. grandifolia,* and *P. bleo* in the size and distributional patterns of its vessels, in its density due to a high proportion of libriform fibers, in its scanty paratracheal parenchyma, and in the variations in size and form of its fully lignified multiseriate rays, as well as in the form and orientation of its ray cells in different parts of an adult plant, particularly in passing from the first-formed to the outermost secondary xylem.

The earlier formed secondary xylem in stems of *Pereskia colombiana* and *P. guamacho* resembles the wood of *P. cubensis* and *P. portulacifolia* in its density and grosser anatomical features. But precocious changes to softer (i.e. more succulent) forms of xylem occur in subsequently formed tissue. This arises by formation of relatively broad concentric zones of wood parenchyma and by reduction in the proportion of libriform fibers in the outer secondary xylem as a whole. However, it is in the roots of these four species, as in those of *P. aculeata* and the Andean pereskias, that enhanced succulence is phylogenetically attained by the elimination of secondary walls and lignification in ray cells and wood parenchyma.

The structural similarities in the xylem may be interpreted as an indication that the four taxa are more closely related genetically one to another than they are to other species of *Pereskia*. Furthermore, the very close anatomical similarities in roots and stems of *P. colombiana* and *P. guamacho* strengthen the conclusion of those taxonomists who argue that the two taxa are conspecific.

SUMMARY OF ANATOMICAL EVIDENCE OBTAINED FROM THE PHLOEM AND XYLEM OF VARIOUS TAXA OF THE GENUS PERESKIA

From the point of view of the phylogeny of the dicotyledons as a whole, the leaf-bearing genera, *Pereskia*, *Pereskiopsis* and *Quiabentia* have attained a high level of structural specialization in the cambium and its xylem and phloem derivatives (Bailey & Srivastava, 1962). This is evidenced in the cambium by the much reduced length of fusiform initials and their tendency to occur in stratified or "storied" patterns; *in the xylem*, by short vessel members having simple porous perforation plates, short wood parenchyma strands and septate and non-septate libriform fibers which store starch, and the phylogenetic elimination of uniseriate rays; *in the phloem*, by reduction in length of fusiform parenchyma and parenchyma strands and by the short length and structural modifications of sieve tube members. It should be emphasized in this connection that these salient end-products of evolutionary specialization closely parallel those which occur in trees and woody shrubs of a number of other dicotyledonous families.

Within the genus *Pereskia*, *P. sacharosa* (Bailey, 1962), *P. grandifolia*, and *P. bleo* (Bailey, 1963c) appear to have persisted at this general high level of structural specialization in both stems and roots without conspicuous evidences of special additional trends of evolutionary modification. On the contrary, particularly in the xylem of roots of the Andean pereskias (Bailey, 1963a), *P. colombiana*, *P. guamacho*, *P. cubensis*, and *P. portulacifolia*, and in both roots and stems of *P. aculeata* (Bailey, 1962), there are evidences of a tendency toward increasing succulence due to the elimination of secondary walls and lignification in ray and wood parenchyma. The occurrence of broad zones of lignified wood parenchyma and reduction in the proportion of libriform fibers in the later-formed secondary xylem of stems of *P. colombiana* and *P. guamacho* may likewise possibly be interpreted as additional evidence toward the formation of softer tissue.

In all taxa of *Pereskia* there is a more or less conspicuous tendency in immature stems of largest diameter toward increase in diameter of the parenchymatous interfascicular parts of the eustele and concomitant increase in diameter of the pith during later stages of the development of the primary body of stems. This form of structure leads at times to an increase in width of the inner part of the first-formed multiseriate rays and to modifications in the form and orientation of ray cells. In the case of *P. conzattii*, *P. autumnalis*, and *P. nicoyana* (Bailey, 1963b) this tendency becomes greatly accentuated in the basal parts of the trunks of the trees, where the pith may expand to a diameter of more than six centimeters. The cells in the inner parts of the multiseriate rays remain unlignified and capable of division and transverse enlargement, thus facilitating increase in circumference of the eustele and concomitant expansion of the pith, long after cambial activity is initiated in the fascicular parts of the eustele.

As demonstrated in the second paper of this series (Bailey, 1961), the genus *Pereskia* may be divided anatomically into three distinct categories of taxa upon the basis of consistently stable differences in the form and distribution of sclereids in the secondary phloem. *Pereskia aculeata*, the pereskias of Peru and Bolivia, and those of southern Mexico and Central America belong in one category; *P. sacharosa*, *P. grandifolia*, *P. bleo*, and *P. tampicana* in a second category; and *P. colombiana*, *P. guamacho*, *P. cubensis*, and *P. portulacifolia* in a third category. Within the second and third categories salient structural similarities may be interpreted as indications of relatively close genetic relationships. In the case of the first category salient structural differences raise some question regarding the degrees of genetic relationships between *P. aculeata*, the Andean pereskias, viz. *P. humboldtii*, *P. weberiana*, and *P. diaz-romeroana*, and *P. conzattii*, *P. autumnalis*, and *P. nicoyana* of southern Mexico and Central America.

It should be emphasized in this connection that anatomical details in xylem of pereskias (i.e. in wood which does not exhibit evidence of highly divergent trends of phylogenetic specialization) vary greatly, not only in the same clone when grown under varying environmental influences, but also in different parts of a single mature plant. As previously noted (Bailey & Srivastava, 1962), diagnostic anatomical criteria commonly utilized by wood anatomists in the differentiation of closely related taxa are of questionable reliability in *Pereskia* unless based upon statistical analyses of many specimens from different localities. When such ranges of potential structural variability are taken into consideration in harmony with evidence from salient trends of divergent specialization in rays and wood parenchyma, available data at least suggest that *P. humboldtii*, *P. vargasii* H. Johnson, *P. weberiana*, and *P. diaz-romeroana* may ultimately prove to be geographical variants of a single species. Similarly *P. grandifolia*, *P. bleo*, and *P. tampicana* may ultimately be shown to be conspecific as also *P. pititache* Karw., *P. conzattii*, and *P. autumnalis*, and *P. colombiana* and *P. guamacho*.

The initial stages in *Pereskia* toward elimination of secondary walls and lignification in ray and wood parenchyma, and toward increase in circumference of the eustele and diameter of the pith after cambial activity is initiated in fascicular parts of the primary body, are particularly significant in dealing with the xylem of *Pereskiopsis* and *Quiabentia* which will be discussed in the next paper of this series.

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EXPLANATION OF PLATES

PLATE I

FIGS. 1–4. Transverse sections of the secondary xylem of *Pereskia colombiana* [*Romero*], × 34. 1, First-formed tissue of a large stem. 2, Outer secondary xylem of a large stem. 3, Outer secondary xylem showing increase in wood parenchyma and reduction of libriform fibers. 4, Outer secondary xylem of a large root.

PLATE II

FIGS. 5–8. Transverse and tangential longitudinal sections of secondary xylem. 5, *Pereskia guamacho* [*Steyermark*]. Transverse section of first-formed secondary xylem of a large stem, × 34. 6, *Pereskia guamacho* [*Pittier 12157*]. Transverse section of outer secondary xylem of a large stem, × 34. 7, *The same*, tangential section of the outer secondary xylem, × 43. 8, *Pereskia cubensis* [Atkins Gard.] tangential section of a root, × 43.

PLATE III

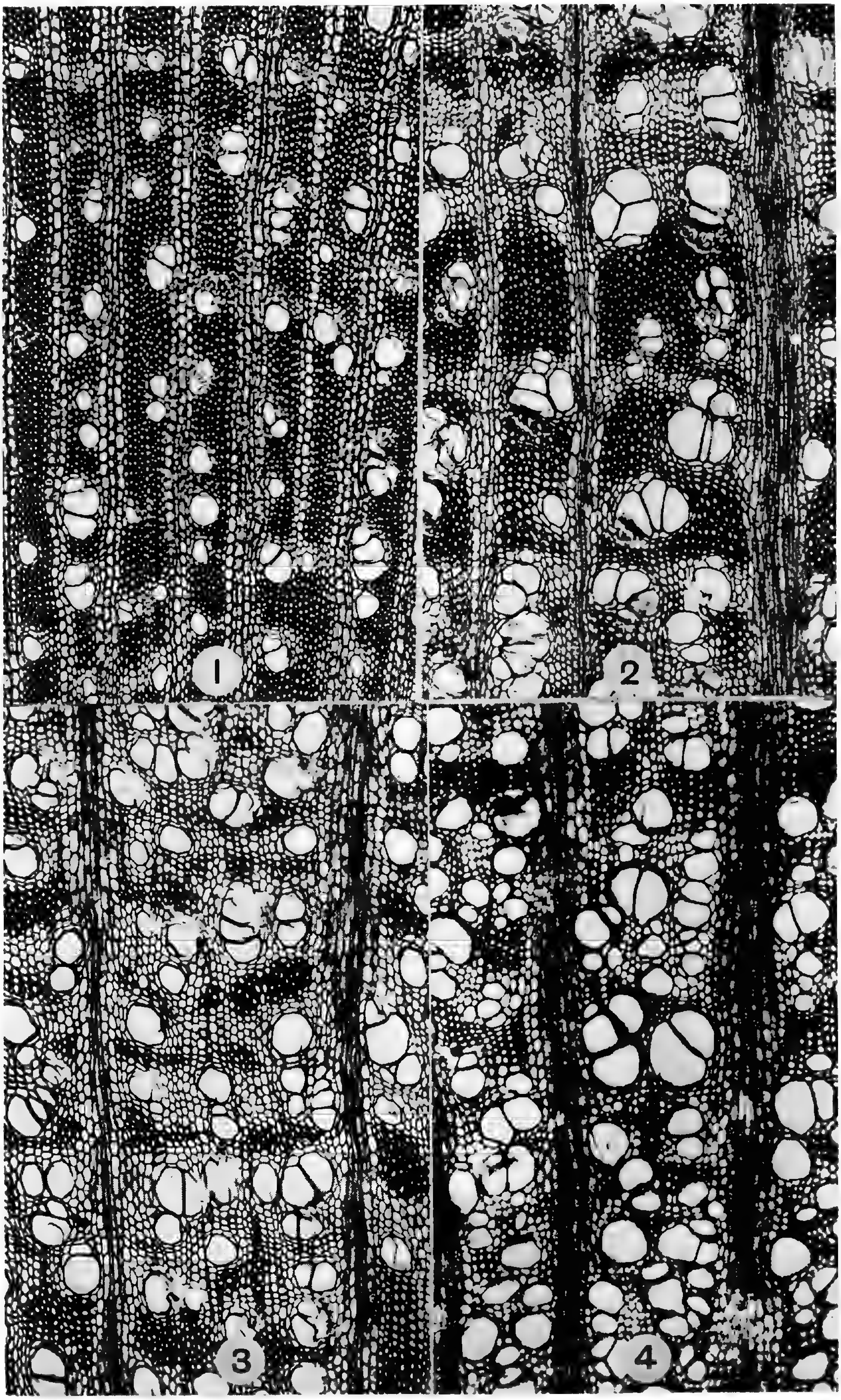
FIGS. 9–12. Tangential longitudinal sections of secondary xylem, × 43. 9, Outer secondary xylem of large stem of *Pereskia colombiana* [*Romero*]. 10, *The same*, root. 11, Outer secondary xylem of large stem of *P. guamacho* [*Steyermark*]. 12, *The same*, root.

PLATE IV

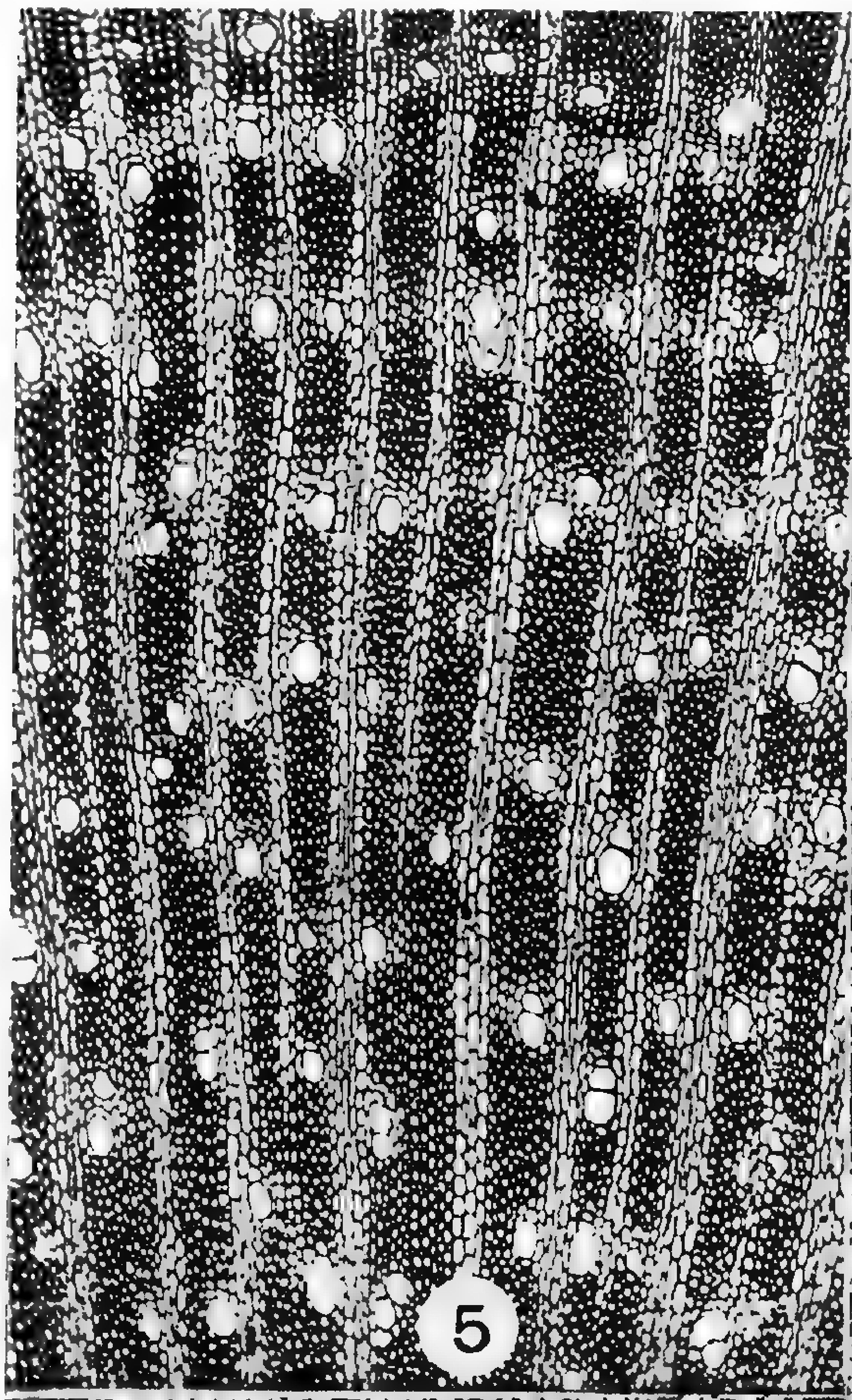
FIGS. 13–16. Transverse and tangential longitudinal sections of the secondary xylem of *Pereskia cubensis* [Atkins Gard.]. 13, Transverse section of innermost secondary xylem of a large stem, × 34. 14, Transverse section of outer secondary xylem, × 11. 15, Tangential section of outer secondary xylem, × 43. 16, Transverse section of root treated with phloroglucin-HCl, showing unlignified parts (white) of multiseriate rays, × 34.

PLATE V

FIGS. 17–20. Transverse and tangential longitudinal sections of the secondary xylem of *Pereskia portulacifolia* [*Jiménez*]. 17, Transverse section of stem, × 11. 18, Transverse section of root, × 11. 19, Tangential section of outer secondary xylem of large stem, × 43. 20, Transverse section of root treated with phloroglucin-HCl, showing unlignified parts (white) of multiseriate rays, × 34.



Bailey, Leaf-bearing Cactaceae, X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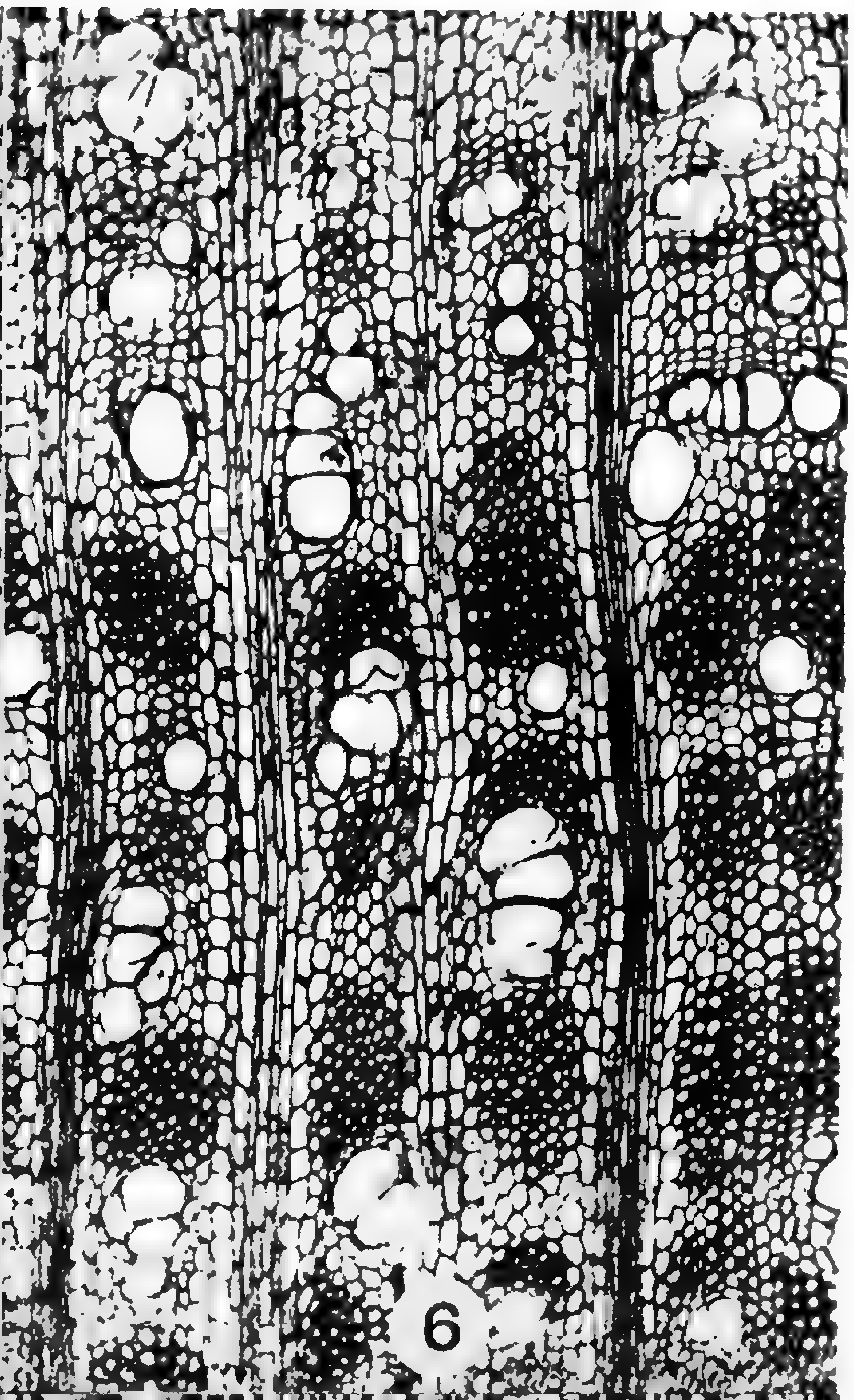
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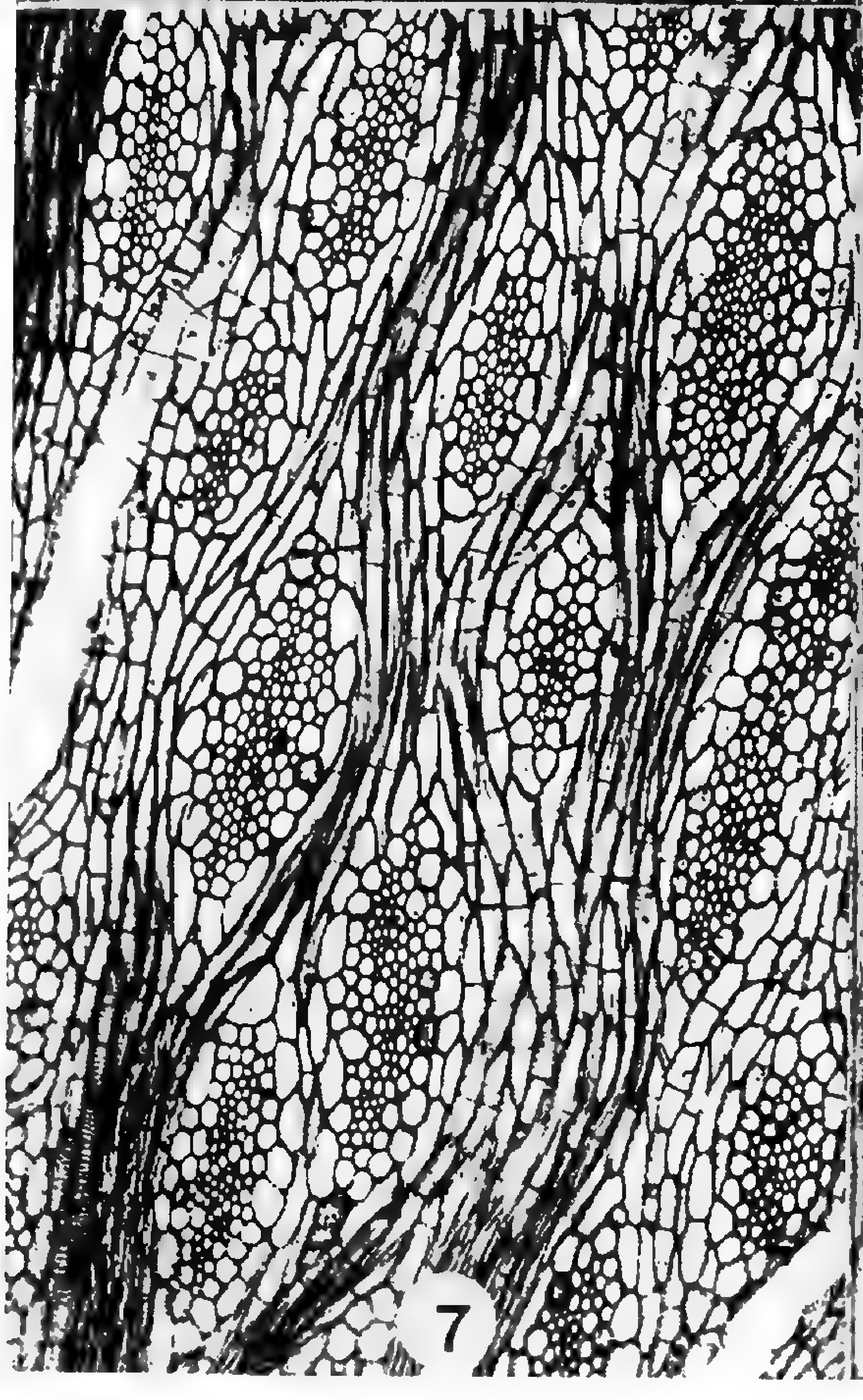
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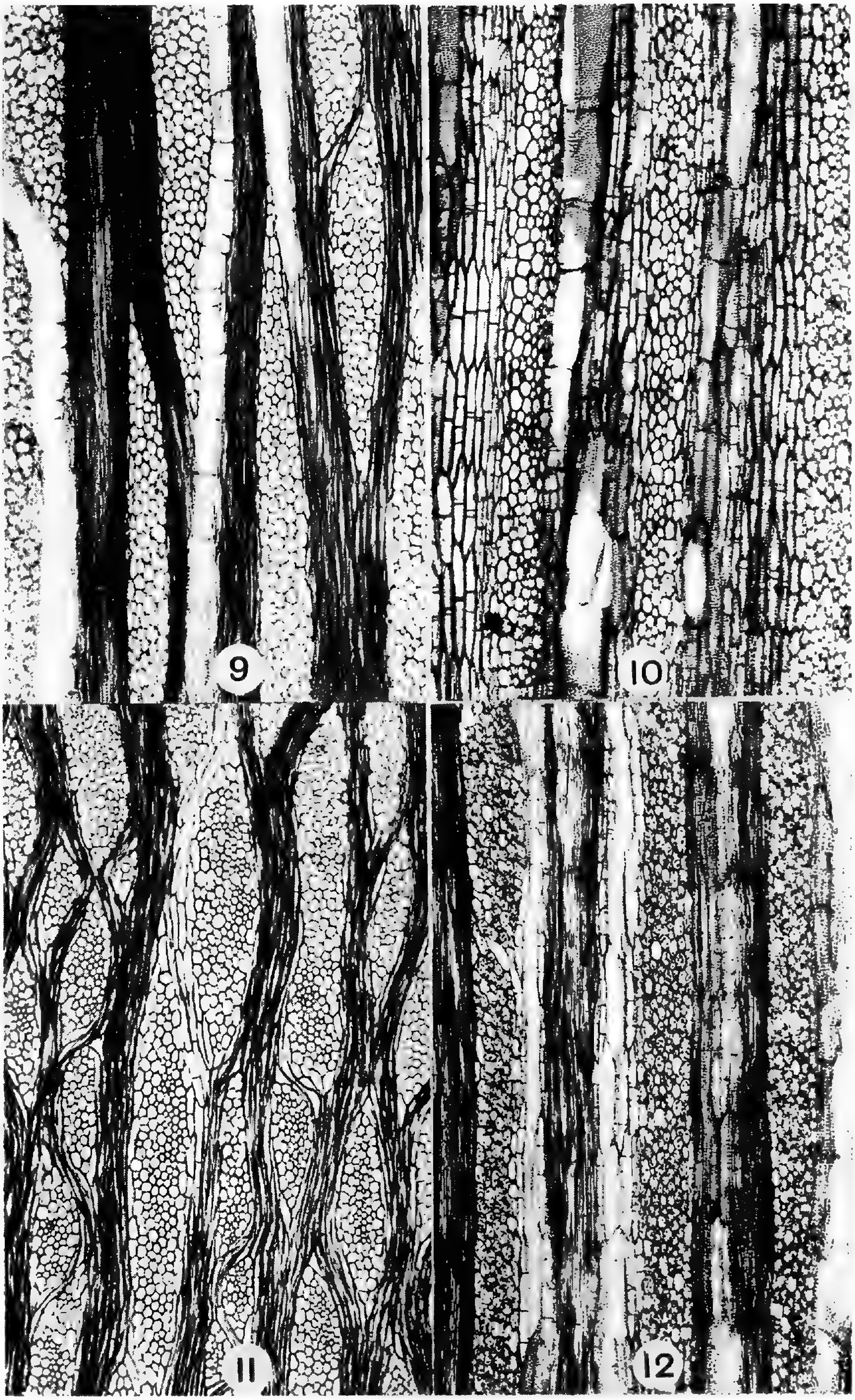
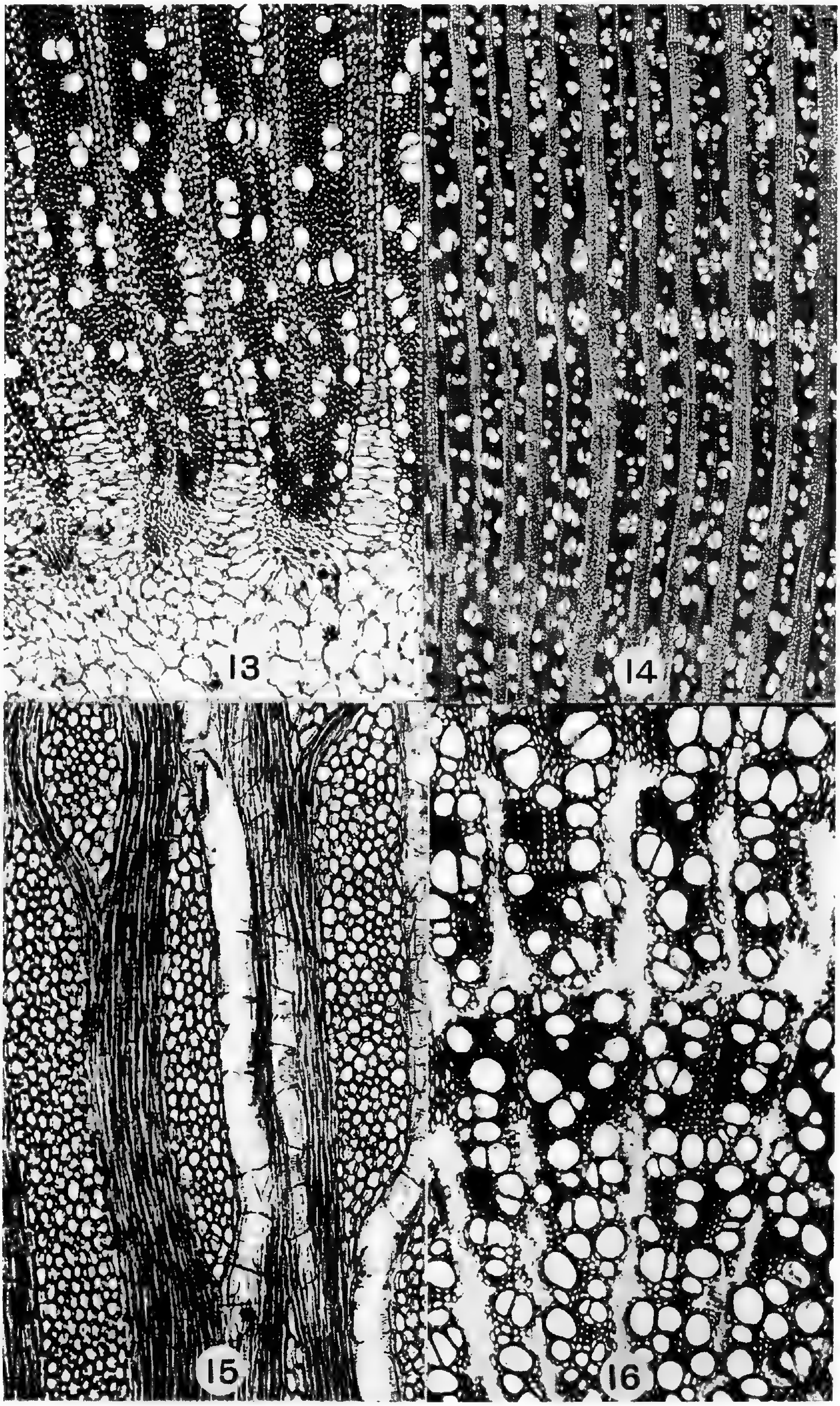


BAILEY, LEAF-BEARING CACTACEAE, X

PLATE IV



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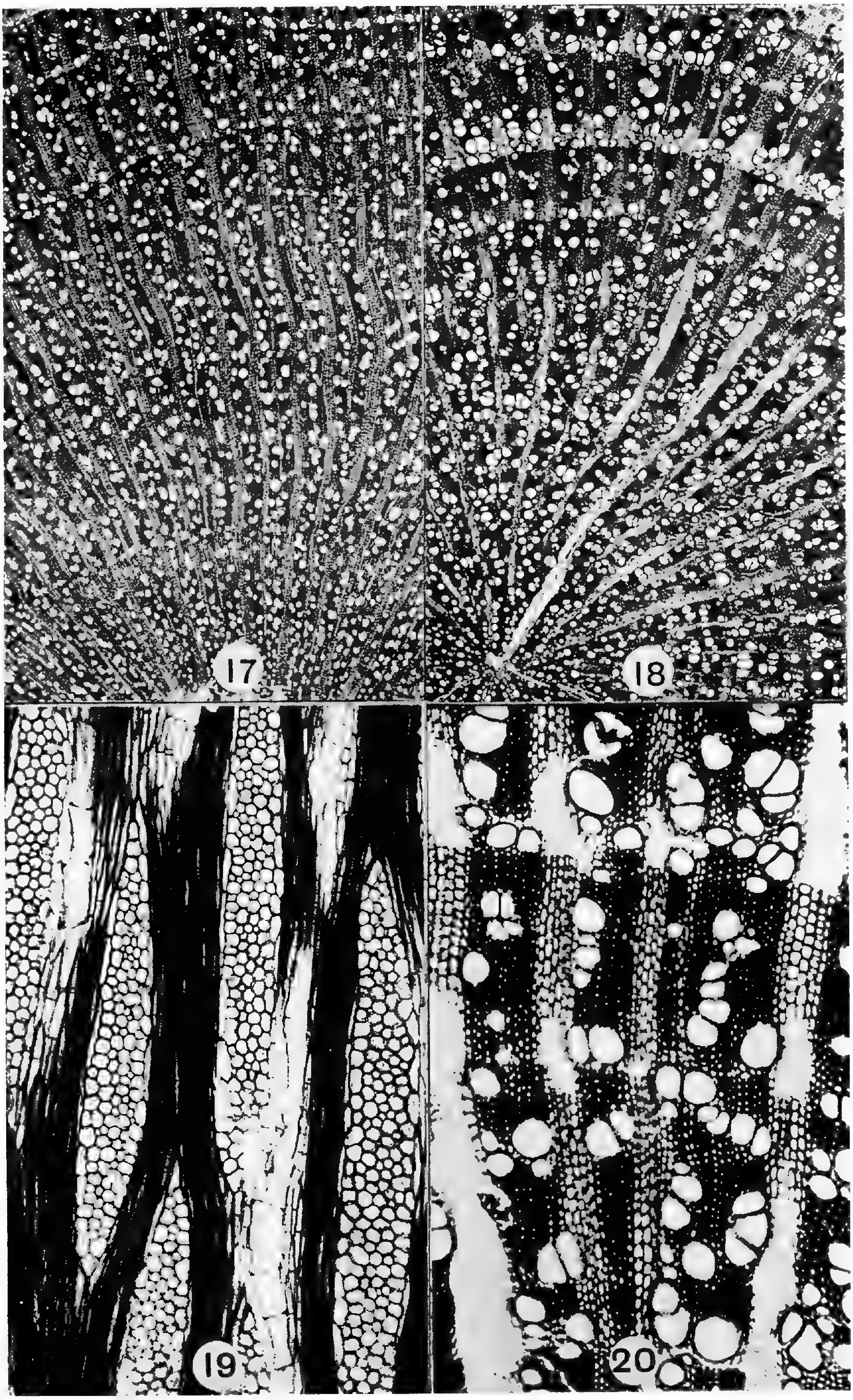


BAILEY, LEAF-BEARING CACTACEAE, X

NOTES ON DAPHNOPSIS

LORIN I. NEVLING, JR.

AS A RESULT OF CONTINUING studies in the genus *Daphnopsis* (Thymelaeaceae) I have accumulated information either lacking previously or temporarily lost, which clarifies some taxonomic and nomenclatural problems. In addition, a reappraisal of the systematic position of one species has been made. These observations and conclusions are presented briefly in alphabetical order by species.

Whenever specimens are cited the abbreviations are according to Lanjouw & Stafleu, *Index Herbariorum*, Pt. I, Ed. 4 (Regnum Vegetabile **15**. 1959). To the directors and curators of these institutions I am most grateful, and extend my thanks for their cooperation. The illustrations of *Daphnopsis pseudosalix* Domke are the careful work of Miss Judith A. Kroll.

Daphnopsis americana (Mill.) J. R. Johnston ssp. **cestrifolia** (HBK.). Nevl. Ann. Missouri Bot. Gard. **46**: 312. 1959.

Daphne cestrifolia HBK. Nov. Gen. **2**: 150. 1817.
Hargasseria cestrifolia (HBK.) Endl. Gen. Suppl. **4**(2): 68. 1847.
Daphnopsis cestrifolia (HBK.) Meissn. in DC. Prod. **14**: 523. 1857.
Daphnopsis incerata Cuatr. Brittonia **14**: 50. 1962.

Several months after the publication of *Daphnopsis incerata* Cuatr. I was permitted to examine the holotype deposited at Kew (COLOMBIA. Nariño: Gorgona Island, on edge of jungle, close to beach; flowers greenish yellow, collected by J. B. Hicks, July 1924. *St. George Expedition No. 352*). Cuatrecasas published a photograph (his Fig. 1) of the holotype to accompany the description which, it must be noted, was arranged from unmounted material and included only one-half the total gathering. Subsequently, when the material was mounted at Kew, all of the gathering was included on a single sheet. Future workers, therefore, will find the type sheet more complete than Cuatrecasas's figure.

In his discussion of this new species (p. 51) Cuatrecasas states that it has "its inflorescences, leaf-form and venation" similar to *Daphnopsis americana* but differs from the latter species in its floral structure and in having a cereous layer which covers the undersides of the leaves, young branchlets and inflorescences. Since I think the similarities cited are correct, I shall limit my remarks to the cited dissimilarities.

Since the flowers on the holotype are few and poorly preserved, I limited my observations to only two. The floral morphology of these differed in no important respect from that of *Daphnopsis americana* ssp.

cestrifolia. One minor difference noted was in the lack of reduced anthers borne on the staminodia, an unusual feature of this subspecies (other subspecies seem variable in this character); the staminodia, however, were well developed (to 0.25 mm. long).

On first examination the holotype looked as though it had been dipped in some undetermined solution which had precipitated on it. The "cereous layer" seemed too regular to have been formed in this manner, so a leaf fragment was hand sectioned and stained with Sudan IV in 80% ethyl alcohol. Microscopic examination showed the waxy layer to be an integral part of the leaf structure which had the positive staining reaction with Sudan IV typical of waxes and other fatty substances. This characteristic seems to be the only outstanding feature of the plant, which I believe is synonymous with *Daphnopsis americana* ssp. *cestrifolia*. For those desiring formal recognition of minor variations it could be adequately treated as a form of ssp. *cestrifolia*.

Daphnopsis crispotomentosa Cuatr. Brittonia **14**: 51. 1962.

Recently Cuatrecasas described two new species of *Daphnopsis* from Colombia. The second of these, *D. crispotomentosa*, is based upon the following collection: "COLOMBIA: MAGDALENA: Sierra Nevada de Santa Marta, southeastern slopes, Hoya de Río Donachuí: Cancurúa, fields and forests, 2400–2650 m alt.; a tree, the leaves coriaceous, yellowish, green above with cinereous tomentum beneath, 10 Oct 1959, *José Cuatrecasas & Rafael Romero Casteñada 24694*." I have had the opportunity to examine the holotype and have made the following observations.

In his comments following the description of the new species Cuatrecasas indicates the relationship of *Daphnopsis crispotomentosa* with *D. caracasana* Meissn., *D. macrophylla* (HBK.) Gilg, and *D. purdiei* Meissn. I have treated these three older species (Ann. Missouri Bot. Gard. **46**: 277–281. 1959) as members of a former "Rassenkreiss" since they show, better than any other species-group in the genus, evidence of sharing common ancestry. If *D. crispotomentosa* is closely related to any of them it would be reasonable to assume that its relationship is with that species which it approaches most closely in terms of geography and geology, *D. purdiei*. This species was collected once at Ocaña on the southern extension of the Sierra de Perija, a mountain range which is separated from the Sierra Nevada de Santa Marta by a river-valley system. Indeed, on the basis of vegetative characteristics, excepting perhaps pubescence, *D. crispotomentosa* agrees well with *D. purdiei*.

The principal distinguishing characteristic of *Daphnopsis crispotomentosa* is in the strongly crisped trichomes found on all parts. In comparison, the trichomes of *D. macrophylla* are slightly crisped, those of *D. caracasana* (see particularly young leaves, stems, and mature leaf margins of *Killip & Smith 17886*, GH) may be strongly crisped, and those of *D. purdiei* are sometimes slightly crisped. In no single specimen of these three species are the trichomes as densely arranged and at the same time as strongly crisped as in *D. crispotomentosa.* This characteristic, nevertheless, is not unique as Cuatrecasas implies.

Precise floral comparison cannot be made, for *Daphnopsis crispotomentosa* is known from immature fruit (Cuatrecasas's floral description is based on a few persistent calyces) whereas, *D. purdiei* is known only from staminate material. However, comparison of the pistillate "flowers" with those of *D. caracasana* shows that the two are similar; but differ in pubescence of the calyx, in shape of the ovary, and in the sessile stigma.

It is my opinion that it is necessary to recognize *Daphnopsis crispotomentosa* until more material is available when the possibility that it is the pistillate phase of *D. purdiei* should be investigated.

Daphnopsis fasciculata (Meissn.) Nevl., comb. nov.

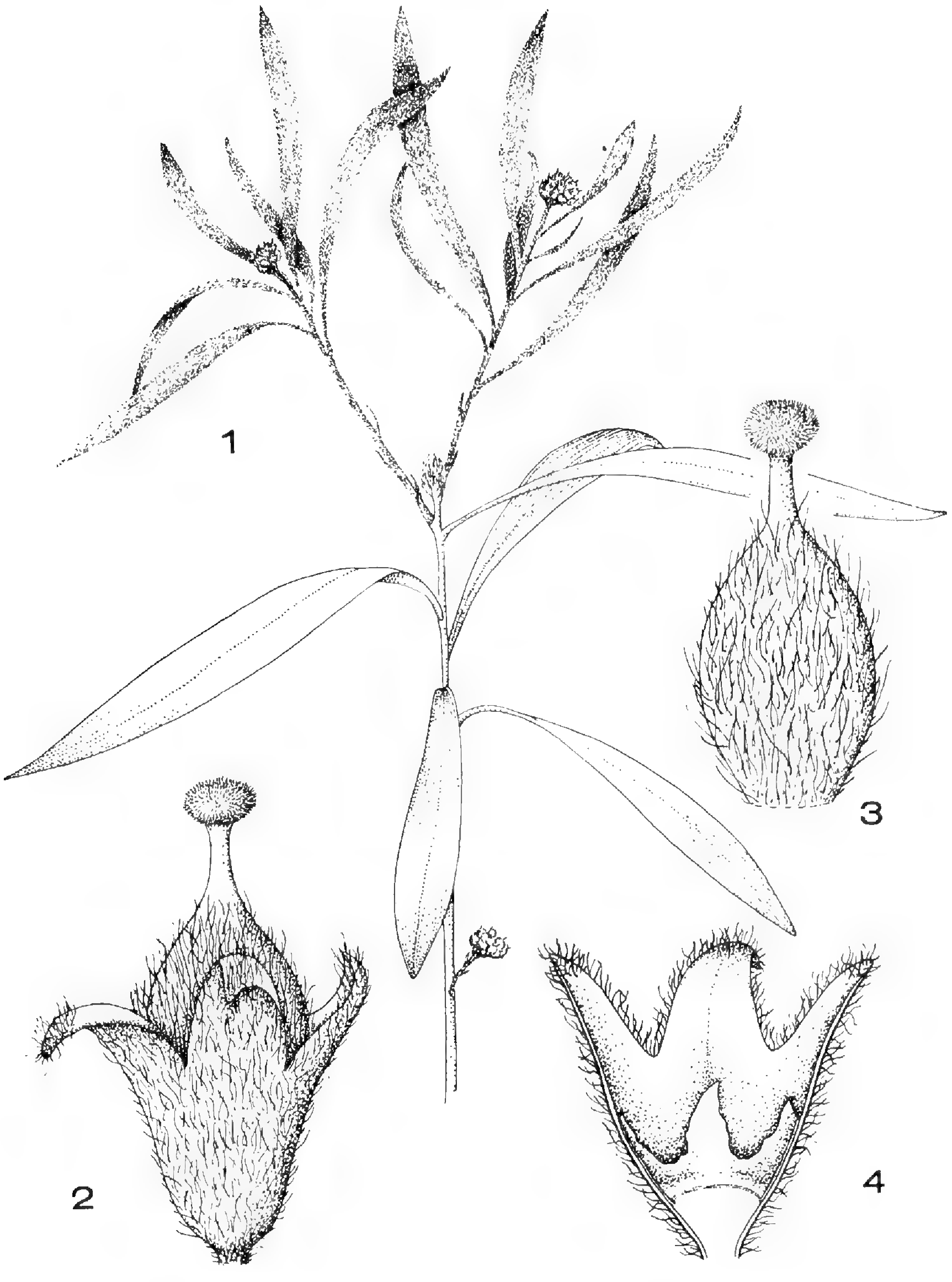
Funifera fasciculata Meissn. in Mart. Fl. Bras. **5**(1): 68. 1855.
Daphnopsis beta Taub. in Engl. Bot. Jahrb. **12**(Beibl. 27): 5. 1890.
Daphnopsis longifolia Taub. *ibid.*

Historically there has been considerable nomenclatural and taxonomic confusion in the Brazilian genus *Funifera* C. A. Mey., the cause of which seems obscure. *Funifera* is composed of a small number of species which, perhaps, gave the impression that there was little to be done. In the process of preparing a preliminary survey of the genus, I discovered, unhappily, that an isotype of *Funifera fasciculata* Meissner (*Widgren 1025*) had been cited among the specimens which I referred (344–346. 1959) to *Daphnopsis beta* Taubert. This specimen (NY) is a fragment of the holotype (from Herb. Sonder) kept by Meissner. It consists of a single leaf and flower; on the packet in Meissner's hand is written "Daphnopsis fasciculata nob (6 Oct. 1853)." I mistakenly believed this to be only a manuscript name, which it is in this particular combination, but it was published as *Funifera fasciculata* by Meissner in 1857. As the publication of *Funifera fasciculata* antedates that of *Daphnopsis beta* by nearly thirty-five years it is evident that a new combination is required because the species, regardless of its epithet, is clearly a member of the genus *Daphnopsis.*

Daphnopsis pseudosalix Domke, Notizbl. **12**: 724. 1935; Nevling, Ann. Missouri Bot. Gard. **46**: *322, fig. 32.* 1959.

Pistillate flowers of *Daphnopsis pseudosalix* have not been previously described. In a loan from the herbarium at Hamburg (HBG) a specimen of this species in young fruit has made it possible to prepare a description of pistillate flowers. For the sake of completeness a full specific description, with specimen citation, and illustrations (FIGS. 1–4) are presented.

Shrubs to 5 m., the young branches densely woolly and glabrescent. Leaf blades narrowly elliptic, 4–12.5 cm. long, 1–2 cm. broad, acuminate, acute or sometimes more or less obtuse at the apex, gradually tapered to the base, chartaceous, woolly and glabrescent above, becoming sericeous beneath, the midvein plane to immersed above, prominent beneath, mar-



FIGS. 1–4. Illustration of pistillate flowers and habit of *Daphnopsis pseudosalix* (*Ule 504*). FIG. 1, Habit, × ⅗. FIGS. 2–4, mature pistillate flowers, × 9; 2, whole flower; 3, gynoecium; 4, calyx tube opened to show interior, note especially lack of corolla and androecium as well as presence of lobed disc.

ginal vein present, the margin somewhat revolute; petiole 1–7 mm. long. Staminate inflorescences borne from the young leafy stem, racemiform, woolly, the primary peduncle 1–1.8 cm. long, the rachis 1–6 mm. long, the secondary peduncles 1–3 mm. long. Staminate flowers: (7–)10–15 per inflorescence; pedicel ca. 2 mm. long; calyx tube narrowly campanulate, ca. 2 mm. long, 1–1.5 mm. broad at the orifice, tomentulose without, glabrous within; calyx lobes unequal, puberulent within, the outer ca. 1.5 mm. long, 1 mm. broad, the inner 1–1.25 mm. long, 1 mm. broad; petals absent; antisepalous stamens inserted at the orifice, subexserted, the alternisepalous stamens inserted below the orifice, included, the anthers suborbicular, ca. 0.5 mm. long and broad, sessile; disc annular, free, less than 0.25 mm. tall, more or less entire, glabrous; pistillode nearly lageniform, ca. 0.75 mm. long, glabrous. Pistillate inflorescences borne from the young leafy stems or from axillary short-shoots on the older wood, umbelliform, woolly, the primary peduncle 1–1.5 cm. long, the rachis 1–2 mm. long, the secondary peduncles to 1 mm. long. Pistillate flowers: 8–15 per inflorescence; pedicel to 0.5 mm. long; calyx tube broadly campanulate, 1–2 mm. long, 1.5–2 mm. broad at the orifice, densely tomentulose without, glabrous within; calyx lobes subequal, tomentulose within at least toward the apex; petals absent; staminodia absent; disc annular, free, to 0.75 mm. tall, irregularly lobed, glabrous; ovary ellipsoid, ca. 2.5 mm. long, 1 mm. in diameter, strigose, the style thick but filiform, ca. 1 mm. long, the stigma capitate, papillose, ca. 0.75 mm. in diameter, exserted. Mature fruit not seen.

Brazil. SANTA CATARINA: prope Blumenau, *Schwacke & Müller 5981* (RB ♂); Itajahy [Itajaí], *Ule 504* (HBG ♀); without precise locality, *Saint Hilaire 1749* (P ♂), *Nadeaud s.n.* (F, P ♂).

This species is known from too few specimens for me to have any idea of the limits of its variation. It is hoped that Brazilian botanists will collect additional material soon. I have been unable to locate the type (*Pabst 546*) which, according to Domke, was collected "bei Desterro."

Daphnopsis racemosa Griseb. Symb. Fl. Arg. 134. 1879.

Daphnopsis leguizamonis Griseb. ex Gilg, in Engl. Pflanzenfam. 3(6a): 236. 1894, *pro syn.*

Daphnopsis racemosa var. *leptostachys* Chod. & Hassl. Bull. Herb. Boiss. II. 3: 811. 1903.

Daphnopsis longiracemosa Gilg ex Domke, Notizbl. **12:** 728. 1935.

Daphnopsis umbelluligera Domke, *ibid.* 730. 1935.

No material referable to *Daphnopsis umbelluligera* Domke was located at the time of my revision (1959). The holotype (*Ule 4765* ♂ "Estado de Rio de Janeiro. Strauch auf der Insel Cabo Frio. October 1899") having been destroyed at Berlin during World War II. Domke's excellent description of the new species led me to believe that it might be synonymous with *D. racemosa* Griseb., with which he also indicated a close relationship. Examination of an isotype, deposited at the Staatsinstitut für allgemeine Botanik, Hamburg (HBG) confirms this opinion.

The Ule isotype agrees in all vegetative characteristics save two with those of *Daphnopsis racemosa*: (1), the shape of the leaf bases are conspicuously cuneate whereas an auriculate or subauriculate base is typical of *D. racemosa* (one exception with a cuneate base is *Dusen 8055* [GH]) and, (2), the petioles tend to be slightly longer, i.e., to 7 mm. *vs.* to 4 mm. long. The position, structure, and size of the staminate inflorescence is precisely that of *D. racemosa.* The staminate flowers do not deviate from the norm of this latter species, even having the peculiar orange-colored disc with yellow apices. Therefore, although the Ule specimen appears to be unique, it falls well within the total range of variation already demonstrated for *D. racemosa* and must be referred to it. There seems to be no need for recognizing any infraspecific categories. The addition of the Insel Cabo Frio locality to the distribution of *D. racemosa* extends the geographical limits of that species insignificantly. The staminate branchlet of *Ule 4765* deposited at Hamburg (HBG) is designated as the lectotype of *D. umbelluligera* Domke, to replace the holotype destroyed at Berlin.

Daphnopsis schwackeana Taub. in Engl. Bot. Jahrb. 12 (Beibl. 27): 6. 1890.

Daphnopsis ulei Gilg ex Domke, Notizbl. 12: 725. 1935.

The holotype of *Daphnopsis ulei* was destroyed, as was that of the preceding species, in Berlin during World War II. An isotype (*Ule 3754* ♂ "Serra do Itatiaia. Blühend in Januar 1986 [1896]") however, was located recently at Hamburg (HBG) with Gilg's penciled identification, but lacking Domke's annotation.

Examination of the Ule isotype reveals that it is a staminate specimen of *D. schwackeana* Taub. It has slightly shorter and more obtuse leaves than the average specimen of this species but deviates in no other way. The specimen has several inflorescences upon which are borne a few buds. Examination of one of the larger buds indicates complete agreement with the floral morphology of *D. schwackeana.* The most striking features of the staminate flowers of this species are the petals connate into a faucal annulus, and the well-developed disc surrounding a rather large fusiform pistillode.

The staminate specimen of *Ule 3754* deposited at Hamburg (HBG) is designated as the lectotype of *Daphnopsis ulei* Gilg ex Domke to replace the holotype destroyed at Berlin.

Daphnopsis weberbaueri Domke, Notizbl. 12: 722. 1935.

Shrubs to 2 m. tall, dichotomously branched, the young branches golden puberulent and glabrescent, the bark reddish brown, rugose with small white lenticels. Leaf blades obovate, oblong-spatulate, or oblong-elliptic, 3–7 cm. long, 1–3 cm. broad, more or less obtuse at the apex, cuneate at the base, membranaceous, glabrous above, sparsely sericeous to glabrescent beneath, usually with a tuft of trichomes at the apex forming a false mucro, the lateral veins prominulous; petiole 1–2 mm. long. Inflorescences terminal but soon appearing lateral, umbelliform, puberulent, the primary peduncle 1–2.5 cm. long, the rachis 1–2 mm. long, the secondary peduncles ca. 1 mm. long. Staminate flowers: 6–25 per inflorescence; pedicel 1–3 mm. long; calyx tube infundibuliform to subcampanulate, 3.5–5 mm. long, 1.5–2.5 mm. broad at the orifice, puberulent without, glabrous within; calyx lobes deltoid, ca. 2 mm. long, 1.5 mm. broad, glabrous within, reflexed; petals 8, papilliform to squamelliform, ca. 0.25 mm. long, inserted in pairs immediately above the alternisepalous anthers; stamens 8, inserted in two whorls, the upper whorl antisepalous, inserted on the base of the calyx lobes, exserted, the lower whorl alternisepalous, inserted about an anther's length below the orifice, included, the anthers oblong to nearly round, 0.5–0.75 mm. long and broad, sessile; disc completely adnate; pistillode lageniform, 0.75–1 mm. tall, glabrous. Pistillate flowers: 3–7 per umbel; pedicel 3–5 mm. long; calyx tube urceolate to subcampanulate, ca. 3 mm. long, 1.5–2.5 mm. broad at the orifice, puberulent to subsericeous without, glabrous within; calyx lobes unequal, glabrous within, the outer ca. 1.5 mm. long, 1.25 mm. broad, the inner ca. 1 mm. long, 1.5 mm. broad; petals 8, papilliform; staminodia 8, papilliform, minute; disc basally adnate, the free apex entire to undulate, glabrous; pistil 4–4.5 mm. long, the ovary obovoid, glabrous, the style 1.5 mm. long, eccentric, the stigma capitate, slightly exserted. Fruit not seen. FIG. 5.

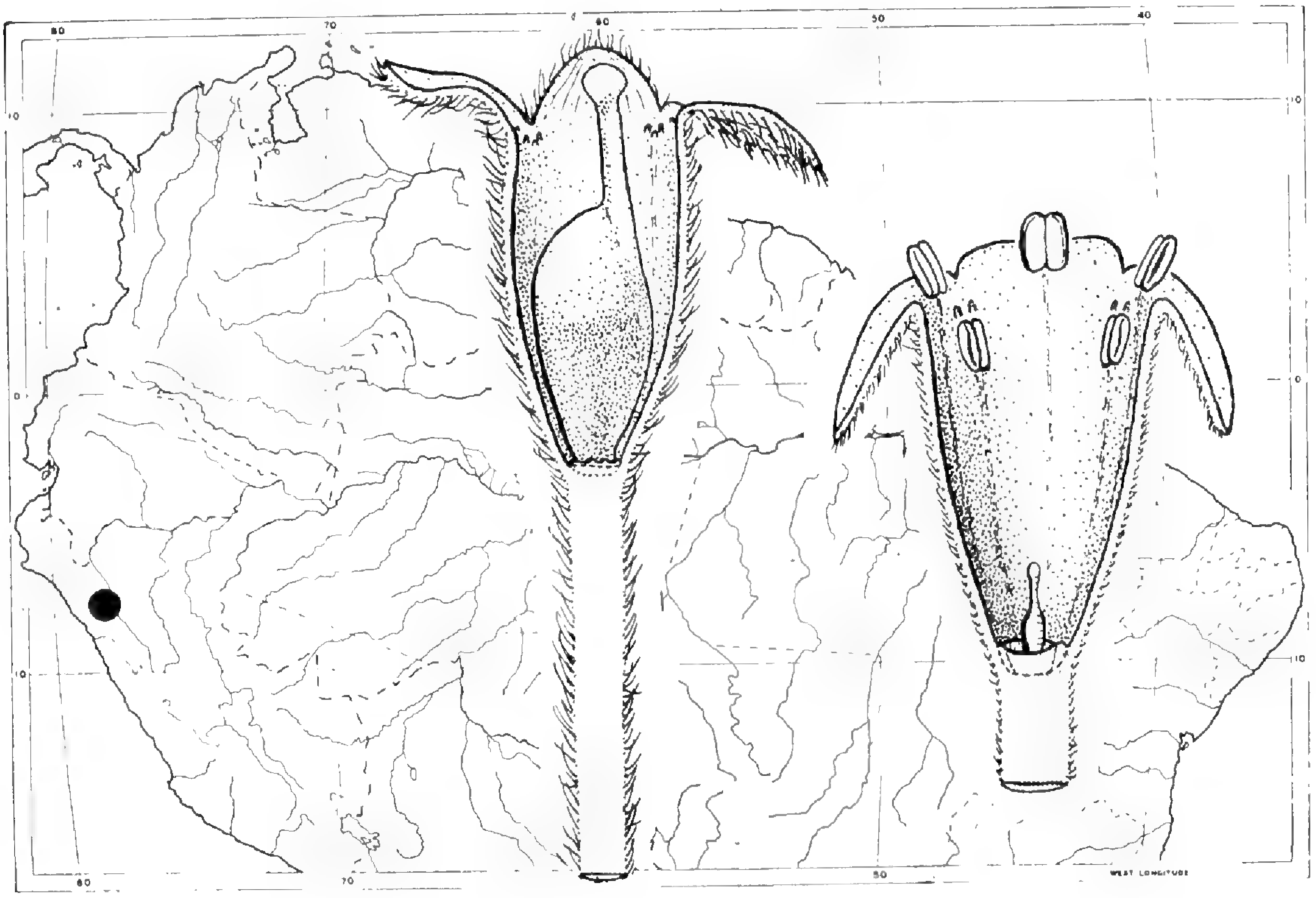


FIG. 5. Illustration of pistillate (*Weberbauer 7219*) and staminate flowers (*Weberbauer 7217*) of *Daphnopsis weberbaueri*, × 9.

Collected once, flowering in December, at an altitude of 3200 meters. Flowers greenish.

Peru. CAJAMARCA: valley of the river Tequeltepeque above Namas, *Weberbauer 7217* (F, GH ♂), *7219* (F–lectotype ♀).

Domke cites *Weberbauer 7217* as "mannl. Typus" and *7219* as "weibl. Typus." The designation of a lectotype clearly is required. Equal emphasis is given in Domke's description to staminate and pistillate material but it seems preferable to choose the pistillate element (*7219*) for important taxonomic characters are found there. In addition, the sheet of this number in the Chicago Natural History Museum bears an annotation, probably in Domke's hand; the original Weberbauer collections were presumably destroyed at Berlin. The Chicago (F) specimen is the only duplicate I have seen of *Ule 7219* and is here designated as the lectotype.

The position of *Daphnopsis weberbaueri* has caused some difficulty ever since its discovery. The collector, Von Weberbauer, thought he had a species of *Ovidia* (a conclusion which I believed correct at the time of my revision of *Daphnopsis*). Domke disagreed with Weberbauer and described the material as *Daphnopsis* because of superficial similarities in leaves, disc, and possibly in the sessile anthers, as well as in the geographic distribution.

The most important characteristic which indicates relationship with *Ovidia* is the eccentric position of the style in pistillate flowers. This character, which does not vary within a species, is considered taxonomically reliable at the specific level. In most genera it is reliable at the generic level but in others such as *Thymelaea* Endl. and *Gnidia* L. it is apparently inconsistent. It is precisely this character, in conjunction with others it is true, which is used to separate *Dirca* L., *Drapetes* Banks ex Lam., *Funifera* C. A. Mey., and *Ovidia* Meissn., from other American genera. An eccentric style is considered more advanced than a terminal or centric one (the implication is that a style in the terminal position indicates a gynoecium composed of two equally expanded carpels). Heinig (Am. Jour. Bot. **38**: 113–132. 1951) interpreted the gynoecium of *Dirca*, which has an eccentric style similar to that of *Ovidia*, to be composed of two carpels: one fertile and expanded, the other sterile and unexpanded. The ovular trace is derived from both placentae of the fertile (expanded) carpel. Therefore, it is necessary to assume carpel polymorphism to explain the gynoecium in *Dirca*. A nearly identical vascular pattern is found in *Linostoma* Wall. ex Endl. which has a terminal style. Heinig's explanation is questionable, however, for in other plant families in which the application of the theory of carpel polymorphism has been re-examined it has been shown to be incorrect. A re-examination here, or at least a reinterpretation, seems to be in order.

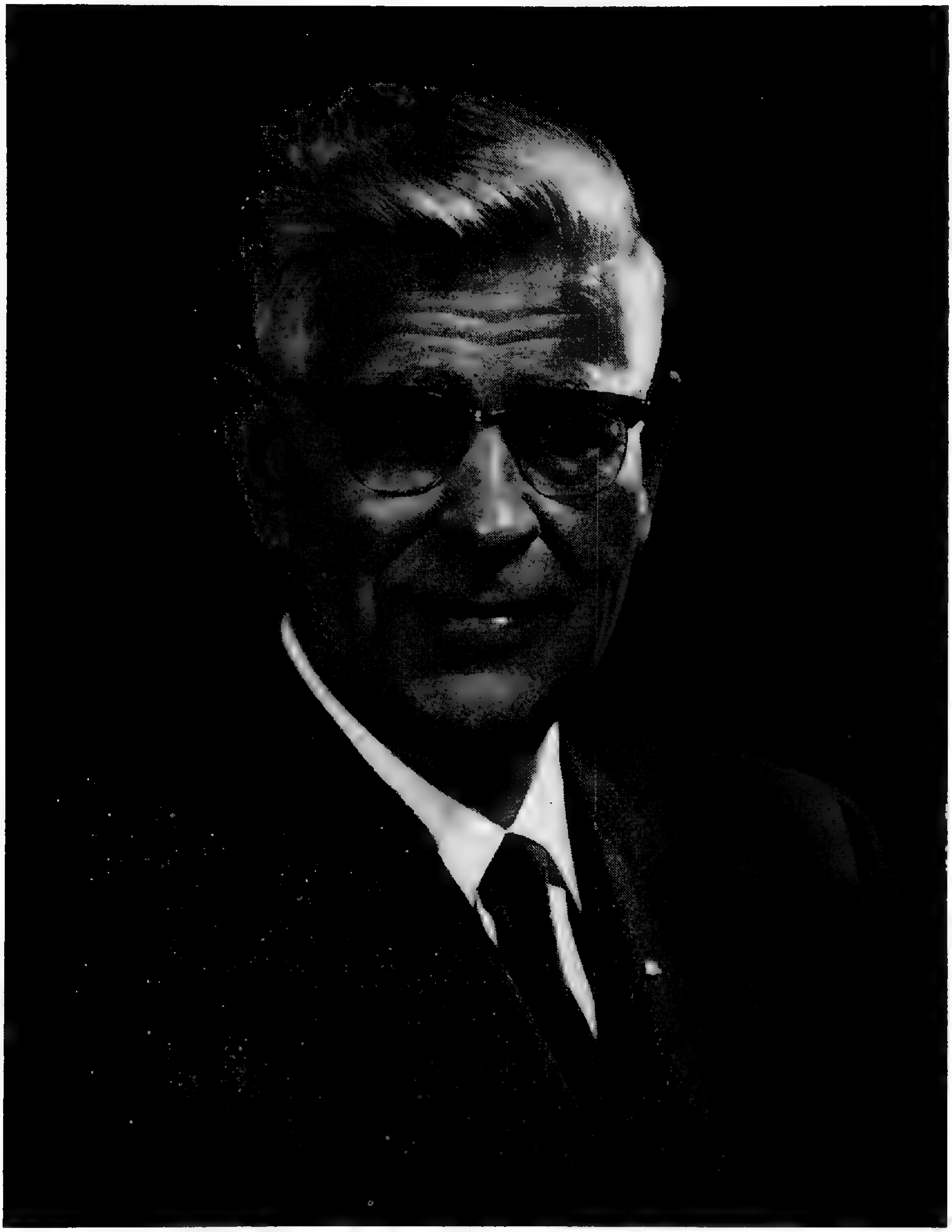
The leaf shape, size, membranaceous nature, position in clusters at the branch apices, coupled with the poor development of extraxylary fibers seem to indicate relationship of Weberbauer's material with *Ovidia*. Internal anatomical characteristics of the leaf do not show close similarity with the latter genus but, unfortunately, information is not available to allow comparison with *Daphnopsis*.

The similarity of the disc to that of *Daphnopsis* (pointed out by Domke) seems to be no greater than its similarity to *Ovidia*. Considerable variation in disc shape, size, connation, and adnation is found in *Daphnopsis*, making it possible to relate almost any disc type in the family to it. The disc characteristics seem to be of little generic significance in this particular case.

Sessile anthers are not found in *Ovidia* but nearly sessile ones are, i.e., with filaments only 0.25 mm. long. As in the disc, a range of variation in filament length also is found in *Daphnopsis* so that relationship in any direction may be postulated. This character, however, is not pertinent to the discussion.

One point of considerable significance which has been previously overlooked is that the plants of this species are dioecious. *Ovidia* exhibits gynodioecism only. *Daphnopsis* is in the main dioecious, although a few species occasionally seem to show tendencies toward gynodioecism (i.e., staminate plants sometimes set a few fruits; the viability of these fruits, however, has never been ascertained).

The geographic distribution is very important since the species falls well outside the range of *Ovidia* but within that of *Daphnopsis*. This fact, coupled with the morphological information presented above, becomes an almost insurmountable barrier to placing *D. weberbaueri* in *Ovidia*. When considered from this viewpoint, and when one attempts to relate the species to one of *Daphnopsis*, it appears that *D. weberbaueri* is most closely related to *D. macrophylla* (HBK.) Gilg, and should be placed near it. There is no question that the species is somewhat anomalous for *Daphnopsis* but it scarcely has the necessary prerequisites to constitute a new genus. The most important hypothesis to be derived from this problem is that style position probably has shifted at several times and in relatively independent groups within the family during its evolutionary history.



Clarence Emmeren Kobuski

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CLARENCE EMMEREN KOBUSKI, 1900–1963

RICHARD A. HOWARD

With portrait *

CLARENCE EMMEREN KOBUSKI, who died on May 9, 1963, in his 64th year, will be remembered by those who knew him well and worked with him as one of the kindest men on the present American botanical scene. In his little-publicized roles as curator, editor, hospital corpsman, singer, and friend, he touched the lives of more people than may ever refer to his published scientific work. In the lives of many of us there is a gap that could have been left only by the death of a man of his character and generosity.

Kay, as he preferred to be called, was born in Gloversville, New York, on January 9, 1900. His ancestry can be traced to Polish nobility through his father, but after the arrival of the latter in the United States, the family name was shortened for convenience. Kay, one of the first of his family to enter college, graduated from Cornell University in 1924 with a Bachelor of Science degree. While there, his future career was shaped by his teachers in languages and science, including K. M. Wiegand and A. J. Eames. His outstanding scholastic record earned for him a Rufus J. Lackland Fellowship at Washington University, St. Louis, where he pursued his studies in conjunction with the herbarium and taxonomic activities at the Missouri Botanical Garden. He was awarded the degree of Master of Science, in 1925, for "A Revision of the Genus *Priva*" (Verbenaceae) and the degree of Doctor of Philosophy, in 1927, with his thesis "A Monograph of the American species of *Dyschoriste*" (Acanthaceae), both accomplished under the direction of Dr. J. M. Greenman. His future research was not again to touch on these families.

For a number of years Professor Alfred Rehder, curator of the Arnold Arboretum, had been corresponding with Dr. Greenman, seeking from the Henry Shaw School of Botany an assistant for the herbarium. It is clear from the correspondence that Rehder was overburdened with routine herbarium work and that he wished time for his own research. Greenman suggested Kobuski, and it was this position, as assistant, which Kobuski

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* Photograph by Fabian Bachrach, December, 1961.

accepted in the fall of 1927. Kay delighted in telling of his first days on the job at the Arboretum. Charles Sprague Sargent, director for 50 years, had just died; E. H. Wilson was acting as director; and Rehder was swamped with the responsibilities of editor and curator. On Kobuski's arrival, Rehder presented him with two massive piles of specimens. The first was to be filed "as soon as possible" in the herbarium, which was located for him with a vague sweep of the hand. The second was to be identified "as soon as possible," and there would be "other tasks as well." Not a word was said of "time for research." Although there were other assistants in the herbarium, Kay soon became the backbone of the curatorial staff, and, during the 36 years he served the collection, unmistakeable signs of his care and devotion to it became increasingly apparent. Kay's meticulous observance of details in his professional work, and in his personal life as well, marked his career. Over the years at the Arnold Arboretum he inaugurated or implemented a system of accessions, loan records and exchange forms, and of procedures for processing and identifying collections which subsequent students have taken to other institutions, with the result that many are becoming standard in American herbaria.

Kobuski and Rehder presented a great contrast in personality and appearance. Kay was over six feet tall and striking in appearance, with jet black hair. He was friendly and outgoing in his personal relationships with everyone. Rehder, on the other hand, was slight of frame, short, and exceedingly retiring in nature. Despite their differences in physique and temperament there developed between the two men a relationship of lasting quality and mutual benefit. Both were scholars well versed in languages and were masters of Latin and Greek. At this period they complemented each other editorially. Kobuski could polish a sentence; Rehder, with an insight gained from long experience, could resolve the most complex botanical and horticultural problems. Together, they worked on the numerous, challenging collections continuously arriving at the Arboretum from collectors in Asia. Together, they prepared the *Journal of the Arnold Arboretum* and later read the proofs for Rehder's books. Together, these men continued for nearly two decades, through the trials and errors of successive directors or supervisors, the work for which the Arnold Arboretum is noted.

Kay's many other achievements were less well known. He had a powerful, naturally pleasing baritone voice with an unusually high tenor range, nearly perfect in pitch. He liked to sing, although he had had no formal training until, in 1935, he was persuaded to begin vocal instruction. His first teacher was Theo Carreiro, of Boston, through whose encouragement Kay's inherent love of music gained purpose and direction. Kay bought a piano, began to amass a significant collection of recordings and sheet music, and concentrated on the theory of music. His understanding of languages and of melody allowed more accurate interpretations than is often usual among singers. In 1938, Kobuski became a pupil of H. Wellington Smith, of New York, who taught in Boston one day a week. Before a year had passed, Kobuski was being groomed for an audition at the

Metropolitan Opera. The realization that at his age an operatic career would necessarily be short and that for it he would have to give up taxonomy, after years of botanical training, caused him to decide, regretfully, that his singing should remain largely an avocation. Kay sang often, although botanists, as a group, heard him just once, at a testimonial dinner for J. M. Greenman during the AAAS meetings in Indianapolis in 1937. He sang professionally throughout New England and for over two years was baritone soloist at the Church of St. John the Evangelist, under the direction of Everett Titcomb. The parts assigned to him were demanding, but his strong, clear voice could be heard over a full choir. He enjoyed giving pleasure to his audience, and few who heard him ever forgot the experience. Unfortunately, his wartime service terminated his singing. His love for music persisted however, and he continued to be a devotee of opera until the end.

In October of 1942, Kobuski was drafted in the U. S. Army at an age barely days below the upper age-limit for conscription. His hair was graying when I, nearly 20 years his junior, saw him on an obstacle course at Camp Pickett, Virginia, training to carry a litter in a hospital battalion. His Ph.D. degree brought him only enlisted-man training as a hospital laboratory technician and an assignment to a hospital ship. Kay worked as hard at this as at any professional assignment, and his medical knowledge eventually rivalled that of the younger medical officers under whom he served. In the years following, Kay made twenty-six crossings of the Atlantic under wartime conditions in convoys and in unaccompanied hospital ships, bringing wounded servicemen back from the African and Mediterranean theatres. Perhaps a good corpsman should be impersonal, but Kay carried the burdens of his patients who frequently became a personal concern. Many he cared for remained his friends through the years. Kobuski returned from the service in August, 1946, physically affected by his experience. For therapy he was advised to take up needle-work, but only few of his close friends knew that the many pieces of needlepoint in his home were of his own design and creation.

Several years after his return to civilian life Kay took into his home an ill amputee he had transported as a patient during the war; he cared for this man during the latter's final years of illness. Kay's guest, however, worked at intervals in an antique shop. With the interest of his patient at heart Kay undertook to learn about antiques and soon began to collect them for his own satisfaction. His specialty became lamps, china, and glass, and his collection developed into that of an expert. He amassed not the largest but probably one of the most complete sets of crossed-swords, blue, onion-pattern Meissen china in private ownership. In each of the areas of his interest Kay made and kept friends.

In 1949, Kobuski was appointed both editor of the *Journal of the Arnold Arboretum* and curator of the herbarium. In both posts his influence became widespread through the years. He had served as associate editor of the *Journal* from 1932 until he left for military service. On his return, though the *Journal* was being issued by an editorial board, Kay did a large share of the work without assuming the full responsibility. He served as editor from 1949 until he asked to be relieved of the duty in 1958. During his twenty-six years of association with the *Journal* hundreds of manuscripts passed through his hands. Countless students, colleagues, and fellow botanists benefited from his suggestions concerning both the style and content of their manuscripts. Meticulous in detail and insistent on accuracy Kay never could be said to edit "by marking for the printer." On papers submitted to him, he always corrected the Latin descriptions (sometimes supplying words left out by the author), often checked references, verified citations of specimens, or had the manuscript retyped. He was insistent that only clean copy be submitted to the printer, and more than one of the printers who worked on his material expressed pleasure over the manuscript, a credit to the editor rather than the author. Only Kay might have appreciated fully the fact that one of his death notices appeared with a letter in an incorrect font of type.

Kobuski as a curator was unsurpassed. He believed that specimens were in the herbarium to be studied, but he valued more than the majority of botanists the heritage that is the curator's responsibility. Kay was the strict but impartial guardian of the herbarium. If the situation warranted, he would refuse a request from an old friend as readily as one from a complete stranger. An ambiguous letter elicited a reply requesting clarification before specimens were sent out; but that loan when sent was certain to contain the material requested and all unidentified specimens that might be of interest to the investigator. His scorn was deep, however, for the botanist who returned those specimens in poor condition or without annotations; it was limitless for one who cited the specimens incorrectly.

In 1954, a decision was made that a portion of the herbarium of the Arnold Arboretum was to be moved to Cambridge, Massachusetts, to a new building more integral to the University and its students. It was Kobuski's task to prepare the Arboretum herbarium for this move and to establish, with me, which specimens of cultivated plants might most profitably be left as a working unit with the living collections in Jamaica Plain. Here his long experience in the efficient use of an herbarium for the identification of plants under cultivation proved to be of inestimable value. Over 100,000 specimens were selected from the general collections of the Arnold Arboretum to be the basis for future work in horticultural plant taxonomy. Kay then moved with the remainder of the collections to Cambridge and, in 1954, he was appointed jointly as curator of the Arnold Arboretum and of the Gray Herbarium to implement the reorganization of the two herbaria into one workable unit. He also served as supervisor of the entire Harvard University Herbarium Building. For a period of five years Kay directed the project involving the reorganization of almost two million specimens and their rearrangement in proper systematic and geographic sequence, as well as the recognition and annotation of type specimens and their arrangement in special folders. The Arnold Arboretum and the Gray Herbarium had used different systems of arrangement, and their respective botanists, Rehder and Fernald, did not always agree on names or species limits. Characteristically, Kay undertook the processing of difficult groups such as the Fagaceae and Juglandaceae where many exacting decisions had to be made. The model combined herbarium created as a result of his tremendous effort remains a monument to his knowledge and ability.

Kobuski's role in the administration of this newly organized herbarium was unique. Two organizations, each with its own herbarium, library, staff, and traditions, were to function in one building under two directors with a single head curator. Few people could have recognized, much less defined adequately, the combined responsibility as well as Kay, who served faithfully and honestly the interests of each organization, dealing fairly with old friends and new associates, carefully submerging his own interests or past loyalties with an impartiality deserving of more admiration and recognition than it received at the time. Kay enjoyed his position immensely. Only rarely did a feeling of nostalgia emerge, and on such infrequent occasions it was manifested by a rather wistful comparison of the restricted view from his new city office with the outlook over the broad acres in Jamaica Plain. His office was the focal point of many activities; but he was available at all times to students, staff, and visitors for informal conversation, professional advice, or discussion of personal problems.

Throughout his professional taxonomic career, Kobuski's tasks were largely assigned or were the result of necessity. He joined the staff of the Arboretum at a time when thousands of specimens were arriving from Asia. As an example, Joseph F. Rock's important collections contained over 25,000 numbers. To Kay and his associates fell the task of sorting these collections for study, preparing lists and duplicate labels, sending sets to specialists, selecting the set to be mounted and inserted, and finally, after determinations were completed, of distributing the duplicates. Throughout his long career at the Arboretum, more collections arrived each year than could be mounted or distributed. As the backlog of unworked material increased curatorial problems also increased proportionately.

Like the early routine duties of the herbarium, Kobuski's first piece of research for the Arnold Arboretum also was assigned by Rehder. A research project, initiated by a former staff member who had resigned because of illness, was given to Kobuski to complete. In this way he began his work on the Theaceae which was to continue throughout his career and to be the basis of his most important published contributions. Thirty-five papers on this difficult family treated genera and species in all tropical areas of the world. The one group of Theaceae which he avoided completely was *Camellia*, with its all too numerous variants. His interest in the genus *Jasminum* began in a similar way: a job to be done in order to solve a problem concerning the correct name for a particular cultivated jasmine, led, ultimately, to a research project. Although his publications do not reveal it, Kay was probably the most knowledgeable American botanist in recent years who worked in the area of cultivated woody plants. After

Rehder's death, Kobuski carried on the voluminous correspondence initiated by Rehder, hopefully, toward a revision of his *Manual of Cultivated Trees and Shrubs*, and concerned chiefly with new records and the identification of specimens. It had been Kay's plan, on retirement in 1967, to return to Jamaica Plain to work with the younger taxonomists on such a revised edition of Rehder's work.

Kobuski's published work scarcely indicates the range of other very real contributions. He completely lacked self-ambition but was unswerving in his desire to further the work and the reputation of the institutions with which he was associated. I have never known a more unselfish man. His own research was frequently laid aside in order to help another worker personally or by correspondence. Nearly every major publication of the Arnold Arboretum produced during his career contains his own not insignificant contribution. His help is acknowledged in hundreds of botanical publications, yet an equal number which might well have done so failed to include such acknowledgment.

Kay did not join many societies. He was a member of the American Society of Plant Taxonomists and a charter member of the International Association for Plant Taxonomy. His membership in the New England Botanical Club covered 36 years and he served the club as assistant phaenogamic curator and council member.

Kay had a dramatic personality and a theatrical manner. At the staff luncheon table he always occupied the head chair from which he moderated discussions or regaled the group with anecdotes well told and always in good taste. Others about the table counted on Kay's reaction to their own comments and were not disappointed. The reaction was sometimes explosive, sometimes stoic, or occasionally a mock expression of shock or disbelief, but it was always dramatic.

This dramatic, often explosive manner, combined with his imposing appearance, could be disconcerting to those who did not know him well, and there were those who misunderstood him. He often reacted first, perhaps sounding curt or brusque, but he did not fail to make amends if he realized that he had been misinterpreted. His was a colorful character to which one could not remain neutral.

Kobuski was a bachelor, sometimes seeking solitude, sometimes gregarious. He was a frequent and welcome visitor to the homes of neighbors and friends with families. His kindness to children was unsurpassed, and the love was mutual.

Kobuski is survived by a sister, Agnes Schroeder (Mrs. Henry J.), of Saugerties, New York, and a brother, Lawrence, of Gloversville, New York. He was buried in the family plot in his native town.

There is no simple epitaph for the man who devoted thirty-six dedicated years to one institution. His term of service is exceeded in length only by those of Charles Sprague Sargent and of Alfred Rehder. His heart was truly big. His life was well lived. We miss him.

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STUDIES IN THE THEACEAE, XXXIV
SOME ASIATIC TAXA OF TERNSTROEMIA [1]

† CLARENCE E. KOBUSKI

Ternstroemia elongata (Korthals) Koorders, Exkurzionfl. Java 2: 611, 1912, *in clavi*, as to name, not as to plant.

Reinwardtia elongata Korthals, Verh. Nat. Gesch. Bot. *t. 12.* 1840; text p. 103. 1841.

Ternstroemia gedehensis Teysm. & Binn. Nat. Tijdschr. Ned. Ind. 3: 332. 1852.

Ternstroemia gedeënsis Teysm. & Binn. Nat. Tijdschr. Ned. Ind. 14: 156. 1857, sphalm. = *T. gedehensis.*

Small tree or shrub with erect, terete, grayish-brown branches; branchlets somewhat subtetragonal or compressed, fasciculate or subfasciculate, grayish brown. Leaves coriaceous, fasciculate, congested at the apex of the branchlets, oblong-obovate or elliptic, 7–14 cm. long, 3–4(–5) cm. wide, acuminate at the apex, cuneate at the base, the margin entire, the

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[1] This paper includes eight taxa of *Ternstroemia* for which Dr. Kobuski had written the manuscript (with the exception of the Latin descriptions) prior to the last month of his illness. Before the onset of his difficulties in the fall of 1960 he had begun a revision of the Old World species of *Ternstroemia*, proposing to publish a series of regional studies of this complicated and poorly understood group. He had borrowed specimens from a number of herbaria, had visited important European herbaria in the summer of that year, and had completed a manuscript on the African species which was published in January, 1961. He was able to publish later in 1961 "A Review of the Genus *Ternstroemia* in the Philippine Islands," "Variation in the Fruit of *Ternstroemia kwangtungensis*," and a by-product of his study. "A New Species of *Adinandra* from the Celebes" (all in *Journal of the Arnold Arboretum*, volume 42). He had reached more or less definite conclusions about many of the Asiatic taxa and, at the time of his last hospitalization, was working toward the completion of a manuscript on the species occurring in Sumatra. Failing that, he expressed his desire to publish with a short introduction at least the completed descriptions and notes on *T. patens* and *T. elongata*, which have been confused in the past. These two, along with two new species from Sumatra, two new taxa from the Celebes, a species from Ambon, and one from China, are presented here. With the exception of the manuscript for two additional species, his notes are otherwise only partially complete and are best left untampered with. I have attempted only to correlate his descriptions and notes (which were written at various times) and to check the citations of the specimens against those which he had on loan, but with a minimum of alterations in the data which he included. Lily M. Perry has helped greatly with the translation of some of the collection data. With the aid of Bernice G. Schubert and Robert C. Foster in some of the critical parts, I have also provided the necessary Latin descriptions for the three new species, using as models both those which Dr. Kobuski had published and his completed descriptions of two new species of the Lesser Antilles which comprise an additional paper, the thirty-fifth and, most sadly, the last in this series of studies in the Theaceae.—C. E. Wood, Jr.

midrib canaliculate above, elevated below, reddish, the veins obscure on both surfaces, ca. 4 main pairs, arcuate-ascending, generally anastomosing near the margin, the petiole 1.5–2 cm. long. Flowers axillary, disposed near the apex of the branchlets. Staminate flowers: pedicel 1 cm. or less long, recurved; bracteoles 2, opposite immediately below the calyx, deltoid, ca. 1.5 mm. long, 2 mm. wide at the base, flat on the ventral surface, thickened into a median ridge on the dorsal surface, glandular-apiculate at the apex, the margin with a few glands; sepals 5, unequal, the outer two smaller, rounded, ca. 3 mm. long, 2 mm. wide, the margin entire, hardly scarious, the inner three concave, wider than long, 3.25 mm. long, 4.25 mm. wide, the margin subscarious; petals 5, oblong-obovate, recurved, 6.5 mm. long, 3–3.5 mm. wide, subligulate, broadest near the apex, emarginate; stamens 50–55 in a single series, ca. 4.5 mm. long, the filaments joined at the base and adnate to the base of the corolla, distinctly finely filamentous, 3 mm. long, the anthers ca. 1.5 mm. long; ovary none. Pistillate flowers: pedicel, bracteoles, calyx, and corolla as in the staminate flowers, the ovary globose to conico-globose, ca. 2 mm. long, ca. 3 mm. in diameter, 2-loculate, each locule with as many as 6 ovules pendent from the apex, the style ca. 2 mm. long, the stigma 2-punctate. Fruit not seen.

Sumatra. RES. WESTKUST: "Melintang" [Malintang Mts., nne. of Padang], *P. W. Korthals s.n.* (L [908251–987], lectotype); exact locality lacking, *Korthals 1238* (L [908251–988 and –998], probable isolectotypes); exact locality lacking, *Korthals s.n.* (L [908251–990 and –1000], probable isolectotypes); north of Pajakumbuh [Pajakoemboeh] in Harau ravine, 0° 10′ S., 100° 40′ E., on steep walls of soft tuff stone, alt. 500–600 m., *M. Jacobs 4588* (A, BO, K, L), Aug. 15, 1956 (once seen; shrub 4 m.; leaves dark above, light below; flowers cream; ovary yolk-yellow). RES. BENKOELEN [Benkulen]: Belirang-Sekintjau gebergte [Sekintjau-Belirang Mountains], alt. 1500 m., *F. W. Rappard 62* (A, BO, L, NY), Aug. 12, 1936; Soeban Ajam [Soebanajam], *Ajoeb* (Exped. Jacobson) *271* (BO), July 5, 1916. RES. RIOUW: Indragiri [Inderagiri], Bovenlanden, Moeara Padjanki, in primary forest, few meters alt., *P. Buwalda 6407* (BO, L), Apr. 7, 1939. **Cultivated.** JAVA: "Cult. in hort. Bog." (BO [134748], possible type material of *T. gedehensis*; [134749, 134750], possibly from the same plant); without data except "Teysmann misit 1867" (L [925250–335], possible type material of *T. gedehensis*).

In 1840, illustrations of *Reinwardtia elongata* Korthals and *R. patens* Korthals, representing the two taxa of the new genus *Reinwardtia*, were published. However, the descriptive text for the genus and species did not appear at the same time but in a later fascicle published the following year. The genus *Reinwardtia* retained its identity until 1912, when Koorders, in a key to the flora of Java, transferred *R. elongata* to *Ternstroemia*, making the combination *T. elongata*. Unfortunately, as is clearly shown in Koorders and Valeton, Atlas Baumarten Java 3: *t. 584*. 1915, the material on which the transfer was based belonged to the second species, *T. patens* (Korthals) Choisy. Furthermore, according to my interpretation, and as far as I know, *T. elongata* has been collected growing spontaneously only in Sumatra. Nomenclaturally, the combination *T.*

elongata (Korthals) Koorders is correct, but taxonomically it has been misinterpreted.

Following the original description of *Reinwardtia elongata* the localities were given as "*Crescit juxta Doekoe, etc.:* SUMATRA." One might expect to find the type in either the Bogor or Leiden herbaria, but at neither institution is there a specimen labeled with the locality Doekoe. However, at Leiden there are five sheets which can be related to the binomial *Reinwardtia elongata* Korth. These specimens were collected by Korthals, and four sheets bear one or two notes in his handwriting. All are either without locality, other than Sumatra, as *Korthals 1238*, or with a locality but without a number, as "Melintang" [= Malintang], *Korthals s.n.* These are obviously the "etc." of the original citation. It is quite evident when examining these specimens and comparing them with the original illustrations (in bud) that these were used for the drawings and description. I have recorded the Malintang specimen as the lectotype, but number *1238* and the two other sheets without collection numbers probably were taken from the same original specimen. One finds often in these earlier collections rather haphazard labeling. Some obviously were not furnished with the original "bits" of paper with the scribbled localities and now possess rather formal labels.

The characters which set off this species are (1) the two-loculate ovary with up to six ovules in each locule, (2) the subulate style (ca. 2 mm. long), and (3) the two-tipped, punctate stigma.

Ternstroemia gedehensis Teysm. & Binn. was described in 1852 from cultivated material growing in Java. It agrees with *T. elongata* in the distinctive characters mentioned immediately above. Possible type material is represented by a specimen in the Bogor herbarium labeled "Ternströmia gedehensis T et B." in Miquel's hand and by one at Leiden (no. 925250–335) which was sent by Teysmann.

Ternstroemia patens (Korthals) Choisy, Mém. Soc. Phys. Hist. Nat. Genève 14: 107 (Mém. Ternstr. 19). 1855; in Miq. Fl. Ind. Bat. Suppl. 1: 476. 1862.

Reinwardtia patens Korthals, Verh. Nat. Gesch. Bot. *t. 12.* 1840, text p. 102. 1841.

Shrub or small tree, up to 5 m. high; branchlets smooth, quite terete, reddish brown, often subverticillate. Leaves thin-coriaceous, subverticillate, near the apex of the branchlets, obovate, abruptly acute at the apex, tapering at the base, usually 7–11 cm. long, 3–4 cm. wide (rarely up to 18 × 7 cm.), the veins 3 or 4 pairs (5 or 6 pairs on largest leaves), arching upward and anastomosing near the entire margin, the petiole usually less than 1 cm. long. Flowers axillary. Staminate flowers: pedicel 1.5–2.5 cm. long; bracteoles 2, alternate, quickly caducous, the upper bracteole scar 3–5 mm. below the calyx, the lower bracteole scar 5–7 mm. below the calyx; sepals 5, imbricate, unequal, the outer two smaller, rounded, 2–2.5 mm. long, 2.5–3 mm. wide, the inner three 3 mm. long, 3 mm. wide, the margin scarious or subfimbriate; petals 5, obovate, lightly unguiculate, rounded at the apex, 7.5–8 mm. long, 5–6 mm. wide. Stamens numerous, ca. 85, ca. 3 mm. long, in three or more series; filaments flattened, ca. 1 mm. long, connate entire length, free from the petals; anthers linear, ca. 2 mm. long, each anther locule subtruncate at apex; pistillodium mound-like, 5-ridged, sterile. Pistillate flower: bracteole scars and calyx as in staminate flower, the bracteoles rarely seen, linear, ca. 1 mm. long, ca. 0.5 mm. wide; petals not seen; staminodium not seen (if present, falling with petals); ovary glabrous, ovoid, ca. 3 mm. long, 2 mm. in diameter at base, one-loculate, with a single pendulous ovule; style very short or none; stigma peltate or disciform, 2-lobed, the margin pendulous, irregularly scalloped or incised. Fruit ovoid, ca. 2 cm. long, 1.3–1.5 cm. in diameter near base, orange, with very thin pericarp (ca. 0.25 mm. thick), still crested by the minute peltate stigma. Seed solitary, hippocrepiform, ca. 1.5 cm. long, 1 cm. wide, covered with a red-orange aril.

Sumatra. RES. WESTKUST: precise locality lacking, *P. W. Korthals s.n.* (L [908251–984, lectotype; 908251–986, probable isolectotype]); Padang, "Sungei bulu" [Sungei Balu], at sea level, *O. Beccari 904* [transcribed on label as *902*] (L), *939*(L), Sept. 18, 1878; Priaman [Pariaman?], Dalik badak, *H. Diepenhorst 2150 H B* (BO, L); Priaman, *J. E. Teysmann s.n.* (A, BO, L). RES. RIOUW: W. Indragiri [Inderagiri], Taluk [Taloek] Region, Hutan Pulau Lawas, near Taratak Air Hitam, on flat sandy soil of lowland forest of Dipterocarpaceae, *W. Meijer 4365* (L), Jan. 16, 1956 (shrub with orange fruit, seeds carmine-red). RES. BENKOELAN [BENKULAN]: Enggano Island, Malakoni, near the river Malakoni, in forest, *W. J. Lütjeharms 4842* (A, BO, L), June 20, 1936 (small tree, ± 5 m. high). Without locality: *Teysmann* (L [908251–985]).

Java. PROV. MID. JAVA: Res. Banjoemas [Banjumas], Subdivision Tjilatjap, Noesa Kambangan, *S. H. Koorders 1901B* (BO, L), Dec. 10, 1891; same locality, *Koorders 9997B* (L), Dec. 7, 1891. PROV. W. JAVA: Bantam, in mountain forest, *C. L. Blume s.n.* (L [908251–995]); without locality but apparently parts of the preceding collection, *Blume s.n.* (L [908251–989 and –999]).

From the specimens examined, this species appears to be confined to the islands of Sumatra and Java. It is very distinct from all other species of *Ternstroemia* in this area. The fruit, with its single locule and single seed, probably was the basic character on which Korthals based his new genus *Reinwardtia*. This character alone separates it from all other taxa of *Ternstroemia* in the Eastern Hemisphere. The very thin pericarp is also most unusual in the genus. A single sheet (apparently from Java) in the Leiden herbarium (no. 908251–982), the collector unknown to me, has a drawing and a brief description attached. Dissections of the fruit on this specimen show that the author-artist mistook the conduplicate character of the seed for a bilocular, two-seeded fruit.

In the above description, the staminodium of the pistillate flowers is mentioned as "not seen (if present, falling with the petals)." There is a brief disc-like area surrounding the pistil which causes the author to believe that a staminodium may have been present. The base of the staminodium may have been adnate to the base of the corolla, a characteristic usually found in this genus. However, in the staminate flower of this taxon the stamens are free from the base of the corolla, which is not the usual finding.

Korthals in his original description refers to the stigma as "decem sulcatum." I could not duplicate this observation. I found the stigma to be irregularly scalloped, but not necessarily in tens.

As with his *Reinwardtia elongata*, Korthals gave the original locality as Doekoe, noting that both species were growing in forests a little above sea level. No specimens of *Ternstroemia patens* with this locality are present in either the Bogor or Leiden herbaria, but at Leiden there are two collected by Korthals which match well the original illustration of *Reinwardtia patens* which was almost certainly based at least in part on this material. One of these specimens labeled as *Reinwardtia patens* by Korthals is chosen as lectotype; the other, which bears a small label with "Nieuwlandia littoralis" in Korthal's hand and another with "Reinwardtia patens Krths." in Blume's is apparently from the same plant.

It is this taxon that Koorders incorrectly called *Ternstroemia elongata* in making the transfer from *Reinwardtia* to *Ternstroemia*. This was an unfortunate error which has caused considerable misunderstanding about the two species *T. elongata* and *T. patens*.

Ternstroemia foetida, spec. nov.

Tree 10–18 m. high; branchlets terete, very light gray, thick (7–10 mm. in diameter), with conspicuous large leaf and flower scars. Leaves subcoriaceous, oblong-obovate to oblong-elliptic, 20–35 cm. long, 7–10 cm. wide, acuminate at the apex, cuneate at the base, tapering into a sturdy petiole 1–2 cm. long, the midrib impressed above, elevated below, the margin entire, the primary veins ca. 13 or 14 pairs, occasionally branching, anastomosing near the margin, secondary veins occasional. Flowers bisexual, solitary; pedicel sturdy, ca. 3 cm. long, curved or straight at the apex, 4–5 mm. in diameter at the base; bracteoles 2, subopposite ca. 5 mm. below the calyx, quickly caducous, broadly linear, 8–10 mm. long, 4 mm. wide, rather thick through the center, thinning along the margin; sepals 5, thick through center and at base, entire, unequal, the outer ones broadly ovate, ca. 10 mm. long, 9–10 mm. wide, the inner ones rounded, 13–15 mm. long, 13–14 mm. wide, scarious at the margin; petals 5, large, concave, thickened (fleshy) in center, unequal, the outer ones broadly ovate, ca. 23 mm. long, 19–23 mm. wide, the inner ones rounded, 25–28 mm. long, ca. 25 mm. wide; stamens numerous, ca. 250, 5 or more seriate, very crowded, unequal, rising from a disk 10 mm. in diameter, the outer ones ca. 12 mm. long, concave, adnate to only the inner petal at the base, the filaments 3 mm. long, thin, broad as anthers, the anthers ca. 6 mm. long, projection flat, as wide as anthers, 2 mm. long, blunt at apex, the inner stamens ca. 8 mm. long, filaments fused, negligible in length, anthers 6 mm. long, the projection 2 mm. long; ovary ca. 5 mm. long, 3.5 mm. in diameter, 2-loculate with 2 pendent ovules in each locule; style thick, 4–5 mm. long, split nearly the whole length (3 mm.), each part branched two or three times, then rebranched with the sub-branches topped by a peltate arrangement of ruffled overlapping stigmas. Fruit rounded, 5 cm. long, 3.5 cm. in diameter, with persistent styles, 2-loculate, each locule 2-seeded; pedicel sturdy, as much as 7 mm. in diameter at the apex. Seeds large, elongate, 2.6 cm. long, 1 + cm. wide, covered with an oily aril.

Arbor 10–18 m. alta, ramulis teretibus, griseis, crassis (7–10 mm). Folia subcoriacea, oblongo-obovata vel oblongo-elliptica, 20–35 cm. longa, 7–10 cm. lata, apice acuminata, basi cuneata in petiolis crassis 1–2 cm. longis attenuata, margine integerrima; costa supra canaliculata, subtus elevata; venis primariis ca. 13 vel 14 paribus. Flores bisexuales, solitarii; pedicellis ca. 3 cm. longis, basi 4–5 mm. diametro; bracteolis 2, suboppositis, caducis, late linearibus, 8–10 mm. longis, 4 mm. latis; sepalis 5, inequalibus, margine integerrimis, exterioribus late ovatis, ca. 10 mm. longis, 9–10 mm. latis, interioribus rotundatis, 13–15 mm. longis, 13–14 mm. latis, margine scariosis; petalis 5, magnis, concavis, inaequalibus, exterioribus ca. 23 mm. longis, 19–23 mm. latis, interioribus 25–28 mm. longis, ca. 25 mm. latis; staminibus ca. 250, 5 vel plus seriatis, inaequalibus, e disco 10 mm. diametro, exterioribus ca. 12 mm. longis, concavis, basi ad petalum interiore adnatis, filamentis 3 mm. longis, antheris ca. 6 mm. longis connectivis apice truncatis 2 mm. projectis, staminibus interioribus ca. 8 mm. longis, filamentis paene in toto coalitis, antheris 6 mm. longis connectivis 2 mm. projectis; ovario ca. 5 mm. longo, 3.5 mm. diametro, 2-loculato, loculis 2-ovulatis, ovulis pendulis; stylo crasso, 4–5 mm. longo, paene in toto diviso (3 mm.), partibus 2- vel 3-ramosis, deinde in ramulis ordinis tertii divisis, his stigmatibus peltatis imbricatis coronatis. Fructus 5 cm. longus, 3.5 cm. diametro, stylis persistentibus, 2-loculatus, loculis 2-seminatis, pedicello crasso apice 7 mm. diametro. Semina magna, elongata, 2.6 cm. longo, 1 + cm. lata, arillata.

Sumatra. GOUVT. ATJEH: Simulue [Simaloer, Simalur, Simeuloeë] Island: "Eil Simaloer," *Achmad 395* (A, BO, L), Apr. 24, 1918; *Achmad 520* (A, BO, L), July 5, 1918; *Achmad 621* (BO [135060], holotype; A, BO [135061], L [922,70–392 and –406], isotypes), Sept. 15, 1919 (10 m. high, crown 7 m. diam.). Tapah Island: "Landschap Tapah (Dèfajan)," *Achmad 1518* (A, BO, L), Nov. 24, 1919.

Although only four collections of this unusual species were available for study, the number of duplicates found at the Arnold, Bogor, and Leiden herbaria numbered over twenty. Ample material of both flowers and fruit was available. It appears that the taxon is limited in distribution to the two small islands of Simulue (note variant spellings) and Tapah off the northwestern coast of Sumatra.

The two features of this species which are immediately noticeable are the unpleasant odor and the generally large size of the stem, leaves, flowers, and fruit. The objectional odor is not unusual in the genus. Dr. Kostermans, of Bogor, had told me earlier that while collecting in Indonesia he was able to detect the presence of members of the group at quite a distance by the odor. The leaves measure up to 35 cm. in length. However, in most of the specimens examined the average length is 20–25 cm. The flower parts are all large and quite fleshy. Especially noticeable are the petals, which, as far as I can determine, never open flat but continue concave. Only the stamens opposite the inner petal appear to be adnate to the corolla, which is different from most species of the genus. The filaments of the outer row of stamens appear to be joined the whole length in a sort of collar. They are quite thin but equal or nearly so to the width of the anther. The filaments in the inner rows are so fused that they appear as a single mass and cannot be separated. Accommodating this arrangement of filaments for so large a number of stamens (250) is a disk about a centimeter in diameter (including the pistil).

The ovary is quite typical of the genus. The style is sturdy, measuring five millimeters or less, and is split in two nearly to the base. In the fruit the two parts are entirely separated. Each portion of the style branches several times and is finally topped by a circular peltate stigma consisting of the combined ruffled, overlapping surfaces of the several stigmas.

Ternstroemia palembangensis, spec. nov.

Small tree 15–18 m. tall; branchlets terete, thick, light gray-brown, with large leaf scars. Leaves large, coriaceous, oblong-obovate, 20–35 cm. long, 8–10 cm. wide, acuminate at the apex, long-cuneate at the base, tapering into a thick petiole ca. 1 cm. long, the midrib impressed above, elevated below, the primary veins 10–12 pairs, anastomosing near the entire margin. Buds tight, globose, ca. 1 cm. across, very hard, difficult to dissect. Flowers bisexual; pedicel 2–2.5 cm. long, straight, erect; bracteoles 2, opposite ca. 3 or 4 mm. below the calyx, linear, ca. 3 mm. long; sepals green, unequal, grading gradually from outer to inner, the outermost broadly ovate, acute at the apex, 4 mm. long, 4.25 mm. wide, the innermost unguiculate, rounded at the apex, 9 mm. long, 10 mm. wide, the claw 4.5 mm. wide; petals fleshy, ivory white, the outermost nearly 2 cm. long; stamens numerous, ca. 150, 4-seriate, dirty white, ca. 5 mm. long, the filaments free, 1.5 mm. long, flattened, as wide as anthers, the anthers ca. 3.5 mm. long, the projection less than 1 mm. long, deltoid to a point, the projections tending to stick together; disk 8 mm. across; ovary long-conical, ca. 10 mm. long, tapering into the entire style ca. 3 mm. long, 2-loculate, probably with two pendent ovules in each locule (only a single ovule seen in one locule); stigmas 2, linear and undulating (almost threadlike) in bud, linear at anthesis and coiled back. Fruit ovoid, 4 cm. long, 3 cm. in diameter, terminating in a strong beak ca. 5 mm. long formed from the persistent style, 2-loculate, each locule 2-seeded; calyx persistent, appearing fused at base into a single unit. Seeds large, 2.5 cm. long, 1.5 cm. wide.

Arbor 15–18 m. alta, ramulis teretibus, crassis, griseo-brunneis. Folia magna, coriacea, oblongo-obovata, 20–35 cm. longa, 8–10 cm. lata, apice acuminata, basi cuneata in petiolis crassis 1 cm. longis attenuata, margine integerrima; costa supra canaliculata, subtus elevata; venis primariis 10–12 paribus. Flores bisexuales; pedicellis 2–2.5 cm. longis, erectis; bracteolis 2, oppositis, linearibus, ca. 3 mm. longis; sepalis viridibus, inequalibus, exteriori late ovato, apice acuto, 4 mm. longo, 4.25 mm. lato, interiori unguiculato, apice rotundato, 9 mm. longo, 10 mm. lato; petalis carnosis, exteriori ca. 2 cm. longo; staminibus ca. 150, 4 seriatis, ca. 5 mm. longis, filamentis liberis, 1.5 mm. longis, antheris ca. 3.5 mm. longis, connectivis deltoideis minus quam 1 mm. longis; disco 8 mm. diametro; ovario longe conico, ca. 10 mm. longo, 2-loculato, loculis probabiliter 2-ovulatis; stylo ca. 3 mm. longo; stigmatibus 2, in alabastro linearibus undulatis, anthesin linearibus recurvatis. Fructus ovoideus, 4 cm. longus, 3 cm. diametro, perrostratus, rostro ca. 5 mm. longo ex stylo persistente, 2-loculatus, loculis 2-seminatis; sepalis persistentibus basi connatis. Semina magna, 2.5 cm. longa, 1.5 cm. lata.

Sumatra. RES. PALEMBANG: "Ond. Afd. Banjoeasin en Koeboestreken bij Bajoenglintjir" [Subdivision Banjuasin and Kubu region near Bajunglintjir; ca. 165 km. nw. of Palembang], alt. 15 m., *L. J. W. Dorst 69T–1P–125* (BO [135020], holotype; BO [135018, 135019], L [922253–245], isotypes), buds collected Nov. 13, 1920, flowers Feb. 27, 1921; "Ond. Afd. Banjoeasin en Koeboestreken," *A. Thorenaar 69T–1P–125* (BO), June 15, 1921; same locality and altitude, *C. J. van der Zwaan 69T–1P–125* (BO), Aug. 6, 1922; same locality, alt. 20 m., *W. Grashoff 817* (BO, L), fruit, Nov. 15, 1915.

This new species appears to be most closely related to *Ternstroemia foetida* in its very large leaves and large flowers and fruit. Both have sturdy pedicels with rather large linear bracteoles located a few millimeters below the calyx. In *T. foetida*, however, the smallest calyx lobe (10 mm.) is longer than the largest 9–10 mm.) found in the present species. The stamens are also more numerous (250 +) and are arranged in more series (five or more). The filaments, except for those of the outer series, are negligible in length and cannot be separated, and the projection is broad and flat at the apex. The style of *T. foetida* is two-parted nearly its entire length, branching and rebranching and topped by a peltate arrangement of overlapping stigmas. The fruit is rounded, topped by the persistent style and stigma.

In *Ternstroemia palembangensis* the filaments are 1.5 mm. long and free their whole length. The projection is distinctly deltoid. The style is entire at first, later splitting and topped by filiform stigmas. The ovary and fruit are long-conical. The persistent style splitting slightly forms a definite beak to the fruit.

Ternstroemia kjellbergii, spec. nov.

Tree 3 m. high; branchlets terete, thick, 6–7 mm. in diameter. Leaves large, coriaceous, oblong-obovate, 25–32 cm. long, 11–14 cm. wide, rounded at the apex, abruptly apiculate, cuneate at the base, the midrib deeply canaliculate above, very prominently elevated below, the primary veins 12–16 pairs, occasionally branching, conspicuous below, anastomosing near the margin, the petiole crassate, as much as 5 mm. in diameter, 2 cm. long. Flowers not seen. Fruiting pedicel ca. 3.5 cm. long, thick, ancipitous; bracteoles 2, caducous, the scars subopposite below the calyx; sepals subequal, the outer two narrower, all rounded at the apex, ca. 10 mm. long, 8 and 11 mm. wide, joined at the base up to 5 mm. Fruit oblong, 4 cm. long, ca. 2 mm. wide, topped at the apex by a broken style, 2-loculate, each locule 2- or 1-seeded, the locules not occupying the whole fruit but measuring only 2 cm. long near the apex, the lower half of fruit represented by a pyramidal mass of spongy, undifferentiated tissue tapering into the central thickening between the walls of the locules. Seeds quite black when dried, hippocrepiform, ca. 1.8 cm. long, 1 cm. wide, covered with a darkened aril.

Arbor 3 m. alta, ramulis teretibus, crassis, 6–7 mm. diametro. Folia magna, coriacea, oblongo-obovata, 25–32 cm. longa, 11–14 cm. lata, apice rotundata subito apiculata, basi cuneata; costa supra canaliculata subtus prominenter elevata; venis primariis 12–16 paribus; petiolo crasso ad 5 mm. diam., 2 cm. longo. Flores non visi. Pedicellus fructiferus ca. 3.5 cm. longus, crassus, ancipitus; bracteolis 2, suboppositis caducis; sepalis subaequalibus 2 exterioribus angustioribus, omnibus apice rotundatis, ca. 10 mm. longis, 8 et 11 mm. latis, basi connatis ca. 5 mm. Fructus oblongus, 4 cm. longus, 2 cm. latus, apice coronatus stylo fracto, 2-loculatus, loculis 2- vel 1-seminatis, loculis ad apicem fructus, loculis tantum 2 cm. longis, dimidio inferiore fructus textu spongioso pyramidali, attenuato inter loculos. Semina nigra in siccis, hippocrepiformia, ca. 1.8 cm. longa, 1 cm. lata, arillata.

Celebes. CENTRAL CELEBES: Lelewao [Lelewaoe] Distr., Preho, tropical rain forest, alt. 600 m., *G. Kjellberg 2517* (S, holotype; BO [134991], isotype), Oct. 15, 1929.

This taxon differs from all others found in the Celebes in the extremely large leaves, the rounded apex of which is sharply prolonged into an apiculate extension. The fruit in the dried state appears quite oblong, but in the fresh condition the diameter may register larger (by as much as a centimeter) than is recorded above. The inner structure of the fruit varies considerably from that found in the other species of the genus which I have examined. Ordinarily the seeds and the locules which contain them occupy the whole structure of the fruit. In this taxon the locules and seeds are confined to the upper half of the fruit. In the lower half below the seeds one finds an unusual pyramidal mass of spongy tissue which tapers at the apex into the center thickening which is found between the inner walls of the locules. Considering the overall size of the fruit, the seeds are unexpectedly small.

Ternstroemia urdanatensis var. crassifolia, var. nov.

A typico *T. urdanatense* differt foliis crassis, 5–6 cm. longis, 2–2.5 cm. latis, venis 5–7 paribus, supra impressis, subtus obscuris.

Celebes. SW. CELEBES: Onderafdeeling [Subdivision] Enrekang, Pokapindjang [one of the Latimodjong Mountains], alt. 2800 m., *P. J. Eyma 613* (A, holotype; BO [134979], L [951166–220], isotypes), June 16, 1937 (fruit wine-red).

Like *Ternstroemia urdanatensis* (Elmer) Kobuski var. *urdanatensis* (see description in Jour. Arnold Arb. **42**: 268. 1961), this variety is characterized by a globose fruit (ca. 9 mm. long and 10 mm. in diameter) topped by a short style (2 mm. long) and a two-parted punctate stigma. In each locule of the fruit were found eight to ten small seeds so crowded that several were misshapen. Of these seeds, probably only four to six would develop to maturity in each locule. The seeds measured 4 mm. long by 3 mm. in diameter and were covered by a mealy aril, bright in color, probably orange or red.

Since this taxon was observed as a single fruiting collection, I do not designate the relationship with *Ternstroemia urdanatensis* with any certainty. The leaves vary from those of the typical variety in their thickness and impressed veins on the upper surface. It may be that when flowers are found and examined this taxon will prove to be specifically distinct.

Ternstroemia robinsonii Merrill, Interp. Rumph. Herb. Amboin. 3: 369. 1917.

Ichthyoctonos montana Rumphius, Herb. Amboin. 3: 214, *t. 139*. 1743.

Tree 15–20 m. high; branchlets thick (8–10 mm. in diameter), reddish brown, occasionally grayish brown, striate in the dried stage, interrupted by large leaf scars; leaves congested at the apex of the branchlets, oblong-obovate, 15–25 cm. long, 5–9 cm. wide, deep purple-brown when dried, thick-coriaceous, the apex obtusely acuminate, cuneate at the base, the midrib canaliculate above, elevated beneath, the veins 15–20 pairs, curving upward near the apex but not anastomosing, the petiole stout, ca. 1 cm. long. Mature flowers not seen. Pistillate bud ca. 1 cm. across; pedicel sturdy, 1.5 cm. long, 0.5 cm. in diameter; bracteoles 2, opposite, quickly caducous, the scars ca. 4–5 mm. below the calyx; calyx-lobes unequal, the outer two rounded 7 × 9 and 8 × 8 mm., the inner three unguiculate, 8–11 mm. long, ca. 11 mm. wide at the upper portion, 5 mm. wide below, all lobes much thickened and joined at the base into a wide, shallow tube; corolla lobes inseparable in the tight bud; staminodia in four series at base of the ovary, ± 200, deltoid, ca. 1 mm. long; ovary broad, flattened dome-shaped, 2 mm. high, 3–5 mm. across, 2-loculate, each locule 2-ovulate, the ovules pendent from apex of the locule; style short, thick, 1 mm. or less long, two-parted, each part three-branched, each branch topped by a broad, spreading stigma as much as 3 mm. across with undulate margin. Fruit ellipsoid to rounded, 5–6 cm. long, 4–5 cm. wide, bright red when fresh, brown when dried, two-loculate, each locule two-seeded; fruiting pedicel ca. 2.5 cm. long, spreading at the apex into the broad, persistent, much-thickened, rugose calyx measuring 2.5–3 cm. across. Seeds 3–4 cm. long, 2–3 cm. across, covered with a dense, red, mealy aril.

Moluccas. AMBON (Amboina): Hitoe messen, in forests, alt. 350 m., *C. B. Robinson* (*Pl. Rumph. Amb.*) *275* (GH, lectotype; BO [134825], L [920191–385], isotypes), Oct. 18, 1913; Haitoe besar, alt. 280 m., *Neth. Ind. For. Serv. bb 10135* (*F. de Bell 8*) (BO), June 26, 1926; Waai, alt. 100 m., *Neth. Ind. For. Serv. bb 25979* (*P. Buwalda 634*) (A, BO, L), Sept. 26, 1938.

Up until now, *Ternstroemia robinsonii* has been known only from fruit. The pistillate structures enumerated above have been drawn from the dissection of a single flower bud. The measurements, of course, will not hold for the mature opened flower, when encountered, but the basic morphology has been made available for comparison with other species.

This species shows a great resemblance to *Ternstroemia philippinensis* in size of flower, fruit, and leaves. However, in *T. philippinensis* the thickening at the base of the fruit is between the fruit and the calyx-lobes, whereas in the present species the thickening is found below the calyx-lobes. Also, the calyx-lobes in *T. philippinensis* are all rounded, although similar in size to those of *T. robinsonii*, in which the thick inner lobes are unguiculate. In *T. philippinensis* the style is longer and sturdier and often persists in the fruit, giving the appearance of a double beak. The stigma is never persistent. In the present species, when persistent, the style is so short that the stigmata often continue into the mature fruit, lying flat at the apex of the mature structure.

Since the original holotype no longer exists because of the destruction of the Philippine herbarium during the war, the duplicate deposited in the Gray Herbarium has been designated as the lectotype.

In studying the description and crude illustration of *Ichthyoctonos montana* Rumphius, published in 1743, I agree with Merrill that they correspond closely enough to represent this species. However, I do not agree that *Ichthyoctonos litorea silvestris latifolia*, described immediately preceding *I. montana*, belongs here. The serrate or undulate leaf, the obvious style, and the size of the fruit, along with the shape of the terminal bud, remind one more of *Adinandra* or *Eurya*.

The range of this species may extend to the adjacent island of Buru (Boeroe). Four sterile specimens appear to belong here. Three collected by *P. S. P. Oersipuny* (*167* [*Neth. Ind. For. Serv. bb 22825*]) at Kak Toea, alt. 800 m., 24 May 1937 (A, BO, L), resemble *Ternstroemia robinsonii* very much. A fourth specimen (*L. J. Toxopeus 491* [BO-134826]), collected at Fakal, at an altitude of 1250 m., September 1, 1921, is less carefully preserved and is mentioned here without too much assurance.

Ternstroemia nitida Merrill, Jour. Arnold Arb. **8**: 10. 1927.

Small tree, 7–12 m. high; branches and branchlets terete, fairly smooth, brownish gray. Leaves disposed near or at the end of the branchlets, chartaceous to thin-coriaceous, shiny, oblong-elliptic to oblong-obovate, 6–10 cm. long, 2.5–4 cm. wide, acuminate at the apex, cuneate at the base, the midrib canaliculate above, elevated below, primary veins 5–7 pairs, somewhat obscure, arching upward and anastomosing near the margin, secondary veins occasional, the petiole 1–1.5 cm. long. Plants dioecious. Staminate flowers axillary, solitary; pedicel unusually slender, tenuous, 1–2 cm. long; bracteoles 2, opposite, immediately below the calyx, minute, deltoid, 2 mm. long, 1.7 mm. wide at the base, sharply pointed at the apex, with few (2 or 3) glandular denticulations along the margin; calyx-lobes unequal, the two outer lobes ovate, 3–4 mm. long, ca. 3 mm. wide, the margin entire, the three inner lobes ovate, rounded at the apex, 5–6 mm. long, ca. 4 mm. wide, the margin scarious; corolla-lobes obovate, somewhat concave, 5–7 mm. long, 4–5 mm. wide near the apex, rounded at the apex, joined lightly at the base; stamens uniseriate, ca. 35, unequal, 3.5–4.5 mm. long, the filaments 1–2 mm. long, joined at the base and adnate to the base of the corolla, the anthers 2–2.5 mm. long; pistillodium flat, undeveloped, with a pseudostyle projected 1 mm. upward. Pistillate flowers not seen. Fruit ovoid to obpyriform, recurved, purple, ca. 1 cm. long, 0.8 cm. in diameter, 2-loculate, each locule with a single seed pendent from the apex of the locule; fruiting style usually partly broken off, occasionally intact, 3–4 mm. long, usually two-parted at the apex for 1 mm., often appearing entire (line of separation visible under the lens), the stigmas two, subpeltate or peltate (?). Seed hippocrepiform, tawny in color, 5–6.5 mm. long, 4–5 mm. in diameter, covered with a tawny colored aril.

China. KWANGTUNG: Lung T'au Mountain, right side of Iu village, forest in K'i ravine, *Canton Christian College no. 12590 (To, Tsang & Tsang* — Wulsin Exped.) (US, holotype [fide L. B. Smith]; A, BM, isotypes), June 26, 1924 (tree 12 m.; flowers white, fragrant). KIANGSI: S. Kiangsi, Tai Au Hong, sw. of Sungwu, above stream in forest, alt. 550 m., *J. L. Gressitt 1596* (A), July 5, 1936 (tree with orange flowers); Kiennan Distr., Sai Hang Cheung, Tung Lei village, in thicket along stream on a dry, gentle loam slope, *S. K. Lau 4061* (A), Aug. 1934 (woody; 7 m. high); Lungnan Distr., Oo Chi Shan, near Lam Uk Tung village, on dry, steep, clay slopes in forest, *S. K. Lau 4501* (A), Sept. 16–30, 1934 (rare, woody, 5 m. high); Yi-feng, Tung-ho, Hwang-kan Shan, in woods along stream, *Y. K. Hsiung 6460* (A), Oct. 15, 1947 (common tree). CHEKIANG: south of Pang Yung, in woods, *R. C. Ching 2063* (A, K, paratype collection), July 11, 1924 (fairly common, small tree, 10 m.). ANHWEI: S. Anhwei, east Wu Yuan, on open, rocky stream bank, alt. 600 m., *R. C. Ching 3314* (A, K), Sept. 4, 1925 (rare, low shrub, 1.5 m.; with evergreen, pale, shiny leaves; fruit nodding, purplish in color). KWANGSI: Lien Chuen Distr., along stream in woods, *Z. W. Chung 83702* (A), Sept. 9, 1937 (tree); Kwei-lin Distr., Chin-kang Shan, Ta-chiang-yuan and vicinity, in swampy thickets, *W. T. Tsang 28262* (A), Sept. 1–17, 1937 (fairly common, woody, 3 m. high).

This species is easily recognized by two very unusual and obvious characters: its disagreeable odor and slender pedicels. All of the parts (leaves, flowers and fruit) give off a strange, obnoxious odor, easily recognized at quite a distance in herbarium specimens. When material for dissections is being boiled up, the strong odor will pervade the halls and rooms nearby. The only other species studied so far with a similar odor is *Ternstroemia foetida*, quite unrelated in other characteristics to *T. nitida* and confined solely to the islands of Simulue and Tapah, off the northwestern coast of Sumatra.

The flowers and fruit are both very small for the genus. The fruit, measuring only ca. 1 cm. in length, is purplish in color and quite ovoid in shape. Each of the two locules is single seeded. The style, which remains intact in the fruit, is quite long (3–4 mm.) in comparison with the size of the fruit and is usually two parted for a third of its length at the apex. When not separated, the two "separating" parts of the style are obvious under a hand lens. It is difficult to designate accurately the shape of the stigma from the dried-up stage found on the fruit. It appears to be subpeltate, but to what extent, one cannot be certain. The pistillate flower, although not seen in this study, can almost be reconstructed from the fruit, with the exception of the stigma and the presence of a staminodium or stamens. The pedicels are very slender, almost threadlike, recurved by the weight of the fruit.

STUDIES IN THE THEACEAE, XXXV
TWO NEW SPECIES OF TERNSTROEMIA FROM THE LESSER ANTILLES[1]

† CLARENCE E. KOBUSKI

Ternstroemia proctoriana, spec. nov.

Materiari-arbor grandis, 25–30 m. alta, ramulis crassis teretibus brunneis. Folia subcoriacea, obovata, 8–12 cm. longa, 3–5.5 cm. lata, apice rotundata vel late obtusa, basi cuneata, margine subintegerrima, costa supra canaliculata, subtus elevata, venis ca. 10-paribus subobscuris, petiolis ca. 1 cm. longis. Flores axillares vel apice ramulorum congesti; pedicellis ca. 1 cm. longis; bracteolis 2, oppositis, inaequalibus, decurrentibus, eglandularibus, 2–2.5 mm. longis, 1.5–2 mm. latis; sepalis 5, imbricatis, albidis, ovatis, apice subrotundatis, inaequalibus, 6–7 mm. longis, 4.5–5 mm. latis, margine integerrimis; petalis 5, aureis, inaequalibus, extus duobus ovatis, 9–10 mm. longis, 4.5–5 mm. latis, intus tribus longe ovatis, 9–10 mm. longis, 2.75–3 mm. latis, apice subapiculatis; staminibus uniseriatis, ca. 15, inaequalibus, 5 longis (8.5–9 mm.), 10 brevioribus (ca. 6 mm.), filamentis 2–3 et 1–1.5 mm. longis, subcrassis; antheris 4–5 mm. et 3–3.5 longis, connectivis attenuatis, 1.5–2.5 et 1.5 mm. projectis; ovario subgloboso vel subconico, ca. 3 mm. diam., 3-loculato (subinde 5- vel 6-loculato apparento), loculis 2-ovulatis; stylo attenuato, ca. 4 mm. longo, basi subcrasso; stigmate punctiformi. Fructus non visi.

St. Lucia: Forestière district, ca. 1 mile due southeast of Trois Pitons, ca. 1100 ft., *G. R. Proctor 18229* (A, holotype; IJ, isotype), June 9, 1958 (large timber tree; sepals white, petals yellow; "merise").

Mr. George R. Proctor, the collector of the type specimen and for whom the species is named, told me that this species, although not common, was one of the large timber trees of the area. Several characters are very distinctive. The sepals are white in the fresh state, while the corolla is clearly a sharp, deep yellow. Both of these colors are unusual in *Ternstroemia*. In the majority of species, the sepals are reddish brown and the corolla white or creamy white.

The stamens, about fifteen in number, are arranged in a single series with five long stamens and ten shorter ones. The five long stamens are located between the petals with two short stamens alternating with each long one. Irregularity in the size of the stamens is very characteristic in the genus. However, this is the first time that I have recognized a definite pattern, especially in a single series arrangement. In a multiseriate ar-

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[1] See also "Studies in the Theaceae, XIV. Notes on the West Indian species of *Ternstroemia*," Jour. Arnold Arb. **24**: 60–76. 1943, and "A New Species of *Ternstroemia* from Jamaica, B. W. I.," Rhodora **59**: 36–38. 1957.

rangement one finds the longer stamens in the outer series and the shorter stamens in the inner, with a gradation in size from the outer to the inner series. In some flowers there were sixteen, and even eighteen, stamens. The variation in number was found in the shorter stamens.

The arrangement of the locules of the ovary might appear confusing. Actually, there are three locules to the ovary with two ovules in each. However, cross-sections nearer the top of the ovary show what appear to be five locules or six locules with a single ovule in each. In the latter situation the placentae appear joined to the locule wall giving a six-loculate appearance. Not having seen the fruit, one can hardly conjecture what the appearance of a cross-section might be. Often the seeds grow to a size completely filling the locules, sometimes causing the placentae, as well as the locule walls, to be distorted.

The bracteoles beneath the calyx are distinctly decurrent the entire length of the pedicel. When one attempts to remove the bracteoles, a strip of tissue adheres to the base of the bracteole. In this instance no scar is left on the pedicel, as is usually the case.

Ternstroemia sanctaluciae, spec. nov.

Arbor 3–4 m. alta, ramulis teretibus griseis. Folia coriacea, obovata, apice ramulorum congesta, 4–6 cm. longa, 1.5–2 cm. lata, apice rotundata; basi in brevissimis (ca. 3 mm.) petiolis attenuata, margine in sicco revoluta, integerrima, pauce minuta glanduloso-denticulata, costa supra canaliculata, subtus elevata, venis ca. 5-paribus. Flores solitarii, pedicellis ca. 2 cm. longis; bracteolis 2, oppositis, inaequalibus, extus ovato, 3 × 2 mm., apice acuto, apice apiculato; intus subdeltoideo, 3 × 3 mm., eglandulari; sepalis 5, imbricatis, inaequalibus, exterioribus duobus ovatis, ca. 8 mm. longis et 6 mm. latis, interioribus tribus 9–10 mm. longis, 7–8 mm. latis, subrotundatis, apice retrorse apiculatis, margine integerrimis; petalis 5, 7.5–8 mm. longis 3.5–4 mm. latis, basi connatis, supra aureis, subtus roseis; stamina ca. 50, triseriatis, inaequalibus, 6–8 mm. longis, filamentis 1–1.5 mm. longis, basi ad corollam adnatis, antheris 2.5–4 mm. longis, oblongis, connectivo longe caudato, 1.5–2.5 mm. projecto; pistillo ca. 9 mm. longo, ovario conico vel subgloboso, ca. 3 mm. longo, 2-loculato, loculis pauciovulatis, stylo attenuato, ca. 6 mm. longo, stigmate punctiformi. Fructus ignotus.

St. Lucia. Vicinity of Linnis Point, south of Dennery, ca. 100 ft., scrub woodland near sea-cliffs, *G. R. Proctor 18041* (A, holotype; IJ, isotype), May 17, 1958 (tree 3.5 m. tall).

Ternstroemia sanctaluciae differs from the preceding species, *T. proctoriana*, primarily in the number of locules in the ovary and the number of stamens arranged in three series. Another difference is that the bracteoles of this species are not decurrent and when removed leave scars. While in the preceding species the corolla is colored a deep yellow throughout, in *T. sanctaluciae* the upper half of the petals exhibits the same color but the lower half is a distinct pink in the fresh state, drying a rather dark red.

THE TRIBES OF COMPOSITAE IN THE SOUTHEASTERN UNITED STATES[1]

OTTO T. SOLBRIG

COMPOSITAE Giseke, Praelect. Ord. Nat. Pl. 538. 1792, nom. cons. (SUNFLOWER FAMILY)

Annual or perennial herbs, shrubs [or small or large trees], rarely trailing or scrambling vines or aquatics; often stoloniferous, rhizomatous, or with tubers or fleshy roots; laticiferous or resinous; often spiny, hairy tomentose or woolly-felty, or glandular. Leaves opposite, alternate, fascicled, or rarely whorled, rosulate and/or cauline [or absent], entire, lobed or dissected, but never truly compound with articulate leaflets, [sometimes fleshy,] exstipulate, petiolate or sessile [seldom terminating in a tendril]. Heads (capitula) solitary at the end of the branches or scapes or arranged in various types of "inflorescences." Flowers (florets) always borne in a many to [rarely 1] flowered head (capitulum) on a flat, convex, or, more frequently, concave receptacle, sometimes provided with receptacular bracts (paleae), and surrounded by involucral bracts (phyllaries) of varied sizes and shapes arranged in one to several series. Florets basically either bisexual or ♀, or by abortion of the pistil ♂ or neuter; heads with bisexual (heterogamous) and/or unisexual (homogamous) florets (if unisexual the plants then either monoecious or dioecious). True calyx absent or trans-

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[1] Prepared for a biologically oriented generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University which has been made possible through the support of George R. Cooley and the National Science Foundation, and under the direction of Reed C. Rollins and Carroll E. Wood, Jr. This treatment follows the style established in the first paper of the series, Jour. Arnold Arb. **39**: 296–346. 1958 (and continued through volume 44). The area covered, as in earlier treatments, is bounded by and includes North Carolina, Tennessee, Arkansas, and Louisiana.

On account of the large size of the family, with about 120 genera in the southeastern United States, it was deemed convenient to subdivide the work. This treatment covers only the tribes; treatments covering the genera under each tribe are to follow. The descriptions apply primarily to the plants of the area of the flora, with supplementary information in brackets. Nevertheless, descriptions of all the tribes in the family, including those not native to this area have been included, in the hope that the work may be of use to workers outside the specific area covered by the flora.

I am very grateful to Dr. John Beaman for information on apomixis in the family and to Dr. George R. Cooley for checking material for me in other herbaria. I am particularly indebted to Dr. Carroll E. Wood, Jr., for his advice and expert editorial assistance throughout the work. The illustrations were prepared by Mrs. Dorothy H. Marsh; microscopical details are my own finished in ink by Mrs. Marsh. The manuscript was prepared by Mrs. Gordon W. Dillon.

formed and replaced by a pappus of bristles, awns, or scales which aids in the dissemination of the seed. Corollas sympetalous, 5-merous, regular, tubular, filiform, bilabiate, or ligulate (with the ligule often 2–5-toothed). Stamens 5, inserted on the corolla, united by the anthers (or rarely only by the filaments), forming a tube surrounding the style; anthers bilocular, with an apical appendage (rarely absent) and a connective, a rounded, auriculate, or tailed (caudate) basal appendage present or absent on each anther-half; pollen globular, generally tricolpate, or occasionally tetracolpate, often covered with sculpturings or spines. Gynoecium syncarpous, 2-carpellate; ovary inferior, unilocular, with an erect, basal, anatropous ovule; style normally 2-branched, the branches usually with stigmatic papillae inside and diverse types of "collecting" or "brushing" hairs on the outside; styles of the ligulate and tubular flowers in a head usually of different types. Fruit a glabrous or variously appendaged cypsela ("achene" of most authors), often crowned by the pappus, with a single erect seed. Endosperm lacking; embryo straight. (ASTERACEAE Dumortier, Comment. 55. 1822, nom. alt.; including Acarnaceae Link, Ambrosiaceae Dumort., Anthemidiaceae Link, Arctotidaceae Bess., Calendulaceae Link, Carduaceae Small, Cichoriaceae Juss., Coreopsidaceae Link, Elichrysaceae Link, Eupatoriaceae Link, Heleniaceae Bess., Helianthaceae Bess., Inulaceae Bess., Lactucaceae Bess., Mutisiaceae Link, Partheniaceae Link, Perdiciaceae Link, Senecionaceae Bess., Vernoniaceae Bess.) TYPE GENUS: *Aster* L.

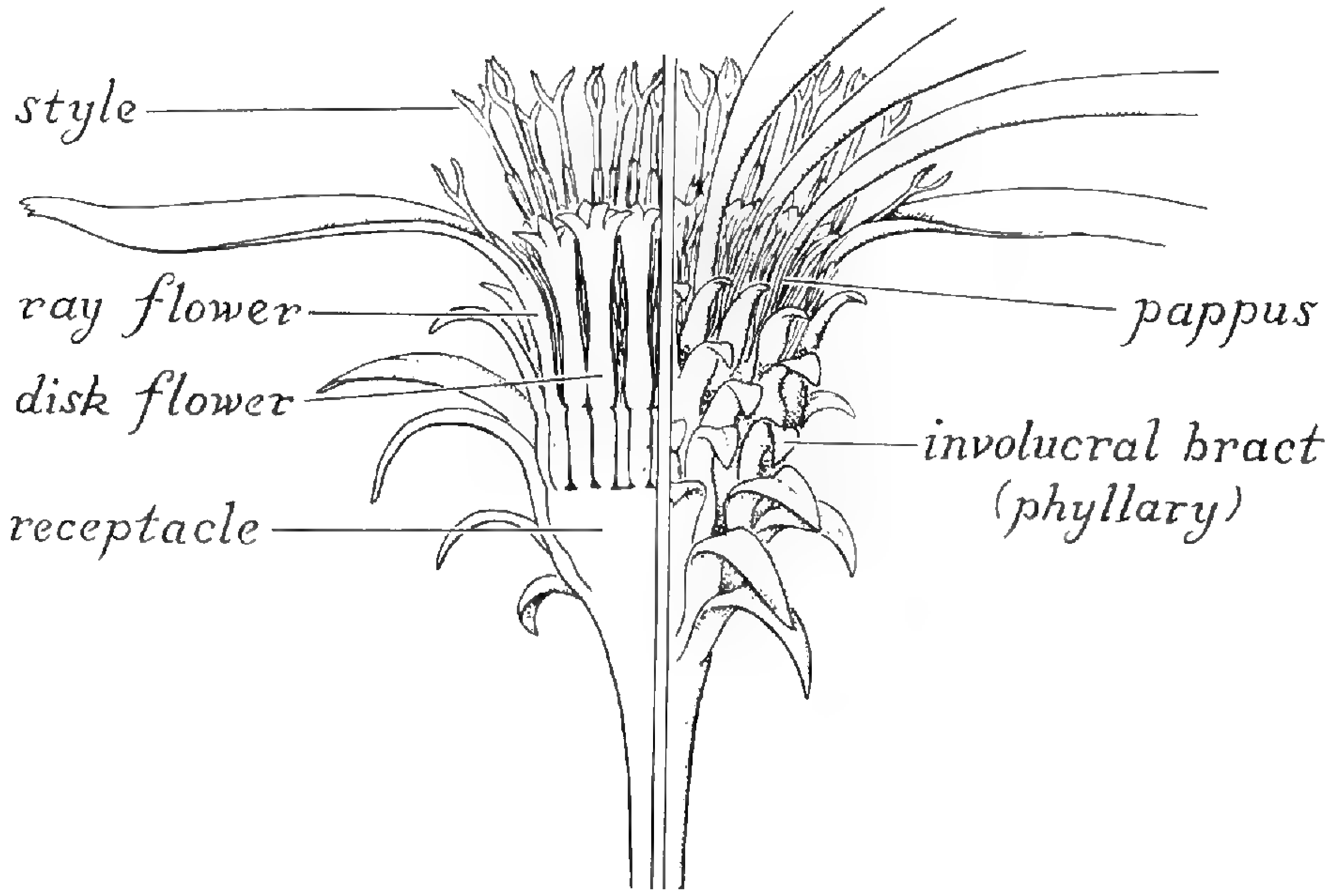

FIG. 1. View and section of a head of *Aster spectabilis* Ait., showing the principal component parts, × 2.

Some 1000–2000 genera and about 20,000 species account for Compositae usually being considered the largest family of flowering plants. The family is truly cosmopolitan, extending from the Arctic to the subantarctic islands (but absent from the Antarctic Continent) and from sea level to snow line of the highest mountains. Although they have successfully invaded all types of habitats, perhaps with the exception of the aquatic (only a few species are truly aquatic), Compositae are particularly conspicuous in dry areas and in montane regions. The family includes both small, isolated, well-marked genera and some of the largest, cosmopolitan, polymorphic complexes in the plant kingdom, with indistinct generic and specific limits (e.g., *Senecio*, with over 1000 species). About 120 genera occur in our area.

Compositae are characterized by having their flowers grouped into heads (capitula), which only rarely are single flowered. (Single-flowered heads are, however, generally associated in secondary heads.) The receptacle of the head is usually flat or slightly convex, occasionally conical, or more rarely concave. The surface of the receptacle is either scrobiculate, foveolate, areolate, fimbrillate, setiferous, or alveolate, or is paleaceous, with membranaceous scales, each subtending a floret. The capitulum is surrounded by a number of modified leaves, the involucral bracts in one or more series, often with the outermost series much reduced forming a calyculus. The involucral bracts, of various shapes and varying consistency from herbaceous to woody-coriaceous, are often armed with spines and/or hooks (particularly in Cardueae). The heads as a rule possess two types of florets: one or more rows of pistillate, ligulate, or filiform florets on the outside, and bisexual, tubular florets in the inside; but all the florets can be either tubular or ligulate (in which case they usually are all bisexual). The florets are usually yellow, but they can be white, orange, red, blue, or violet. The Compositae are further characterized by united anthers, bifid style, calyx modified into a pappus, and bicarpellate inferior ovary with a single, erect ovule, which develops into a characteristic fruit.

The family is predominantly herbaceous or subshrubby, particularly in the temperate zones, but woody members, including large trees 20 m. in height, are not rare. The Compositae are most likely primitively woody. A more or less developed "excretory apparatus," found in all but two of the genera studied, is represented by two distinct tissues: schizogenic canals inclosing oleoresins and fundamentally deriving their origin from the endodermic cells; and laticiferous cells, either isolated or anastomosed, found in the pericycle, near the primary phloem, or in the midst of the secondary phloem parenchyma. One type or the other may be characteristic of species, genera, or tribes (*q.v.*).

The ovary wall in many Compositae contains calcium oxalate crystals, the form of which varies characteristically from species to species. Some have visible markings; others reveal complex structures when heated or treated with acids. These bodies seem to be organized inclusions of the cell, of unknown function.

The Compositae form a distinct group, often treated as comprising the order Asterales. The relationships of Compositae to other families are not entirely clear. They have been considered allied to Campanulales on account of the connate anthers, milky juice, Composite-like heads, and similar vegetative aspect of some species of Campanulaceae, particularly those of subfam. Lobelioideae. Calyceraceae and Dipsacaceae have also been cited as possible ancestral groups on account of their involucrate inflorescences and one-seeded fruits, but both have the single ovule pendulous from the top of the ovary, while in Compositae the ovule is basally attached. Finally, an alliance to the Rubiales has also been considered because of the pappus-like calyx, the differentiation of the marginal flowers, and the tendency towards a 2-carpellate, uniovulate ovary, features which occur in different families and species of the Rubiales.

The flowering heads of Compositae are often very showy. Pollination is largely by insects, although ornithophily is also known. Anemophily is the rule among the ragweeds (*Ambrosia* spp.) and their allies, the pollen of which is among the most important causes of hay fever. Wind pollination has been accompanied by a series of special adaptations, such as free stamens, inconspicuous heads with reduced involucre, and reduction in the number of flowers per head. Polyploidy and hybridization are frequent in many genera. Most Compositae are self-sterile.

Apomixis has been shown in 16 genera, and for eight others there are reports of triploids and unbalanced chromosome numbers, possible indications of apomixis. In view of reports that apomixis is common in Compositae, this is a rather low figure. Nevertheless, some widespread genera such as *Hieracium*, *Taraxacum*, *Rudbeckia*, *Erigeron*, and *Antennaria* have many apomictic species. The most common types of apomixis are either diplospory or apospory followed by parthenogenesis. Some species have nonagamospermous apomixis.

Dispersal of fruits is mostly by animals or wind. Adherence of the fruit to animals may be obtained by glandular structures or mucilaginous pericarps; by hooks, which may be in the involucre as in the cockleburs (*Xanthium* spp.) or in the pappus; or, more frequently, by hairs. The more common situation is dispersal by wind, the chief dispersal mechanism being the pappus, which acts as a kind of sail, as well as parachute and helicopter rotor. Dispersal by wind is further aided in many species by the involucral bracts, which can be hygroscopic, recurving under dry conditions. The pappus also often responds to changes in humidity and extends fully only when the relative humidity is under 70%. Dispersal of the fruits by water is also aided by the pappus which traps a bubble of air and helps flotation, but this type of dispersal is rare.

Classically, the Compositae have been subdivided into a number of tribes on the basis of such characters as differences in the styles of the bisexual flowers, the basal appendages of the stamens, the presence or absence of receptacular bracts, the shape of the corolla, and the type of pappus. It is also customary to consider one tribe, the Cichorieae, as forming a subfamily, the Cichorioideae Kitamura (Liguliflorеae, of authors), on account of the uniqueness of their heads of only ligulate florets and the universal presence in this tribe of anastomosed latex canals; all the other tribes are grouped under the subfamily Asteroideae (Tubuliflorae, of authors). The major tribal categories are fairly well agreed upon, although different authors vary in according either subtribal or tribal status to some groups; most accept either 12 or 13 tribes.

The phylogenetic and evolutionary relationships within the family are not clear. Certain tribes, such as Cichorieae, Astereae, and Calenduleae, appear to be fairly specialized and advanced. The Heliantheae are considered by many as the most primitive tribe, but the Mutisieae, Vernonieae, Cardueae, and even Senecioneae have also been suggested. Characters considered to be primitive, together with others considered advanced, are present in many tribes, pointing to a mosaic type of evolution. Although there is an enormous array of vegetative variations, the family is basically very uniform, and discussions on phylogeny are necessarily concerned with minute details.

Economically the family is important as the source of sunflower oil and seed, safflower oil, and wormwood; several garden crops, particularly lettuce, artichokes, chicory, endive, salsify, etc., as well as some of the most cherished garden flowers, such as *Chrysanthemum, Dahlia, Cosmos, Tagetes*, and *Ageratum*. Rubber is found in extractable quantities in guayule (*Parthenium argentatum* Gray) and kok-saghyz (*Taraxacum kok-saghyz* Rodin). Alkaloids have been reported from many Compositae, but are of little commercial importance. On the negative side, some of the most obnoxious garden and field weeds are members of this family.

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In the following key and treatment of the tribes of Compositae, the Calenduleae and Arctoteae are included, neither being native nor naturalized in the southeastern United States, although *Calendula officinalis* L. and *Arctotis calendulacea* L. are cultivated and may be found occasionally as waifs or escapes from cultivation. A short account of both tribes is presented in order to include all 12 of those generally recognized and to make the treatment more complete and useful for workers outside the area of this flora. The tribes are arranged alphabetically, and no phylogenetic interpretation should be attached to this ordering. Figure references in the key and text refer to the text figures.

ARTIFICIAL KEY TO THE TRIBES OF COMPOSITAE IN THE SOUTHEASTERN UNITED STATES

(Based primarily upon flowering material and fruits, with subsidiary vegetative characters.)

- A. Flowers of the disc tubular or 2-lipped, never ligulate (subfam. Asteroideae).
  - B. Styles of bisexual flowers thick, very slightly divided at the apex, abruptly contracted near the middle, and continued to the base as a narrower column. .... ARCTOTEAE.
  - B. Styles not contracted near the middle, the undivided part of uniform width.
    - C. Anthers conspicuously sagittate at the base (FIG. 3g).
      - D. Styles with a ring of hairs below the point of bifurcation (FIG. 2 l); plants generally ± spiny ("thistly"). .... CARDUEAE.
      - D. Styles of the bisexual flowers without a ring of hairs below the point of bifurcation; plants very seldom with spines.
        - E. Heads with marginal flowers ♀, filiform (FIG. 3c). .... INULEAE.
        - E. Heads with marginal flowers ligulate (FIG. 3b).
          - F. Bisexual flowers tubular (FIG. 3a); pappus absent. .... CALENDULEAE.
          - F. Bisexual flowers 2-lipped; pappus formed by hairs. .... MUTISIEAE (*Chaptalia*).
    - C. Anthers with a short, auriculate or semisagittate basal appendage or none.
      - G. Branches of the style linear, acute, covered with hairs some distance below the point of bifurcation (FIG. 2c); heads with isomorphic flowers (except *Stokesia*), all bisexual, never yellow. .... VERNONIEAE.
      - G. Branches of the style short or large, but without hairs below the point of bifurcation.
        - H. Branches of the style linear, large or clavate, generally obtuse, covered with very short papillae which begin above the point of bifurcation (FIG. 2d); heads with isomorphic flowers, all bisexual, fertile, never of a true yellow color. .... EUPATORIEAE.
        - H. Branches of the style short or large, with well-developed collecting hairs at the upper part (very seldom without collecting hairs in flowers which have a sterile gynoecium); heads with isomorphic or dimorphic flowers; bisexual flowers generally yellow.
          - I. Pappus of hairs or bristles.

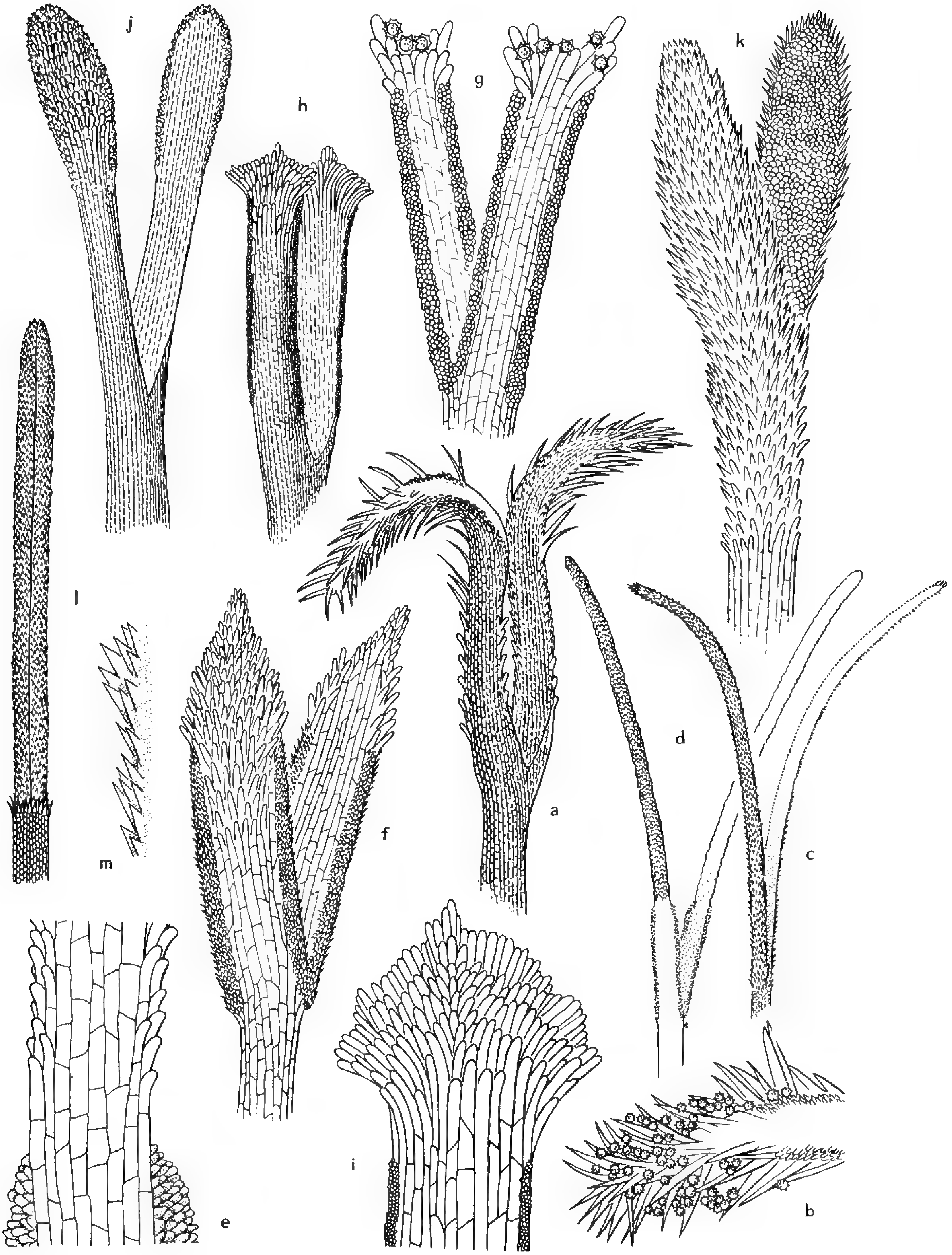

FIG. 2. Different types of styles. a, b, *Helianthus microcephalus* Torr. & Gray, × 75 & 150; c, *Vernonia noveboracensis* Willd., × 50; d, e, *Eupatorium dubium* Willd., × 50 & 400; f, *Aster umbellatus* Mill., × 75; g, *Pterocaulon undulatum* Mohr, × 100; h, i, *Senecio tomentosus* Michx., × 75 & 250; j, *Chaptalia tomentosa* Vent., × 100; k, *Achillea Millefolium* L., × 100; l, m, *Cirsium pumilum* (Nutt.) Spreng., × 50 & 500.

- J. Involucral bracts imbricate, composed of 2 to many series; branches of style of bisexual flowers lanceolate or triangular at apex (FIG. 2f). .... ASTEREAE.
- J. Involucral bracts in one series, sometimes with external bracteoles; branches of style of bisexual flowers truncate at the apex with a crown of hairs or a linear-hairy appendage (FIG. 2h). ... SENECIONEAE.
- I. Pappus of scales or chaffy bracts or absent.
  - K. Involucral bracts with dry-scarious or membranaceous margins; pappus poorly developed or absent. .... ANTHEMIDEAE.
  - K. Involucral bracts without dry margins; pappus paleaceous, well developed or absent. .... HELIANTHEAE.

A. Flowers all ligulate, the apex of the ligules 5-toothed; plants with latex (subfam. Cichorioideae). .... CICHORIEAE.

Anthemideae Cassini, Jour. Phys. Chim. Hist. Nat. Arts **88**: 192. 1819.

Mostly strong-scented or aromatic herbs, rarely subshrubs or shrubs, with a woolly, glutinous, or hispid indumentum. Leaves alternate, some or all finely dissected, pinnately parted, or pinnatifid, except in a few species. Bracts of the involucre in several rows, imbricated, commonly dry and scarious, or at least the inner ones with scarious margins or tips. Receptacle naked or pubescent or with deciduous chafflike bracts. Florets white, yellow, or greenish, all bisexual or the outer ones ♀ or neuter. Pappus none or a short scarious cup or crown. Ray florets present or absent, the ligule 3-toothed at the end or entire. Anthers not tailed, usually obtuse at the base, and with a terminal appendage. Style branches of disc florets obtuse or truncate, without appendages (FIG. 2k). Achenes usually rather small, often angular and truncate at the top, or those of the ray florets dorsally flattened and sometimes winged. TYPE GENUS: *Anthemis L.*

About 50 genera, with 1000 species, with very few exceptions Old World, chiefly extratropical, the tribe rather uniform; represented in our area by eight genera: *Achillea* L., *Anthemis* L., *Artemisia* L., *Chrysanthemum* L., *Matricaria* L., *Santolina* L., *Soliva* Ruiz & Pavon, *Tanacetum* L.

The tribe is characterized by the strongly scented and/or aromatic, usually finely dissected, pinnately parted or at least pinnatifid leaves; the usually dry and scarious phyllaries; and the truncate style branches of the disc florets which are much more constant in their shape than in the majority of the tribes of Compositae. A fairly uniform and not very large tribe, it is not easily subdivided into well-marked subtribes. The classical division into subtribes Anthemidinae Dumort. and Chrysantheminae Less., based on the presence or absence of receptacular bracts, is clearly artificial.

Anthemideae are largely insect pollinated, but some, notably *Artemisia*, are wind pollinated. Anemophily in Anthemideae has not been accompanied by the same floral morphological specializations as in *Ambrosia*

(Heliantheae), although there is a striking resemblance in gross morphology between the two genera.

The pollen grains in Anthemideae are normally tricolpate, with furrows of medium length and a characteristic coarse-granular exine. A great deal of variation in the number and size of pollen grains exists between the wind- and insect-pollinated species, the former tending to have smaller, smoother grains while the latter have pollen grains with broadly conical, sharp-pointed spines which are often rather large in size.

Gametic chromosome numbers of $n = 8$, 9, 10, and 17 have been reported, with the majority of the species and genera having $n = 9$. Polyploidy, particularly multiples of 9, is widespread. Most genera of Anthemideae studied embryologically have a normal type of embryo sac. Notable exceptions are *Chrysanthemum*, with species with mono-, bi-, and tetrasporic embryo sacs; *Matricaria*, with mono- and tetrasporic embryo sacs; and *Anthemis*, with tetrasporic embryo sacs in all the species so far investigated. Species in this last genus can have embryo sacs with 8 to 12 cells. Apomixis is reported in one sterile species of *Artemisia* which reproduces by rhizomes.

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Arctoteae Cassini, Jour. Phys. Chim. Hist. Nat. Arts **88:** 159. 1819, "Arctotideae."

Rosette-forming or spreading herbs (or rarely shrubs), with white-woolly indumentum, or glabrous; occasionally spiny. Leaves radical or alternate, usually lobed or divided, sometimes spiny-toothed. Involucral bracts in several series, imbricated, sometimes partly scarious, hardening after flowering, pungent or spiny-toothed. Receptacle usually epaleaceous, sometimes alveolate or even truly paleaceous. Heads heterogamous and radiate, occasionally homogamous due to loss of the ray florets. Pappus wanting, or coroniform, or paleaceous. Disc florets bisexual or occasionally partly sterile with a regular, 4- or 5-lobed, mostly yellow corolla; ray florets ♀ or sterile, with a trimerous spreading ligule, entire or toothed, yellow, reddish, or purple. Anthers with a terminal appendage, and usually also with a short, auriculate basal appendage, but with no well-developed tails. Style branches of the disc florets linear or oblong, usually obtuse and papillose outside, the papillae extending below the point of bifurcation. Achenes mostly rather thick, angular or winged, never beaked, glabrous or more or less hairy or woolly. TYPE GENUS: *Arctotis* L.

A very small tribe of about 20 genera and some 200 species, Old World (chiefly South African) in distribution; possibly represented in our area by one introduced species.

Characterized by the style with papillae below the point of bifurcation and the tailless, but often auriculate, anthers, Arctoteae are morphologically between Anthemideae and Cynareae. *Arctotis calendulacea* L., sometimes cultivated as an ornamental, has been found as an escape in at least South Carolina and Florida. It is possible that it may grow in other areas also, although there is no good evidence that it is established in the Southeastern States.

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Under family references see BENTHAM and CRONQUIST.

Astereae [Cassini, Jour. Phys. Chim. Hist. Nat. Arts **88**: 195. 1819.]

Mostly perennial herbs, sometimes annuals, or shrubs [rarely small trees], with alternate, entire or toothed, or occasionally divided, leaves, often somewhat resinous or gummy. Heads heterogamous or rarely unisexual. Bracts of the involucre commonly imbricated in several rows. Receptacle naked. Disc florets (FIG. 3a, e) mostly yellow or white, pentamerous or rarely tetramerous, perfect in all our genera except *Baccharis*. Ray florets (FIG. 3b) present or seldom absent, yellow or more often bluish, reddish, or white; ligule often showy, trimerous, entire or toothed. Pappus copious, mostly of setae or bristles, seldom paleaceous, or absent. Anthers obtuse at base [or rarely sagittate or auriculate], always with a terminal appendage (FIG. 3f). Style branches of bisexual flowers flattened, conspicuously margined by the stigmatic lines, tipped with a subulate or triangular appendage covered with collecting hairs (FIG. 2f). Achenes small, flat, ribbed or with nervelike margins, rarely beaked. TYPE GENUS: *Aster* L.

Over 100 genera with about 2000 species, mostly in temperate and montane regions; represented in our area by 15 genera and over 100 species.

Astereae are characterized by the imbricated involucral bracts in two or more series, the naked receptacle, the tailless anthers, and the appendages of the style branches of the hermaphrodite flowers. The tribe has been subdivided into six subtribes based on such characters as homochromous *vs.* heterochromous heads, types of pappus, and unisexual *vs.* bisexual heads. At least some of the subtribes, particularly those based on flower color and type of pappus, are artificial. A specialized tribe, it is morphologically similar to Senecioneae and Inuleae, although it seems to be derived from Heliantheae or some protoheliantheaceous ancestor.

Although predominantly perennial herbs and subshrubs, some genera have truly woody members, notably the South Pacific and Australasian genus *Olearia* Moench, which has species of a definite arboreal habit; *Baccharis* L., formed largely by woody shrubs; and to a certain extent several other genera such as *Haplopappus* Cass., *Chrysothamnus* Nutt., and *Gutierrezia* Lag. A few species and genera have a pulvinate or semipulvinate habit.

The wood of Astereae shows advanced characteristics, such as the vessels usually grouped in various specialized patterns and the abundant vascular tracheids, characteristic components of specialized woods with extremely narrow vessels. The relatively short vessel-element length in the tribe as a whole probably corresponds to a more advanced position within Compositae than Heliantheae or Mutisieae. Another characteristic of the wood of Astereae is the abundance with which various types of helical vessel sculpturing, particularly fine and coarse bands, are represented.

Most Astereae are bisexual, self-incompatible, outbreeding, insect-pollinated plants with showy heads; *Baccharis* L. is dioecious. A few genera are self-compatible, notably *Conyza* L., in which many species are weedy.

The pollen is spheroidal or slightly flattened and provided with characteristic well-developed, uniform, evenly distributed conical spines. There is little variation in pollen characteristics throughout the tribe, suggesting a close relationship of the taxa.

The lowest chromosome number so far known in the plant kingdom is a member of the Astereae, *Haplopappus gracilis* (Nutt.) Gray, with $n = 2$. Gametic chromosome numbers of two to ten and multiples up to 72 have been reported. Two-thirds of the species and 60% of the genera so far counted are on the base of nine, presumed to be the basic number.

A monosporic type of embryo-sac development is found in all the genera so far studied embryologically, with the exception of *Erigeron* and *Townsendia*, which have bisporic and tetrasporic embryo sacs. These two genera are the only ones of the tribe known to have species with an apomictic type of reproduction.

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Calenduleae Cassini, Jour. Phys. Chim. Hist. Nat. Arts **88**: 161. 1819.

Herbs or small shrubs, much branched or spreading; leaves alternate or sometimes opposite, entire, lobed or toothed, seldom divided. Heads heterogamous, the ray florets in a single row, ♀ or neuter; disc florets bisexual, ♂, or sterile. Involucral bracts narrow, herbaceous, with or without scarious margins, in 1 to 3 series. Receptacle naked, or slightly setaceous. Pappus always absent. Corollas mostly yellow or orange, all of the same color; those of the ray florets trimerous, spreading or reduced; those of the disc florets pentamerous and regular. Anthers with a terminal appendage and with short, pointed or obtuse basal appendages. Styles of fertile disc florets with truncate and penicillate tips. Achenes of various and irregular shapes, often curved and winged, or thick and hard. TYPE GENUS: *Calendula* L.

About ten genera, chiefly African and Mediterranean; in our area possibly one introduced species (*Calendula officinalis* L.).

This is the smallest tribe of Compositae, closely allied with Senecioneae with which it shares the characters of the style. It is differentiated by the lack of a pappus, by the involucral bracts often in more than one row and more massive, by the presence of sterile florets, and by the heteromorphic achenes. All the characters by which Calenduleae differ from Senecioneae are considered as advanced characters in the family, and the tribe is most likely a specialized offshoot from Senecioneae.

Gametic chromosome numbers of $n = 7, 8, 9$, and 10 have been reported. Some species are polyploids, and different numbers have been reported for the same species in instances.

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Cardueae Cassini, Jour. Phys. Chim. Hist. Nat. Arts **88**: 155. 1819, "Carduineae."

Thistles, or thistle-like herbs, with a cottony or woolly, rarely silky or hispid indumentum. Leaves alternate, sinuate, lobed or divided, rarely entire, mostly prickly or spiny. Heads mostly large, homogamous, the florets all perfect; or sometimes heterogamous, the marginal florets then radiatiform and commonly neuter or ♀. Bracts of the involucre imbricated in several rows, usually prolonged into a spine or bristle, or provided with a membranous edge. Receptacle often thick and hard, or fleshy; bristly or hairy, seldom with true bracts; or naked. Pappus bristly or plumose, rarely paleaceous or wanting. Corolla of the ray florets, when present, never with a trimerous ligule; the ligule, if present, either bilabiate or pentamerous and deeply cleft. Tubular corollas split into long, narrow lobes. Anthers with elongated appendages at the tip, sagittate at the base. Style branches short, commonly united up to the obtuse or acute tips, usually with a pubescent ring below (FIG. 21, m). Achenes usually narrow or flat, sometimes produced into a narrow beak. (Including Cynareae Less., nom. illegit.) TYPE GENUS: *Carduus* L.

About 50 genera and 1500 species, basically Northern Hemisphere and Old World, a few genera common in the New World in both North and South America; represented in our area by the indigenous *Cirsium* Mill. and the naturalized *Arctium* L., *Centaurea* L., *Cnicus* L., *Onopordum* L., and *Silybum* Adans.

Cardueae are characteristically robust herbs with spiny or prickly leaves, stems, and involucres. The anthers are provided with long tails, and the style branches are short, with a typical ring of hairs below the point of bifurcation. The corollas are all tubular or, if ligulate, never with a trimerous ligule; the receptacle usually is massive. Although particular genera show exceptions to these characteristics, no one genus combines all exceptions. The subtribes into which the Cardueae have been divided are not very well marked and possibly are somewhat artificial. The tribe is morphologically related to Arctoteae and Mutisieae, but possibly as a result of parallel or convergent evolution, rather than of a recent common origin. Chiefly on account of the tubular corollas, Cardueae have sometimes been considered as primitive, and even as the ancestral tribe within Compositae. The modified and obviously specialized habit, involucre, style, and possibly also anthers and receptacle make this view rather unlikely.

Gametic chromosome numbers of 8, 9, 10, 11, 12, 13, 15, 17, 19, and multiples have been reported; $n = 17$ has been proposed as basic, the lower numbers being interpreted as a reduction series. The embryo sac is of the normal, monosporic, 8-celled type; the endosperm is of the nuclear type, with a varied number of free cells, or in subtribe Echinopinae it can be cellular. Apomixis is suspected in species of *Carduus* and *Cirsium*. The ovary walls have crystals of calcium oxalate which seem to be characteristic of different genera and of taxonomic importance.

Cardueae are often adapted to disturbed and ruderal conditions, where they are often very aggressive, and due to their size and spininess constitute obnoxious weeds. Their seeds are particularly well adapted to wind dispersal; man has also aided in the process. They are especially harmful in semicultivated grasslands, and, for example, in the Argentine pampas many square miles of good range are covered by species of *Carduus*, *Cirsium*, and *Silybum*.

Some species of *Carduus* and *Cirsium* which show narrow ecological tolerance, particularly in respect to nitrate and organic matter deficiency and drainage, are good indicators of soil conditions.

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Cichorieae Dumortier, Anal. Fam. Pl. 30. 1829.

Herbs [and low shrubs or, exceptionally, small trees] with milky juice and alternate or radical, entire, toothed or pinnatifid, rarely much-divided leaves. Heads always homogamous. Involucral bracts membranous or herbaceous, rarely scarious, imbricated in several rows, or equal in a single row. Receptacle naked or with chafflike bracts, nearly always flat. Florets bisexual, the corolla ligulate, the ligule 5-toothed at the truncated apex; corollas after flowering twisted into a caplike mass which often remains on the achene or involucre for some time. Pappus usually with 1 or more rows of simple or plumose setae, rarely of paleae, awns, or wanting. Anthers sagittate or auriculate at base, commonly with thin, rather short appendages at summit. Style branches slender, semicylindric, narrowed towards the end or almost obtuse, stigmatic on their inner surface for their whole length. Achenes often excavated at the base, with a short stipe, and often with a slender beak at the summit (Lactuceae Cassini, Jour. Phys. Chim. Hist. Nat. Arts **88**: 151. 1819, has priority over Cichorieae and must be used when subfamily Cichorioideae is not recognized). TYPE GENUS: *Cichorium* L.

Seventy-five genera and about 1000 species, essentially Northern Hemisphere and Old World, although relatively abundant on the American continent; represented in our area by some 14 genera.

This, the best-defined tribe in the family, is easily characterized by the homogamous heads with the corollas all expanded into a 5-merous, truncate, 5-toothed ligule and by the milky juice. Although the tribe is essentially herbaceous, subshrubs, shrubs, and even small rosette-trees are known.

The wood of Cichorieae shows many advanced anatomical characteristics, such as very short storied fibers; large groupings of vessels; and either very scanty or very abundant vasicentric parenchyma. Woody Cichorieae show clear anatomical adaptations to environment, complicating considerably the elucidation of over-all phylogenetic patterns. The distribution, as isolated groups in different parts of the world, including oceanic islands, and the advanced floral morphology of most of the woody Cichorieae point to a possible secondary origin from herbaceous progenitors, but the possibility that they are derived from extinct woody ancestors cannot be ruled out.

Although some generic variation is present, the pollen grains of Cichorieae are relatively uniform. They are globular; generally tricolpate or infrequently tetracolpate; echinolophate or occasionally echinate, with 12 to 20 lacunae and high ridges, and prominent sharp, conical spines; and are characterized by an elaborate and beautiful system of sculpturing.

Fifty-three of the 65 genera recognized in the latest treatment of the tribe are known cytologically. Every number from $n = 4$ to 10 is known, with $n = 9$ being by far the most frequent. Morphological and distributional evidence also point to 9 as the original basic number of the tribe. Polyploidy is known to occur, but is not as frequent as in other tribes.

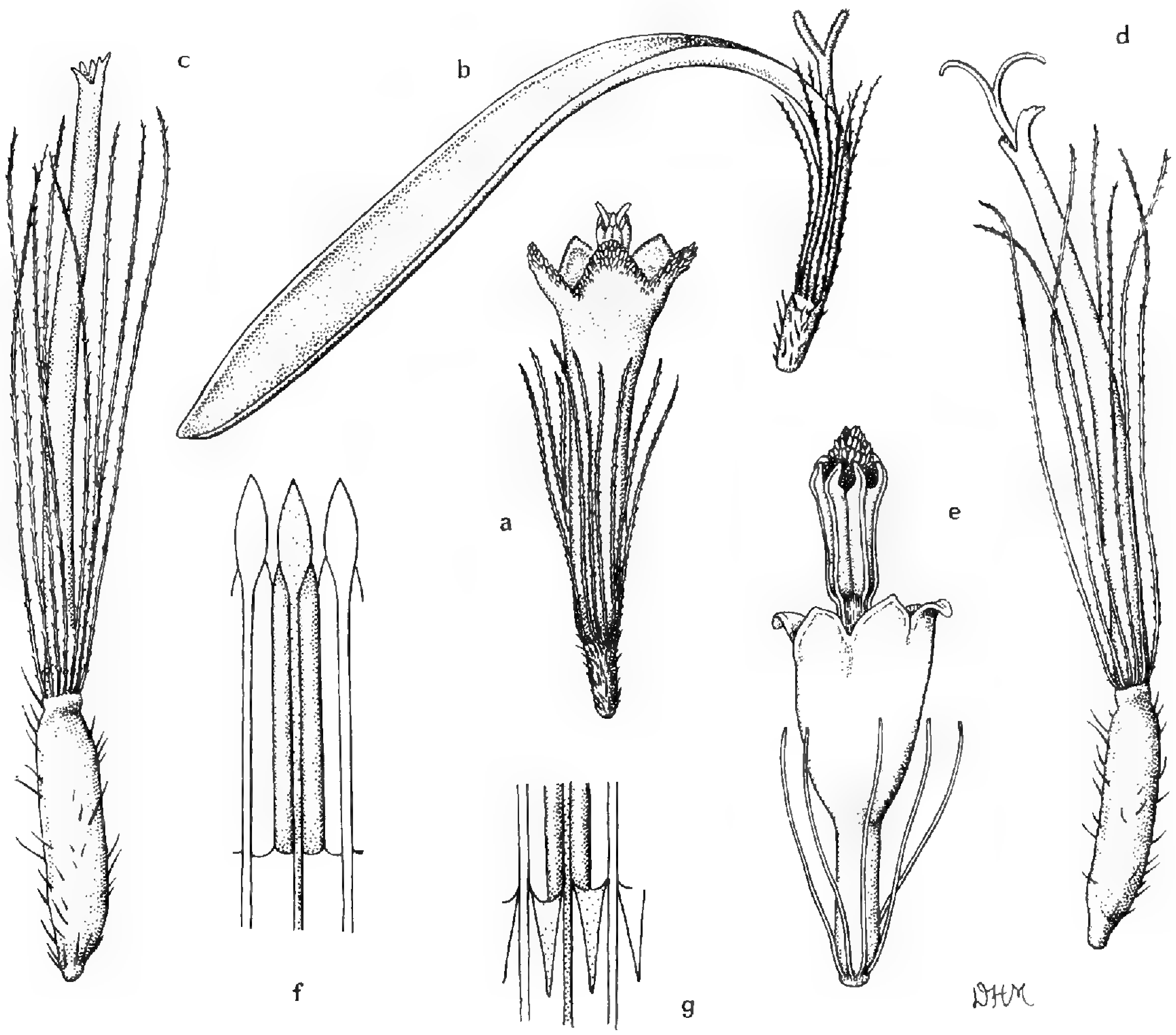

FIG. 3. Florets and stamens. a, b, *Erigeron annuus* (L.) Pers.: a, tubular flower, × 20; b, ligulate flower, × 20. c, d, *Conyza bonariensis* (L.) Cronq.: c, filiform corolla, style not visible, × 20; d, ligulate corolla, × 20. e, *Amphiachyris dracunculoides* (DC.) Nutt., tubular flower, ♀ sterile. f, *Aster umbellatus* Mill., anthers, × 25. g, *Pterocaulon undulatum* Mohr, detail of anthers showing tails, × 25.

Apomixis, known in several genera (e.g., *Hieracium*, *Taraxacum*, *Crepis*), is either obligate or facultative, the embryo being formed either as a result of apospory or, more commonly, diplospory followed by parthenogenesis. The lack of understanding of this phenomenon in these genera, particularly in *Hieracium*, has often led to the description of apomictic forms as species, resulting in much taxonomic confusion.

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Eupatorieae Cassini, Jour. Phys. Chim. Hist. Nat. Arts **88**: 202. 1819.

Herbs or shrubs, rarely annuals, with opposite, whorled or alternate, mostly undivided leaves. Heads always discoid and the florets bisexual and fertile, very rarely reduced to a single flower. Involucral bracts imbricated, in several rows, or nearly equal and in about 2 rows. Receptacle flat or somewhat convex, rarely spherical, almost always naked. Pappus of rigid setae or rarely plumose, scaly, or absent. Corolla tubular, regular, pentamerous, very rarely tetramerous, purple, reddish, bluish, or white, never true yellow. Anthers rounded at base, terminal appendage present or absent. Style branches semicylindric, elongated, more or less clavate or thickened upward, obtuse, with the more or less inconspicuous stigmatic lines only near the base (FIG. 2d, e). Achenes terete, 4- or 5-angled, 10-ribbed, or flattened. TYPE GENUS: *Eupatorium* L.

A very homogeneous tribe with some 50 genera of almost exclusively American distribution, in our area represented by 11 genera: *Ageratum* L., *Brickellia* Ell., *Carphephorus* Cass., *Eupatorium* L., *Garberia* Gray, *Hartwrightia* Gray ex Watson, *Kuhnia* L., *Liatris* Schreb., *Mikania* Willd., *Sclerolepis* Cass., *Trilisa* Cass. (including *Litrisa* Small).

Eupatorieae are best defined by the characters of the style, with its elongated, terete or somewhat flattened style branches which are obtuse or club shaped towards the end, minutely papillose but not hairy, with the stigmatic lines rather obscure on the inner surface and towards the base. Another diagnostic character is the heads of tubular florets which are purple, reddish, bluish, or white, but never true yellow. Generic limits within the tribe are difficult to define, and specific delimitations are also difficult, especially in some of the large tropical genera, such as *Mikania, Ageratum,* or *Eupatorium.* Subtribe Piqueriinae Benth. & Hook. is characterized by lack of the terminal stamen appendages which are almost universal features in the family. *Liatris* with its corms ("bulbs"), alternate leaves, and corollas is also slightly aberrant and approaches the Vernonieae in some characters.

On account of the tubular corollas, Eupatorieae have sometimes been considered as the basic tribe in the family. The question of whether a tubular or radiate head is primitive is not easily resolved, and opinions vary. It is nevertheless unlikely that this small American tribe is the ancestral one, although it is likely that it has retained some primitive characteristics, while acquiring some advanced ones, such as the characters of the involucre and involucral bracts.

Gametic chromosome numbers of 9, 10, 11, 17, 19, and multiples have been reported for the tribe, with $n = 10$ apparently being the modal number. Apomixis is reported in some species of *Eupatorium* and suspected in others.

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Heliantheae Cassini, Jour. Phys. Chim. Hist. Nat. Arts **88**: 189. 1819.

Herbs or shrubs with more or less scabrous or hirsute, rarely silky indumentum. Leaves entire or divided, opposite or alternate. Heads homogamous and discoid; or heterogamous with ♀ or neutral ray florets and bisexual or ♂ disc florets; or unisexual, the plants then either monoecious or dioecious. Involucral bracts generally more or less herbaceous, sometimes dry and rigid or membranaceous, biseriate, with a difference between outer and inner rows, or imbricated in several rows. Receptacle with a chafflike bract subtending each floret or bristly, hairy, or naked. Ray florets mostly yellow, with a trimerous ligule, or reduced to a short tube, or none; disc florets with a regular corolla with 5, rarely 4, lobes; ♂ florets in some groups with the corolla none or a mere rudiment. Pappus of scales, paleae, awns, or wanting. Anthers obtuse at base, not tailed, with a terminal appendage in all but a few species; in some genera anthers distinct or scarcely coherent. Style of the bisexual disc florets varying from truncate to subulate, with or without appendages, but never with appendages below the point of bifurcation (FIG. 2a, b). Achenes thick or flattened contrary to the subtending chaffy bract, never parallel with it. (Including Helenieae Benth. & Hook., Ambrosiaceae Link, and Ambrosieae Cass.) TYPE GENUS: *Helianthus* L.

A varied group comprising some 200 to 300 genera, essentially American, and chiefly tropical or subtropical, with a very few endemic Old World genera and species; the most abundant tribe in our area, where it is represented by some 45 genera.

Heliantheae are characterized by being usually rather coarse herbs or subshrubs, with generally a more or less scabrous or hirsute, rarely felty-tomentose or woolly, indumentum. The leaves are usually entire or toothed, and at least the lower ones are usually opposite. The heads are radiate with yellow florets and are often few in number. Also typical of the tribe is the development and usual persistence of the receptacular bracts, which, when present, subtend the individual florets. The tailless anthers and the pappus either formed by a few rigid awns or paleae or absent are also typical.

As circumscribed here, the Heliantheae is probably the largest tribe in the family. The tribe is usually divided into ten subtribes unequal in size and degree of distinction and in the extent to which they form natural groupings. Helenieae Benth. & Hook., a rather artificial assemblage, the result of convergent and parallel evolution in the one common technical character, the loss of receptacular bracts, is considered here as not deserving tribal status. Most of the genera of Helenieae belong with Heliantheae; others are better placed elsewhere.

Subtribe Ambrosiinae Less., the familiar ragweeds, has been considered as a separate tribe, subfamily, and even as a separate family in the past. A small, strictly American group of some ten genera and 50 species, they are remarkable for their free but closely approximate anthers, forming the usual cylinder and sometimes slightly cohering. The heads of Ambrosiinae are either bisexual or unisexual, the florets always unisexual by abortion. The corolla of the ♀ florets is much reduced or often absent; in those species with unisexual heads, there is often in each head only one naked floret surrounded by the involucral bracts, usually four or five such heads then being aggregated into a secondary head. These extreme reductions are the result of adaptation to wind pollination and are accompanied by corresponding changes in pollen morphology. In addition, the heads of Ambrosiinae are further specialized for seed dispersal by animals. Particularly in the genera *Xanthium* and *Franseria*, the common cockleburs, the involucre is fused around the single fruit at maturity, and is provided with sharp spines or hooks, which adhere to the fur of animals.

Heliantheae are often considered as the most primitive tribe of Compositae on account of their opposite leaves; few, large heads; leafy involucres; chaffy receptacles; yellow corollas; carpellate ray florets and bisexual disc florets; tailless anthers; style branches with no clearly differentiated stigmatic portion; and a chaffy pappus often of five members, all characters usually considered primitive within Compositae. On the other hand, the tribe is primarily herbaceous, a presumably derived condition. As is true for Compositae in general, the Heliantheae are an advanced and specialized group, the species showing, in general, a remarkable adaptation to all kinds of ecological and environmental conditions. Consequently, both primitive and advanced characteristics occur, as a result of a mosaic type of evolution. No subtribe or genus is truly primitive; all show some advanced characteristics. Some groups among Heliantheae probably have the highest concentration of primitive characters in the family; others, particularly the Ambrosiinae, are highly advanced and specialized. But more than any particular feature, the array of primitive and advanced characteristics and the remarkable diversity and variation exhibited by Heliantheae are indications of a long history.

The secondary xylem of woody species of Heliantheae shows a great deal of variability in vessel-element length and diameter, in the number of vessels per group, in the pittings and striations in the vessel wall, etc. Narrow vessels aggregated in large numbers; the presence of helical striations in vessels and vascular tracheids; wood rays composed of thin-walled, unlignified cells; and the presence of vascular tracheids are among the characters considered as advanced within the tribe. Although some species of woody Heliantheae seem to have some primitive characteristics, no definite conclusions as to the position of the tribe within Compositae can be drawn from wood characters alone. Since the Compositae are a highly advanced family, no absolute primitive characteristics in the wood can be expected.

Pollen grains are tricolpate, with the exine moderately to exceedingly thick, with long, slender, conical spines in the insect-pollinated species, the spines greatly reduced or absent in the wind-pollinated species.

Gametic chromosome numbers of 4, 6, 7, 8, 9, 10, 11, 12, 13, 15, 17, 19, and multiples have been reported for the tribe. In general, the lower numbers correspond to the more advanced groups within the tribe; 12 seems to be the most frequent number, but no definite basic number has been proposed. Apomixis is known in *Parthenium*, *Rudbeckia*, and *Ambrosia*; diplospory with parthenogenesis appears to be the most prevalent mechanism in the first two genera, although apospory, which occurs in the one apomictic species of *Ambrosia*, is also known.

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Inuleae Cassini, Jour. Phys. Chim. Hist. Nat. Arts **88**: 193. 1819.

Herbs, shrubs [or rarely trees] mostly with white-woolly or glandular herbage. Leaves alternate or opposite, entire, or rarely more or less lobed or dentate. Heads rather small and discoid or ligulate, homogamous or heterogamous, dioecious in some genera. Involucral bracts imbricated in several rows, commonly white or scarious, often very hirsute. Receptacle usually epaleaceous. Ray florets short and slender, filiform or ligulate, the ligule trimerous and minutely toothed at the apex. Disc florets tubular, with 5 or 4 lobes, usually light yellow or white. Pappus capillary, rarely paleaceous, or none. Anthers with an upper appendage and always tailed at base, the tails free or united in pairs (FIG. 3g). Style branches of various forms, but mostly obtuse or truncate, with marginal stigmatic lines on the inner surface, and always devoid of stylar appendages (FIG. 2g). Achenes usually very small, flat, terete, angled, or elongated. TYPE GENUS: *Inula* L.

A cosmopolitan group, with some 300 genera and 2000 or more species, abundant in the Old World, especially South Africa and Australia; ten genera in our area: *Anaphalis* DC., *Antennaria* Gaertn., *Evax* Gaertn., *Facelis* Cass., *Filago* L., *Gnaphalium* L., *Inula* L., *Pluchea* Cass., *Pterocaulon* Ell., and *Sachsia* Griseb.

Inuleae are characterized by anthers more or less strongly tailed (caudate) at the base; flattened style branches with marginal stigmatic lines; mostly capillary pappus; and heads often discoid or when ligulate then usually homochromous and yellow. A large and cosmopolitan tribe, the generic limits are often characteristically blurred. Inuleae are superficially morphologically similar to Astereae from which they can be easily separated by the usual appendages to the anthers and by the absence of terminal appendages on the style branches. The heads are often small and discoid or are ligulate with short, inconspicuous ligules, while the involucre is frequently very hairy. Although resembling Astereae, Inuleae are most likely related to and derived from Heliantheae, the similarities with

Astereae being the result of parallel evolution, as is often the case in Compositae.

Anatomical studies of secondary wood show a series of specialized characteristics. The vessels tend to be rather narrow, with grooves interconnecting apertures of a few or many pits adjacent in a helix on the vessel wall. The libriform fibers are occasionally very short, although always longer than the vessel elements in any given species. Both uniseriate and multiseriate rays are found, but the former appear to be very scarce. Wood anatomy seems to indicate a relationship with Vernonieae, but since advanced characteristics are involved, there is always the possibility of parallelisms.

Several species, particularly those of the New Zealand genus *Raoulia*, the "vegetable sheep," have a pulvinate type of growth. An extreme reduction in the leaf has taken place in this genus, resulting in minute leaves with an open type of venation.

Gametic chromosome numbers of 5, 7, 8, 9, 10, 11, and 13 are known in the tribe. Many genera are based on 5 and 7, but the tribe is not as well known cytologically as many of the others in the family. The large genus *Antennaria* has many apomictic species, with diplospory followed by parthenogenesis the usual apomictic mechanism. Many *Antennaria* species seem to be obligate apomicts.

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Mutisieae Cassini, Jour. Phys. Chim. Hist. Nat. Arts **88**: 199. 1819.

Herbs [or mostly shrubs or rarely twining or arborescent plants]. Leaves [alternate or] radical, entire [toothed or pinnatifid, very rarely much divided or prickly]. Heads [homogamous, the florets all bisexual and the corolla bilabiate, or] heterogamous and then usually more or less radiate, with the corollas being gradually enlarged from the center to the circumference of the head [or the ray florets irregular or 4- or 5-merous]. Involucral bracts usually imbricate in several rows, rarely forming a single row of equal bracts, with or without small outer ones. Receptacle mostly naked. Pappus setose, simple [or plumose, or formed of narrow paleae, very rarely wanting]. Corollas [either regular, or] bilabiate, or expanded into a ligule, of various colors, but ray and disc corollas always of the same color. Anthers with long tails at the base, and an elongated upper appendage. Style branches of perfect flowers not appendaged, usually short and blunt, without a ring of hairs below the point of bifurcation (FIG. 2j). TYPE GENUS: *Mutisia* L.f.

Some 55 genera and over 500 species, mainly South American, but also North American, African, and Asian; in our area represented only by *Chaptalia nutans* (L.) Hemsl. and *C. tomentosa* Vent.

Mutisieae are characterized by all or some of the corollas being bilabiate, by the naked receptacle, and by the tailed anthers. There is in the tribe a great amount of variation and a wide latitude of expression of characters, including the diagnostic ones cited above. Mutisieae are also quite varied in habit, including trees up to 20 m. tall; shrubs; subshrubs; rosette trees, shrubs, and herbs; leaning and climbing vines; and perennial and annual herbs.

Some of the Mutisieae studied anatomically show what can be considered rather primitive characteristics in their secondary xylem. These include relatively wide vessels which are solitary or in small groupings; no tendency towards ring porosity in the vessels, which also lack prominent spiral thickenings; absence of vascular tracheids; and nonstoried wood. In other species, some or all of these are replaced by more advanced features. Primitive wood characteristics are often correlated with primitive characters in the floral organs, suggesting that at least some genera of Mutisieae are primitive in the family.

The tribe is subdivided into three to five subtribes, which in general seem to represent natural assemblages, although there is still a considerable amount of knowledge needed before a true understanding is reached.

The pollen grains also show a great deal of variability. They vary from spheroidal to markedly elliptical and may be with or without a thickened exine, with short or long furrows, and short or long spines. In some instances, characters of the pollen can be of taxonomic importance in the separation of genera.

Chromosome numbers of $n = 18$, 23, 24, and 27 have been reported. These represent a departure from the lower numbers characteristic of other tribes of the family, but relatively few species have been studied so far.

Pollination is entomophilous, in general, but some South American species of *Mutisia* are apparently adapted to pollination by hummingbirds. *Chaptalia* is suspected of being apomictic.

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Senecioneae Cassini, Jour. Phys. Chim. Hist. Nat. Arts **88**: 196. 1819.

Herbs or shrubs, or a few species arborescent. Indumentum soft, cottony and whitish, sometimes glutinous, rarely coarsely hirsute. Leaves mostly alternate or radical (seldom opposite), entire, variously toothed, or divided. Heads with bisexual tubular disc florets and ♀ or neutral ligulate ray florets, or the ligulate wanting, the heads then discoid. Involucre mostly of a single series of similar herbaceous or membranaceous bracts, sometimes with an outer calyculate series, rarely imbricated in several rows. Receptacle nearly always naked. Pappus of numerous fine bristles, rarely subpaleaceous. Corollas yellow or, less frequently, white or purple; ray florets with a trimerous, entire or toothed spreading ligule. Anthers mostly round at the base and with a well-developed apical appendage. Style branches of bisexual flowers usually flat, the truncate tips penicillate, and the nearly marginal stigmatic lines not meeting (FIG. 2h, i). Achenes usually angular or terete and striate, truncate or shortly contracted at the end, not beaked, occasionally somewhat flattened but never winged. TYPE GENUS: *Senecio* L.

About 50 genera, with over 2000 species, distributed in all regions; five genera in our area: *Arnica* L., *Cacalia* L., *Erechtites* Raf., *Gynura* Cass., *Senecio* L.

Relatively small in number of genera, this tribe is rich in species due to the genus *Senecio*, which is not only the largest genus among Compositae, but one of the largest among the seed plants, and certainly the most widely dispersed. Truly cosmopolitan and ubiquitous, *Senecio* abounds in local species in almost every region of the globe, in the Old and the New World, from the Equator to the Arctic and Subantarctic.

Senecioneae are characterized by their involucre, which generally consists of a single inner row of equal, more or less herbaceous, free or united phyllaries, with or without an outer row of smaller bracts (often called a calyculus); by the truncate stylar branches, with or without terminal appendages; and by the tailless anthers.

Over two-thirds of the genera of Senecioneae have been examined cytologically, but this figure is somewhat misleading, since the chromosome numbers of only a relatively small number of species of *Senecio* are known. Gametic chromosome numbers of 5, 7, 9, 10, 11, and euploid and aneuploid multiples of these are known. It has been proposed that the base number for the tribe is 10, which also seems to be the most frequent number, with a reduction series accounting for the lower numbers and polyploidy for the higher ones. The chromosomes in Senecioneae are often small and difficult to count, and a fair number of reports are only tentative. In general, Senecioneae have a monosporic, normal type of embryo-sac development. Some species, especially of *Arnica*, are apomictic, and species in some other genera are also suspect.

The tribe is usually divided into subtribes Liabinae Less., Othonninae Less., and Senecioninae, based primarily on characteristics of the involucres and the phyllaries. Generic limits are very much confused and have been the subject of much controversy. Particularly difficult is the delimitation of *Senecio*, vegetatively one of the most polymorphic genera of angiosperms, but relatively constant in its floral characters. The delimitation of species in *Senecio* is based largely on vegetative characters.

Senecioneae have been proposed by Small as the most primitive tribe of Compositae, largely on the basis of Willis' "Age and Area" hypothesis, although a detailed analysis of the morphology of the tribe was supposed to corroborate the primitiveness of the tribe. However, this is most likely an advanced and specialized tribe (as evidenced by the involucre, the receptacle, and the pappus) derived from helianthoid ancestors. Morphological similarities between Senecioneae and tribes other than Heliantheae are also present, particularly Eupatorieae.

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Vernonieae Cassini, Jour. Phys. Chim. Hist. Nat. Arts **88**: 203. 1819.

Perennial herbs or shrubs, rarely small trees, or very rarely annuals, with alternate, occasionally opposite leaves. Heads homogamous (except *Stokesia*), with all the florets bisexual (or rarely slightly unisexual, sometimes reduced to a single floret). Involucral bracts many, imbricated in several rows (except in a very few and anomalous genera reduced to 2 equal rows or to a small definite number). Pappus usually setose and copious, the setae in some genera flattened into paleae and in a very few others much reduced or lacking. Corollas tubular (and ligulate in *Stokesia*), reddish purple to white, seldom blue, never yellow; anthers with a terminal appendage; basal appendage of the anthers auriculate [or very short tailed] or absent. Style branches slender, acute, or scarcely obtuse, uniformly and shortly hirsute, the stigmatic papillae on the inner surface towards the base and not very conspicuous (FIG. 2c). Achenes usually terete or slightly flattened, usually 1-ribbed (sometimes 4- or 5-ribbed). TYPE GENUS: *Vernonia* Schreb.

One large genus, *Vernonia*, with nearly 1000 species, and some 50 small, closely related genera, largely pantropical, particularly abundant in South America, but also frequent in North America and Africa; only three genera in our area: *Elephantopus* L., *Stokesia* L'Hér., and *Vernonia* Schreb.

Vernonieae are characterized by the uniformly homogamous heads with bisexual florets which are never yellow. They are usually perennial herbs, with alternate, entire or toothed leaves.

The tribe is not as well known cytologically as others in the family. Gametic chromosome numbers of 9, 10, 11, and 16 have been reported. The pollen grains of Vernonieae show a great deal of variation. In general, they are spheroidal in shape, with an elaborate system of ridges or crests inclosing depressions or lacunae. The size, shape, and number of the ridges and lacunae are varied, but there does not seem to be any adaptive value to these modifications.

The Vernonieae appear to be allied to the Cardueae. They are also related to the Mutisieae through the anomalous genus *Stokesia,* which has the anthers, styles, and pollen of Vernonieae, but the outer florets ligulate and rather deeply 5-lobed as in Mutisieae. Anatomical characters tend also to link Vernonieae somewhat with Mutisieae (*q.v.*), as do palynological characteristics. Since Mutisieae and Cardueae are apparently closely related, this relationship of Vernonieae with both tribes is not surprising.

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THE GENERA OF SAPINDALES IN THE SOUTHEASTERN UNITED STATES [1]

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RECENT RESEARCH in the fields of floral morphology and anatomy, embryology, palynology, comparative anatomy, biochemistry, etc., has made possible more accurate determination of the systematic positions of many families and their arrangement into more natural affinity-groups or orders than was attainable at the time when the classical Englerian system was proposed. Since orders usually form the skeleton of every proposed scheme for a "natural system" of the angiosperms, the achievement of the greatest possible homogeneity seems to be of primary importance. With regard to this, the splitting of at least some very large and heterogeneous orders of the Englerian system (e.g., Geraniales, Sapindales), followed in some instances by rearrangement of the families among and/or within the segregated orders, appears to be expedient. Such changes have been carried out more or less successfully in several recent systems (e.g., Hutchinson, 1926 & 1959; Gundersen, 1950; Cronquist, 1957; Takhtajan, 1959).

Although the sequence of a number of families of the southeastern United States which have been surveyed by the author in the *Journal of the Arnold Arboretum* (vols. 43 & 44, 1962 & 1963) generally corresponds with that of Engler's system (1936), Takhtajan has been followed primarily in the delimitation of the orders. Thus, the families Rutaceae, Simaroubaceae, Burseraceae, and Anacardiaceae (as well as Meliaceae, unpublished) are regarded as members of the order Rutales; the families Sapindaceae, Aceraceae, and Hippocastanaceae (as well as several others occurring beyond

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our limits) constitute the order Sapindales; and Aquifoliaceae, Celastraceae, and Hippocrateaceae represent the order Celastrales. The families Empetraceae (Wood & Channell, Jour. Arnold Arb. **40**: 162–164. 1959) and Cyrillaceae (Thomas, *ibid.* **42**: 96–102. 1961) have been removed from Sapindales and are regarded as members of Ericales, views which accord with those of Takhtajan. Contrary to Takhtajan's view on Staphyleaceae as a primitive member of Sapindales, this family is here excluded from Sapindales and will be treated within Cunoniales (or Saxifragales *sensu lato*), where it seems to belong (cf. C. G. G. J. van Steenis, Fl. Males. I. **6**: 49. 1960).

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SAPINDACEAE A. L. de Jussieu, Gen. Pl. 246. 1789, "Sapindi," nom. cons.

(SOAP-BERRY FAMILY)

Trees, shrubs, or woody (rarely herbaceous) vines climbing by axillary tendrils [or very rarely erect herbs], often containing saponine in the tissues of the stem and/or fruit. Leaves usually alternate, compound to decompound, often even-pinnate, rarely simple, exstipulate or rarely stipulate, persistent or deciduous. Plants (polygamo-) monoecious or dioecious; flowers in terminal and/or axillary thyrses [or simple or compound racemes, or rarely solitary], small, hypogynous, regular or more rarely irregular, usually unisexual by abortion, occasionally also bisexual. Sepals usually 4 or 5, distinct or ± connate, usually unequal, deciduous or persistent, imbricate [or valvate]. Petals usually 4 or 5, distinct, clawed, often with petaloid appendages ("scales") on the interior surface just above the claw, imbricate, rarely wanting. Nectariferous disc extrastaminal (except in *Dodonaea*), continuous and regular or unilateral and oblique. Stamens 6–10[–12], often 7 or 8, distinct or connate at base, inserted within or on the disc, short and sterile or wanting in ♀ flowers; anthers versatile, introrse (extrorse only in *Melicoccus*), longitudinally dehiscent. Gynoecium syncarpous, usually 3–, rarely 2– or 4[–6]-carpellate, rudimentary in ♂ flowers; stigma simple or lobed, or stigmas 3; style short or elongate, sometimes ± cleft at apex; ovary superior, 2–4[–6] (usually 3)-locular, the placentae axile; ovules usually 1 or 2 in each locule, campylotropous to anatropous, apotropous or more rarely epitropous. Fruit a drupe, berry, capsule (sometimes winged), or schizocarp splitting at maturity into drupelike [nutlike or samaroid] mericarps, often 1-locular and 1-seeded by abortion. Seed usually solitary in a locule, often provided with an aril; [2] seed coat bony, crustaceous, or coriaceous (rarely fleshy); endosperm usually wanting or scanty; embryo usually curved. (Including Dodonaeaceae Link.) TYPE GENUS: *Sapindus* L.

A pantropical family of nearly 150 genera with about 2000 species, a few extending into warm-temperate areas. The number of genera occurring in America, Asia, and Africa (including Madagascar) is almost equal (with fewer in Australia with Oceania), but the greatest number of species is New World. The large genus *Allophylus* L. is pantropical; the primarily American *Cardiospermum* and the almost exclusively Australian *Dodonaea* have two and one species, respectively, of pantropical distribution. A few genera are extratropical (e.g., the Asiatic *Koelreuteria* Laxm. and *Xanthoceras* Bunge), while some largely tropical genera have extratropical species (e.g., *Sapindus*). The family has been subdivided by Radlkofer into 14 very natural tribes.

One of the peculiarities of the flowers of the family is the frequent presence of variously shaped, more or less petaloid, interior "appendages" to the petals. According to Leinfellner, the diversity of appendaged and unappendaged petals of Sapindaceae is a result of phylogenetically fixed lateral and/or median-ventral splittings of originally peltate-funnelform petals, sometimes also followed by various secondary connations or eventual suppression in development of the separated (split-off) parts.

Chromosome numbers known at present (23 species in 17 genera) form an aneuploid series, $2n = 20, 22, 24, 28, 30, 32$.

Sapindaceae are most closely related to Hippocastanaceae and Aceraceae, but are also allied to Anacardiaceae, Burseraceae, Meliaceae, Simaroubaceae, and Rutaceae. Evidence from wood anatomy (Heimsch) supports this scheme of relationships suggested by Radlkofer (1890, 1895, 1932–1934).

Indigenous to French Guiana, *Talisia pedicellaris* Radlk., which differs from *Melicoccus* (*q.v.*) mainly in the 5-merous perianth, introrse stamens, and septate ovary, was included in the flora of the Southeastern States by Small. This record was based on a poor herbarium specimen (NY) collected by Harshberger in Brickell Hammock, Miami, Florida, in December, 1910. Apparently neither Small nor Sargent, both of whom seem to have been much interested in Harshberger's discovery, ever relocated this species. Because Brickell Hammock since has been destroyed by the growth of

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[2] Van der Pijl (p. 620) proposed the following definitions of the aril and aril-like structures: "I propose to define the aril more or less in the same way as Gaertner did of old, viz. as a secundary, usually postfloral outgrowth of the funicle and therefore entirely free from the seed. This definition is independent of whatever view we may hold with regard to the phylogenetical origin of the aril. While maintaining the old term 'arillode' for an outgrowth of the integument in the vicinity of the micropyle, I shall use the term 'arilloid' for every kind of outgrowth on or near the seed that resembles the apparently independent aril." Since only a few families and not all the genera of Sapindaceae with arillate seeds have been investigated in regard to the morphological nature of their "arils," it is preferred here to use the term aril in a broad descriptive sense, applying it to all the categories of seed out-growths defined by Van der Pijl.

metropolitan Miami, there seems to be no reason for the inclusion of *Talisia* in the flora of the southeastern United States at present.

The eastern Asiatic *Koelreuteria paniculata* Laxm., $2n = 22$, 30(?), and *Xanthoceras sorbifolium* Bunge are often grown as hardy ornamentals; the former is beginning to spread from cultivation in at least the northeastern United States (Fernald, Gray's Man. Bot. ed. 8. 990. 1950). The less hardy *K. formosana* Hayata, $2n = 22$, is grown in the warmer areas of the southern United States. Lychee, *Litchi chinensis* Sonn., $2n = 28$, 30, a native of southeastern Asia, where it has also been in cultivation for over 2000 years, is now widely grown in tropical countries for its edible fruit pulp (seed aril) and seeds (edible when roasted). It is being cultivated commercially in Florida. The closely related *Euphoria Longana* Lam., longan, $2n = 30$, a native of India or southern China, widely planted in the Tropics (especially in Asia), is grown as an ornamental fruit tree (edible seed arils) in southern Florida, as well as in southern California. The caffeine-bearing seeds of the South American *Paullinia Cupana* HBK. find application in medicine (guarana, pasta guarana, guarana bread). Fruits and crushed shoots of many species of various genera are used for poisoning fish in the Tropics because of their saponine content.

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KEY TO THE GENERA OF SAPINDACEAE

General characters: *trees, shrubs, or vines; leaves alternate, usually compound or decompound, very rarely simple, mostly exstipulate; flowers small, regular or more rarely irregular, hypogynous, usually unisexual by abortion; perianth usually double, 4– or 5-merous; petals clawed, often with interior appendages above the claw, rarely absent; nectariferous disc usually extrastaminal; stamens often 6–8; gynoecium commonly 3-carpellate, syncarpous; ovary superior; ovules 1 or 2 in each locule, campylo- to anatropous, usually apotropous; fruits various, often 1-locular and 1-seeded by abortion.*

A. Plants herbaceous or suffruticose, climbing by axillary tendrils; leaves usually biternate, minutely stipulate; flowers irregular; disc unilateral, 2-glandular; fruits subglobular to top-shaped bladdery capsules, 1.5–4.5 cm. long. .... 1. *Cardiospermum.*

A. Plants woody, trees or shrubs; leaves never biternate, exstipulate; flowers regular; disc continuous; fruits various, never bladdery capsules.

  B. Leaves simple, covered with minute resiniferous glands, often viscous, appearing varnished; petals wanting; disc intrastaminal, minute; fruit a (2)3(4)-winged capsule. .... 5. *Dodonaea.*

  B. Leaves compound; petals always present; disc extrastaminal; fruits not winged.

    C. Leaves 3-foliolate, leaflets, small, up to 6 cm. long by 2.5 cm. broad; fruit an ovoid or ellipsoidal black drupe, 6–9 mm. long. . 6. *Hypelate.*

    C. Leaves usually even-pinnate; leaflets medium sized to rather large; fruits various, larger.

      D. Leaves with 6–18 entire or toothed leaflets; petals mostly appendaged.

        E. Leaflets entire, opposite or alternate, often conspicuously inequilateral, acute or acuminate at apex (if obtuse or rounded, the rachis winged); fruit of 1 or 2 (3) brown to black, drupe-like, subglobular mericarps with rudiment(s) of aborted carpel(s) at base, 1.2–2 cm. in diameter; seed not arillate. .... 2. *Sapindus.*

        E. Leaflets toothed or at least repand, alternate, ± equilateral, obtuse or rounded at apex; fruit a triangular-top-shaped stipitate capsule, 10–15 mm. long and broad; seed with cup-shaped aril. .... 4. *Cupania.*

      D. Leaves usually with 4 (2–6) entire, opposite or subopposite leaflets; petals unappendaged.

        F. Flowers in slender simple or panicled racemes terminating lateral branches; leaves usually 4-foliolate, leaflets acute at apex; berry ellipsoidal or obovoid, about 3 cm. long and 2 cm. broad, green, the pericarp thick and firm; seed ellipsoidal; seed coat fleshy, edible. .... 3. *Melicoccus.*

        F. Flowers in axillary, subterminal, corymb-like thyrses; leaves 2- or 4(rarely 6)-foliolate, leaflets obtusish to rounded or notched at apex; berry usually subglobular, 10–14 mm in diameter, dark purple, the pericarp thin; seed subglobular; seed coat crustaceous. .... 7. *Exothea.*

Tribe PAULLINIEAE HBK. emend. Radlk.

1. **Cardiospermum** Linnaeus, Sp. Pl. 1: 366. 1753; Gen. Pl. ed. 5. 171. 1754.

Herbaceous or suffruticose vines climbing by axillary tendrils; nodes trilacunar. Leaves biternate, sometimes also 3-foliolate with 3-lobed leaflets, or subbipinnate, petioled, minutely stipulate; leaflets usually coarsely toothed. Plants (polygamo-) monoecious or dioecious; flowers in axillary, corymb-like, reduced thyrses bearing two opposite tendrils below the summit of the peduncle, small, irregular, unisexual by abortion, sometimes also bisexual. Sepals 4 [5], the two exterior nearly half as long as the interior, imbricate. Petals 4, short clawed, appendaged, the petaloid scales of the two upper petals equilateral, cucullate crested, bearing below the apex a tongue-like "appendage" pointing downward, those of the two lower petals inequilateral, with a dorsal, winglike crest. Disc unilateral, with a gland opposite each of the two upper petals. Stamens 8, of unequal length, deflexed, shorter and sterile in ♀ flowers; filaments slightly connate at base; pollen medium sized, 3-colpate, heteropolar (one polar area bulging, the other ± flat or slightly concave), triangular in polar view, reticulate. Gynoecium 3-carpellate, rudimentary in ♂ flowers; stigmas 3, filiform, spreading; style short; ovary 3-locular, the placentae axile; ovules solitary in each locule, anatropous, apotropous, ascendent, 2-integumented, with a thick nucellus. Fruit a membranaceous or subchartaceous bladdery capsule, subglobular, obovoid or top shaped, 3-angled and slightly 3-lobed, septifragal [or septicidal]. Seeds subglobular, black, with an inconspicuous aril (arillode, "pseudoaril") leaving a whitish, reniform to semicircular abscission scar ("hilum," "pseudohilum") in the micropylar area; testa thick-crustaceous; endosperm very scanty or wanting(?); embryo curved; cotyledons fleshy, unequal (the shorter, exterior one incurved, the longer, interior transversely biplicate); radicle short. TYPE SPECIES: *C. Halicacabum* L. (Name from Greek, *cardia*, heart, and *sperma*, seed, in allusion to the heart-shaped abscission scar on the seeds of the type species.) — BALLOON-VINE, HEART-SEED, HEART-PEA.

A largely tropical American genus of 12 species; *Cardiospermum grandiflorum* Sw. also occurs in tropical West Africa (introduced?), and two species of pantropical distribution extend into our area. *Cardiospermum Halicacabum* var. *Halicacabum*, $2n = 22$, usually an annual vine with biternate leaves and seeds with a heart-shaped to reniform "hilum," occurs sporadically in waste places, moist thickets, and cultivated grounds in our area and west to Texas and Oklahoma, north to Missouri, Ohio, Illinois, Pennsylvania, and New Jersey. It is considered to be an introduced and naturalized species. The perhaps indigenous var. *microcarpum* (HBK.) Blume, sometimes regarded as a distinct species, *C. microcarpum* HBK., differing in its somewhat smaller leaves and leaflets and smaller fruits more or less truncate at the apex, has been collected in the hammocks, pinelands, and swamps of the Florida Keys and peninsular Florida as far north as Lake County. The closely related *C. Corindum* L. (*C. keyense* Small), a suffruticose vine with usually biternate, rarely subbipinnate leaves, and seeds with a semicircular "hilum," occurs in hammocks on the Florida Keys, where it apparently is indigenous. Some authors include this species in *C. Halicacabum*.

Our knowledge of the genus as a whole in regard to biology, floral anatomy, embryology, and cytology is almost exclusively based on studies on *Cardiospermum Halicacabum*. The tendrils below the summit of the peduncle are regarded as modified lowermost lateral branches of the inflorescence. Since the flowers usually are unisexual, and the occasional bisexual ones are proterandrous (Nair & Joseph), cross-pollination should be the rule if *Cardiospermum* is dioecious, as has been assumed. Recently, however, Hauman characterized the genus as monoecious. Although observations made on herbarium material agree with Hauman's view, at least in regard to *C. Corindum* and *C. grandiflorum*, further field observations are necessary. It is possible that both mono- and dioecism occur within the genus and even within the species. The conditions of pollination and fertilization in monoecious plants should also be investigated. Insect-pollinators have not been specified, but bees probably take part in pollination, since "Balloon vine is reported as the source of considerable honey in Texas" (Pellett). The placentation of the ovaries is axile in the ovule-bearing region, although a tendency toward a parietal condition has been indicated (Nair & Joseph). There is no positive knowledge in regard to the fruit-dispersing agents. Although Radlkofer (1895, p. 295) and Engler (p. 265) assumed winds to be responsible for the transportation of capsules for long distances, Guppy (1906) believed that granivorous birds "probably carry about the seeds of *Cardiospermum halicacabum*."

Fossil leaves (resembling those of *Cardiospermum Halicacabum*, but coriaceous) from two Oligocene localities in Colorado have been referred by MacGinitie (pp. 143, 144) to this genus.

The genus is most closely related to the tropical American *Urvillea* HBK., which extends into Texas with at least two species. Relationships with *Serjania* Schum. and *Paullinia* L. are also unquestionable.

The common balloon-vine, *Cardiospermum Halicacabum* (as well as *C. Corindum* and *C. grandiflorum* in the Tropics) is often cultivated as an ornamental. Roots, stems, and leaves of this species, as well as of *C. Corindum*, find various applications in local medicine in tropical countries. The leaves and young stems of *C. Halicacabum* are eaten in the East Indies.

REFERENCES:

Under family references see DAVID (pp. 693–698), ENGLER (pp. 265, 268, 269), GUÉRIN (pp. 337–340), GUPPY (1906, p. 417), HAUMAN (pp. 284–287), LUBBOCK (pp. 357–359), MACGINITIE (pp. 143, 144), VAN DER PIJL (pp. 620–636), RADLKOFER (1867, pp. 25, 26; 1895, pp. 295, 306–308; 1932, pp. 317–414), and SELLING (pp. 218, 220).

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PELLETT, F. C. American honey plants. 297 pp. *front.* Hamilton, Ill. 1920. [*Cardiospermum*, 28.]

Tribe SAPINDEAE

2. **Sapindus** Linnaeus, Sp. Pl. **1:** 367. 1753; Gen. Pl. ed. 5. 171. 1754.

Evergreen or deciduous trees or shrubs. Leaves even-, rarely odd-pinnate, [very rarely simple](petiolate, exstipulate; leaflets (4) 6–18, entire; rachis winged or wingless. Plants monoecious or dioecious; flowers in ample terminal thyrses with minute deciduous bracts and bractlets, regular, small, unisexual by abortion. Sepals 4 or 5, unequal, the two outer smaller than the inner, connate at base, imbricate, deciduous. Petals 4 or 5, equal, longer than the sepals, unguiculate, with a single bifid scale or 2 scales above the claw on the interior surface, or without scales, imbricate. Nectariferous disc annular, fleshy, lobulate. Stamens 8(–10), inserted within the disc, exserted in the ♂, short and with rudimentary anthers in ♀ flowers. Gynoecium 2–4(usually 3)-carpellate, rudimentary in ♂ flowers; stigma small, 3-lobed; style short, columnar, 2–4 (usually 3)-sulcate; ovary sessile, 2–4(usually 3)-locular and -lobed; ovules solitary in each locule, ascendent, campylotropous, apotropous, 2-integumented, with a thick nucellus. Fruit a schizocarp of 3 mericarps (or more commonly of 1 or 2, with rudiments of the aborted locules); mericarps drupelike, yellow to black, subglobular or obovoid, 1-locular, 1-seeded; the flesh resinous, rich in saponine, crustaceous when dried; endocarp pergamentaceous, silky-hairy inside around the seed insertion. Seed globular or obovoid, exarillate; seed coat bony, smooth, black or dark brown; endosperm wanting; embryo curved; cotyledons fleshy, superposed, the dorsal cotyledon incurved, almost inclosing the transversely conduplicate ventral cotyledon; radicle short, inferior, directed toward the hilum. TYPE SPECIES: *S. Saponaria* L. (Name a contraction of Latin, *sapo*, soap, and *indicus*, Indian, i.e., Indian soap, referring to the saponaceous properties and use of the fruits in the West Indies for washing linen.) — SOAPBERRY.

A primarily tropical genus of about 13 species distributed in the Americas (three species), eastern and southeastern Asia (six), Oceania exclusive of Australia (three), and Hawaii (one). At least two species are extratropical. All three American species (included with a few Asiatic and Oceanic ones in sect. SAPINDUS [§ *Eusapindus* Radlk.]) occur in our area. The primarily tropical American *Sapindus Saponaria*, southern soapberry, a tree with winged leaf rachises (unwinged in f. *inaequalis* (DC.) Radlk.) and unappendaged petals, ranging from northern Argentina to Peru, north to Mexico and the West Indies, is known from hammocks in southern peninsular Florida (Dade, Monroe, and Collier counties) and on the Keys. It is also considered to be indigenous and represented by a distinct form, f. *microcarpus* Radlk., in the Philippines and some southern Pacific islands (including New Guinea), as well as (f. *inaequalis*) on the Mascarene and Hawaiian Islands, but is introduced and naturalized in some parts of Africa. The extratropical *S. marginatus* Willd., Florida soapberry, with narrowly margined or marginless leaf rachises and with appendaged petals, a rare and possibly rather primitive species, occurs on the Coastal Plain from central Florida (Manatee County) to eastern Georgia (Liberty and Chatham counties). It has been recorded from Cuba, but the records are apparently referable to *S. Saponaria* f. *inaequalis*, which resembles *S. marginatus* in the wingless rachises and usually falcate leaflets but lacks appendages on the petals. Since no authentic records indicating an overlap of the ranges of *S. Saponaria* and *S. marginatus* at the present time have been available, the intergradation between the two species "along their boundary in Florida," presumed by LaMotte (1935, p. 35), appears to be questionable. The also extratropical *S. Drummondii* Hook. & Arn. (*S. Saponaria* var. *Drummondii* (Hook. & Arn.) Benson), western soapberry, very closely related to and perhaps only a variant of *S. marginatus*, ranges from western Louisiana and central Arkansas north to southwestern Missouri, west to Kansas, southern Colorado, western and southern New Mexico, and Arizona, and from Texas to northern Mexico. It appears to intergrade with *S. Saponaria* in Baja California, where the ranges of both species overlap (LaMotte, p. 35).

Little is known about the floral biology of the genus. The flowers usually are unisexual, and the plants have been characterized as (polygamo-)dioecious, although Hauman considers *Sapindus Saponaria* to be monoecious. At least some herbarium specimens of *S. marginatus* and *S. Drummondii* show monoecism. Possibly both di- and monoecism may occur within a species.

Fruit dispersal by frugivorous bats has been observed in Trinidad, as well as in Java (Van der Pijl, 1957, p. 632). In addition, "the indications of West Indian beach-drift and the stranding of the seeds in a germinable condition on the shores of Bermuda point unmistakably to the agency of the current . . . the buoyancy [of seeds] arising from the fact that the kernel [embryo] incompletely fills the seed-cavity. When, however, the cavity is entirely occupied, the seed sinks" (Guppy, 1917).

"The genus seems to have first appeared in late Lower Cretaceous time in western America as *Sapindopsis magnifolia* Fontaine of the Fuson of Crook County, Wyoming, and *S. variabilis* Fontaine from the same beds. These forms, as figured, may represent a *Eusapindus*-like ancestor to the genus" (LaMotte, 1935, p. 36). Several more definitely outlined species of *Sapindus* are known in western North America from the Paleocene, Eocene, and Miocene. The Eocene species were, in general, large leaved like the living *S. Saponaria* and *S. Mukorossii* Gaertn. (a native of Japan and southeastern China). *Sapindus oregonianus* Knowlton, known from the Miocene of Nevada, Oregon, and Idaho, seems to have been especially close to *S. Mukorossii*, which, in turn, is considered by LaMotte to be the most primitive living species of sect. SAPINDUS.

The genus is closely related to the African *Deinbollia* Schum. & Thonn., which reportedly differs from *Sapindus* mainly in fruits devoid of saponine.

The flesh of fruits of *Sapindus Saponaria* and other species rich in saponine has been used as a substitute for soap in tropical countries. Bony seeds of several species are strung for necklaces and bracelets.

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See also under family references BERRY (1916, pp. 272–277; 1924, pp. 71–74), DAVID (pp. 698, 699), GUPPY (1917, pp. 156–158), HAUMAN (pp. 330, 332), HOLDEN (pp. 53–57), MACGINITIE (pp. 146, 147), MAURITZON (pp. 168–173), RADLKOFER (1895, p. 315; 1932, pp. 630–668), SARGENT (1922, pp. 711–714), and WEST & ARNOLD (p. 135); under Aceraceae see KURZ & GODFREY (pp. 227, 228).

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Tribe MELICOCCEAE Blume emend. Radlk.

3. **Melicoccus** P. Browne, Civ. Nat. Hist. Jamaica 210. 1756.

Large, usually glabrous, evergreen trees. Leaves alternate, 4 (rarely 6) [or 2]-foliolate, occasionally simple on the lower branches, petioled, exstipulate; leaflets opposite or subopposite, subsessile, membranaceous to subcoriaceous, entire, usually conspicuously inequilateral; rachis and petiole sometimes winged. Flowers manifestly pediceled, in terminal (and sometimes axillary) slender, simple or panicled racemes with minute subulate or abortive caducous bracts, small, greenish white to white, 6–8 mm. in diameter (when expanded), regular, hypogynous, unisexual by abortion, (polygamo-)dioecious (or monoecious?). Sepals 4, nearly distinct, subequal, petaloid, usually deciduous, imbricate. Petals 4, oblong-obovate to obovate, very shortly clawed, nearly twice as long as the sepals, nonappendaged [or with an interior bifid scale above the claw], imbricate. Nectariferous disc extrastaminal, large, flat, glabrous, yellow [or red], with undulate to crenate margins. Stamens 8, as long as or longer than the petals in ♂, short and with nonfunctional anthers in ♀ flowers; filaments filiform, much longer than the anthers in ♂ flowers; anthers extrorse, attached to the filaments above the base on the adaxial side, oblong-ovate in outline, sagittate-cordate at the base, 2-locular at anthesis. Gynoecium 2(3)-carpellate, syncarpous, rudimentary in ♂ flowers; stigma large, peltate, 2(3)-lobed; style short, stoutish; ovary superior, sessile, obovoid or ellipsoid, glabrous, 1-locular to imperfectly 2-locular (when 3-carpellate); ovules 2 (3), ascendent from the base, campylotropous, apotropous. Fruit an ellipsoid to subglobular "berry" 2–4 cm. long, with green to yellowish, leathery pericarp, usually 1-locular and 1-seeded. Seed ellipsoid, 1.5–2 cm. long, exarillate; the outer seed coat fleshy, white, yellowish, or yellowish pink, sour-sweet or sour, the inner seed coat leathery to crustaceous; endosperm wanting; embryo straight; cotyledons fleshy, orbiculate, planoconvex; radicle minute, inferior. TYPE SPECIES: *M. bijugatus* Jacq. (*Melicocca bijuga* L.).[3] (Name derived from Greek, *meli,* honey, and *coccos,* grain, seed, berry, i.e., honey-seed or honey-berry, apparently referring to the usually pleasant, sour-sweet taste of the seed coat.) — SPANISH LIME, GENIP.

A genus of two species of tropical continental America. *Melicoccus bijugatus*, $2n = 32$, native to northern South America (Surinam to Colombia) and perhaps to Central America (north to Nicaragua), has been widely naturalized from cultivation in the West Indies and perhaps elsewhere in tropical America. It has been grown in southern Florida as an ornamental and shade fruit-tree (the fleshy seed coat and roasted seeds are edible) and appears to have become established in subtropical Florida.[4] *Melicoccus lepidopetalus* Radlk., differing from our species in the unijugate leaves and appendaged petals, has been recorded from Bolivia and Paraguay.

Since little is recorded about the biology of the genus, Lunan's observations (1814) on *Melicoccus bijugatus* are of special interest: "This tree sheds its leaves annually, in the spring, when the new leaves and blossoms make their appearance together; and, in rainy weather, the progress of its

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[3] The genus *Melicoccus*, established as monotypic by Browne, was given a combined specifico-generic description and is therefore validly published. Since Browne did not use binary nomenclature, the single species remained unnamed until 1760, when Jacquin (Enum. Syst. Pl. Ins. Carib., p. 19) published *Melicoccus bijugatus.* Although Jacquin did not provide a specific description, the binomial is valid and legitimate, for he gave a complete reference to Browne. In 1762, however, Linnaeus (Sp. Pl. ed. 2. 1: 495) changed both the generic and specific names and introduced *Melicocca bijuga*, the binomial which has been in general use ever since. There was, however, no justification for these changes, and the correct name for the species is *Melicoccus bijugatus* Jacq.

[4] Monroe County: Cudjoe and Little Knock'emdown keys (cf. Dickson, Woodbury, & Alexander, p. 197); Upper Matecumbe Key, *F. C. Craighead*, 13 May 1962 (FLAS). Hendry County?: hammock, 20 mi. se. of La Belle, *T. H. Carlton*, 4 Apr. 1932 (FLAS).

vegetation is so rapid that the new leaves are completely budded and unfolded in the short space of forty-eight hours, the old foliage, yet in a green state, which ornamented the tree only yesterday, is forced off and strewed withering on the ground. When the blossoms open they diffuse their agreeable fragrance to a very considerable distance, and attract towards them, during that time, swarms of bees and humming birds to feed upon their honey. It has been observed that these trees, when young, bear blossoms two or three years without being succeeded by any fruit; and it is also remarkable that the leaves of old trees lose their foliated margin [wings] upon the common middle rib, which is only to be seen in the leaves of the young ones."

The genus is closely related to the tropical continental American *Talisia* Aubl. which extends as far north as the Yucatán Peninsula, Mexico (two species).

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Under family references see RADLKOFER (1932, pp. 820–826), and RECORD & HESS (p. 491).

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POPENOE, W. Manual of tropical and subtropical fruits. xv + 474 pp. New York. 1920. [*Melicoccus*, 332, 333.]

Tribe CUPANIEAE Reichenb. emend. Radlk.

4. **Cupania** Linnaeus, Sp. Pl. 1: 200. 1753; Gen. Pl. ed. 5. 93. 1754.

Evergreen trees or shrubs. Leaves usually even-pinnate, rarely odd-pinnate (in cultivated specimens), petioled, persistent, exstipulate; leaflets (2) 6–14 [20], usually alternate [or subopposite], medium sized, chartaceous, ± dentate to subentire, shortly petioluled. Plants (polygamo-) dioecious; flowers pediceled, in axillary [or terminal] thyrses with usually small bracts and bractlets, small, regular, unisexual by abortion. Sepals 5, distinct, in 2 series, broadly imbricate. Petals 5, whitish [or yellowish], as long as [or shorter than] the sepals, [or rarely wanting], each provided with 2 scales above the claw, imbricate. Disc continuous, annular, crenulate to lobulate, puberulous [tomentose or glabrous]. Stamens 8(–10), inserted within the disc, exserted in ♂, short and sterile in ♀ flowers. Gynoecium 2–4(usually 3)-carpellate, rudimentary in ♂ flowers; stigmas 3 [or stigma 3-lobed], style nearly as long as [or shorter than] the ovary, [sometimes 3-fid at apex]; ovary 2–4(usually 3)-locular, usually pubescent outside [and sometimes also within], ovules solitary in each locule, ascendent from near the base of the axile placenta, campylotropous, apotropous. Fruit a stipitate, turbinate-triangular [laterally 3-lobed, sometimes also 3-winged], (2)3(4)-locular capsule, apiculate with remnants of the style, loculicidally dehiscent. Seed ellipsoidal to subglobular, covered to half its length by a cup-shaped, fleshy aril; seed coat crustaceous [or coriaceous]; embryo thick, curved; cotyledons fleshy, plano-convex; radicle short, inflexed. TYPE SPECIES: *C. americana* L. (The name commemorates Francis Cupani, 1657–1710, a Sicilian monk, physician, and botanist.)

A tropical American genus of nearly 45 species, extending south to Argentina and Peru, north to Mexico and southern Florida. *Cupania glabra* Sw. of the West Indies, Mexico, and Central America (as far south as Costa Rica) occurs in hammocks on the Florida Keys (Big Pine Key). The species was first collected by Blodgett in the 1840's on Key West, but the specimen was identified only in 1901 by Britton. The species was thought to have been exterminated in Florida until it was rediscovered by Small in 1921 on Big Pine Key, where it has since been collected by several botanists.

Two fossil species, *Cupania oregona* Chaney & Sanborn (resembling the living South American *C. vernalis Cambess.*) and *C. Packardii* Chaney & Sanborn (resembling the living South American *C. americana* L.) are known from the Goshen and Chalk Bluff floras (Upper Eocene-Lower Oligocene) of central Oregon. Several species of the presumably very closely related fossil *Cupanites* Schimper are represented by leaves in the Eocene of the southeastern United States and by both leaves and fruits in certain European Tertiary deposits (cf. Berry, 1916, p. 269).

The genus is very closely related to the tropical American *Matayba* Aubl.

REFERENCES:

See also under family references BERRY (1916, pp. 269, 270; 1924, p. 70), RADLKOFER (1895, p. 337; 1934, pp. 1020–1062), and WEST & ARNOLD (p. 134).

BRITTON, N. L. *Cupania* on Pine Key, Florida. Torreya **1**: 132. 1901. [Blodgett's collection, labeled *Paullinia*, was identified by Britton as *Cupania glabra*.]

CHANEY, R. W., & E. I. SANBORN. Contributions to paleontology. The Goshen flora of west central Oregon. Carnegie Inst. Publ. **439**: 1–103. *pls. 1–40.* 1933. [Age of Goshen flora between Upper Eocene and Lower Oligocene; *Cupania*, 82, 83.]

MACGINITIE, H. D. Contributions to paleontology. A Middle Eocene flora from the central Sierra Nevada. Carnegie Inst. Publ. **534**: 1–178. *pls. 1–47.* 1947. [*Cupania*, 144.]

RADLKOFER, L. Ueber *Cupania* und damit verwandten Pflanzen. Sitz-ber. Akad. München II. **9**: 457–678. 1879. [Relationships, 457–494.]

Tribe DODONAEEAE HBK. emend. Radlk.

5. **Dodonaea** Miller, Gard. Dict. Abr. ed. 4. 1754.

Evergreen shrubs [sometimes low and ericoid] or small trees, mostly resinous-viscous. Leaves alternate [rarely subopposite], simple [or pinnate], usually subchartaceous, entire or repand [or ± toothed], with ± numerous parallel lateral veins, usually appearing varnished, viscous, ±

covered with resiniferous glands, petioled to subsessile, exstipulate. Plants (polygamo-) monoecious or dioecious; flowers pediceled, [solitary or] in terminal [or axillary] thyrses [or panicles] with small bracts, small, regular, unisexual by abortion, often (in ours) also bisexual. Sepals 3–7, usually 4 or 5 (more rarely 3), connate at base, valvate or narrowly imbricate, usually deciduous. Petals wanting. Stamens distinct, 6–10[–12] in ♂ and bisexual, sterile or wanting in ♀ flowers; filaments very short; anthers linear-oblong in outline, obtusely quadrangular in cross section, apiculate at apex, much longer than the filaments; pollen medium sized, 3-colpate, prolate-spheroidal, subtriangular in polar view, smooth or minutely reticulate. Nectariferous disc intrastaminal, obsolete (minute) in ♂, stipelike in bisexual and ♀ flowers. Gynoecium 2–4[–6](usually 3)-carpellate, rudimentary in ♂ flowers; stigmas 2–4, usually 3, small; style filiform, sometimes 2–4-fid at apex, at least 3 times as long as the ovary, deciduous; ovary 2–4[–6] (usually 3)-locular, slightly raised on a short, gynophore-like disc, mostly densely covered with resiniferous glands; placentation axile; ovules 2 in each locule, superposed (the upper ascendent, apotropous, the lower pendulous, epitropous), sessile on the outgrowths of the placenta, campylotropous, 2-integumented, with a thick nucellus. Fruit a chartaceous [membranaceous or coriaceous], septifragal [or septicidal] capsule, usually 3–, rarely 2– or 4[–6]-locular, the locules boat shaped, manifestly [or narrowly] winged, 2(or by abortion 1)-seeded. Seeds lenticular or obovoid [or subglobular], with a callus-like outgrowth of the carpel wall around the abscission scar; seed coat crustaceous [or coriaceous]; endosperm wanting; embryo coiled; cotyledons linear; radicle elongated. TYPE SPECIES: *Ptelea viscosa* L. = *D. viscosa* (L.) Jacq. (Named in honor of Rembert Dodoens, or Dodonaeus, 1518–1585, Dutch physician and herbalist.) — HOPBUSH, VARNISH-TREE.

A primarily Australian genus of nearly 60 species, with one in Madagascar, three in Hawaii, and one (*Dodonaea viscosa*) pantropical. *Dodonaea viscosa* (including *D. jamaicensis* DC., *D. microcarya* Small), $2n = 28, 32$, extremely variable in shape and size of leaves, size of capsules, and size and shape of seeds, occurs in our area primarily in coastal habitats and hammocks from the Florida Keys northward to Volusia and Hernando counties, Florida. The taxonomy of this perplexing complex apparently has been based almost exclusively on the study of herbarium material, and the numerous varieties and forms have been distinguished primarily on the basis of vegetative characteristics. The lines between taxa are weak, and there seem to be many transitional specimens. The limits of variability of leaves (size and shape) on individual plants have not been studied, but may be rather broad, since in some instances two sheets of the same collection of *D. viscosa* have been cited as different varieties. As delimited by Sherff the species comprises three pantropical varieties (including 11 forms) and var. *Stokesiana* F. Br. restricted to Fiji, the New Hebrides, Society, and Tubuai (Austral) islands of the southern Pacific. The lack of field observations and ecological and cytological data for this complex makes impossible any conclusion regarding the nature and delimitation of infraspecific categories of *D. viscosa.*

On the basis of Sherff's treatment, all three pantropical varieties, sometimes regarded as distinct species, are represented in Florida. *Dodonaea viscosa* var. *viscosa* f. *viscosa* (var. *vulgaris* Benth. f. *repanda* (Schum. & Thonn.) Radlk.), a shrub with oblong or obovate leaves 7–15 cm. long by 1.5–4 cm. broad and subcircular to oblate capsules 1.5–2.5 cm. broad, seems to be restricted to the mainland in our area, while var. *linearis* (Harv. & Sond.) Sherff f. *angustifolia* (Benth.) Sherff (var. *angustifolia* Benth.; *D. jamaicensis* DC.), a shrub or small tree (?), with linear-oblong to narrowly oblanceolate leaves 6–9 cm. long by 0.5–1 cm. broad and capsules 1.2–1.6 cm. broad, has been collected both on the mainland and the Keys. The var. *arborescens* (Cunn.) Sherff (var. *spathulata* Benth.), a shrub or small tree with spatulate leaves, is represented on the mainland by the rare f. *arborescens*, with narrowly spatulate, sinuate-dentate leaves, and by similar but more frequent f. *spatulata* (Smith) Sherff in which the leaves are entire or slightly sinuate; on the Keys (very rarely on the mainland?) occurs the very distinctive f. *elaeagnoides* (Rudolphi ex Ledeb. & Adlerst.) Brizicky[5] (*D. microcarya* Small), a small tree with subcoriaceous, broadly spatulate to obovate-cuneate leaves 3.5–5 cm. long by 1.6–3 cm. broad and small, oblate capsules only 0.8–1[–1.6] cm. broad. Forma *elaeagnoides* (f. *Ehrenbergii*) is known also from the Bahamas, Cuba, Hispaniola, and the Lesser Antilles. Sherff comments (1947, p. 304), "It cannot be emphasized too strongly that in certain localities the f. *Ehrenbergii* may easily appear widely and specifically different from f. *arborescens.* Future authors of floristic works restricted to such localities will perhaps, therefore, be tempted to treat it so." In view of the broad tropical distribution of the infraspecific taxa of *D. viscosa,* these apparent geographical restrictions within our area are of interest.

Both dioecism and monoecism have been recorded in *Dodonaea viscosa;* apparently the former is more frequent. Delpino concluded that pollination is by wind. Parthenocarpy has been reported by Joshi. Both Radlkofer and Engler considered wind to be mainly responsible for fruit dispersal in *D. viscosa,* but Guppy (1917, p. 207) concluded "that if we placed the agencies of dispersal in their order of effectiveness they would be, first granivorous birds, then currents, and lastly man."

About 15 fossil species of *Dodonaea,* represented by leaves and/or fruits have been described from the Tertiary deposits (Oligocene and Miocene) of various parts of western Europe. A few species, based on leaves or fruits, are known from the Lower Eocene (e.g., *D. Wilcoxiana* Berry, *D. Knowltonii* Berry) and the Middle and Upper Eocene (e.g., *D.*

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[5] **Dodonaea viscosa** (L.) Jacq. var. **arborescens** (Cunn.) Sherff forma **eleagnoides** (Rudolphi ex Ledeb. & Adlerst.) Brizicky, comb. nov. Basionym: *D. viscosa* (L.) Jacq. var. *spathulata* Benth. f. *elaeagnoides* (Rudolphi) Radlk. Pflanzenreich IV. **165**(Heft 98g): 1371. 1934. *Dodonaea viscosa* var. *arborescens* (Cunn.) Sherff f. *Ehrenbergii* (Schlechtend.) Sherff, Am. Jour. Bot. **32:** 214. 1945; *D. elaeagnoides* Rudolphi ex Ledeb. & Adlerst. Diss. Bot. Sist. Pl. Doming. Decad. 18. 1805; D. *Ehrenbergii* Schlechtend. Linnaea **18:** 36. 1844.

viscosoides Berry) of the southeastern United States (Mississippi, Tennessee, Louisiana), the Oligocene of Colorado (*D. umbrina* MacGinitie), the Miocene of southern California (*D. californica* Axelrod), the Pliocene of Bolivia, and the late Tertiary of Brazil. Axelrod states that material of *D. californica* "cannot be separated from the living *Dodonaea viscosa* . . . . In fact, the affinity of the Miocene to the modern species is so much closer that it seems desirable to recognize a new species."

A modern revision of the genus, eventually of *Dodonaea viscosa*, based on population studies accompanied by cytological investigations, is very desirable.

The genus is most closely related to the Australian *Distichostemon* F. Muell.

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See also under family references BERRY (1916, pp. 270–272; 1924, pp. 70, 71), ENGLER (pp. 265, 285–287), GUPPY (1906, pp. 338–341; 1917, pp. 206, 207), LUBBOCK (pp. 365, 366), MACGINITIE (p. 144), MAURITZON (pp. 168–173), RADLKOFER (1895, pp. 356, 357; 1933, pp. 1350–1404), SELLING (pp. 224–226), and WEST & ARNOLD (p. 134).

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SMALL, J. K. A new varnish-leaf tree from the Florida Keys. Torreya **25:** 38, 39. 1925. [*D. microcarya.*]

SUTARIA, R. N. Meiosis in *Dodonaea viscosa* L. Proc. Indian Sci. Congr. Assoc. **17:** 297. 1930.*

Tribe DORATOXYLEAE Radlk.

6. **Hypelate** P. Browne, Civ. Nat. Hist. Jamaica 208. 1756.

Evergreen trees or shrubs. Leaves 3-foliolate, petioled, exstipulate; leaflets relatively small, 3.5–6 cm. long by 1.3–2.5 cm. broad, obovate-cuneate or oblanceolate, sessile, entire, thin-coriaceous, with close, parallel, lateral veins. Plants monoecious; flowers slender pediceled, in axillary or subterminal, loosely branched, few-flowered, long-peduncled thyrses (as long as or longer than the leaves) with small caducous bracts and bractlets, small, regular, unisexual by abortion. Sepals (4) 5, reddish, unequal, the two exterior smaller than the interior, imbricate, deciduous. Petals (4) 5, white, as long as the sepals, unappendaged, flabellate veined, imbricate. Disc annular, fleshy, shallowly 5-lobed, (7)8-sulcate, glabrous. Stamens (7) 8, inserted on the lobes of the disc, exserted in ♂, short and with sterile anthers in ♀ flowers. Gynoecium 3-carpellate, rudimentary in ♂ flowers; stigma obtuse, 3-lobed; style short, curved near apex; ovary 3-locular; placentae axile; ovules 2 in each locule, superposed (the upper ascendent and apotropous, the lower pendulous, epitropous), campylotropous. Fruit a small (ca. 8–9 mm.) drupe, black, subglobular, slightly 3-sulcate, crowned with remnants of the persistent style; flesh thin, sweet, containing saponine; stone thick-crustaceous, 1-locular by abortion, 1-seeded. Seed ellipsoidal or obovoid, exarillate; seed coat thin, leathery, rugulose, reddish brown; endosperm wanting; embryo curved; cotyledons thin, curved, the exterior nearly infolding the circinate interior; radicle long, incumbent, directed toward the fruit apex. TYPE SPECIES: *H. trifoliata* Sw. (The ancient Greek name for *Ruscus* [Liliaceae], butcher's broom, applied by Browne to this genus.) — WHITE IRONWOOD.

A monotypic genus of the West Indies and the hammocks or rarely pinelands (Big Pine Key) of southernmost Florida (Florida Keys). This large shrub or small tree (occasionally up to 12 m. tall and 45 cm. in diameter) is one of the rarest tropical plants indigenous to our area (cf. *Cupania*).

The staminate and carpellate flowers occur in separate inflorescences on the same plant. The occurrence of occasional bisexual flowers seems to be possible. Nothing is known in regard to pollination.

The wood is very heavy, hard, very durable in contact with the soil, and has been valued in Florida for posts; it is also used elsewhere in shipbuilding and for handles of tools.

The genus is closely related to the monotypic Cuban *Euchorium* Ekm. & Radlk. and to *Exothea* Macfad.

REFERENCES:

See also under family references RADLKOFER (1895, p. 358; 1933, pp. 1407–1410), and SARGENT (1922, pp. 716, 717).

SARGENT, C. S. *Hypelate.* Silva N. Am. **2**: 77, 78. *pls. 80, 81.* 1891.

7. **Exothea** Macfadyen, Fl. Jamaica **1**: 232. 1837.

Evergreen trees. Leaves even-pinnate, 2–6[–8] (most often 4)-foliolate, very rarely 3- or 1-foliolate, petiolate, exstipulate; leaflets opposite usually thin, entire, obscurely veined, lustrous on the upper surface, subsessile or shortly petiolulate. Plants (polygamo-)dioecious; flowers shortly pediceled, in axillary, subterminal, corymb-like thyrses with minute, deciduous bractlets, small (ca. 1 cm. in diameter), regular, unisexual by abortion, rarely also bisexual. Sepals 5, connate at base, tomentulose, reflexed after blooming, persistent, imbricate. Petals 5, whitish, short-unguiculate, unappendaged, 1-nerved, about as long as the sepals, imbricate. Nectariferous disc fleshy, patelliform, lobulate, puberulous, orange to red. Stamens 7–10, usually 8, inserted on the disc in small depressions near its margin, as long as or somewhat longer than the petals in ♂ and bisexual, short and sterile in ♀ flowers. Pollen small, 3-colpate, spheroidal, spinulose. Gynoecium 2-carpellate, rudimentary in ♂ flowers; stigma large, obtuse, subbilobed or indistinctly 3–4-lobed; style short, stoutish; ovary sessile, pubescent, 2-locular; ovules 2 in each locule, collateral, suspended from the summit of the axile placentae, anatropous, epitropous. Fruit a berry, dark purple to black, juicy (crustaceous and brownish when dried), crowned with remnants of the style, surrounded at the base by reflexed sepals, usually nearly globular, 1.2–1.6 cm. in diameter, 1-locular and 1-

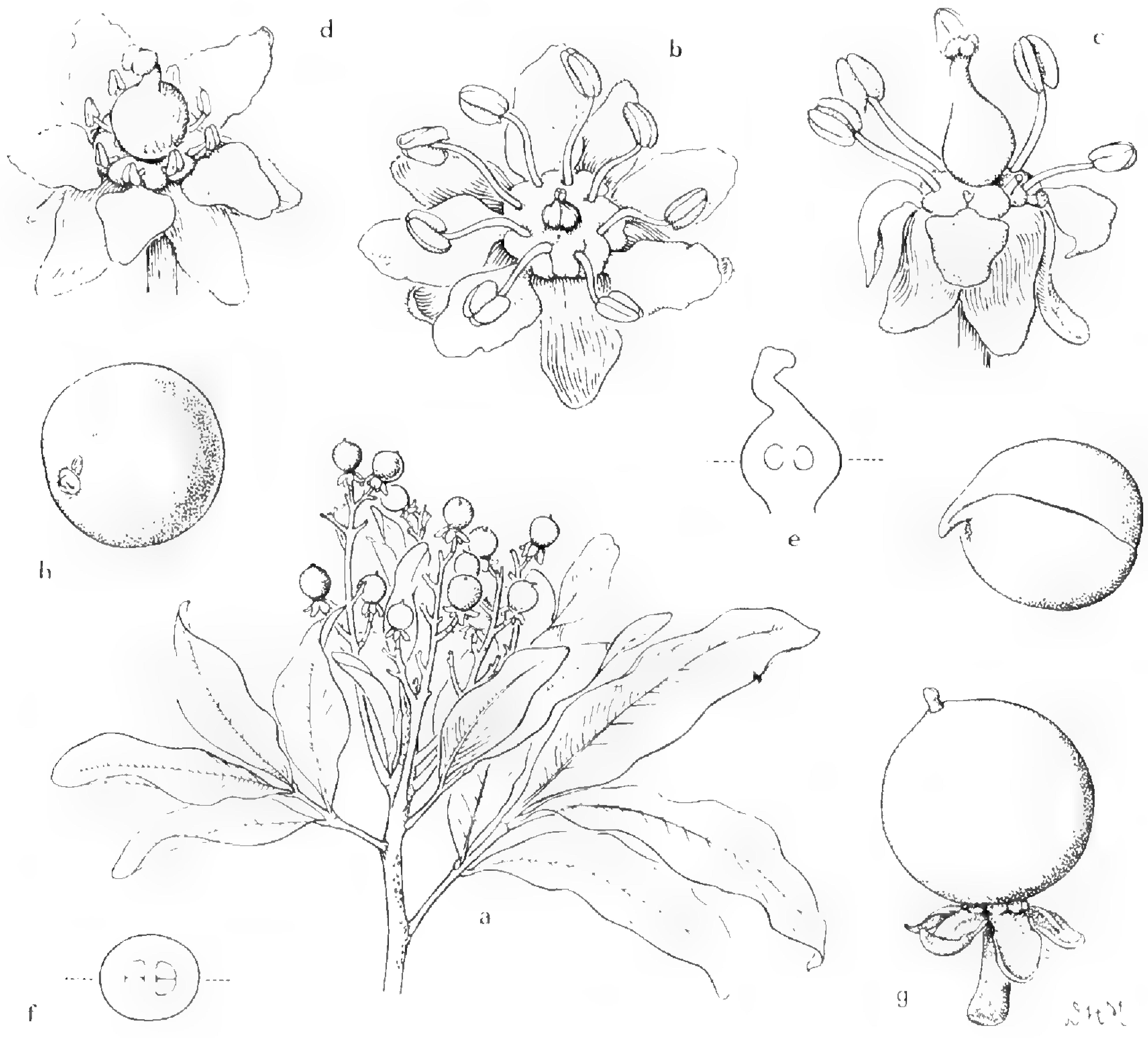

FIG. 1. **Exothea.** *E. paniculata*: a, twig with immature fruits, × ½; b, staminate flower, showing disc and pistillodium, × 4; c, bisexual flower, two stamens removed, × 4; d, carpellate flower, showing staminodia, × 4; e, gynoecium in vertical section in plane marked by broken line in "f," × 6; f, gynoecium in horizontal section in plane marked by broken line in "e," showing the four ovules, × 6; g, fruit, × 2; h, seed, × 2; i, embryo, lateral view, × 2; e, f, diagrammatic.

seeded by abortion, rarely transversely ellipsoidal, 2-lobed, 2-locular and 2-seeded. Seed globular, exarillate; seed coat thin, crustaceous, reddish brown, lustrous; endosperm wanting; embryo curved; cotyledons fleshy, plano-convex, puberulous; radicle superior, very short, incumbent, turned toward the small hilum and inclosed in a lateral cavity of the seed coat. TYPE SPECIES: *E. oblongifolia* Macfad. = *E. paniculata* (Juss.) Radlk. (Name derived from Greek, *exotheo*, to remove, in allusion to the separation of this genus from Amyrideae, with which group it was thought to be related.) — INKWOOD, BUTTERBOUGH.

A tropical American genus of three species, distributed in the West Indies, southern Florida, Mexico, and Central America, south to Costa Rica. *Exothea paniculata* occurs in hammocks and on calcareous soils and shell mounds (kitchen middens) in southern peninsular Florida (northward on the east coast to Volusia County) and on the Florida Keys, southward beyond our limits in the West Indies and Central America. Apparently birds are responsible for fruit dispersal. The wood is very hard and heavy, resistant to the attacks of teredo, therefore valuable for piles; it is also used for cabinet-work, boat-building, and small articles.

The genus is closely related to *Hypelate* and *Euchorium*.

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See also under family references RADLKOFER (1895, p. 358; 1933, pp. 1411–1415), SARGENT (1922, pp. 714–716), and WEST & ARNOLD (p. 133).

SARGENT, C. S. *Exothea*. Silva N. Am. 2: 73–76. *pls. 78, 79.* 1891.

ACERACEAE A. L. de Jussieu, Gen. Pl. 250. 1789, "Acera," nom. cons.
(MAPLE FAMILY)

Trees or shrubs distinguishable from the closely related Sapindaceae by the opposite, largely simple leaves; regular flowers; often intrastaminal nectariferous disc; regularly 2-carpellate gynoecium; and schizocarpous fruit (a "double samara") splitting into 2 winged mericarps. TYPE GENUS: *Acer* L.

A family of two genera, chiefly of the Temperate Zone of the Northern Hemisphere. In contrast to the polymorphic and widely distributed *Acer*, *Dipteronia* Oliv. (differing from *Acer* in naked buds, pinnately multifoliolate leaves, ample thyrses, and mericarps winged all around) is known only from central and western China (two species), although, in the Tertiary it was represented in western North America by *D. insignis* (Lesq.) R. W. Br., similar to the extant *D. sinensis* Oliv.

A close relationship of Aceraceae to Sapindaceae has generally been assumed, an assumption fully supported by evidence from external and internal morphology, palynology, and biochemistry. The relationship to Hippocastanaceae also is unquestionable, but that to Staphyleaceae, presumed by some taxonomists (cf. Takhtajan), has not been demonstrated satisfactorily.

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1. **Acer** Linnaeus, Sp. Pl. 2: 1054. 1753; Gen. Pl. ed. 5. 474. 1754.

Trees or shrubs. Leaves opposite, simple and usually palmately 3–9 [–11]-nerved and -lobed, or rarely pinnately compound, 3–7-foliolate [or palmately 3–5-foliolate], membranaceous or subcoriaceous [or coriaceous], deciduous [rarely persistent]; nodes 3[4, 5]-lacunar. Inflorescences usually terminal raceme- or corymb-like thyrses, racemes, corymbs, or umbel-like fascicles on short, few-leaved or leafless branchlets developing from the apical and/or lateral buds, before, with, or after leaves. Flowers small or minute, regular, usually hypogynous, ♂ sometimes perigynous, greenish yellow or yellow, rarely red [or white], unisexual by abortion, sometimes also bisexual. Sepals 5(4), ± distinct, or more rarely connate, imbricate. Petals 5 (4), distinct, not rarely sepal-like, imbricate, rarely wanting. Nectariferous disc thick, annular, often lobed, sometimes deeply 5-parted, extra- or intrastaminal, rarely wanting. Stamens 4–10, usually 7 or 8, distinct, hypogynous or perigynous (at least in ♂ flowers) or inserted in the middle of the disc, commonly exserted in ♂, short and generally abortive or rarely wanting in ♀ flowers; filaments filiform; anthers oblong or linear in outline, nearly basifixed, 2-locular at anthesis, introrse, longitudinally dehiscent; pollen medium sized, 3-colpate, prolate, the surface reticulate to striate [or exceptionally spinulose]. Gynoecium syncarpous, usually 2-carpellate (sometimes 3- or 4-, rarely to 8-carpellate), rudimentary or wanting in ♂ flowers; stigmas 2, spreading, often recurved, short to elongate and narrow; style single, elongate to very short; ovary superior, usually 2-locular, much compressed perpendicular to the partition; ovules 2 in each locule, collateral or superposed, campylotropous to anatropous, 2-integumented, with a thick nucellus, nearly sessile, the funicle very short and broad. Fruit a winged schizocarp ("double samara"), composed of 2 mericarps (samaras) separating after maturity from the persistent axis (carpophore), the nutlike, usually 1-seeded, body ("nutlet") of each mericarp produced on the back into a chartaceous or coriaceous, reticulated, ± obovate (sometimes ± falcate) wing thickened on the lower margin. Seed without endosperm; testa membranaceous; embryo conduplicate, sometimes coiled [rarely straight]; cotyledons foliaceous or fleshy, variously irregularly plicate or rarely flat, incumbent or accumbent on the elongated descending radicle turned toward the hilum. Germination usually epigeous (hypogeous in *A. saccharinum*). (Including *Negundo* Boehm. in Ludw., *Rulac* Adans., *Saccharodendron* (Raf.) Nieuwl., *Crula* Nieuwl., *Argentacer* Small, and *Rufacer* Small). LECTOTYPE SPECIES: *A. Pseudo-Platanus* L.; see N. L. Britton, N. Am. Trees 638. 1908. (The classical Latin name of the maple; etymology obscure.) — MAPLE.

A genus of nearly 150 species, primarily of the North Temperate Zone, a few extending into the subarctic in Europe (e.g., *Acer platanoides* L., up to 63° N. Lat. in Sweden) and North America (e.g., *A. glabrum* Torr., up to 59° N. Lat. in Alaska), as well as into the Tropics in Central America (*A. Skutchii* and *A. Negundo* in Guatemala) and in Asia (*A. niveum* Blume in the mountains of Java, Sumatra, Celebes, and Timor). The genus is centered in eastern Asia where about two-thirds of the species and several endemic sections occur. The species in general are components of various associations and forest types of deciduous and mixed forests of moderately warm and humid climates. Only *A. monspessulanum* L. and its allies seem to have become adapted to the arid conditions of the Mediterranean region.

The classification of *Acer* followed here is basically that of Pax (1902), emended by Rehder (1905, 1940). The genus is subdivided into 14 sections, five of which occur in our area. The monotypic and endemic sect. GLABRA Pax (presumably related to the eastern Asiatic sect. ARGUTA Rehd.) is represented by *A. glabrum* Torr., and the otherwise eastern Asiatic sect. PALMATA Pax by *A. circinatum* Pursh in Pacific North America. The sections are based on the characteristics most adequately known at present: type of inflorescence; floral structures; gross morphology of fruits, especially of the nutlets (seed-bearing portions); number and arrangement of the scales of winter buds; and external (and partially internal) features of leaves.

In the early Tertiary, the genus was widely distributed throughout the boreal zone, and the ranges of some sections were much more extensive than at present. Thus, in the Oligocene, and perhaps even the Eocene, species of sect. RUBRA, which is now restricted to eastern North America and Honshu, Japan, occurred in Eurasia and North America (as far north as Greenland). In the Miocene this section was still represented in Pacific North America (e.g., *Acer Chaneyi* Knowl., from Oregon), and in the Pliocene and even the Quaternary in northern Italy. Members of the now exclusively American sect. SACCHARINA Pax have been described from the Miocene of Hungary (e.g., *A. Jurenakii* Stur.) Fossil species of sect. NEGUNDO have been recorded from the Oligocene (Colorado) and the

Miocene (Oregon) of North America, and from the Miocene of Europe (Bohemia) and eastern Asia (Shantung Prov., China).

KEY TO THE SECTIONS OF ACER IN THE SOUTHEASTERN UNITED STATES

A. Leaves simple, palmately 3–5-lobed or -cleft; plants usually monoecious; flowers 5-merous, entomophilous; stamens usually 7 or 8, rarely 5 or 6.
  B. Flowers in thyrses or racemes; petals and disc present; leaves 3 (or slightly 5)-lobed (our spp.); winter buds with 2 outer scales.
    C. Inflorescences slender, upright, subcylindrical thyrses; petals linear or linear-spatulate; disc extrastaminal; nutlets of the samaras convex, strongly ribbed; bark of trunk and branches brown or darker, not striped; leaves coarsely serrate. . . . . Sect. ACER.
    C. Inflorescences slender, pendulous racemes; petals obovate; disc intrastaminal; nutlets of the samaras somewhat flattened, ribless; bark of young trunk and branches green, with longitudinal pale or dark stripes; leaves finely doubly-serrate. . . . . Sect. MACRANTHA.
  B. Flowers in corymbs or fascicles; petals and/or disc present or absent; winter buds with several to many imbricate scales; leaves 3–5-lobed or -cleft.
    D. Flowers on long, filiform, pendulous pedicels, in ± many-flowered, umbel-like corymbs produced from the terminal buds of the leading shoot and short lateral branchlets, appearing with or a little before the leaves; plants monoecious; petals wanting; disc extrastaminal; leaf lobes entire or sparingly coarsely sinuate-dentate or lobulate, the the sinuses between lobes rounded. . . . . Sect. SACCHARINA.
    D. Flowers subsessile or pediceled (the pedicels not pendulous), in 3–7-flowered umbel- or headlike clusters produced from aggregated lateral buds, appearing long before the leaves; plants monoecious or dioecious; petals and an intrastaminal disc present, or both wanting; leaf lobes serrate or coarsely dentate, the sinuses between lobes usually acute; if rounded, the middle lobe considerably narrowed toward its base. . . . . Sect. RUBRA.
A. Leaves pinnately compound, 3–7(–11)-foliolate; plants dioecious; flowers 4- or 5-merous, anemophilous, the staminate fascicled and pendulous on long, filiform pedicels, the pistillate in slender, drooping racemes; petals and disc wanting (our sp.); stamens 4–6; winter buds with 2 outer scales. . . . . Sect. NEGUNDO.

The Eurasian-North American sect. ACER (§ *Spicata* Pax, §§ *Gemmata*, *Microcarpa*, and *Trilobata* Pojark.), comprising about 30 species and centered in eastern Asia, is represented in our area by *Acer spicatum* Lam., mountain maple, $2n = 26$, which occurs from Newfoundland and southeastern Labrador to Hudson Bay, Manitoba, and Saskatchewan, and southward in cool, damp, rocky woods at higher elevations in the Appalachians to western North Carolina, eastern Tennessee, and northern Georgia. This species is closely related to the Japanese-Manchurian *A. ukurunduense* Trautv. & Mey. The Pacific North American *A. macrophyllum* Pursh, $2n = 26$, usually placed here, perhaps represents a section of its own. The European *A. Pseudo-Platanus* L., sycamore-maple, $2n =$

52, much planted as an ornamental in the Northeastern States, has become established there locally, and the eastern Asiatic *A. Ginnala* Maxim., $2n$ = 26, is locally established from Maine to Connecticut and western New York. Section Acer, as delimited here, seems to be somewhat heterogeneous.

The almost exclusively eastern Asiatic sect. Macrantha Pax, including about 20 species, is represented in North America only by *Acer pensylvanicum* L., striped maple, $2n$ = 26, a primarily northeastern species extending into our area along the Appalachians, usually in cool, damp soil at elevations above 3000 feet, to Tennessee, North Carolina, and northern Georgia. It seems to be closely related to the Manchurian-Korean *A. tegmentosum* Maxim.

The entirely North American sect. Saccharina Pax (*Saccharodendron* Nieuwl.) consists of two to six species (depending upon the taxonomy adopted). The species concept followed here is that based on population studies by Desmarais (1952), who regarded *Acer saccharum* Marsh. emend. Desm. as a complex species comprised of six subspecies (five formerly regarded as distinct species), four of which occur in our area. The subspecies have been distinguished mainly on the basis of the general leaf outline, the types of which appear to have definite geographical patterns and to show some correlation with the color and the degree (amount) and type of the pubescence of the lower leaf-surface. All these characters intergrade in the areas where the ranges of the subspecies overlap.

The northeastern American *Acer saccharum* subsp. *saccharum* (*A. saccharodendron* K. Koch; *A. nigrum* var. *glaucum* (Schmidt) Fosb.; *Saccharodendron barbatum* Nieuwl., not *A. barbatum* Michx.), sugar maple, $2n$ = 26, extends southward into our area, being abundant in eastern Tennessee and western North Carolina, but sparse in central North Carolina, northeastern Alabama, and northeastern Georgia. "It attains its greatest abundance in the northern part of its range, forming in some places almost pure stands. Farther south along the Appalachians, it is still an important element of the flora, but grows with many other species of trees. From the Appalachians west its abundance gradually decreases, until it is replaced by subsp. *nigrum*" (Desmarais). Subspecies *nigrum* (Michx. f.) Desm. (*A. nigrum* Michx. f.; *S. nigrum* (Michx. f.) Small), black maple, $2n$ = 26, ranges from southern Quebec to southern Minnesota southward, reaching its southern limit in Arkansas, Tennessee, and western North Carolina. Its occurrence in Georgia and Alabama (cf. Fernald, Gray's Man. Bot. ed. 8. 987. 1950) should be verified. Records from Louisiana are possibly based on planted specimens. "The black maple, covering a wide range, is really abundant only in Illinois and Iowa, where it forms pure stands in the valleys along the rivers. It is a very variable group, and seems to be gradually eliminated by subsp. *saccharum* where the two grow together" (Desmarais). Intermediates between subsp. *saccharum* and subsp. *nigrum* have been grouped by Desmarais into a "*saccharum-nigrum*" cline. Subspecies *floridanum* (Chapm.) Desm. (*A. barbatum* Michx. fide Fernald; *A. floridanum* (Chapm.) Pax; *A. nigrum* var. *floridanum* (Chapm.) Fosb.; *S. floridanum* (Chapm.) Nieuwl.), Florida maple, occurs on the Coastal Plain and in the Piedmont, from southeastern Virginia south to central Florida (Hillsborough County), west to Louisiana, north to Arkansas and Tennessee, and beyond our limits in the Ozark Plateau of Missouri and along the Mississippi Valley in southern Illinois and western Kentucky. Subspecies *leucoderme* (Small) Desm. (*A. leucoderme* Small; *A. nigrum* var. *leucoderme* (Small) Fosb.; *S. leucoderme* (Small) Nieuwl.), chalk-maple, is a tree mostly of the deep valleys of the southern Appalachians and Piedmont, as well as at the inner edge of the Coastal Plain, from western North Carolina south to northernmost Florida (Gadsden and Liberty counties), west to Louisiana, north to Arkansas and Tennessee. Generally rare and local, it is apparently most abundant in Georgia and Alabama. This subspecies presents a homogeneous population intermediate between subspp. *nigrum* and *floridanum*, with which it is often confused. Subspecies *Schneckii* (Rehd.) Desm. (*A. saccharum* var. *Schneckii* Rehd.), "intermediate between *saccharum, floridanum*, and *grandidentatum* . . . is found along a zone where the ranges of *saccharum* and *floridanum* meet" (Desmarais). Although apparently unrecorded from our area, its occurrence in at least the northwestern part seems to be possible. The range of subsp. *grandidentatum* (Torr. & Gray) Desm. (*A. grandidentatum* Torr. & Gray, including *A. sinuosum* Rehd.), bigtooth maple, lies to the west and northwest of our area, and there are no authentic records of its occurrence east of Comanche County, Oklahoma. Since the subspecies of *A. saccharum* distinguished by Desmarais, "although treated on the same level in the nomenclatural system, are not of equal rank and do not have the same relationships" (Desmarais), further taxonomic changes are to be expected.

The poorly known *Acer Skutchii* Rehd. occurs in the mountains of Tamaulipas, Mexico, and Zacapa and Quiché, Guatemala. Combining the leaf outline of subsp. *nigrum* (but the leaves glaucous, glaucescent, or green on the lower surface), the pubescence of subsp. *Schneckii*, and fruits larger and smoother than those of *A. saccharum*, it should be studied in the light of variation in *A. saccharum*. It is considered to be an Arcto-Tertiary element in the Mexican [and Guatemalan] montane biota (Martin & Harrell).

Section SACCHARINA is supposed to be closely related to sect. GONIOCARPA Pojark. (§ *Campestria* sensu Pax, exclusive of *Acer campestre* L.[6]) of the Mediterranean region.

Section RUBRA Pax (*Rufacer* Small, *Argentacer* Small) includes two eastern North American and one endemic Japanese species, *Acer pycnanthum* K. Koch, closely related to *A. rubrum*. The red maple, *A. rubrum* L., (*Rufacer rubrum* (L.) Small), $2n = 78, 104$ (flowers in umbel-like clusters, usually red, rarely yellow, pediceled; sepals distinct; petals and disc present; wings of samaras slightly divergent), ranges from Newfoundland, the Gaspé Peninsula, southern Quebec, and Ontario, southward, in a wide

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[6] Following Pojarkova (1936) and Fernald (Gray's Man. Bot. ed. 8. 986. 1950), the writer regards *Acer campestre* L. as a member of sect. PLATANOIDEA Pax. Consequently, the sectional name *Campestria* Pax is replaced by GONIOCARPA Pojarkova.

variety of habitats, throughout our area, except the extreme southeastern part of peninsular Florida (Dade County) and the Florida Keys, westward to Texas and Oklahoma. Two doubtful varieties, var. *Drummondii* (Hook. & Arn.) Sarg. (*Rufacer Drummondii* (Hook. & Arn.) Small) and var. *tridens* A. Wood (var. *trilobum* K. Koch; *Rufacer carolinianum* (Walt.) Small), occur on the Coastal Plain south to Florida. The taxonomy of this polymorphic species remains obscure; extensive population studies are desirable. The existence of chromosomal races within *A. rubrum* has been suggested (Taylor, Duffield). The silver maple, *Acer saccharinum* L. (*A. dasycarpum* Ehrh.; *Argentacer saccharinum* (L.) Small), $2n = 52$ (flowers in headlike clusters, usually yellow, rarely red, subsessile; sepals connate; petals and disc wanting; wings of samaras much divergent), a characteristic bottomland species similar in its silvical features and general range to the red maple, occurs in the Piedmont and at moderate elevations in the mountains, as well as on the Coastal Plain, especially in river valleys, locally throughout our area south to northern Florida and west to Louisiana. "The likelihood of the formation of distinct races within relatively small distances (about 100 miles) in the climatically uniform Middle West" is presumed (Wright, 1949, pp. 301, 302). The position of sect. RUBRA within the genus seems to be rather isolated. Anatomically it seems to be close to sect. GLABRA Pax (cf. Warsow).

The eastern Asiatic-North American sect. NEGUNDO (Boehm. in Ludw.) Maxim.[7] emend. Rehd., 1940 (*Negundo* Boehm., *Acer* subg. *Negundo* (Boehm.) Momotani), includes three species, one American. *Acer Negundo* L. (*Negundo aceroides* Moench, *N. Negundo* (L.) Karst.), box-elder, ash-leaved maple, water maple, $2n = 26$, ranging throughout most of the United States, north to southern Canada and south to Mexico and Guatemala, occurs scattered in the valleys of the lower mountains, along sandy banks and bottoms in the Piedmont, and along the larger rivers on the Coastal Plain, throughout our area south to central Florida (Hernando County). This polymorphic species includes several apparently intergrading varieties (sometimes regarded as distinct species) which differ mainly in the shape, thickness, and dentation of the leaflets, and the hairiness of leaflets and/or branchlets and fruits. Its closest allies are *A. cissifolium* (Sieb. & Zucc.) K. Koch, $2n = 26$, from Japan, and *A. Henryi* Pax, $2n = 26$, from central China, both with petaliferous flowers with an intrastaminal disc. The position of the section within the genus seems to be rather isolated, and its relationships are obscure.

Although the flowers of *Acer* usually are unisexual by abortion, occasional bisexual (morphologically, at least) flowers and rarely even individuals

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[7] In his *Bibliography of Cultivated Trees and Shrubs* (1949, p. 428a), Rehder cited Pax (Bot. Jahrb. **6**: 327. 1885) as the author of the sectional name *Negundo*. In a footnote he pointed out that it could not be attributed to K. Koch, since Koch used the informal "term 'Gruppe' for his four divisions which are published with descriptions but without names; in Gruppe 4 the name '*Negundo* Mnch. meth. 334' is obviously cited as a synonym and is not intended as the name of the group." Although correct in regard to Koch, Rehder apparently overlooked the earlier publication of the name by Maximowicz (Bull. Acad. Sci. St. Pétersb. III. **26**: 450. 1880).

with prevailingly bisexual flowers occur. In general, however, polygamy seems to be relatively rare within the genus. In most species the plants are monoecious (dioecism being of extremely rare occurrence, e.g., in *A. platanoides*, *A. Pseudo-Platanus*) and entomophilous, bees being recorded as most frequent pollinators. *Acer saccharinum* and *A. rubrum* are either monoecious or dioecious and pollinated by insects and wind; and *A. Negundo* is dioecious and wind pollinated. Cross-pollination seems to be the rule, bisexual flowers being proterogynous (e.g., in *A. Negundo* × *platanoides*; see Beskaravainaya) and close-pollination in monoecious plants being obstructed by differences in position of staminate and carpellate flowers on the tree and by their expansion at different times (male-female or vice versa) (cf. Mushegian, Stout). Some species have been found to be self-fertile (e.g., *A. campestre*, *A. Ginnala*, *A. Pseudo-Plantanus*, and perhaps *A. rubrum*), others self-sterile (e.g., *A. platanoides*, *A. saccharinum*, *A. spicatum*; cf. Pjatnitzki). Parthenocarpy and rarely apomixis have been recorded in *A. Negundo* and its hybrids with *A. platanoides*.

Chromosome numbers have been investigated in about 31 species, all of which are diploid (*A. platanoides* also sometimes triploid) with $2n = 26$, except three tetraploids (*A. Pseudo-Platanus*, *A. saccharinum*, and *A. carpinifolium*), and *A. rubrum* ($2n = 78, 104$). It has been suggested that the basic number 13 might have arisen either through multiplication of an original chromosome set of 5 (Takizawa, 1952) or from one of 12 (Meurman).

With the exception of *Acer* × *Bornmuelleri* Borbas (*A. campestre* × *monspessulanum*), all of about 18 known intra- or intersectional hybrids are either artificial or of spontaneous garden or nursery origin. The at least partly fertile artificial hybrid, *A. Negundo* ♀ × *platanoides* ♂, reported from the U.S.S.R., is of special interest as being between species of presumably very remotely related sections.

Floral anatomy, investigated in 11 species (Hall, 1951, 1961), revealed eight different anatomical types mostly corresponding to Pax's sections. On the basis of leaf anatomy (studied in 85 species by Warsow), a few changes in Pax's classification have subsequently been made by Rehder (1905, 1940), Pojarkova (1936), and Momotani (1962). Petiole anatomy, investigated in 55 species (in great detail in 42 species by Watari), though variable and complicated, seems mostly to be in agreement with Koidzumi's delimitation of the sections (slightly different from that of Pax) and is hardly in favor of any generic segregation. Fruit histology (Momotani, 1961) for about 55 species seems to support the classification of the genus used here. Seed proteins have been investigated in 45 species (Momotani, 1962), but the data are quite incomplete in terms of the whole genus; further investigations in this field are very desirable.

Many species, domestic and foreign, yield valuable timbers. The sap of *A. saccharum* is the source of maple syrup and sugar of considerable economic importance. Numerous species are of high ornamental value as garden and park plants and/or shade trees (cf. Mulligan).

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HIPPOCASTANACEAE A. P. de Candolle, Prodr. 1: 597. 1824, nom. cons.
(Horse-chestnut Family)

Trees or shrubs distinguishable from the closely related Sapindaceae by the opposite, 5–11-foliolate, palmately compound leaves; relatively large, showy, irregular flowers in ample terminal thyrses [or panicles]; and capsules with large chestnut-like seeds. (Paviaceae Horaninow, 1834; Aesculaceae Lindley, 1836.) Type genus: *Aesculus* L.

A family of two closely related genera, *Aesculus*, of the North Temperate Zone, and *Billia* Peyr., of tropical America (southern Mexico to northwestern South America). Hippocastanaceae, the closely related Aceraceae, and perhaps the Bretschneideraceae are regarded as having been derived independently and on different lines from the ancestral Sapindaceae (cf. Hardin, 1957d).

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1. **Aesculus** Linnaeus, Sp. Pl. 1: 344. 1753; Gen. Pl. ed. 5. 161. 1754.

Trees to small shrubs. Leaves opposite, palmately compound, 5–11 (usually 5–7)-foliolate, manifestly petiolate, deciduous; leaflets thin to subcoriaceous [or coriaceous], variable in size and shape, the central leaflet usually the largest, usually petiolulate [or sessile], serrulate to serrate or doubly-serrate [rarely nearly entire.] Plants andromonoecious; flowers showy, irregular, ♂ and bisexual, pediceled, in terminal thyrses composed of cincinni each of which is subtended by a small bract. Sepals 5, whitish, yellowish, or reddish, connate to ⅔ or more [or less] of their length into an equally or unequally 5-lobed [sometimes 1- or 2-lipped] campanulate to tubular calyx often oblique and gibbous at base on the upper side. Petals 4 or 5, subequal or unequal (the upper pair longer and narrower than the lateral), clawed (the claw often wide, with involute margins clasping a staminal filament), white to yellow, scarlet or red. Disc annular or lobed, usually one sided. Stamens usually 6–8 [rarely 5], exserted or included; filaments white; anthers yellow, orange or reddish, usually glandular at the tip and at the base of each anther half; pollen medium sized, 3-colpate, subprolate or prolate, striate-reticulate. Gynoecium rudimentary and stalked in ♂ flowers; stigma terminal, small, simple or obscurely 3-lobed; style single, subulate, elongate, often arcuate, deciduous; ovary sessile, 3-locular (rarely 2- or 4-locular); ovules 2 in each locule, superposed, sessile, campylotropous (or amphitropous?), 2-integumented, with a thick nucellus. Fruit subglobular or obovoid, variable in size; pericarp leathery, thick or thin, pale to dark brown; smooth, tuberculate or spiny; seeds usually 1–3 (occasionally 4–6), dark chestnut-brown to light orange-brown, with a pale "hilum" (pseudohilum) of variable size; embryo large, filling the seed cavity at maturity (nuclear endosperm abundant in early stages); cotyledons unequal, thick, hemispherical, usually inseparable (conferruminate), incurved on a short radicle lying in a pocket formed by an infolding of the testa; plumule distinctly 2-leaved. LECTOTYPE SPECIES: *A. Hippocastanum* L.; see N. L. Britton, N. Am. Trees 657. 1908. (The ancient Latin name of some oak, applied by Linnaeus to this genus; etymology of name obscure.) — HORSE-CHESTNUT, BUCKEYE.

A genus of about 13 species in five sections, of disjunct distribution in the North Temperate Zone in North America (7), Asia (5), and the Balkan Peninsula of Europe (1 species). One Asiatic species, *Aesculus assamica* Griff., extends into the Tropical Zone as far south as northern Siam and northwestern Indochina. Five species occur in our area;[8] *A. californica* (Spach) Nutt. ex Torr. & Gray (§ CALOTHYRSUS (Spach) Koehne) is restricted to California, and *A. Parryi* Gray (§ PARRYANAE Wiggins) to northwestern Baja California.

Including only a single distinctive species, sect. MACROTHYRSUS (Spach) Koehne (Deutsche Dendrol. 384. 1893), comprises spreading shrubs or small trees with elongate columnar inflorescences (20–30[–50] cm. long);

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[8] In taxonomic treatment and distribution of the taxa Hardin's *Revision* (1957d) is followed here.

petals 5, white, subequal; and stamens 3–4 times the length of the petals. *Aesculus parviflora* Walt. (*A. macrostachya* Michx.), bottlebrush buckeye, $2n = 40$, apparently is endemic to Georgia and Alabama. It occurs "in the Coastal Plain of southwestern Georgia and southeastern Alabama (along the Apalachicola River), and through central Alabama from Clarke, Butler, and Monroe Counties north and off the Coastal Plain into Franklin, Blount, and Etawah Counties." Early records of the occurrence of this species in eastern Georgia, South Carolina, and Florida have been questioned, but the type specimen of *A. macrostachya* was collected "ad ripas amnis *Savannah*, juxta urbiculam *St. Augusti* [Augusta, Richmond County, Georgia]" (Michaux, Fl. Bor.-Am. 1: 220. 1803). This species is stoloniferous and is usually found in dense colonies or clones in rich woods on calcareous soils, on shady hillsides, on river and stream bottoms, or on rocky and sandy banks. The species seems to be most closely related to those of the Asiatic-western American sect. CALOTHYRSUS.

The exclusively eastern North American sect. PAVIA (Mill.) Walp. (Repert. Bot. Syst. 1: 423. 1842) comprises four highly variable, closely related, sympatric species characterized by broad pyramidal inflorescences (10–15[–25] cm. long); petals 4, yellow or red, nearly equal or mostly unequal; and stamens included or exserted to twice the length of the petals. Hybridization and introgression between the species seem to be common; flowering dates for all four species overlap.

Of wide range, *Aesculus glabra* Willd. var. *glabra*, Ohio buckeye, $2n = 40$, a tree 10–30 m. tall, or a shrub, with exserted stamens, yellowish, nearly equal petals, fruits usually spiny-tuberculate, and leaves with 5–7 oval-oblong to elliptic-obovate leaflets, occurs in our area in northern Alabama, central Tennessee (with outlying stations in eastern Tennessee, central Alabama, and east-central Mississippi), and western Arkansas. It extends to Missouri, Iowa, Indiana, southern Michigan, eastern Pennsylvania, and Kentucky. The distinctive var. *arguta* (Buckl.) Robins., a shrub or small tree, the leaves with 7–11 narrow leaflets attenuate at both ends, intergades with var. *glabra* in western Arkansas; its principal range is beyond our limits in Kansas, Oklahoma, and Texas. Both varieties usually grow in fertile bottomlands of rivers and streams, or in rich calcareous soils on hillsides and in flat woodlands.

Primarily Appalachian, *Aesculus octandra* Marsh. (*A. flava* Ait.), yellow or sweet buckeye, $2n = 40$, usually a large tree 20–30 m. tall, with included stamens, yellow, unequal petals, stipitate glands on the pedicels, and smooth or somewhat scaly or pitted fruits, ranges from northern Georgia, northeastern Alabama, and central Tennessee, through eastern Tennessee, western South and North Carolina, western Virginia, eastern Kentucky, and West Virginia to southwestern Pennsylvania and southern Ohio, thence along the Ohio River bluffs to southern Indiana and Illinois. A plant of rich forest soils, "it is often a dominant, or more often the co-dominant, with *Tilia heterophylla*, *Liriodendron tulipifera*, and *Acer saccharum*, in the cove forests of the Blue Ridge, Smoky, and Cumberland Mountains."

Usually a shrub 1–3 m. tall, more rarely a tree to 15 m., *Aesculus sylvatica* Bartr. (*A. neglecta* of many authors, not Lindley), the Georgia buckeye, further characterized by yellow to often reddish petals and eglandular pedicels, occurs mainly in the Piedmont from southern Virginia south through the Carolinas and Georgia to northeastern Alabama and northward into eastern Tennessee, growing in many different habitats and soil types. "Many populations of *A. sylvatica* are quite variable in many characters, as a result of introgression from *A. Pavia* or *A. octandra*, or both. . . . The great variation in the [petal] color (yellow to red), characteristic of many populations is thought to be due to introgression with *A. Pavia*" (Hardin 1957d; cf. 1957a, b). *Aesculus Pavia* L., red buckeye, $2n = 40$, also a shrub or small tree, with scarlet, red, yellowish-red, or yellow petals, the petals stipitate-glandular on the margins and surface, occurs from central Florida (Orange County) northward to eastern North Carolina and westward to eastern Texas, extreme southeastern Oklahoma, Arkansas, western Tennessee, southeastern Missouri, and southern Illinois. It is usually a plant of well-drained soils in pinelands, mixed pine and broad-leaved forests, and oak-hickory flatwoods. *Aesculus Pavia* has often been separated into several varieties or even species. "When the entire species is examined, however, there is no real degree of discontinuity which would separate any of the variants. . . . A conspicuous clinal variation exists from east to west in two characters, the calyx length and the pubescence of the lower leaf-surface. The calyx becomes shorter and more campanulate westward, and there is a gradual increase westward in the percentage of shrubs in a population with tomentose or woolly leaves." The yellow color of the petals "in eastern populations, and west to Texas, is considered a result of the influence of *A. sylvatica* and *A. glabra* through introgression. On the other hand, the populations of *A. Pavia* [representing a variant] in the extreme western part of its range are typically yellow."

This section is considered by Hardin to have been evolved on a line independent from that of the four other more or less interrelated sections, and its closely related species "were presumably derived from an ancestral form (or forms) which was a relic of the Arcto-Tertiary forest that persisted through late Tertiary and Pleistocene in the Appalachian refugium." The genus itself presumably was derived from a *Billia*-like ancestor, and Central or South America is supposed to be its center of origin.

Although only staminate and bisexual flowers have been recorded in our species, at least in *Aesculus Hippocastanum* occasional carpellate flowers with the stamens either losing their anthers before dehiscence or having more or less closed anthers with nonfunctional (shriveled) pollen seem to occur. The bisexual flowers are either proterogynous (e.g., *A. Hippocastanum, A. glabra*) or proterandrous (e.g., *A. parviflora*). Close-pollination in an inflorescence seems to be prevented by the expansion of male and bisexual flowers at somewhat different times, apparently in a male-bisexual sequence. An extensive study of the floral biology of our species, however, has not been available. *Aesculus Hippocastanum* is believed to be self-fertile. Bumblebees are considered to be the main pollinators in all the species except *A. parviflora*, which appears to be pollinated by moths. The reported occurrence of polyembryony in *A. Hippocastanum* (see Penzig, p. 222) should be verified. Chromosome numbers, known in six species representing four sections and in a few hybrids, are invariably $2n = 40$, except $2n = 80$ in *A.* × *carnea* Hayne (*A.* × *rubicunda* Loisel.), an amphiploid intersectional hybrid between *A. Hippocastanum* and *A. Pavia*, and $2n = 60$ in *A.* × *plantierensis* André, a sterile backcross between *A.* × *carnea* and *A. Hippocastanum*. Both of these hybrids are of garden origin. Intrasectional hybrids are known only within sect. PAVIA. Hardin (1957b) mentions seven hybrids, both under cultivation and/or in natural populations. Two of these, both of garden origin, are triparental, i.e., *A.* × *arnoldiana* Sarg. (*A. glabra* × [*A. octandra* × *A. Pavia*]), and *A. woerlitzensis* Koehne (*A. octandra* × [*A. Pavia* × *A. sylvatica*]), the latter apparently also occurring wild.

Many species, varieties, and hybrids of *Aesculus* (e.g., *A. Hippocastanum* of southeastern Europe, *A.* × *carnea* Hayne, *A. parviflora*, and species of § PAVIA) are planted for ornament or shade, and a few species are a source of commercial timber. The glucoside aesculin, present in all organs, but especially in the bark and bud scales of *A. Hippocastanum*, seems to have some application in plant cytology (see Sharma). All species of our area are considered poisonous to livestock.

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THE DIRECTOR'S REPORT

The Arnold Arboretum During the Fiscal Year Ended June 30, 1963

The work of the Arnold Arboretum includes the maintenance and study of a collection of living plants, the preservation and use of herbarium specimens and library books, and the pursuit of botanical and horticultural research with the results being made available through publications and by educational programs. In each of these areas the annual records are cumulative. In our northern temperate climate the variations of the environment from year to year are readily observable in the flowering of the trees and shrubs of the living collections. The records of the institution, many dating back nearly ninety years, allow comparisons. The past winter with its unusual ice storms adversely affected some plants, but proved favorable for others, and the spring season was marked by an unusually beautiful flowering display of crab apples, lilacs, and evergreen rhododendrons. An active staff published collectively over 65 papers during the year, while continuing its regular curatorial activities involving the many collections. A large number of educational programs, ranging from lectures and guided tours to courses and correspondence, were also part of another busy year.

Staff:

The staff was saddened by the death of Dr. Clarence E. Kobuski, on May 9, at the age of 63. Dr. Kobuski came to the Arboretum in 1927, and his death ended 36 years of contribution to the Arnold Arboretum, interrupted only by wartime service in the United States Army. His was a period of dedication second in length only to those of Charles Sprague Sargent and Alfred Rehder. In his early years he came to know well woody plants under cultivation, as an assistant to Rehder, and later as an editorial assistant in the preparation of Rehder's *Manual of Cultivated Trees and Shrubs* and the *Bibliography of Cultivated Trees and Shrubs*. His research, involving difficult groups, began as studies of cultivated plants in the families Theaceae and Oleaceae. As an editor of the *Journal of the Arnold Arboretum* and as senior curator of the Arboretum collections, Dr. Kobuski served and helped every staff member. His efficiency, his hard work, his knowledge, and his good humor were basic to our everyday activities. Although the diagnosis of Hodgkin's disease more than two years ago was known to all, his death was a personal loss to each of us. An account of his life and a list of his publications is being published in the *Journal of the Arnold Arboretum.*

Three new appointments were made during the year. Dr. Theodore R. Dudley joined the staff as Assistant Horticultural Taxonomist on May 1, after completing studies on the genus *Alyssum* at the University of Edinburgh. Dr. Mary E. Sanders was appointed Research Associate for one year to complete her studies of the cytology and genetics of *Sorghum*, using the Arboretum facilities. Mr. William Grime was appointed Curatorial Assistant in February, 1963. Dr. Wood completed a one year appointment as supervisor of the Harvard University Herbarium Building. In addition, Miss Dulcie A. Powell, of the Institute of Jamaica, Kingston, Jamaica, was awarded a Mercer Research Fellowship for the year, to work on the history of early plant introductions and the history of the garden of Hinton East, in Jamaica. The appointment of Dr. Lalit M. Srivastava as Mercer Research Fellow was renewed to permit him to continue his studies of the cambium and its vascular derivatives. Mrs. Claude Weber was awarded a James R. Jewett Fellowship from the funds of the Arnold Arboretum, to support her work on the genus *Chaenomeles* for the year.

Mr. Don M. A. Jayaweera, having completed a series of studies of the genus *Mussaenda* and his tenure as a Mercer Research Fellow, returned to his position as Superintendent of the Royal Botanic Gardens, Peradeniya, Ceylon. Dr. Wallace R. Ernst, who has been working on the generic flora of the southeastern United States, under Dr. Wood's direction, resigned at the end of the fiscal year to accept a position at the United States National Museum.

Several members of the staff received honors or special committee assignments during the year. Dr. Donald Wyman was appointed chairman of the Awards Committee of the American Horticultural Society and was elected vice-president of the International Dendrological Union. Dr. Shiu-Ying Hu was one of two individuals selected as the first honorary members of the Korean Botanical Society. Mr. Peter Green was appointed to the committee of the International Organization for the Study of the Taxonomy of Cultivated Plants. This committee, formed at the XVI International Horticultural Congress, will function as an organization within the International Association for Plant Taxonomy. Dr. Schubert was appointed to the Publications Committee of the Association for Tropical Biology.

Horticulture:

The past year was notable for its cool summer and a winter made scenically beautiful by a series of ice storms. Unfortunately, these same storms severely damaged many flower buds and killed to the ground plants of *Ilex*, *Weigela*, and *Deutzia*. This damage to particular genera was common in the northeastern states and also occurred as far west as Ohio. One storm in January that began as a freezing rain coated all plants with ice which persisted for seven days in protected locations. Fortunately no wind accompanied this storm, and breakage of branches was minimal. This was but one of seven occasions in January and February when ice coated the living collections for periods exceeding 24 hours. In contrast to the damage to above-ground portions of these genera, the quality and time of flowering was noticeably altered in *Forsythia*, *Magnolia*, and the azaleas. On the other hand, these same winter conditions appear to have favored the ornamental crab apples which flowered profusely nearly a week ahead of their normal time, the lilacs which persisted in peak of bloom for nearly two weeks, and the evergreen rhododendrons which seemed more floriferous than usual.

Two major improvements were made on the grounds during the year. The Department of Parks and Recreation of the City of Boston continued its program of road improvements in the Arboretum, completing the resurfacing of a section of road near the *Fagus* collection and the circular road on Peters' Hill. The top of Peters' Hill, one of the highest points in Boston, has often been suggested as an ideal point for a vista over the Arboretum grounds. Previously only accessible in dry weather, the Department of Parks and Recreation has now begun an all-weather roadway to the area. Two large dry wells were built to handle the road drainage and the approach road has been started. Eventually a circular drive, forming a turn-around at the top of the hill, will make this area easily available to visitors.

A division of costs with the City of Boston permitted the installation of a new concrete storm sewer across the lower portion of the greenhouse tract of land from Centre Street to the linden collection. The existing ancient sewer had collapsed in places, creating a hazard to visitors and permitting flooding in the *Tilia-Aesculus* collections after heavy rains.

The meadow area of the Arboretum in front of the Administration Building, has been subject to flooding in recent years, and the resulting high water table has had a damaging effect on the meadow-road plantings. With the installation of the storm sewer at the greenhouse area the water level in the meadow can be controlled by cleaning out the silt-filled ditches. This effort succeeded in improving the drainage pattern so that the water table was reduced by one foot.

New gates, installed at the Bussey Street entrances to the conifer collection and to the Peters' Hill area, not only improved the appearance of these areas, but has allowed better control of the properties during off hours. A fence was placed along South Street and around the property at 383 South Street for increased protection of this entrance to the grounds.

The area behind the Administration Building which was largely occupied by mass plantings of *Forsythia* and *Cornus* was cleared in part, to allow room for expansion of the *Magnolia* collection. Opposite the Administration Building and adjacent to the Arborway, another area was cleared during the winter to improve the growth of the willow collection and to allow the establishment of plantings of colorful azaleas which will be visible across the meadow in the future. The wooden trellis holding many of the climbing plants in the Arboretum collection was in need of repair and now has had most of the overhead cross pieces replaced.

An unusually large amount of compost and mulch materials, as well as of top soil, became available in the Boston area during the year and was purchased or accepted as gifts, with gratitude. This was placed on the living collections or stock-piled for future use. The large supply of cocoa shells resulted from the closing of a cocoa processing plant which in recent years has made available large amounts of valuable mulching material. Again, we must renew our search for additional low-cost mulch material.

In the previous fiscal year the efforts of the grounds staff were concentrated on removing Arboretum collections from the property of the Bussey Institution, in re-establishing the hedge collection, and on landscaping the greenhouse area. With this work completed during the autumn months, the work described above could be undertaken and the regular planting program renewed. During the year over 500 specimens of trees and shrubs from the nurseries at the Case Estates were planted in the collections at Jamaica Plain.

During the spring we completed the first year of operations in the Charles Stratton Dana Greenhouses. As these structures differed in size and plan from those formerly used it was expected that a period of adjustment to the new physical arrangements and environments would be required. Greenhouses do have individual environmental characteristics and the experimental program of the past year has indicated the methods of optimal use of each. A mist propagation system, formerly out-of-doors and usable only in the summer months has been established in one house; a second house is devoted to plastic tent propagation techniques as well as the processing of seeds and the grafting of plants; while the third house contains the teaching and research collections used by the staff. The new class facilities of the Dana Greenhouses were used by Mr. Fordham in conducting a plant propagation class of ten sessions. The laboratory for cytology and morphology has been used by Dr. Sanders and other members of the staff.

Two of our interesting collections were enhanced by special gifts. Through the kindness of Mr. William T. Gotelli, of South Orange, New Jersey, Mr. Fordham was able to obtain propagating material of 84 dwarf or abnormal conifers not previously represented in our collections. Mr. Gotelli had previously donated 20 cultivars of tree peonies in 1958, and an additional 14 in 1961. During this year his gift of 34 more cultivars has been added to the collection located near the *Viburnum* plantings. In this locality the plants have prospered and, in the spring, flowered profusely.

The activities of the men in the plant propagation area of our operations are practical and experimental, concerning both the established plants and the introduction of new taxa. Some of the very old plants in the Arboretum are approaching senescence, while others are failing because of storm damage or insect attacks. Regular surveys of the grounds are made to locate and propagate such plants for replacements. Plants which have done well but are few in number are also propagated for proper preservation or display. During the year 382 species and varieties in our established collections were processed for such reasons. In addition, new taxa were received for trial as living plants, cuttings, or seeds. During the past fiscal year the Arboretum received 174 shipments of plant materials representing 700 species and varieties from 14 countries, not including the United States, and 80 shipments of seeds representing 132 taxa from 24 countries, not including the United States. To aid the staff in taxonomic or analytical problems 172 different kinds of plants were propagated. To acquire propagation data on species difficult to reproduce 74 taxa were handled experimentally.

PAEONIA cv. HUKUO-JASHI. One of the most floriferous of the tree peonies in the collections of the Arnold Arboretum.

Still another aspect of the work of the plant propagation staff is the distribution of plant materials for hardiness trials, for other experimental purposes on request, or as gifts or exchanges when the required material is not readily available from other sources. During the year the shipments of plants as living specimens, including seeds, numbered 321 shipments comprising 1227 species and varieties to a total of 15 different countries. The cost of this aspect of our activities in labor, supplies, and postage is compensated by the receipt of equivalent materials in exchange from other organizations, by similar cooperation for our research needs, and by the invaluable factor of the good will established both in the United States and abroad.

The program of plant distribution to cooperating nurserymen described in previous reports was continued during the year by making available twelve authentically identified species and varieties of plants with outstanding horticultural characteristics. Thirty-five nurseries and botanic gardens in 25 states and 5 foreign countries requested materials from a list supplied to them. Fulfilled requests for specific materials amounted to 123 shipments of 442 taxa to nurseries and botanic gardens. Unusual requests for soil samples; plant parts for analysis, cancer chemical screening, or animal nutrition studies; preserved stems, or flowers, or pollen for breeding programs represented shipments of 639 taxa during the year.

Surplus plants were supplied for three widely separated hardiness trial programs of interest to the staff of the Arboretum. The Vermont Agricultural Experiment Station, Burlington, Vermont, received 70 species and varieties over the past two years; the Regional Plant Introduction Station, Ames, Iowa, was sent 51 different kinds of plants for trial and evaluation in the North Central Regional Plantings of the Ornamental and Shelter Plant Introduction Program. Other plants for tolerance of hardiness experiments were sent to the Mustilla Arboretum, Elimaki, Finland, the northernmost arboretum in the world, and to gardens in Puerto Rico, Trinidad, and Honduras for checking of their tolerance of heat.

We receive requests from newly formed arboreta for surplus plants, or specific plants, and attempt to aid these institutions as well as schools which request material to diversify their plantings for educational purposes. During the year we supplied collections ranging in number from 17 to 150 species and varieties to such places as the Bristol County Agricultural School; the town committees of Chelmsford and of Weston, Massachusetts; the Meeting House School, West Rindge, New Hampshire; and Union College in Schenectady, New York. A specific request for plants cultivated in the 18th century in New England was received from the Board of Managers of historic Gore Place, in Waltham, where an attempt is being made to recreate the original landscaping of the grounds. A number of species and a few available old cultivars were supplied as a gift.

Work in the taxonomy of cultivated plants is a major effort of the staff. One recent issue of *Arnoldia* described the new cultivars registered by the Arboretum during the past year. A new registration list of cultivars for *Chaenomeles* and a supplementary list for *Syringa* were published. Some of the new cultivars and recent introductions received by the Arboretum present special taxonomic problems. Mr. Green undertook a survey of a selected number of the plants introduced to the Arboretum in recent years to check the nomenclature adopted. Some interesting problems encountered will be discussed by him in papers in appropriate journals later.

Two machines for preparing labels were purchased during the year to add efficiency to our methods of labeling specimens in the living collections. An electrically operated Graphotype Embosser, manufactured by the Addressograph Company, will replace the more limited hand-operated machine used previously. A Green Pantograph Engraver was purchased to prepare labels from black and white laminated plastic for collections of small-sized plants. Such labels have been placed on the lily test-plots, the ground covers, and perennial garden collections in Weston, and on the *bonsai* and dwarf conifer collections at the Dana Greenhouses. Both machines produce attractive resistant labels at greater speed than could be realized by our former techniques.

Case Estates:

During 1963 the town of Weston, the location of the Case Estates of the Arnold Arboretum, marked the 250th anniversary of its founding. The staff of the Arboretum was asked to cooperate by assisting in the committee work for the occasion and by scheduling the annual Open House at Weston during the celebration by the town. The Arboretum is fortunate in occupying a prominent geographic position in this lovely town and is aware of its privileges and its responsibilities as a tax exempt organization there. Dr. Wyman has served for many years on the park, cemetery, and the beautification committees of Weston. He has also assisted in the design of a new park area. The Arnold Arboretum has contributed 150 trees and shrubs for the landscaping of it and other localities in the town. Dr. Howard, Dr. Wyman, and Mr. Draper, all resident on the Case Estates, were responsible for tours of the Estates during the anniversary celebration.

The plantings of the Case Estates are always open to residents of the town, and many of them take advantage of the labeled displays for study, or participate in the classes and tours offered. Main roads of the town pass along the boundaries of the Case Estates and road-edge plantings of crab apples, established in recent years, reached a peak of bloom this year in time for the ceremonies.

A committee of the town of Weston concerned with the identification of the oldest houses for the anniversary celebration, verified the location of its fifty oldest buildings. One Arboretum house, at 131 Wellesley Street, was built by or for Thomas Rand in 1790, and is now identified on town maps and marked by a bronze plaque. The town has requested that all measures be taken to insure the preservation of these historic buildings.

During the year, Dr. Scott Pauley and Mr. Albert Johnston, representing the Cabot Foundation, examined the clonal collections of trees which have been maintained on the Case Estates for a number of years. Their report compares the same genetic material planted in twenty-five test locations in Massachusetts. There are numerous clones of *Populus* and *Pinus*, and smaller numbers of other genera. The species and hybrids, as well as the selections for geographic areas, including altitudinal variations, could be compared when grown in pure stands or in various combinations in one test plot. Over the years of their existence the plots have shown survival ratios from zero to ninety percent for the material outplanted in Weston and reveal definite indications of potentially profitable breeding combinations, not only for growth, but for hardiness and borer and weevil resistance. The test plots were originally established on standard planting intervals for trunk development. The most promising plants have now been propagated, following the Scott and Johnston report, for growth as specimen plants both in Jamaica Plain and in Weston. The value of these plants lies in the detailed genealogical records and the long and careful selection studies which document them.

ABOVE: A frame house built around 1791 by or for Thomas Rand is located on the Case Estates of the Arnold Arboretum in the town of Weston.

BELOW: A commemorative plaque, donated by the town of Weston and placed on one of the houses of the Case Estates, marks it as one of the 50 oldest buildings in the town.

Herbarium:

Additional competent help became available during the year, making possible a major effort to distribute duplicate specimens to herbaria with appropriate interests. In recent years this aspect of our taxonomic work has had to be neglected in favor of the reorganization of the herbarium and the insertion of mounted material. In contrast to the previous fiscal year, when only 483 specimens were sent out in exchange, 24,482 specimens were distributed during the fiscal year just ended. These constituted primarily collections from Indochina and from New Guinea, made by Arboretum-sponsored expeditions immediately after the close of World War II. The Arboretum received during the year 35,431 specimens, either in exchange, or by subsidy, gift, or purchase. The largest single collection included was from Dr. Hugh Raup of the Harvard Forest, a collection made by him in 1948 in Alaska and the Yukon Territory, when he was a staff member of the Arboretum. Particularly valuable material was received from Mr. Myoshe Furuse as a set of 1072 specimens collected on a subsidy. Included in the total number of specimens received were 10,967 specimens obtained in exchange programs with other herbaria and 1900 specimens received as gifts or for identification. We are particularly grateful for valuable duplicates of historical collections received from the Muséum National d'Histoire Naturelle, Paris.

It is worthy of notice that the number of specimens of cultivated plants received for identification continues to increase. This is in part associated with the efforts of the staff in the registration of cultivars, for the nurseryman and the layman both are aware of the value of correctly identified plants. Fortunately, the majority of the specimens received are worthy of preservation and will therefore constitute an important part of the record of the distribution of cultivated plants. Other botanical gardens are now distributing specimens collected from the plants they have under cultivation, either for checking of the identifications or for records of growth in a certain area. Mr. Don M. A. Jayaweera, former Mercer Research Fellow, arranged for the Arboretum to receive a collection of specimens of plants currently under cultivation in the Royal Botanic Gardens, Peradeniya, Ceylon. The plants of this garden formed the basis of records for H. F. MacMillan's *Tropical Planting and Gardening*, and many of the species received were new records for our herbarium in Jamaica Plain.

During the year 19,112 specimens were mounted and added to the herbarium, bringing the total collection to 763,928 specimens. The research program of the staff requires the study also of herbarium specimens borrowed from other institutions. In the past year requests were made for 77 loans of specimens from 41 institutions, 22 in the New World and 19 in the Old World. The incoming loans totaled 4421 specimens, or an average of 57 sheets per loan. The staff received requests for the loan of its herbarium material from 51 institutions and sent out 128 loans averaging 145 specimens for a total of 18,643 sheets from the herbaria of the Arnold Arboretum and the Gray Herbarium.

In addition to the published papers the taxonomic staff has many research projects in progress. Dr. Brizicky is studying the generic limits within the Sapindales and Geraniales for the generic flora of the southeastern United States. He completed, in the past year, studies on the genera of Anacardiaceae and detailed studies on the generic limits of *Rhus*, as well as treatments of genera of the Sapindaceae, Aceraceae, Hippocastanaceae, Celastraceae, and Hippocrateaceae. Dr. Dudley completed field work in Turkey early in the summer and then organized the collections of that expedition. His field studies of *Alyssum*, made in the type localities of many of the species, produced 160 specialized collections of this genus. The specimens, as well as viable seeds, were basic to his monographic studies. Since *Alyssum* is well represented in the Near East he has agreed to prepare treatments for several regional floras being assembled by european colleagues.

Dr. Ernst completed treatments of Capparaceae, Moringaceae, Loasaceae (with Dr. H. J. Thompson), Hamamelidaceae, Platanaceae, Berberidaceae, Lardizabalaceae, and Menispermaceae for the southeastern flora project. Mr. Green continued his work on the Oleaceae, giving special attention to the genera *Osmanthus* and *Nestegis*. Dr. Howard received contrasting collections for special study during the year. One was of old specimens collected in the botanic garden at Saint Pierre, Martinique, before its destruction by the eruption of Mt. Pelée. The other was a collection made on Inagua, in the Bahamas, during the winter of 1962–63, which pointed out the immediate need for field work in areas threatened by the rapid expansion of tourism in the West Indies. Dr. Hu continued her work on the identification of the accumulated, incompletely identified Asiatic herbarium material received by the Arnold Arboretum. As these identifications are completed the duplicate specimens will be distributed to other herbaria. Dr. Hu has also been assisting botanists in Asia with the verification of identifications of specimens collected on Hong Kong and Quemoy. Quemoy, an embattled island, is closed to collectors and the materials under study were obtained by a Nationalist Chinese soldier stationed there. During his illness, Dr. Kobuski attempted to continue his work on the Asiatic species of *Ternstroemia*. Unfortunately much of this remains unfinished, but a few completed portions are being published posthumously.

Dr. Nevling had the opportunity of studying *Daphnopsis* species in Puerto Rico and continued his work on the family Thymelaeaceae. Dr. Perry is completing her studies of the medicinal plants of Southeast Asia and their various uses throughout their geographic range. Dr. Schubert, in addition to serving as editor of the *Journal of the Arnold Arboretum*, continued her studies of the genera *Begonia*, *Desmodium*, and *Dioscorea*. Dr. Wood, who is editing and coordinating the manuscripts prepared by various individuals for the generic flora of the southeastern United States, continued the direction of these studies, his own work in this area, and the compilation of the basic data and materials for the project. In addition to a number of peripheral papers, treatments of forty-eight families of flowering plants, comprising over 500 pages of the *Journal of the Arnold*

Arboretum, have been published since the series was begun. Dr. Wood has also continued his critical work in connection with the nomenclature of the families of seed plants.

Library:

A notable increase in the use of the library during the year by students and visiting scholars was attributable, we believe, to the developing cross-reference system of file cards in the catalogue. This work has progressed slowly over the past few years and was reflected again this year in the statistical records of the librarian. Four hundred nineteen bound volumes were added to the library during the year, making a total number of 51,453. Of this number, 104 deal primarily with horticultural topics and are housed in Jamaica Plain. Five hundred eighteen items were added to the pamphlet collection, increasing its total to 18,926. Although 937 accessions were recorded by the librarian, the number of reference cards added to the main card catalogue totalled 1976, reflecting the effort of Mrs. Schwarten and her assistants to make the library of increasing value. The annual issues of the Index to American Botanical Literature, the Card Index of American Plants issued by the Gray Herbarium, and of the Index Nominum Genericorum issued by the International Association for Plant Taxonomy were all added to the existing files.

The librarian has also undertaken to arrange the available duplicate reprints of former staff members for eventual distribution as requested, and to prepare volumes of the collected works of former and present staff members. In many cases this has involved locating obscure periodicals not necessarily in our library and obtaining reproductions of the appropriate articles.

Several outstanding additions were made to the library resources during the year. Through the kindness of Mr. Philip J. McNiff, of the Harvard College Library, 92 of the original Linnaean Dissertations were obtained in an exchange program with the library of the University of Helsinki, in Finland. Between the libraries of the Arnold Arboretum and the Gray Herbarium, 132 of the original 186 Linnaean theses published are now available for research use. Also of special value are the manuscripts, photographs and documents used in the preparation of *The Lilac* and *Botanical Exploration of the Trans-Mississippi West*, which were a gift of the author, Mrs. Susan Delano McKelvey. During the year we were able to purchase the manuscripts and notes of Dr. A. K. Schindler, of Düsseldorf, Germany, whose work comprises studies of many genera of the Leguminosae. We acknowledge with gratitude the many other books and periodicals received as gifts, including a copy of *Flora Nasuensis*, edited by the Biological Laboratory, Imperial Household, and presented by Emperor Hirohito of Japan.

In a cooperative program with the Gray Herbarium, microfiche reproductions of the herbarium which formed the basis of the many volumes of the DeCandolle *Prodromus*, and of the herbaria of Thunberg and Burser, were purchased during the year.

Mrs. Schwarten continued her contribution to the preparation of the

Index to American Botanical Literature in cooperation with the editors of the *Bulletin of the Torrey Botanical Club.*

Comparative Morphology:

The wood collection of the Arnold Arboretum received its usual curatorial attention during the year. A large collection of wood samples from the Fiji Islands, collected by Dr. A. C. Smith in 1947, was prepared for sectioning in a cooperative program with the Division of Wood Anatomy of the Smithsonian Institution, United States National Museum. In another cooperative program with the Department of Plant Anatomy, Order of Lenin Forest Academy, Leningrad, U.S.S.R., wood samples of a large number of specimens representing primitive or localized taxa were prepared. In all, 14 requests for anatomical material were processed during the year.

Irving W. Bailey, Professor of Plant Anatomy, *Emeritus,* has continued his research on the leaf-bearing cacti of the genera *Pereskia, Pereskiopsis,* and *Quiabentia,* the results of which have been published in the *Journal of the Arnold Arboretum.* His research reveals incipient trends of phylogenetic specialization in these most primitive surviving representatives of the Cactaceae, which become increasingly accentuated in the Opuntieae and Cereae. Professor Bailey's grant from the National Science Foundation has been extended for a period of two additional years. His studies are now concerned with investigations of the formation of diversified forms of "sphaerites" induced in leaves of *Pereskia* and *Pereskiopsis* during air-drying and alcoholic dehydration of specimens.

Dr. Lalit Srivastava, Mercer Research Fellow, has continued his studies on the ontogenetic and histochemical aspects of the cambium and its vascular derivatives. He has completed his studies of the secondary phloem of the Cactaceae and of the cambium and vascular derivatives of *Ginkgo biloba.* At present he is reviewing the anatomy, chemistry, and physiology of bark for the *International Review of Forestry Research.*

Education:

Through the spring semester Dr. Howard taught a course in horticultural plant taxonomy in the Department of Biology. During the regular spring vacation this class continued its work in Puerto Rico, making its headquarters in the Luquillo Mountains and visiting the University of Puerto Rico, including its agricultural research stations, the forestry nurseries, and plantings of the U. S. Forest Service, as well as other areas of horticultural, agricultural, or floristic interest. The experiment of working with undergraduate students in tropical floras proved stimulating and successful to both instructors and students. The general collections that were made included five taxa new to Puerto Rico and many specimens needed for the herbaria of both native and of cultivated plants. Nearly 100 living plants were collected for growing in our greenhouses to serve as research projects for the students in the next semester.

The informal fall and spring classes conducted by the Arboretum staff were again held both in Jamaica Plain and Weston. Staff members also participated in the seminar series held in the Harvard University Herbarium in Cambridge.

Mrs. Claude Weber completed, for the thesis requirement toward the

The mid-winter meeting of the Northeastern Section, American Society for Horticultural Science, included an inspection of the Charles Stratton Dana Greenhouses.

doctor of philosophy degree, a study of the genus *Chaenomeles*, under the direction of Dr. Howard.

The Northeastern Section of the American Society for Horticultural Science which for a number of years has held a mid-winter meeting in Cambridge, was invited to meet at the Arnold Arboretum. Scientific sections were held in the Administration Building, and an informal dinner was served in the Dana Greenhouses followed by reports of members who attended the International Horticultural Congress in Brussels. Dr. Howard and Dr. Wyman contributed to this meeting while Messrs. Ernst, Fordham, Green, and Wyman, and Mrs. Weber, all presented research papers during the meetings.

Dr. Howard gave the horticultural lecture at the annual meeting of the Garden Club of America, in Philadelphia, and was one of the speakers at the Clara B. Ford Garden Forum, at Greenfield Village, Dearborn, Michigan. He spent several days on the campus of West Virginia Wesleyan College as a guest speaker of the American Institute of Biological Sciences and visited the Inter-American University in San German, Puerto Rico, under the same sponsorship. Talks were also given at the University of Massachusetts and at Framingham State College. Dr. Wyman was a speaker at the annual meeting of the Garden Club Federation of Massachusetts, and at the Universities of Rhode Island, New Hampshire, and Massachusetts, and at Cornell University. Requests for special talks on street trees were received from arborist groups in central and northern New York, New Hampshire, and Massachusetts. These were filled by Dr. Wyman who discussed our trial plots in Weston. Messrs. Ernst, Fordham, Green, Williams, and Wood described the work of the Arboretum or talked about their own research in several seminars and various horticultural meetings.

Exhibits and Displays:

The Arboretum staff prepared four special exhibits during the past year. The largest, entitled "Woody Plant Seeds and their Germination," was the Arnold Arboretum display at the Spring Flower Show of the Massachusetts Horticultural Society. This educational exhibit was designed to show the various methods of seed production and dispersal, seed processing, including treatments for the several types of embryo dormancy, and comparative growth rates of seedlings. The background of this display consisted of mature plants (forced into bloom) of many of the seeds exhibited. The exhibit was planned for convenient study and visitors took advantage of this. The staff was pleased to receive a first prize and a gold medal from the Massachusetts Horticultural Society for its exhibit and to be recipients of the Buckley Medal of the Garden Club of America for the most educational exhibit in the show.

The staff assisted the Horticultural Committee of the Garden Club of America in preparing an educational exhibit on the propagation of herbaceous and tree peonies which was displayed at the Spring Show of the New York Horticultural Society. At the National Capitol Flower and Garden

The exhibit of the Arnold Arboretum at the Spring Flower Show of the Massachusetts Horticultural Society, Revere, Massachusetts, March 16–24, 1963, featured the types of seeds of woody plants and their methods of germination. This exhibit was awarded the Buckley Medal of the Garden Club of America for the most educational display.

Show, in Washington, D.C., the Arnold Arboretum joined other arboreta in an exhibit of which our portion featured hedge plants and two series of kodachrome transparencies of plants and plantings in the Arboretum. In the fall of 1962, a display of plants producing colorful foliage or fruits was arranged for the Fall Show of the Massachusetts Horticultural Society.

Travel and Exploration:

The Arboretum was represented by one or more staff members at various professional meetings including those of the American Association of Botanical Gardens and Arboretums, the American Horticultural Society, the American Institute of Biological Sciences, the American Nurserymen's Association, the American Society for Horticultural Science, the XVI International Horticultural Congress, the National Association of Gardeners, and the Plant Propagators Society. In each case a staff member gave a research paper or presided at a sectional meeting. When these meetings were held in areas outside of Massachusetts staff members were able also to visit nearby Universities, botanical gardens or arboreta, or to undertake field work.

Drs. Howard and Wyman attended the International Horticultural Congress held in Brussels, Belgium, during August. Dr. Howard presided at a meeting and symposium sponsored by the International Association of Botanical Gardens. En route to and from the meetings he visited gardens and herbaria in England and France. Dr. Wyman visited gardens in England, Holland, Germany, France, and Switzerland, in addition to those visited during the Congress tours.

Dr. Wood attended meetings of the Association of Southeastern Biologists at the University of Florida, in Gainesville, and collected herbarium material and living plants in northern Florida in connection with his work on the generic flora of the southeastern United States. Drs. Howard and Nevling made general collections in Puerto Rico, but each also put special emphasis on the accumulation of field data on species of *Coccoloba* and of *Daphnopsis*, in connection with their respective research programs. Dr. Hu visited several collections of *Ilex* and *Sorbus* in Washington and Oregon. Mrs. Weber visited nurseries and arboreta along the East Coast to study the flowering characteristics of *Chaenomeles*. Dr. Ernst continued with Dr. H. J. Thompson, of the University of California in Los Angeles, their program of field work in Texas in connection with studies of Loasaceae. Dr. Howard attended the Neotropical Botany Conference at the Imperial College of Tropical Agriculture, Trinidad, and had the opportunity of collecting selected species in Barbados, Curaçao, Aruba, and Bonaire, en route, applicable to his research program on the plants of the Lesser Antilles. Mr. Fordham made a special trip to collect abnormal forms from native populations of *Taxus*, *Juniperus*, and *Pinus* in New Hampshire and Massachusetts. It is hoped by study of these collections to determine the nature and origin of similar abnormal forms occurring under cultivation.

The general assembly meeting of the 16th International Horticultural Congress held in the Palais du Congres, Brussels, Belgium.

Gifts and Grants:

The many Friends of the Arnold Arboretum renewed their generous support of the horticultural work during the year. We are most appreciative of this continuing annual generosity. Although most gifts are unrestricted, two were gratefully accepted for the care of the Larz Anderson *bonsai* collection and for the care and acquisition of dwarf conifers. A gift from the Boston Edison Company was accepted to complete the collection of street trees maintained in Weston.

The library was enriched with many gifts of individual volumes which are acknowledged as received. Mrs. Susan McKelvey presented to the library the records she has maintained supporting and supplementing her published work on the lilac, and on botanical exploration of the western United States. A large number of botanical journals comprising a gift from Mr. R. W. St. Clair, were particularly useful in replacing several worn volumes. Mr. Edwin Menninger, of Stuart, Florida, presented to the Arboretum the original colored photographs used in preparing his book *Flowering Trees of the Tropics*. This collection has been mounted and placed in the herbarium where it will be of value in complementing herbarium specimens of cultivated plants used constantly for study and demonstration.

Continuing support of the research projects of various staff members by grants from the Public Health Service, the National Research Council, and the National Science Foundation is acknowledged here, and as usual, in the various reports and papers resulting from the research. The project concerned with preparation of a generic flora of the southeastern United States received an additional grant from the National Science Foundation for three years, beginning in September, 1962.

Gifts of plant materials are received annually from many botanic gardens and nurseries to complete or supplement the representation in our living collections. Outstanding collections received during the year were specimens of the genera *Chaenomeles*, *Hosta*, *Lilium*, and *Paeonia* as well as various dwarf conifers.

Publications:

Results of much of the scientific work of the staff is published as research papers in the *Journal of the Arnold Arboretum*. Dr. Wood, who has very ably edited the *Journal* for the past five years turned over this responsibility to Dr. Schubert in January. The four numbers issued during the past fiscal year included 543 pages, containing 31 articles, 25 of which were written by staff members. The six articles by other scientists concerned, in some way, the various collections maintained by the Arnold Arboretum.

The twelve numbers of *Arnoldia* edited by Dr. Wyman and issued during the past fiscal year contained but one article not prepared by a member of the staff. The articles in *Arnoldia* which drew the most attention were reports of the results of trial plots of ground-cover plants and of street-tree plantings as grown in Weston; the first registration list of cultivars in *Chaenomeles*; and two supplementary lists of cultivars recently registered.

During the year the page proof of the *International Directory of Botanical Gardens* was read. Publication of this directory by the International Association for Plant Taxonomy is expected during the summer of 1963.

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1962–1963

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STEPHANNE B. SUTTON, A.B., Business Secretary.
JOHANNA-GERMANA CLAUDE WEBER, M.A., James R. Jewett Fellow.
ROBERT GEROW WILLIAMS, B.S., Superintendent.
CARROLL EMORY WOOD, JR., Ph.D., Associate Curator.
DONALD WYMAN, Ph.D., Horticulturist.

* Appointed jointly with the Gray Herbarium
[1] Resigned April 12, 1963

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