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CRETACEOUS ANGIOSPERM POLLEN OF THE ATLANTIC COASTAL PLAIN AND ITS EVOLUTIONARY SIGNIFICANCE

JAMES A. DOYLE

ONE OF THE MAJOR problems in the study of the evolution of higher plants is the paucity of evidence from the fossil record on the origin and evolution of the angiosperms. Because of the relatively sudden appearance of angiosperms in the fossil record, the lack of recognized angiosperm precursors, and the lack of any striking peculiarities of the macroscopic remains of Lower Cretaceous angiosperms (mostly leaves), almost all conclusions on the origin of the group and the nature of its primitive members have been based on comparative studies of its living representatives. Angiosperm paleobotany has been primarily concerned with the geographic vegetational and floristic changes in the Tertiary, which were due more to migration and extinction than to evolution. The methods of Tertiary angiosperm paleobotany, such as the procedure of identifying modern taxa for paleoecological information, have been far less productive in the Cretaceous, and the problematical nature of the results is undoubtedly largely responsible for the present low level of activity in Cretaceous megafossil paleobotany.

In the past decade a new method has been applied in Cretaceous paleobotany which promises to shed light on the problems of angiosperm origin and evolution. This is the study of fossil pollen and spores. In contrast to the megafossil record, the palynological record shows clear-cut changes in the morphology and diversity of the angiosperms from the time of their first appearance. Most of the information on early angiosperm pollen has been obtained for stratigraphic purposes (cf. Couper, 1964), and is, from a botanical point of view, largely descriptive; the evolutionary implications have been frequently mentioned but not discussed in detail.

The purpose of this paper is to review the characteristics of Lower and early Upper Cretaceous angiosperm pollen floras and to discuss the evolutionary and phylogenetic implications of the record. Much of this discussion is based on my own work on Cretaceous angiosperm pollen of the Atlantic Coastal Plain, which appears to give a fairly representative picture of the world flora. Comparisons will be made with correlative sequences, which are now known in many other parts of the world. Much of the detailed documentation of both the stratigraphic and systematic aspects is in progress and will be presented later in more complete form, but the general results seem clear enough to be summarized in this preliminary paper.

In general, morphological terminology follows Erdtman (1952), though some terms of Pflug (1953) are used in discussing triporate pollen.

GEOLOGICAL BACKGROUND

The Cretaceous is one of the longer geologic periods, covering some 72 million years between about 136 and 64 million years before the present (Casey, 1964). The Cretaceous System is customarily divided into Lower and Upper Cretaceous series, which are subdivided into six stages each (TABLE 1). These stages were first recognized in western Europe and subsequently extended around the world; they are now operationally defined by ammonite zones of the Tethyan province.

Continental or near-shore marine sediments favorable for palynological studies are fairly extensively developed in the Cretaceous, though few areas have large parts of the system represented by continuous continental deposition. For example, the uppermost Jurassic and much of the Lower Cretaceous are well represented in the Purbeck and Wealden of southern England, but late Lower Cretaceous rocks there are marine and only marginally suitable for palynological study. The Upper Cretaceous consists of the wholly unsuitable marine Chalk, and to extend the European Cretaceous pollen record we must go to Central Europe.

TABLE 1. **Subdivisions of the Cretaceous**

SERIES	STAGES	
UPPER CRETACEOUS	Maestrichtian	
	Campanian	Senonian (most common usage)
	Santonian	
	Coniacian	
	Turonian	
	Cenomanian	
LOWER CRETACEOUS	Albian	
	Aptian	
	Barremian	Neocomian (most common usage)
	Hauterivian	
	Valanginian	
	Berriasian	

TABLE 2. **Presumed stratigraphic relations of Atlantic Coastal Plain nonmarine Cretaceous formations**

TIME-STRATIGRAPHIC UNITS		ROCK-STRATIGRAPHIC UNITS				
SERIES	STAGES	SOUTHERN AND CENTRAL MARYLAND AREA			RARITAN BAY AREA, NEW JERSEY	
	—?—?—?—					
	Santonian	Magothy Formation			Magothy Formation	Cliffwood Beds Morgan Beds Amboy Stoneware Clay
	—?—?—?—	Hiatus			Hiatus	
	Coniacian					
	—?—?—?—					
Upper	Turonian				Raritan Formation	Old Bridge Sand South Amboy Fire Clay Sayreville Sand Woodbridge Clay Farrington Sand Raritan Fire Clay
	—?—?—?—					
	Cenomanian				Subsurface Only	
			"Raritan" Formation			
—?—	—?—?—?—	Potomac Group	Patapsco Fm.	Subzone B —Zone II— Subzone A		
	Albian					
Lower	—?—?—?—		Arundel Clay	Zone I		
	Aptian Barremian?		Patuxent Fm.			

An excellent section of the late Lower and early Upper Cretaceous for pollen studies is found in the Atlantic Coastal Plain between Virginia and New Jersey. Pre-Campanian deposition in this area took place mostly in river flood plains and deltas. The result is a seaward-dipping wedge of unconsolidated clays, sands, and gravels, often very rich in organic matter, which is exposed as a wide northeast-trending band several hundred feet thick at the landward margin of the Coastal Plain. The presumed stratigraphic relations are shown in TABLE 2.

In Maryland and adjacent states the basal unit is the Potomac Group, which until recently was defined as consisting of the Lower Cretaceous Patuxent, Arundel, and Patapsco formations (cf. Clark *et al.*, 1911). The Patuxent tends to be feldspar-rich and sandy or gravelly; the Arundel is a huge lens of dark, organic-rich clay with siderite nodules, while the Patapsco is rather heterogeneous, though its red and variegated clays are most characteristic. As is often the case with continental sediments, Potomac Group lithologies are highly variable, and there is much doubt that the formations can be consistently separated in the field. The Arundel, which was apparently deposited in a swamp belt, is the greatest exception to this, and it is an important marker in dividing the Potomac Group; however, it is definitely present only in the area between Washington, D.C., and Baltimore Co., Maryland.

To these three formations have recently been added higher beds traditionally designated Raritan Formation (Weaver *et al.*, 1968), which appear to be earliest Upper Cretaceous. These sediments are generally sandy and lacking in fossils; the few samples that have been examined palynologically (discussed below) indicate an age between the typical Patapsco and the type New Jersey Raritan. In the absence of any distinctive lithological similarity to the type Raritan, this Maryland "Raritan" should probably be considered either part of the Patapsco or a new formation of the Potomac Group.

In the Raritan Bay area of New Jersey, Coastal Plain deposits begin with the Upper Cretaceous Raritan Formation, which appears to be largely of deltaic origin (Owens *et al.*, 1968). The Raritan has been divided into six locally recognizable members, excluding the Amboy Stoneware Clay, which on palynological and other grounds is better associated with the overlying Magothy Formation (Wolfe & Pakiser, ms.). The palynologically important Woodbridge Clay member is dark, massive, highly organic, and siderite-bearing, like the much older Arundel Clay of Maryland, but the South Amboy Fire Clay member is more varied lithologically, with lignitic beds and sands as well as dark, often laminated clays. Most of the Raritan Formation consists of deltaic sands.

The last nonmarine Cretaceous unit, the Magothy Formation, occurs in both Maryland and New Jersey. It unconformably overlies both the Potomac Group and the Raritan Formation; this unconformity represents a considerable hiatus in deposition even in New Jersey, where older Upper Cretaceous is present. The Magothy is lithologically distinctive and unlike the lower units: it consists mostly of alternating sands and dark clays with considerable lignitic material, and it shows much more continuity of individual beds. It appears to be a deltaic deposit, with evidence of tidal influence (Glaser, 1967); it is overlain by the often glauconitic offshore shelf sediments of the Matawan and Monmouth groups.

Unfortunately, controls on the age of the Atlantic Coastal Plain continental units from marine fossils are poor. Except for an aberrant brackish water fauna of uncertain age from a deep well on the Eastern Shore of Maryland (Anderson, 1948), marine fossils are unknown in the Potomac Group. Marine mollusks from the Woodbridge Clay in New Jersey, recently restudied by Sohl (pers. comm.), date that unit as middle or late Cenomanian, while a late Santonian ammonite was recently found in the Magothy Formation of New Jersey (Owens & Sohl, pers. comm.). Biostratigraphic correlations must therefore be based almost entirely on the plant fossils, of which the pollen and spores are by far the most useful and readily obtained. Palynological study reveals a sequence of biostratigraphic zones which are consistent with the regional lithostratigraphy, and which compare closely with better dated sequences in other parts of the world. It is the angiosperms, which were apparently undergoing rapid evolutionary diversification in the mid-Cretaceous, that are most useful in defining these zones. Though questions might be raised on the exact correlation of the angiosperm pollen assemblages in the absence of independent age control, the relative times of appearance of major types are the same as elsewhere, and correlations based on the angiosperms agree well with those made with the spores and gymnosperm pollen alone.

PATUXENT AND ARUNDEL FORMATIONS

The pollen and spore flora of the lower two formations of the Potomac Group, first described in detail by Brenner (1963), is representative of mid-Lower Cretaceous floras of most of the world, just before the appearance of typical angiosperm pollen. It is dominated by pteridophytes and gymnosperms, notably: the fern families Cyatheaceae (or Dicksoniaceae), Schizaeaceae (*Cicatricosisporites*, *Appendicisporites*, and possibly *Trilobosporites*, *Concavissimisporites*, etc.), and Gleicheniaceae, as well as groups of less certain affinities; conifers representing the living families Pinaceae, Podocarpaceae, Cupressaceae (or Taxodiaceae), and Araucariaceae, and extinct forms such as *Classopollis* (which was apparently produced by plants known as the megafossil genera *Cheirolepidium*, *Brachyphyllum*, and *Pagiophyllum*, Pocock & Jansonius, 1961), the possibly related *Exesipollenites tumulus* Balme, and the last of the seed ferns, the Caytoniales (*Vitreisporites*). Smooth monosulcate grains probably represent the gymnospermous orders Cycadales, Bennettitales, and Ginkgoales, while the Gnetales are represented by grains of the *Ephedra* type. The picture of the flora obtained from the pollen and spores is in general agreement with that provided by the megafossils, which are also predominantly ferns, conifers, and cycadophytes (Fontaine, 1889; Berry, 1911).

The genus *Eucommiidites*, common throughout the Potomac Group, is of special interest since it was first described by Erdtman (1948) as a dicot from Jurassic rocks. *Eucommiidites* pollen is smooth and medium-sized, with three furrows which initially suggest the tricolpate condition typical of and restricted to dicots (FIGS. 1a,b). However, one of the furrows is wider and more cycad-like than the others, and the general shape of the grains was shown by Couper (1958) to be more like that of monosulcate gymnosperm than tricolpate angiosperm grains. Subsequently, *Eucommiidites* has been found in the micropyles of gymnospermous seeds in both England (Hughes, 1961a) and Virginia (Brenner, 1963). It was presumably produced by an extinct group of gymnosperms.

The Patuxent-Arundel flora does include one form, *Clavatipollenites* Couper, which has distinctive angiosperm characters. *Clavatipollenites* is generally monosulcate, with the exine finely pilate (clavate), retipilate (with free pila arranged in a reticulum), or reticulate (with the heads of the pila fused to form a true reticulum). Couper (1958), in describing the type species *C. hughesii* from the Barremian of England, pointed out that while the monosulcate aperture condition is prevalent in gymnosperms, pilate or retipilate sculpture is not known outside the angiosperms, and he noted the similarity of the grains to those of *Ascarina* in the dicot family Chloranthaceae. *Clavatipollenites* has been widely reported from the middle and late Lower Cretaceous: the Barremian through Albian of England (Hughes, 1958; Kemp, 1968), the Aptian and Albian of Portugal (as *Apiculatisporis vulgaris* Groot & Groot, 1962), the Barremian through Albian of West Africa and the Aptian and Albian of Central America (Couper, 1964), the Albian of Australia (Kemp, 1966), presumed pre-Albian rocks of southern Argentina (Archangelsky & Gamerro, 1967), and the late (Norris, 1967) and middle (pers. obs.) Albian of the Canadian Plains. A supposed latest Jurassic or earliest Cretaceous species, *C. couperi* Pocock, from Canada (Pocock, 1962) and Egypt (Helal, 1966) is dissimilar in its exine structure and is probably a cycadophyte (Pocock, pers. comm.; cf. Kemp, 1968).

Clavatipollenites is so variable that it undoubtedly represents several natural species. The coarseness of the sculpture varies greatly, and there is every degree of fusion of the heads of the pila, up to a good reticulum with large lumina. The grains usually have a simple sulcus, consisting of a granulate or irregularly sculptured area in the pilate forms (FIGS. 1c–e), or a well-delimited unsculptured membrane in the reticulate ones (FIGS. 1f,g). But especially in the overlying Patapsco Formation, the pilate grains often have a more irregular, sometimes trichotomosulcate aperture (FIG. 1h), as figured by Groot and Groot (1962) as *Apiculatisporis vulgaris* from Portugal, or they may be inaperturate or have several weak colpoid areas (FIG. 1i).[1]

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[1] Recently Hedlund and Norris (1968. Spores and pollen grains from Fredericksburgian (Albian) strata, Marshall County, Oklahoma. Pollen et Spores **10**(1): 129–159) have described polycolpoidate and tetra- and pentachotomosulcate grains from the Middle Albian as species of *Stephanocolpites* and the new genus *Asteropollis*. These grains appear to be essentially identical to the irregular-aperturate specimens of *Clavatipollenites* from the Potomac Group, but they show much more complete

The distinction between retipilate grains with an irregular sulcus and reticulate grains with a clearly defined sulcus and a tendency for the reticulum to detach is important in Kemp's (1968) separation of *Clavati-*

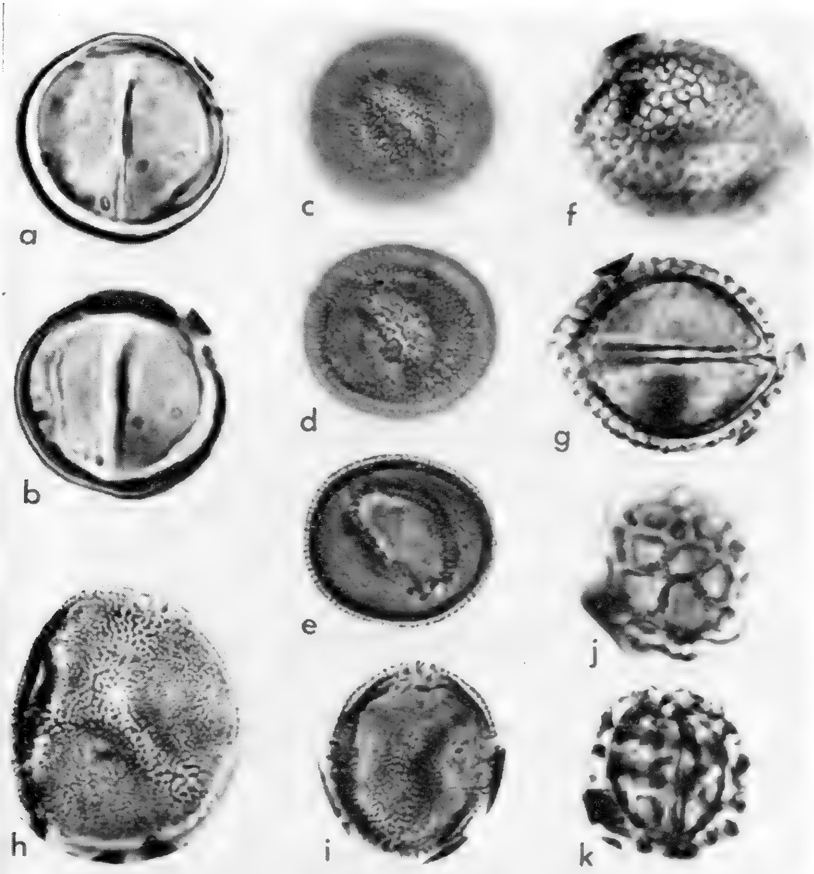

FIG. 1. Potomac Group gymnosperm and probable angiosperm pollen. Numbers in parentheses refer to slides. a and b, *Eucommiidites troedssonii*, grain with main sulcus on upper side, two focal levels (Aq 45–1c: Patuxent Fm., Zone I); c, d, and e, *Clavatipollenites* sp., flattened pilate grain with sulcus on lower side (Aq 27–1g: Patuxent Fm., Zone I); f and g, *Clavatipollenites* or *Liliacidites* sp., reticulate grain, two focal levels (Aq 44–1a: Patuxent Fm., Zone I); h, *Clavatipollenites* sp., trichotomosulcate grain (B 27–1c: Patapsco Fm., Subzone B of Zone II); i, *Clavatipollenites* sp., tetracolpoidate grain (65–1–2a: Patapsco Fm., Subzone B of Zone II); j and k, *Peromonolites* sp. (*sensu* Brenner), grain with sulcus (?) on lower side, two focal levels (Aq 18–1c: Patuxent Fm., Zone I). All figures × 1000.

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intergradation from sulcoidate to colpoidate. This gives further support to the hypothesis that zonaperturate (including tricolpate) pollen is derived from monosulcate through tri-, tetra-, or pentachotomosulcate intermediates.

pollenites hughesii and her species *C. rotundus*. She also found size and shape were reliable characters, but the retipilate forms in the Potomac Group are much more variable in size and shape than *C. hughesii* in England, overlapping considerably with *C. rotundus*, while the reticulate forms often lack the characteristic infolding of the sulcus margin of *C. rotundus* and sometimes have coarser sculpture. Brenner (1963) referred the reticulate forms, which he reported only from the Patapsco, to *Liliacidites dividuus* (Pierce) Brenner. However, the *Liliacidites* type intergrades with *Clavatipollenites* and does occur occasionally in the Patuxent-Arundel, favoring Kemp's treatment of both types as one genus. The status of *C. minutus* Brenner, defined on the basis of smaller size, is doubtful, since Kemp found it falls within the size variation of *C. hughesii*. Another form which should be re-evaluated is the small, coarsely reticulate *"Peromonolites" reticulatus* Brenner, which, as Norris (1967) suggested, may be an angiosperm related to *Clavatipollenites* rather than a perinate spore (FIGS. 1j,k).

Brenner (1963) was skeptical about the angiospermous nature of *Clavatipollenites*, and he suggested that it represents an extinct group of gymnosperms. This possibility cannot be denied, but there is no concrete evidence for it, and it loses its force because definite (tricolpate) angiosperm pollen appears in the next formation, and all the morphological characters are quite at home among the angiosperms. Much of the range of variation (though not all the intermediates) may be found in the Chloranthaceae: *Ascarina* pollen resembles the fine clavate-retipilate forms, *Hedyosmum* the coarser clavate irregular-aperturate ones, while *Sarcandra* pollen is reticulate and nearly inaperturate. Similar retipilate sculpture is seen in the Myristicaceae and many dicots with tricolpate pollen, and variation in the aperture from monosulcate to trichotomosulcate is common in several monocot and "ranalean" families, e.g. Canellaceae (Wilson, 1964). In general, *Clavatipollenites* has more in common with the "ranalean" dicots than the monocots, which tend to have reticulate or tegillate rather than pilate exines.

If *Clavatipollenites* is tentatively regarded as of angiospermous origin, it is the oldest definite pollen record of angiosperms (cf. Couper, 1964). Older reports have gradually been rejected as more has been learned of Mesozoic gymnosperms. *Eucommiidites* has been discussed; the alleged nymphaeaceous pollen from the Scottish Middle Jurassic (Simpson, 1937) appears to have been grains of the coniferous genus *Zonalapollenites* and folded araucariaceous grains (Hughes & Couper, 1958), and Rouse's (1959) Upper Jurassic *Pterocarya* was a corroded *Classopollis* grain (Pocock & Jansonius, 1961). *Classopollis* itself was originally misinterpreted by Pflug (1953) as a tricolpate grain. A possible older occurrence of tricolporates, in the Berriasian-Valanginian of the Netherlands (Burger, 1966), has not yet been restudied.

The presence of primitive angiosperm pollen in the Patuxent-Arundel is consistent with the megafossil record. Fontaine (1889) described dicot leaves, *Ficophyllum*, *Rogersia*, and *Proteaephyllum* (in part), from the

Patuxent near Fredericksburg, Virginia. Palynological study of the matrix (Harvard University Paleobotanical Collections: cf. Fontaine, 1889, p. 5) shows that this locality is indeed of lower Potomac age. Berry (1911) questioned that these leaves were dicots and suggested that they could be *Gnetum*, but reinvestigation by Wolfe (pers. comm.) shows none of the distinctive fine venation or fiber network characters of *Gnetum*, and instead a series of presumed primitive angiosperm characters found in the living Winteraceae. It should be noted that the distinctive permanent tetrads of the Winteraceae are absent in the Potomac Group pollen flora, so a direct affinity is questionable. Isolated entire margined dicot leaves are also reported from the Aptian of the USSR (Vakhrameev, 1952).

No consistent way has been found to subdivide the Patuxent-Arundel palynologically, and Brenner (1963) included both in one biostratigraphic unit, Zone I. The age has not been defined more precisely than Barremian, Aptian, or early Albian. *Clavatipollenites* and ephedraceous pollen (Couper, 1964) and the schizaeaceous spore assemblage (Hughes, pers. comm.) indicate a post-Hauterivian age. The general assemblage suggests middle more than early Lower Cretaceous (cf. Pocock, 1962), and it is very much like the flora described from undifferentiated Aptian-Albian rocks of Portugal (Groot & Groot, 1962). Determinations of an early Neocomian age based on the megafossils (Berry, 1911; Dorf, 1952) were made when younger pre-Albian floras were practically unknown. The upper limit on the age is defined by the absence of tricolpate angiosperm pollen in the Patuxent-Arundel and its appearance at the base of the overlying Patapsco Formation. The appearance of tricolpates, discussed in the following section, is often taken to mark the Aptian-Albian boundary, but the sporadic record of Lower Albian tricolpates leaves open the possibility that the Arundel-Patapsco boundary lies within the Albian.

PATAPSCO FORMATION

Changes in the pteridophyte spore and gymnosperm pollen flora between the Arundel and the Patapsco are rather minor: the entrance of a handful of new species which Brenner (1963) used as index fossils for his Zone II, and the decline of some groups such as *Classopollis* and the Schizaeaceae within the Patapsco. The most important event is the appearance of small reticulate tricolpate grains. This pollen type is unlike the "pseudotricolpate" *Eucommiidites* type in having radial symmetry and a reticulate exine, and it is at present restricted to the dicots. In the lower part of the Patapsco (Brenner's Subzone A) the tricolpates are very uniform and present only in low percentages; in the upper part (Brenner's Subzone B, recognized by the entrance of several distinctive spores and gymnosperm pollen) they become more diverse and abundant; on rare occasions they constitute a majority of the pollen and spore flora. Their percentage variation from sample to sample (Brenner in fact encountered Subzone B assemblages with no tricolpates) suggests that they were restricted ecologically to certain habitats. *Clavatipollenites* also increases in abundance in the Patapsco; forms with irregular aperture morphology are not uncommon (FIGS. 1h,i).

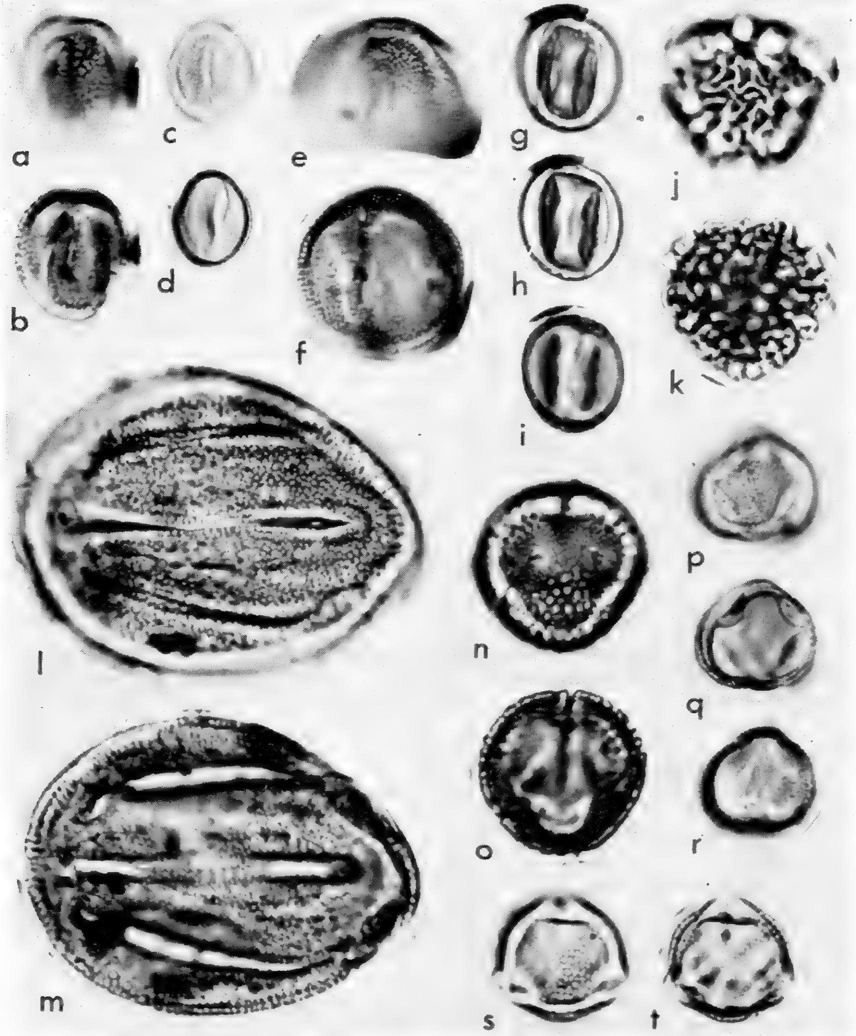

FIG. 2. Patapsco angiosperm pollen. All specimens from Patapsco Fm., Subzone B of Zone II. a and b, *Tricolpopollenites* cf. *micromunus*, two focal levels (65–1–2a); c and d, *Tricolpopollenites* cf. *minutus*, two focal levels (65–S–3h); e and f, Tricolpate type 1, pilate grain, two focal levels (65–1–2a); g, h, and i, Tricolpate type 2, nearly psilate grain, three focal levels (65–0–2g); j and k, "*Retitricolpites*" cf. *vermimurus*, polar view, two focal levels (65–2a–1a); l and m, *Tricolpopollenites* aff. *crassimurus*, two focal levels (65–2a–1b); n and o, Tricolpate type 3, reticulate, operculate grain, two focal levels (65–2a–1c); p, q, and r, Tricolporoidate type 1, grain with geniculate colpi, three focal levels (65–S–3i); s and t, Tricolporoidate type 2, oblate grain with subtriangular amb, two focal levels (65–2a–1j). All figures × 1000.

Patapsco tricolpate pollen shows some differentiation; at least in the upper part of the formation perhaps a dozen form species might be recognized. They are typically small (10–20μ), prolate or spheroidal in shape, with a fairly thin retipilate or reticulate exine, and colpi without any specialized margins or wide membranes. Many of the dominant forms (FIGS. 2a,b. Cf. *Tricolpopollenites micromunus* Groot & Penny, compared by Brenner to pollen of *Tetracentron*, or *Tricolpites albiensis* Kemp) have fine but well-defined retipilate or reticulate sculpture, without a continuous tegillum, and sexine somewhat thicker than nexine (1.0–1.5μ total exine thickness). *Tricolpopollenites minutus* Brenner is very small (11μ average axial dimension), with a reticulum which may be missed without oil immersion (FIGS. 2c,d). Besides these and similar microreticulate species, there are tricolpates with a *Clavatipollenites*-like exine, with free pila not arranged into a reticulum (FIGS. 2e,f), and at another extreme small forms with a nearly continuous smooth tegillum which were not reported by Brenner and are possibly restricted to the upper Patapsco (FIGS. 2g–i). Less common species are *"Retitricolpites" vermimurus* Brenner with a loose vermiculate reticulum (FIGS. 2j,k), and in the upper Patapsco large prolate tegillate grains close to *Tricolpopollenites crassimurus* Groot & Penny (FIGS. 2l,m), and a rather thick-walled spheroidal type with a coarse reticulum in the mesocolpia and internal thickenings (costae) at the margins of the operculate colpi (FIGS. 2n,o).

A previously unmentioned but possibly significant morphological feature of many of the Patapsco tricolpates, especially the *Tricolpopollenites micromunus* and *T. minutus* complexes, is a frequent buckling-out of the center of the colpi, giving them a geniculate appearance and suggesting a rudimentary os. This "tricolporoidate" tendency is prevalent in the upper Patapsco (FIGS. 2p–r). Another tendency, so far seen only in the upper Patapsco and later, results in oblate grains sub-triangular in equatorial outline, with the apertures at the protruding apices instead of sunken, as is the rule in Patapsco forms. These grains show differentiation of the nexine at the aperture and should probably be considered truly tricolporate (FIGS. 2s,t).

The appearance of tricolpate pollen seems to have been a major worldwide event, and in all areas which have been carefully studied there is a zone with small reticulate tricolpates but without triporates or typical tricolporates (cf. Krutzsch, 1963; Muller, 1968). This appearance generally may be dated as early or middle Albian, but refinement is needed in most areas. In England, the Patapsco-type *Tricolpites albiensis* Kemp appears at the base of the Middle Albian, but Kemp (1968) found rare grains of another tricolpate species in one Lower Albian sample. In western Canada tricolpates are reported by Norris (1967) from the base of the Colorado Group, which is considered basal Upper Albian (Norris) or late Middle Albian (Jeletzky, 1968) on the basis of ammonites, while they are reported to be absent from the underlying Mannville Group (Singh, 1964), which is presumably Middle Albian at the top. However, mid-Albian tricolpates cannot be ruled out here since the contact between the two groups is an unconformity, and in fact rare tricolpates occur locally in the upper Mannville (Pocock, pers. comm.; pers. obs.). The same relation holds in the U.S. Western Interior: tricolpates are present in the Thermopolis and Mowry shales of Colorado (lower Colorado Group equivalents; Tschudy & Veach, 1965), and in the Fall River Formation (basal Colorado Group equivalent) of the Black Hills, but they are absent from the underlying Lakota Formation (Cahoon, 1968). In Portugal, they occur in undifferentiated Albian but not in lower Aptian-Albian rocks (Groot & Groot, 1962); there are other reports from Albian rocks in France (Taugourdeau-Lantz & Jekhowsky, 1959), Germany (Krutzsch, 1963), and USSR (Zaklinskaya, 1961). In the central USSR Bolkhovitina (1953) reported tricolpates from the Lower Albian on; Yedemskaya (1960) found them in the Albian of the Caucasus, plus two isolated grains in the Aptian. In the Southern Hemisphere, tricolpates occur in the Upper Albian or Cenomanian of New Zealand (Couper, 1960), and in the Albian of northwestern Australia (Kemp, 1966).

In view of theories of a tropical origin of angiosperms, it would not be surprising to find earlier occurrences of angiosperm pollen or more pollen types in the present tropical areas. However, it appears that here, too, there is a zone with reticulate tricolpates and no triporates, and that the tricolpates do not appear demonstrably earlier than in present temperate areas. In North Borneo the Upper Albian or Cenomanian pollen flora contains angiosperms only of the same tricolpate and tricolporoidate types as in the Patapsco, associated with a very similar pteridophyte and gymnosperm flora (but lacking Pinaceae) (Muller, 1968). In northeast Brazil (Müller, 1966), the first angiosperm pollen is again reticulate tricolpates; the age is early Albian or possibly late Aptian. In higher zones (mid-Albian through Cenomanian, subdivision uncertain) these are joined by *Didymeles*-type tricolpodiorates and polyporates, and later triporates. In Upper Albian samples from Peru, Brenner (pers. comm.) found tricolpates and polyporates but no other angiosperm pollen. A very similar sequence occurs in Africa: in Senegal and the Ivory Coast reticulate tricolpates and tricolporates (tricolporoidates?) are the only angiosperms in the Lower (?) through much of the upper Albian; polyporates and later triporates enter higher in the Upper Albian-Lower Cenomanian interval (Vachey & Jardiné, 1962; Jardiné & Magloire, 1965). The Albian and Cenomanian of Gabon yield similar tricolpates, tricolpodiorates, triporates, and polyporates (Boltenhagen, 1965). The most unusual elements are the tricolpodiorates and polyporates. The latter are compared with the Amaranthaceae, but it should be noted that similar pollen occurs in some monocots (e.g. *Alisma* spp.). These pollen types do appear earlier in South America and Africa: the tricolpodiorates in fact are unreported elsewhere, but rare polyporates are known from the Cenomanian of Oklahoma (Hedlund, 1966) and Bohemia (Pacltová, 1966). Still, the record is consistent with a pre-Upper Albian interval with only tricolpate and tricolporoidate angiosperms.

Brenner (1963) considered the Patapsco to be Albian, and the record of the first tricolpates as reviewed here indicates that it is almost certainly no older than Lower Albian and may in fact be younger. Considering the record in England and the North American Western Interior, it is quite possible, as suggested by Wolfe and Pakiser (ms.), that the underlying Patuxent and Arundel are largely Lower Albian in age. More work on the pollen flora near the Aptian-Albian boundary in well-dated sequences (e.g., in Texas) is clearly in order.

Aside from the Fredericksburg material mentioned above, the first angiosperm leaves in the Atlantic Coastal Plain are found in the Patapsco (Fontaine, 1889; Berry, 1911), where they are still a subordinate element. Similar fossils occur in the (Middle?) Albian lower Blairmore flora of western Canada (Bell, 1956), the Cheyenne Sandstone of Kansas (Berry, 1922), deposits in the Kolyma basin in eastern Siberia (Samylina, 1960), Lower and Middle Albian rocks of Kazakhstan (Vakhrameev, 1952), and the Albian of Portugal (Teixeira, 1948); Vakhrameev (1952) and Takhtajan (1960) have noted the characteristic small size of these Albian leaves and suggested a relation to a still unperfected conductive system.

Brenner (1963) proposed an Upper Albian age for the upper Patapsco (Subzone B) on the basis of a close specific similarity to the Upper Albian-Lower Cenomanian angiosperm pollen flora of Portugal (Groot & Groot, 1962). It is generally in the Upper Albian that tricolpate pollen becomes a characteristic though still subordinate element in the flora and attains a certain low degree of diversity. Similar Upper Albian (-Lower Cenomanian?) floras are seen in the lower Colorado Group of western Canada (Norris, 1967), the Thermopolis and Mowry shales of Colorado (Tschudy & Veach, 1965), and Upper Albian-Lower Cenomanian strata in the USSR (Bolkhovitina, 1953; Bolkhovitina *et al.*, 1963). At the present time it is impossible to rule out a Lower Cenomanian age for part of Subzone B, considering the uncertain dating of the correlative deposits, the general lack of well-dated Lower Cenomanian pollen for comparison, and the only slightly more modernized floras of the Middle Cenomanian (cf. Hedlund, 1966, and below).

It is in the Upper Albian and Lower Cenomanian that we see the first megafossil floras dominated by dicot leaves. Such floras are the Dakota flora of Kansas (Lesquereux, 1892), long considered Upper Cretaceous but now known to be in part correlative with the Upper Albian Mowry Shale, the upper Blairmore flora of western Canada (Bell, 1956), and a series of Upper Albian floras from Kazakhstan (Vakhrameev, 1952). Characteristic for these floras are a variety of entire leaves and a large number of lobate leaves with platanaceous venation which have been referred to several unrelated modern genera (*Aralia, Sassafras, Sterculia, Liquidambar*). A "Dakota" flora has not been described from the Patapsco, but this may be because the early collections were made mostly near the Potomac River, where the Patapsco appears to be pinching out; I have seen upper Patapsco localities (65–2a, 65–S) rich in simple entire marginal leaves of a type not described by Berry (1911).

RARITAN FORMATION

The basal Coastal Plain unit in New Jersey, the Raritan Formation, has not been studied as comprehensively as the Potomac Group. The Woodbridge Clay member, near the base of the formation in the Raritan Bay area, is best known palynologically (Groot, Penny, & Groot, 1961; Kimyai, 1966; Wolfe & Pakiser, ms.). This unit, dated as Middle or Upper Cenomanian by marine fossils, is significantly younger than the typical Patapsco of Maryland: the angiosperm pollen is much more diverse, with several definite tricolporates (the dominant pollen type in modern dicots) and low percentages of the first triporates, the genera *Complexiopollis* Krutzsch and *Atlantopollis* Krutzsch of the Normapolles group of Pflug (1953). Older beds which promise to close the gap between the Patapsco and Raritan are becoming known to the south of Raritan Bay and in the subsurface, as are younger beds of presumed Turonian age (the South Amboy Fire Clay member) in the Raritan Bay area.

The Raritan is the first Coastal Plain unit in which angiosperms clearly dominate the pollen flora, but gymnosperms and pteridophytes are still important elements. These are mostly Pinaceae, Podocarpaceae (including *Phyllocladus*-like forms and perhaps the bizarre genus *Rugubivesiculites* Pierce, with a ruffled central body, which appears in the upper Patapsco but is most typical of the North American Upper Cretaceous), Taxodiaceae, Cupressaceae, Araucariaceae, Cyatheaceae, and Gleicheniaceae; the Schizaeaceae are in decline, and most of the extinct groups represented by *Classopollis, Eucommiidites, Vitreisporites,* etc. are very rarely seen. The angiosperm pollen of the Woodbridge includes reticulate tricolpates of the Albian type, though many appear to be new species, and occasional monosulcates (*Clavatipollenites, Liliacidites*). A larger portion is assumed by small psilate tricolpates and tricolporates (FIGS. 3a–d). Some of the most characteristic of these continue a trend seen in the upper Patapsco: they are oblate and triangular in equatorial outline, with apical apertures (FIGS. 3e,f. Cf. *Tricolporopollenites triangulus* Groot, Penny, & Groot). Besides these small, simple tricolpates and tricolporates, there are larger forms with more complex exine structure (reticulate to completely tegillate) and apertures (e.g., FIGS. 3g–i). An unusual new pollen type is represented by two forms with permanent tetrads: one is larger, with a smooth tegillum supported by large pila, and with somewhat obscure colpi arranged according to Fischer's law (FIGS. 3j,k); the other is smaller, psilate to retipilate, with very irregular colpoid areas (FIGS. 3l,m). Neither is like the familiar tetrads of the Ericaceae; the smaller type is strikingly similar to pollen of the monogeneric family Myrothamnaceae of South Africa and Madagascar.

The most striking new element is the first of the bizarre triporate Normapolles, which are dominant in the Upper Cretaceous and earliest Tertiary of Europe. They are an extinct group, not directly comparable to any living angiosperms, though if the complex protruding apertures of some of the later form genera were reduced somewhat and the grains became less triangular, they might approach pollen of some modern amentiferous

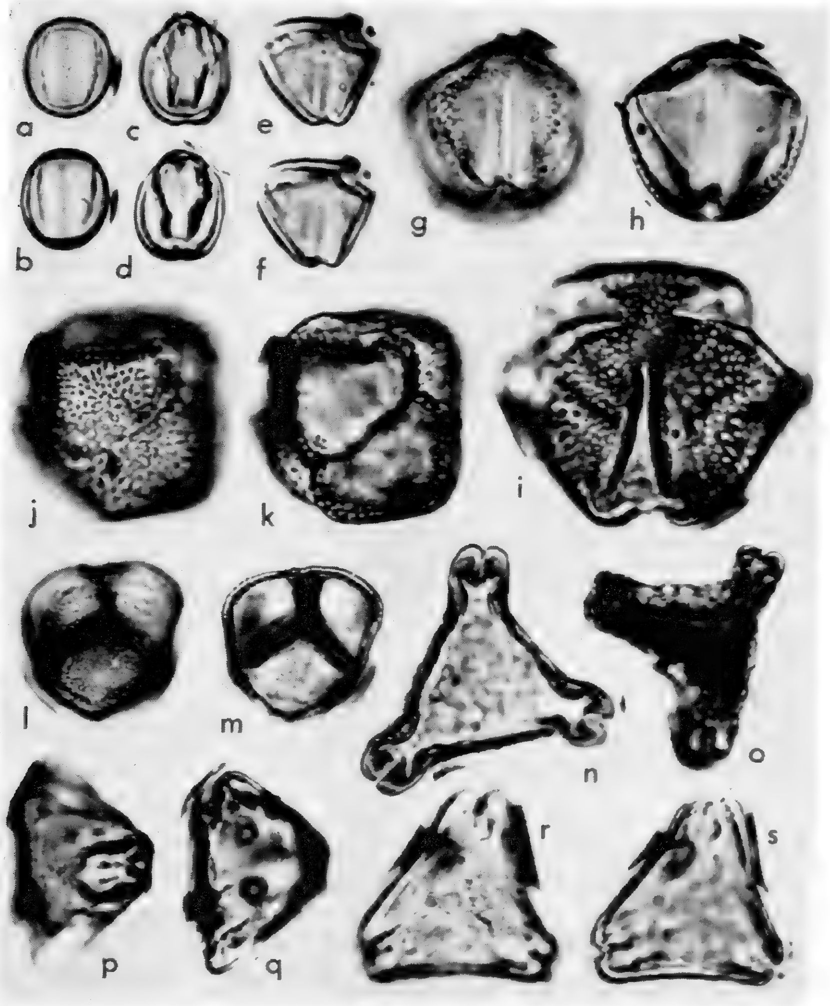

FIG. 3. Lower Raritan and Patapsco-Raritan transition zone angiosperm pollen. All specimens except p–s from Woodbridge Clay member, Raritan Fm. a and b, Tricolpate type 4, prolate, psilate grain, two focal levels (68–10–1b); c and d, Tricolporate type 1, prolate, psilate grain, two focal levels (68–8–1a); e and f, *Tricolporopollenites* cf. *triangulus*, two focal levels (68–10–1b); g and h, Tricolporate type 2, reticulate grain with flat mesocolpia, two focal levels (NJ 2–1a); i, Tricolporate type 3, reticulate grain with marginate colpi (68–8–1a); j and k, Tetrad type 1, large, tegillate grain, two focal levels (NJ 2–1a); l and m, Tetrad type 2, small, retipilate grain, two focal levels (68–10–1c); n, *Complexiopollis* sp. (NJ 2–1b); o: *Atlantopollis* sp. (68–10–1b); p and q, Tricolporate type 4, possible precursor of Normapolles group, oblique view, two focal levels (TR(1551–3)–1c: upper part of Patapsco-Raritan transition zone); r and s, same, polar view, two focal levels (TR(1551–3)–1c). All figures × 1000.

groups (Betulaceae, Casuarinaceae, Myricaceae, Rhoipteleaceae, Juglandaceae, Urticales). In fact, as was pointed out by Góczán *et al.* (1967) in their revision of the group, they cannot be rigidly separated from the Tertiary "Postnormapolles" of Pflug (1953), which include many of the modern "Amentiferae." *Complexiopollis* and *Atlantopollis* are among the oldest Normapolles in Europe. *Atlantopollis* differs from the psilate or scabrate *Complexiopollis* in its coarsely reticulate or (in New Jersey) verrucate sculpture. Apertures in both genera are very short colpi or elongate pores, with the nexine differentiated into an endannular collar just inside the pore (FIGS. 3n,o). The multiple endannular rings seen in European Turonian species and in the upper Raritan (FIG. 4a) are poorly developed in lower Raritan forms.

The Normapolles and other pollen and spores provide an age determination consistent with that from the marine fauna of the Woodbridge. A Normapolles assemblage with only *Complexiopollis* and its relatives was first described from the Lower Turonian of Germany (Krutzsch, 1959), but it has been extended an uncertain distance down into the Cenomanian. The Cenomanian Peruc Formation of Bohemia (Pacltová, 1966; Pacltová & Mazancova, 1966) is probably closest to the Woodbridge: very similar Normapolles are present in very low proportions, while the rest of the angiosperm flora contains reticulate and psilate tricolpates and tricolporates, including a triangular form of the *Tricolporopollenites triangulus* type (but also polyporates unknown in the Raritan). Cenomanian deposits of Portugal (Groot & Groot, 1962) also contain *Complexiopollis* and *Atlantopollis* (as *Latipollis*). In North America, the Tuscaloosa Group of Alabama, believed to be of late Cenomanian age, yields a flora with *Complexiopollis* and *Atlantopollis* almost identical to that of the Woodbridge (Leopold & Pakiser, 1964). *Complexiopollis* (as *Punctatricolporites*) appears near the putative Cenomanian-Turonian boundary in the Eagle Ford Shale of Texas (Brown & Pierce, 1962). Wolfe and Pakiser (ms.) believe the Woodbridge is Upper Cenomanian, and considering the low percentages of Normapolles this is probably correct, though the range data permit a Lower Turonian age as well. It is probably younger than most of the Middle Cenomanian, since Normapolles are not reported from the Middle Cenomanian Woodbine Formation of Oklahoma (Hedlund, 1966), nor the "Dakota Group" of Minnesota (Pierce, 1959), though both these floras have post-Patapsco elements such as psilate tricolporates and similar conifers (diverse *Phyllocladus*-type and *Rugubivesiculites*) and spores (common large *Sphagnumsporites*, *Camarozonosporites*, and *Gleicheniidites*).

Triporates other than Normapolles appear in other parts of the world probably in the Cenomanian, though the age control is lamentably poor. Thus in North Borneo grains with simple round pores appear in a zone loosely dated as Cenomanian to Senonian (Muller, 1968); triporates compared with Sapindaceae or Proteaceae appear near the end of an Upper Albian to Lower Cenomanian interval in Senegal and the Ivory Coast

(Jardiné & Magloire, 1965) and late in the Upper Albian through Cenomanian interval in northeast Brazil (Müller, 1966).

It is becoming clear that there was an interval in the Atlantic Coastal Plain after the typical Patapsco and before the Woodbridge with angiosperm floras including tricolporates, many psilate and some triangular, but without Normapolles. Extinct gymnosperms such as *Classopollis* are often common in these floras. This Patapsco-Raritan transition zone is seen in surface samples from Elk Neck in northern Maryland and near Trenton, New Jersey (Wolfe & Pakiser, ms.), from the uppermost "Raritan" of Bodkin Point, Maryland (pers. obs.), in the subsurface "Raritan" near Delaware City, Delaware (Brenner, 1967), at the top of the "Raritan(?)-Patapsco" in a well near Waldorf, Maryland, and in a well some thirty miles downdip from the Raritan Bay outcrop area on the Toms River, New Jersey (pers. obs.). The data of Wolfe and Pakiser and from the Toms River well suggest that the first "Raritan" elements to appear are the more prolate psilate tricolporates and, soon after, the triangular forms; other "Raritan" elements enter as Lower Cretaceous gymnosperms and ferns decline, until the flora is very close to the Woodbridge except for the absence of Normapolles.

In one of the uppermost pre-Woodbridge samples from the Toms River well, an unusual tricolporate occurs with a shape and sculpture very much like *Complexiopollis* but with longer vestigial colpi and no typical annulus or endannulus. The apertures approach those of some of the more complex Raritan triangular tricolporates, suggesting a link between less bizarre tricolporates and the Normapolles (FIGS. 3p–s).

Wolfe and Pakiser (ms.) characterize the pollen flora of the South Amboy Clay member as essentially the same as the Woodbridge flora except for some new non-Normapolles triaperturates. However, samples from four localities in the upper Raritan, including the classic Kreischerville collections of Hollick (New York Botanical Garden Paleobotanical Collections: cf. Hollick & Jeffrey, 1909), yield floras which appear to be significantly younger than the Woodbridge. Although many of the Normapolles might be considered advanced members of the *Complexiopollis* group (FIG. 4a), most show characters of the mid-Turonian and younger *Plicapollis* and *Vacuopollis* groups. Intergradations render generic separation difficult, but the genus *Pseudoplicapollis* Krutzsch, with rudimentary endoplicae and a characteristic pore structure, is definitely present (FIG. 4b). In most of the grains the apertures tend to protrude less than in *Complexiopollis* and consist of nearly round pores, with the nexinous collar retracted or reduced to produce a true vestibulum (as in *Plicapollis* Pflug) or atrium (as in *Vacuopollis* Pflug). Many show apparently structural folds (FIGS. 4c,d), though these are generally less regular than the "endoplicae" of typical (younger?) *Plicapollis*. Some of the subspheroidal forms approach the myricoid genus *Triatriopollenites* Thomson & Pflug (FIG. 4g). Also present are small psilate triporates perhaps unrelated to the Normapolles (FIGS. 4e,f), and large, oblate brevitricolporates (*Porocolpopollenites*, *sensu* Leopold & Pakiser 1964: FIG. 4h). Other new tricol-

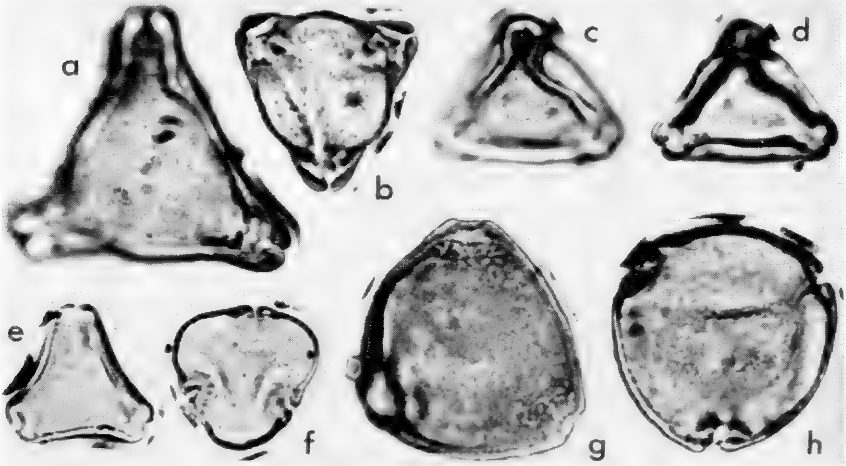

FIG. 4. Upper Raritan angiosperm pollen. a, *Complexiopollis* sp. (68–23–1a: South Amboy Fire Clay member); b, *Pseudoplicapollis* sp. (68–26–1a: South Amboy Fire Clay or Old Bridge Sand member); c and d, aff. *Plicapollis* sp., two focal levels (68–25–1a: South Amboy Fire Clay member); e, Triporate type 1 (68–23–1b: South Amboy Fire Clay member); f, Triporate type 2 (68–26–1b: South Amboy Fire Clay or Old Bridge Sand member); g, aff. *Triatriopollenites* sp. (68–25–1b: South Amboy Fire Clay member); h, *Porocolpopollenites* sp. (*sensu* Leopold & Pakiser) (68–25–1c: South Amboy Fire Clay member). All figures × 1000.

porates appear to be forerunners of typical Magothy species (cf. FIGS. 5h–k). Most of these forms are reported from the McShan and Eutaw formations of Alabama (Leopold & Pakiser, 1964), which are referred to the later Turonian by Wolfe and Pakiser (ms.). Although strictly comparable floras have not been described from Europe, the range data of Góczán *et al.* (1967) suggest a Middle or Upper Turonian age.

MAGOTHY FORMATION

The Magothy Formation, which extends from Maryland through Long Island, has a highly diversified angiosperm flora which has been described by Stover (1964), Groot, Penny, and Groot (1961), and more completely by Wolfe and Pakiser (ms.). As noted by Wolfe and Pakiser, the rich and advanced Normapolles element indicates a sizable break in deposition before Magothy time, though the presence of Turonian in the Raritan may close some of the gap. The Raritan marks the end of the nearly continuous mid-Cretaceous record; remarks on the Magothy flora will hence be only of a general nature.

Normapolles are a dominant element, represented by at least a dozen genera. The *Plicapollis-Pseudoplicapollis* group (with Y-shaped thickenings and vestibula), the *Vacuopollis* group, now represented by typical

Vacuopollis (with large atria and thick annuli made up of minute inward projecting rods), and *Trudopollis* Pflug (with thick annuli and endannuli and a space or interloculum between inner and outer exine) are especially common (FIGS. 5a–d). There are many small Normapolles (*Minorpollis*, etc.) and other simple triporates of the type seen in the upper Raritan (FIG. 5e; cf. FIGS. 4e,f). Such an assemblage must be at least as young

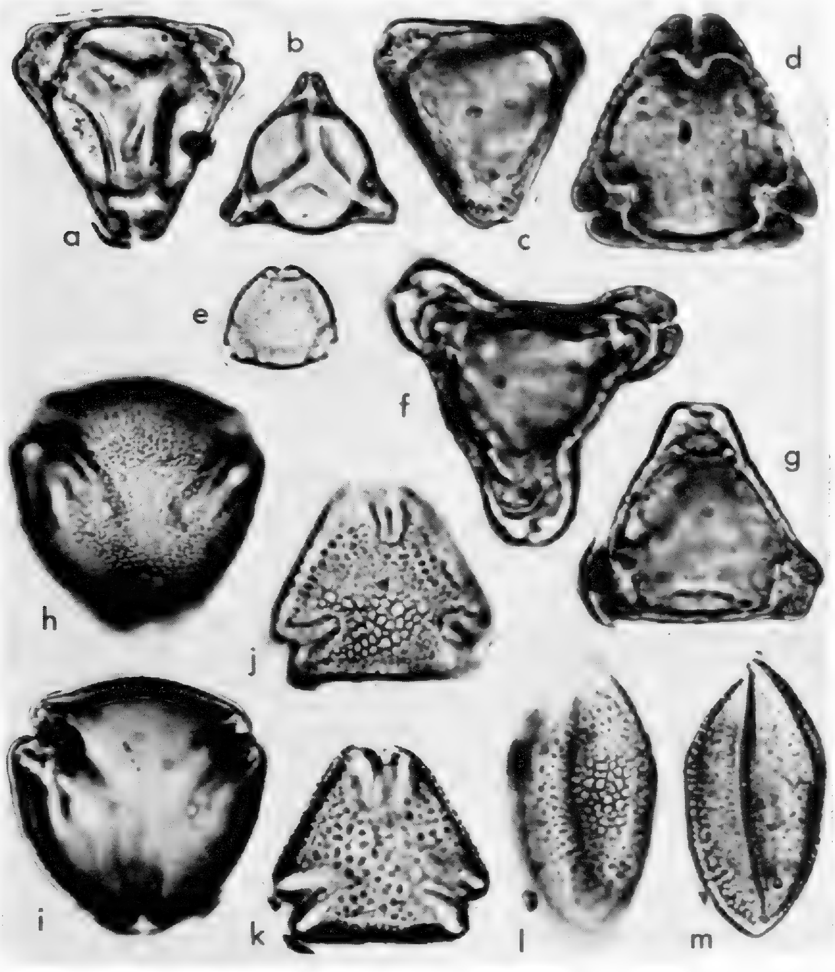

FIG. 5. Magothy angiosperm pollen. a, *Plicapollis* sp. (68–14–1a: Amboy Stoneware Clay member); b, *Pseudoplicapollis* sp. (68–14–1a); c, *Vacuopollis* sp. (68–14–1a); d, *Trudopollis* sp. (68–14–1a); e, Triporate type 3 (68–14–1a); f, aff. *Praebasopollis* sp. (68–14–1a); g, aff. *Pecakipollis* sp. (68–14–1a); h and i, Tricolporate type 5, two focal levels (68–16–1a: Cliffwood beds); j and k, Tricolporate type 6, two focal levels (68–16–1a); l and m, Monosulcate type 1, grain with sulcus on lower side, two focal levels (Ch-Bf 127(441–2)–1b: Magothy Fm. undifferentiated). All figures × 1000.

as mid-Coniacian (cf. Góczán *et al.*, 1967) and is probably younger, since most of these genera become abundant only in the Santonian (Krutzsch, 1957). More specific evidence is provided by close relatives or new species of the mid-Santonian and younger genera *Praebasopollis* Groot & Krutzsch (with two endannular lips extending into the large vestibula: FIG. 5f) and *Pecakipollis* Krutzsch & Pacltová (*Plicapollis*-like grains without clear endoplicae and with some *Trudopollis* traits: FIG. 5g). A Santonian age is verified by a late Santonian ammonite found in the upper Magothy of New Jersey (Sohl, pers. comm.).

Tricolpates and tricolporates, many continuing from the upper Raritan, are highly diverse in the Magothy. Upper Raritan and Magothy pollen types commonly suggest modern families, but most species have anomalous features or characters now found only in related families. Thus the grain in FIGURES 5h and i has some nyssaceous and cornaceous characters but would not be at home in either family, while the grain in FIGURES 5j and k has rhamnaceous apertures but hippocrateaceous or celastraceous sculpture, and the common myricoid grains (cf. FIG. 4g) have more of an endannulus than modern Myricaceae. Reticulate, psilate, and spiny monosulcates very suggestive of modern palms are abundant in some samples (FIGS. 5l,m). Palm megafossils, among the oldest known, are also found in the Magothy (Berry, 1916).

From the Turonian on, the world pollen flora is marked by provincialism which contrasts strongly with the cosmopolitanism of the early Cretaceous. Zaklinskaya (1962) first pointed out the major provinces of the Northern Hemisphere in the Senonian and Maestrichtian: the *Aquilapollenites* province in Siberia and western North America and the Normapolles province in Europe and eastern North America (cf. Góczán *et al.*, 1967). *Aquilapollenites* Rouse is a peculiar extinct form with a prolate, often heteropolar, central body and protruding arms bearing the apertures. It is often associated with pollen of possible proteaceous affinities which is common also in the Senonian of New Zealand, Australia, and Africa. *Aquilapollenites* has been found in equatorial Africa (Jardiné & Magloire, 1965) and Borneo (Muller, 1968), but not in the Normapolles province until the breakdown of provincialism in the Paleocene, when it occurs briefly in the Gulf Coastal Plain (Tschudy, pers. comm.). Normapolles are unknown in Africa and Borneo and very rare in Siberia. There are also strong similarities between the pollen floras of Africa and Brazil in the Upper Cretaceous, but these have not been studied as well (cf. Müller, 1966). The peculiar distribution of the Northern Hemisphere provinces is clearly a reflection of the epicontinental seas which extended from the Gulf of Mexico to the Arctic Ocean and along the east side of the Urals (cf. Tschudy, 1966).

The Magothy flora is a representative of the Normapolles province, but it illustrates that the province should be divided into American and European areas. Though many of the stratigraphically important genera and groups of genera are common to Europe, Wolfe and Pakiser (ms.)

point out that many bizarre forms are restricted to Europe, and many of the Magothy genera are new, being most nearly represented only by relatives in Europe. They note that the *Trudopollis* group is absent from the American Turonian, and that most of the Magothy dicots other than Normapolles are still unreported from Europe. The Atlantic Ocean certainly acted as a barrier to migration in the Senonian, but it is still surprising that it may have been less effective than the epicontinental sea of the American interior.

GENERAL EVOLUTIONARY IMPLICATIONS

In the late Lower Cretaceous the angiosperms are a very subordinate, undiversified element in the pollen flora; by the mid-Upper Cretaceous they are dominant and highly differentiated, though far from modern in total variation. The increase in diversity is regular, with new morphological types appearing not at random but in what can be read as series that permit derivation of each type from an earlier one. Small retipilate monosulcates are joined by small retipilate tricolpates; these pass into tricolporoidates and then tricolporates of more diverse exine structure, and these into the first triporates, which in turn diversify. The pollen record by itself leads unambiguously to the conclusion that we are witnessing a major adaptive radiation of a new group. Since we have the time dimension, we can tell which way to read our series and hence determine which character states are primitive (i.e. ancestral) and which advanced (i.e. derived). The resulting trends of course apply directly only to the plants of the time observed, and many of them have doubtless been reversed in later evolution, but they are relevant to modern groups insofar as the present major alliances are the result of this radiation and much of the ancient range in morphology is retained today. Likewise, we observe directly only evolution in pollen morphology, but this tells us something about general phylogeny insofar as pollen morphology is useful in recognizing taxa today, and as primitive or advanced characters in different organs are loosely correlated as a result of lesser or greater evolutionary rates in a given line (cf. Sporne, 1954).

The pollen record sets some limits on the time and place of origin of the angiosperms. The group must have originated at the beginning of the observed radiation (in the Barremian-Aptian) or earlier, though the possibility that the earliest pollen with angiosperm characters (*Clavatipollenites* and the early Albian tricolpates) was produced by plants which had not reached the angiosperm level in other organs should not be ignored. But at least in the Aptian, the typical dicotyledonous leaf morphology had been attained as well.

So far, the pollen record provides no conclusive evidence on the hypothesis that the angiosperms appeared and diversified first in the tropics. The earliest tricolpates there are similar to those in the temperate zones, though after the Middle Albian some pollen types seem to have appeared earlier in the tropics. There is suggestion of a lag of a third of a stage in invasion of the middle latitudes in reports of Lower Albian and even Aptian tricolpates in Africa and South America on the one hand and their poor record before the Middle Albian in England and North America on the other, but the stratigraphy requires much refinement before this can be considered established. In any case, the tropical belt in the early Cretaceous undoubtedly covered areas which are now temperate. The tree ferns and cycads in the Potomac Group suggest at least an equable (warm temperate?) climate, though the lack of bisaccate conifers in the tropics indicates some latitudinal differentiation.

One area that is ruled out as a center of angiosperm origin and evolution is the Arctic. Megafossil and microfossil floras from northern Siberia and Alaska north of the Brooks Range rarely contain angiosperms until well into the Cenomanian (Teslenko, 1958; Vasilievskaya, 1956; Smiley, 1966; Stanley, 1967; cf. Hughes, 1961b). Most of Seward's Lower Cretaceous angiosperm leaves from the Kome flora of Greenland appear to have come from the Upper Cretaceous, and the status of the one remaining leaf is uncertain (Koch, 1964).

It is certainly possible that primitive, undiversified angiosperms existed as a subordinate part of the flora long before the Barremian. We need only compare the mammals, which originated in the late Triassic but did not undergo major radiation until the Tertiary. Rare angiosperms with cycad-like pollen, as in several "ranalean" families, might easily go unnoticed in the Jurassic or Triassic. However, theories that postulate that the angiosperms not only existed but diversified long before the Cretaceous in isolated areas such as the tropical uplands (e.g. Axelrod, 1952) and simply migrated into other areas in the Cretaceous do become implausible in the light of the progressive appearance of morphological types. While we might expect a gradual increase in the number of types as a result of such migration, we would expect a sequence of unrelated derived types rather than convincing evolutionary series.

The record of early angiosperms is doubtless biased toward prolific pollen shedders and wind-pollinated offshoots. Even so, if much more highly evolved pollen was being produced by strictly insect-pollinated plants, we would expect to see it occasionally. Isolated large, more highly sculptured grains often found in the Potomac Group (e.g. "*Retitricolpites*" *geranioides* (Couper) Brenner or the form in FIGS. 2l,m) may in fact represent such plants, but they are similar morphologically to their smaller and more common associates. The simplest assumption, that the pollen we see preserved is fairly representative of the morphological types that existed at the time, is followed here.

The concept of an evolutionary radiation of angiosperms beginning in the early Cretaceous may appear to be in conflict with the megafossil record. Lower Cretaceous leaves have been placed in such unrelated modern genera as *Populus* and *Sassafras* and form genera (e.g. *Ficophyllum* and *Celastrophyllum*) intended to suggest families as distant as Moraceae and Celastraceae. To reconcile such diversity with the uniformity of the pollen flora by postulating that pollen evolution lagged behind while other organs differentiated to nearly a modern level would require an incredible amount of mosaic evolution in many lines. The pattern of variation in modern angiosperms suggests rather that, in general, pollen morphology has not behaved markedly unlike other character complexes: families may be either very uniform or diverse palynologically. What is needed is a re-evaluation of the leaf determinations, which were made without modern techniques of cuticle and fine venation analysis and apparently without the caution required in studying evolutionarily important fossils. Pacltová (1961) found that cuticles of "*Eucalyptus*" from the Cenomanian of Bohemia bore no specific relation to that genus; the platanaceous venation of Dakota leaves placed in several unrelated genera and Wolfe's case for the winteraceous affinity of *Ficophyllum* have been mentioned. A detailed study of the morphology of Cretaceous leaves might prove of more evolutionary interest than attempts at identification of taxa.

Specific Trends

The most striking evolutionary trends seen in early angiosperm pollen are in the apertures and shape of the grains. Other more questionable trends involve the exine sculpture and size. These trends are summarized in Table 3 (p. 28).

It would appear that the monosulcate condition of *Clavatipollenites*, the first convincing angiosperm pollen, is very primitive. Within this group we see as later variants trichotomosulcates, inaperturates, and grains with several ill-defined colpoid areas. There is a definite trend to fusion of structural elements into a true reticulum, as in *Liliacidites*.

The record is consistent with derivation of the tricolpates, the next most ancient major pollen type, from monosulcates of the *Clavatipollenites* type. The similar retipilate exine structure in *Clavatipollenites* and the earliest tricolpates favors this hypothesis over such alternatives as a completely independent origin or derivation from the *Eucommiidites* type. It is a general principle that in seeking ancestors for a group we should consider its most primitive (here earliest) members rather than advanced (later) forms (Thorne, 1963). There are, unfortunately, no obvious intermediates between monosulcates and tricolpates in the Cretaceous record, but the presence of trichotomosulcate apertures and irregular colpoids in *Clavatipollenites* may be significant. A theory of the origin of the tricolpate condition by loss of the polar connection of the three arms in a trichotomosulcate grain has been advanced by Wilson (1964). However, intermediate forms with three colpi displaced toward the pole are lacking. Another possibility is that the tricolpate condition represents the stabilization of an irregular situation with several colpoids. In the Chloranthaceae a similar process may have produced the longitudinal colpi (usually six) in *Chloranthus*.[2]

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[2] See footnote 1 on page 6.

Within the triaperturate group trends are more readily documented, and the wealth of intermediates leaves no need to invoke independent origin of the more complex forms. Tricolporates may have originated from tricolpates via tricolporoidates with only a slight weakening at the center of the colpus membrane. In some lines this trend was associated with a change in shape from prolate or spheroidal to oblate with a triangular amb and apical apertures. A pervasive trend in all the triaperturate classes (as well as the monosulcates), but most common in the tricolporates, was the fusion of exine structural elements into a complete tegillum, often resulting in psilate grains. Permanent tetrads also appear as a later offshoot in the triaperturate groups.

The small size of the early tricolpates suggests that this may be a primitive character in the triaperturates. However, the occasional presence of large grains suggests size was an unstable trait from the beginning, being subject to changes in pollination ecology. Small grains are often associated with wind pollination, but the Albian forms are even smaller than most amentiferous pollen. A comprehensive comparative study of size-pollination relations in modern angiosperm pollen would be desirable.

The culmination of the trend toward apical apertures is evidently seen in the triporate Normapolles, which may have been derived from conventional dicots through triangular tricolporates in pre-Woodbridge time. The Normapolles show various peculiar trends, such as the evolution of atria, vestibula, and other elaborations of the pores, and the development of endoplicae suggesting the arci of the Betulaceae, Rhoipteleaceae, and Ulmaceae. Soon after the origin of the group, the shape trend was apparently reversed to produce subspheroidal grains, as in most of the modern "Amentiferae." Other triporates, seen in the upper Raritan and parts of the world where Normapolles are lacking, may be of independent origin; they might originate by reduction of the colpus in a tricolporate grain or perhaps by contraction of the colpus in a tricolpate.

Pollen with numerous scattered pores occurs in the Cretaceous of some areas, apparently always after the entrance of tricolpates. Polyporates are found today in both monocots and dicots: the fossil record is consistent with derivation from either monosulcates or tricolpates and does not indicate which alternative is correct. Occasional dicolpate and polycolpate variants of tricolpate Raritan species and tetraporate Normapolles grains are within the normal variation of modern species; apparently such variation did not lead to major trends in the Cretaceous.

The proposed evolutionary relationships among the major pollen types are shown in their stratigraphic framework in FIGURE 6. This scheme is almost identical to the one proposed by Takhtajan (1959, 1966), based on the comparison of the pollen of angiosperms which are believed to be primitive or advanced in other characters. Many of the same trends are implicit in the writings of Bailey and coworkers (e.g. Money, Bailey, & Swamy, 1950) and of Wodehouse (1936). One of Takhtajan's important trends, from monosulcate to monoporate, is not shown since mono-

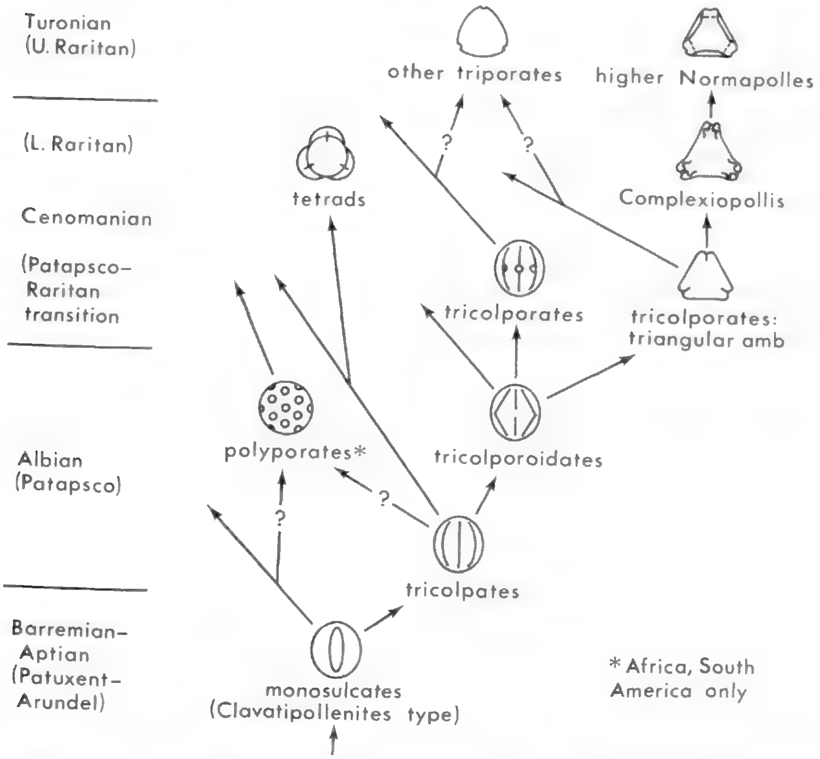

FIG. 6. Suggested evolutionary interrelationships of the major angiosperm pollen types of the Potomac-Raritan interval (Barremian-Turonian).

porates are not reported from Turonian or older rocks, but it is suggested by the record. Monoporates of a graminioid type are known from the Maestrichtian of Africa (Jardiné & Magloire, 1965).

The trends proposed here are very different from those of Kuprianova (1966), who lists as primitive a large number of characters found in such groups as the Santalales, many amentiferous plants, and Upper Cretaceous fossils including the Normapolles which suggest an ancestry with trilete spores. This approach overlooks earlier Cretaceous fossils which point toward simple tricolpate or monosulcate ancestral forms; the fossil sequence clearly shows sporelike Upper Cretaceous forms and their modern analogs are secondarily derived. As a rule, I would suggest that no exclusively post-Middle Albian pollen types can be used directly to reconstruct primitive conditions in angiosperms.

PHYLOGENETIC INFERENCES

Although the Cretaceous pollen record does not show us the origin of the angiosperms, it does allow us to make more secure inferences about the ancestors of the group. Thus the earliest monosulcate angiosperm pollen points to a group of gymnosperms with monosulcate pollen. This suggests an ancestor among the cycadopsids (i.e. the seed ferns and their presumed derivatives) rather than the coniferopsids or pteridophytes. An ultimate seed fern ancestor, making the angiosperms a parallel group to the cycads, Bennettitales, and Caytoniales, is suggested by the comparative morphology of the other plant organs (cf. Takhtajan, 1960; Cronquist, 1968). Clearly more must be known of Triassic, Jurassic, and, as Hughes (1961b) emphasizes, Lower Cretaceous gymnosperms before a more definite hypothesis may be presented.

Discussion of an ancestor of the angiosperms assumes the group is monophyletic, at least in the loose sense of Simpson (cf. Cronquist, 1968). This assumption is consistent with the record, which appears to show one major radiation, with the more ancient representatives of putative lines more instead of less similar to each other. Even the Normapolles may be derived from earlier tricolporates. This argument holds only for the basically tricolpate groups and their immediate monosulcate ancestors (i.e. the bulk of the dicots), and it does not mean all the characters we associate with the angiosperm grade had evolved when the taxon originated. In any case, it is quite likely that still more primitive groups with monosulcate pollen reached the angiosperm level in several lines, resulting in much of the heterogeneity of the living "Ranales."

Speculation on the affinities of early angiosperm pollen might easily lead to unwarranted conclusions on the age of modern taxa. It is not difficult to find modern analogs of Albian pollen: we have seen that much of the morphological variation in the *Clavatipollenites* type may be found in the Chloranthaceae, while similar generalized tricolpates occur in the Lardizabalaceae and Menispermaceae, or the Tetracentraceae, Hamamelidaceae, Platanaceae, and related families of the Trochodendrales and Hamamelidales of Cronquist (1968). However, the monosulcate and tricolpate complexes were young and evolving rapidly in the Albian, and their total diversity could probably be accommodated in two or three closely related orders and perhaps five to ten families. In contrast, the modern families mentioned are relictual and isolated from each other by specialization and extinction. It would probably be a mistake to believe the similarities indicate any more than that such taxa have retained a primitive pollen type, and hence perhaps other primitive characters.

Higher dicot groups (e.g. Salicaceae) may have reticulate tricolpate and tricolporoidate pollen, but unlike the Ranunculales, Trochodendrales, and Hamamelidales they are usually dominated by tricolporate pollen (cf. Fagaceae, Elaeocarpaceae, Flacourtiaceae). In terms of the subclasses of Takhtajan (1966) and Cronquist (1968), it is possible that Albian angiosperms had not evolved beyond the level of the Magnoliidae and lower Hamamelididae, and that the higher Hamamelididae (most of the "Amentiferae"), Dilleniidae, Caryophyllidae, Rosidae, and Asteridae were represented only by ancestors more primitive in pollen morphology and many other characters than their present members. These taxa may have differentiated in the radiation of basically tricolporate groups beginning in the Cenomanian. Some Upper Cenomanian tricolporates already suggest orders of the Rosidae such as the Cornales.

The fossil record indicates that extinct dicot alliances, represented by the Normapolles and *Aquilapollenites*, flourished in the late Cretaceous (cf. Krutzsch, 1963). The possibility of extinct major groups is largely ignored in angiosperm phylogeny, but it is quite relevant, for example, in the "Amentiferae," which may be in large part relics of the group represented by Normapolles pollen.

Since the basic monosulcate pollen type of monocots is common among "ranalean" dicots, the fossil pollen record is ambiguous on the origin of monocots. Though typical *Clavatipollenites* is most like the pollen of some modern dicots, the usually younger reticulate *Liliacidites* type could be either "ranalean" or monocotyledonous. Some Cenomanian pollen is more convincingly monocotyledonous in origin.

The discussion of the last paragraphs shows the consistency of the record with the systems of Takhtajan and Cronquist. In general, "ranalean" theories of angiosperm phylogeny are favored, since the earliest angiosperm pollen is of types characteristic of or restricted to groups considered primitive in such theories. On the other hand, systems which make the wind-pollinated "Amentiferae" primitive become implausible. The Betulaceae, Casuarinaceae, Myricaceae, Rhoipteleaceae, Juglandaceae, and Urticales all have basically triporate pollen (from the Normapolles?), a definitely derived, though ancient, type. The Fagaceae, with generally prolate tricolporate pollen, have a questionable status, but the unusual complex protruding apertures in *Trigonobalanus doichangensis* (Camus) Forman (Erdtman, 1967) suggest a relation to the Normapolles.

CONCLUSIONS

Angiosperm pollen types in the Cretaceous of the Atlantic Coastal Plain appear in essentially the same sequence as in other areas, including the tropics. In the Patuxent and Arundel formations (Barremian?-Lower Albian?) the retipilate monosulcate genus *Clavatipollenites*, apparently the oldest pollen with characters restricted to angiosperms, occurs in a flora dominated by pteridophytes and gymnosperms. Clearly dicotyledonous reticulate tricolpate pollen appears at the base of the Patapsco Formation (Lower-Middle Albian?); tricolpates increase in abundance and diversity in the upper Patapsco (Upper Albian-Lower Cenomanian?), where many show tricolporate tendencies. Definite tricolporates, often psilate and with triangular amb, occur in beds transitional to the Raritan Formation; in the lower Raritan (Upper Cenomanian?) they are joined by the first triporates, *Complexiopollis* and *Atlantopollis* of the extinct (pre-amentiferous?) Normapolles group. In the upper Raritan (Middle-Upper Turonian?), these pass into more advanced Normapolles genera.

The rich flora of the Magothy Formation (Santonian), which includes some forms suggesting modern families, is representative of the Senonian Normapolles province of Europe and eastern North America.

The expansion and diversification of angiosperm pollen in the Cretaceous is believed to reflect the basic adaptive radiation of the group, within which morphological series documenting evolutionary trends and the origin of major types may be recognized. Though the angiosperms may have originated well before the observed radiation, the idea that they were highly differentiated at their first appearance in the fossil record conflicts with the low diversity of Albian angiosperm pollen and the regular sequential appearance of morphological types. Trends such as monosulcate to tricolpate, prolate tricolpate to tricolporoidate to oblate tricolporate to triporate, and retipilate or reticulate to completely tegillate are in good agreement with trends postulated on the basis of comparative morphology and with systems in which the Magnoliidae and lower Hamamelididae are considered primitive and the "Amentiferae" advanced. Considering the evidence for important evolution in pollen characters, it is hoped that the megafossil record of early Cretaceous angiosperms will be re-examined with modern techniques and a more evolutionary-morphological point of view.

TABLE 3. **Evolutionary trends in pollen morphology based on the Cretaceous pollen record**

GENERAL APERTURE TRENDS:
- monosulcate, bilateral symmetry → tricolpate, radial symmetry
- monosulcate or tricolpate → polyporate
- simple colpi → complex apertures

MONOSULCATE GROUP:
- monosulcate → trichotomosulcate, inaperturate, or with several colpoids
- pilate or retipilate → reticulate or completely tegillate

TRIAPERTURATE GROUP:
- tricolpate → tricolporoidate → tricolporate → triporate
- tricolpate → triporate?
- prolate or subspheroidal → oblate, triangular amb, angulaperturate
- retipilate or reticulate → psilate, completely tegillate
- single grains → permanent tetrads
- small size → large size?

NORMAPOLLES GROUP:
- pores nearly simple → pores with atria or vestibula
- no endoplicae → endoplicae
- triangular amb → circular amb

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APPENDIX

LOCALITIES CITED IN TEXT AND FIGURES

PATUXENT FORMATION:

All specimens figured are from the lower Potomac Group exposed in construction of the Susquehanna Aqueduct between Baltimore and Aberdeen, Md., collected by E. T. Cleaves. Locality data are given in Cleaves (1968):

Aq 18 = Cleaves sample no. 18
Aq 27 = " " " 27
Aq 44 = " " " 44
Aq 45 = " " " 45

PATAPSCO FORMATION:

65–1: exposure on E side of parking lot behind Industrial Center on 52nd St., ca. 0.2 mi. N of junction of Kenilworth Ave. (Md. Rt. 201) and Baltimore-Washington Parkway, S of Bladensburg, Md. (Brenner's Station 17). Gray clay bed with cupressaceous twig compressions, 40–50′ above surface of parking lot and Brenner's sample, overlain and underlain by red and gray clay. Subzone B-1 of Zone II, vs. Subzone A of Zone II for Brenner's sample.

65–2a: NW side of West Bros. Brick Co. pit on N side of Sheriff Rd., 1.0 mi. E of Washington, D. C. city limit, ca. 0.7 mi. NW of Highland Park, Md. (Brenner's Station 29). Thin gray clay lens with dicot leaf compressions near top of predominantly red clay, roughly same level as Brenner's collection but toward N side of pit. Subzone B of Zone II.

65–O: exposure on NE corner of Branch Ave. and O St. SE, Washington, D.C. Gray clay lens with lignite bed, grading downward and laterally into red and white clay, and overlain by cross-bedded sands with ironstone concretions ("Raritan" Formation?). Subzone B of Zone II.

65–S: N side of Severn Clay Co. pit, 0.1 mi. N of road connecting Ritchie Highway and Md. Rt. 648, ca. 0.5 mi. SE of Harundale, Md. (Brenner's Station 11). Gray clay lens with dicot leaf compressions just above base of pit, overlain by red clay. Subzone B of Zone II.

B–27: James D. Bethards No. 1 well (Socony-Vacuum Oil Co.), ca. 5 mi. SW of Berlin, Md. (cf. Anderson, 1948). Gray clay core sample from 2735–2751′, provided by Maryland Geological Survey. Subzone B of Zone II.

PATAPSCO-RARITAN TRANSITION ZONE:

68–65: exposure overlooking Chesapeake Bay, ca. 0.6 mi. S of Bodkin Point, Anne Arundel Co., Md. Gray clay exposed just above beach level, passing laterally into red clay, overlain by yellow-white sands with ferruginous ledges. "Raritan" Fm.: Patapsco-Raritan transition zone.

Ch-Bf 127(536–7) and Ch-Bf 127(546–7): well ca. 1.5 mi. NE of Waldorf, Md. (Ch-Bf 127: cf. Hansen, 1968). Medium gray clay core samples from 536–537′ and 546–547′, obtained from Maryland Geological Survey. Near top of "Raritan(?)-Patapsco" Fm.: Patapsco-Raritan transition zone.

TR(1551–3): Toms River Chemical Co. Test Well No. 84, 39° 59′ 3″ N latitude, 74° 14′ 20″ W longitude, Ocean Co., N.J. Gray clay core sample from 1551–1553′, obtained from H. E. Gill through J. P. Owens, U.S. Geological Survey. Near top of Patapsco-Raritan transition zone: samples from 1369–1371′ and 1298–1300′ yield typical Woodbridge pollen and spores.

RARITAN FORMATION:

NJ 2: "Woodbridge, N.J." Light gray clay matrix from specimen of *Magnolia glaucoides* Newberry, N.Y. Botanical Garden Paleobotanical Collections. Woodbridge Clay.

68–8: S side of Sayre & Fisher Brick Co. pit, on S side of Main St., just NE of Sayreville, N.J. Near top of massive dark gray clay exposure. Woodbridge Clay.

68–10: E side of same pit. Medium gray clayey sand at top of massive dark gray Woodbridge Clay.

68–12: NE end of large sand pit ca. 0.5 mi. NNE of Phoenix, N.J. Gray clay capping thick cross-bedded sands. Old Bridge Sand?

68–23: W side of clay pit on N side of Washington Rd., ca. 0.5 mi. E of Parlin, N.J. Near base of thin-bedded gray clay unit, underlain by light gray sand, at low elevations in pit. South Amboy Fire Clay.

68–25: same pit. Near top of same clay unit, exposed just to W and 10–20′ higher. South Amboy Fire Clay.

68–26: same pit. Thin bed of laminated gray clay exposed near top of small hill near NW corner of pit, underlain by white sand, and overlain by thin bed of thinly laminated lignitic sand (68–27). South Amboy Fire Clay or Old Bridge Sand.

68–27: see under 68–26.

68–28: S side of abandoned sand pit off E side of Hillside Ave., just N of high voltage wires, Sayreville, N.J., above and to E of Sayre & Fisher pit (68–8, 68–10). Gray clay lens in predominantly coarse-medium grained sand. Sayreville Sand or South Amboy Fire Clay.

MAGOTHY FORMATION:

68–14: SW corner of Madison Township dump, 0.3 mi. E of U.S. Rt. 9, ca. 0.9 mi. S of junction with Ernston Rd., and 1.5 mi. SSE of Ernston, N.J. Dark gray clay overlain by thin-bedded alternating sands and clays of the Morgan beds of the Magothy Fm., near lowest elevations in dump. Amboy Stoneware Clay (J. P. Owens, pers. comm.).

68–16: bluff overlooking Raritan Bay NE of town of Cliffwood Beach, N.J. Gray silty clay just below contact with glauconitic Merchantville Fm. exposed at top of bluff. Cliffwood beds of Magothy Fm.

Ch-Bf 127(441–2): same well as Ch-Bf 127 samples under Patapsco-Raritan transition zone. Fine gray clayey sand core sample from 441–442′. Near top of Magothy Fm.

Note: Brenner localities are those described in Brenner (1963). Unless otherwise indicated, samples were collected by J. A. Doyle. All slides are located at the Harvard University Paleobotanical Collections.

DEPARTMENT OF BIOLOGY
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COMPARATIVE ANATOMY AND RELATIONSHIPS OF COLUMELLIACEAE

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> Género dedicado á Junio Moderato Columela, antiguo español, colocado por Linneo entre los padres de la Botánica, y que escribó elegantemente en prosa y verso de *Labranza y cultivo de Jardines* — Ruiz and Pavón 1794.

IN 1961, Brizicky summarized information on the Andean genus *Columellia* and presented a taxonomic synopsis of this puzzling group of plants. The genus was described in 1794 by Ruiz and Pavón and David Don established Columelliaceae in 1828. Eleven species have at one time or another been ascribed to the genus and through his critical examination of all available herbarium specimens, Brizicky reduced this number to four more or less well-defined species. Evaluations of the taxonomic position of *Columellia* and Columelliaceae have been set forth from the time of A. L. de Jussieu and Ruiz and Pavón, but even the latest authors have been unable to fix the relationships of these plants conclusively. "With its peculiar combination of opposite, exstipulate leaves; bisexual, epigynous flowers; somewhat irregular, sympetalous corollas; two stamens with plicate and contorted anthers resembling those of some Cucurbitaceae; two-carpellate, imperfectly two-locular ovaries; and imperfectly four-locular capsular fruits, *Columellia* is indeed a unique genus" (Brizicky 1961).

Although several positions have been proposed for *Columellia* and for Columelliaceae, taxonomists agree that a plausible understanding of the relationships of these plants requires comprehensive studies to clarify disputed points and to complete our knowledge of their anatomy. It was with this in mind that the present authors have examined the anatomy of the flower and fruit, node, leaf, and secondary xylem.

Taxonomic position of Columellia

A. L. de Jussieu (1801) considered *Columellia* as a genus of Oleaceae "hoc Genus ad Jasminearum ordinem pertinere." Kunth (1818) placed the genus in Scrophularinae, but noted, "An Gesnereis affinior?" At first Reichenbach (1828) included the genus in Gesneriaceae ("Gesnereae" as a tribe of Bignoniaceae) but later (1837) he transferred it to Oleaceae

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[1] George K. Brizicky died June 15, 1968 in Cambridge, Massachusetts, during the final stages of the preparation of this manuscript. It is to his memory that the surviving authors respectfully dedicate this paper.

("Jasmineae"). Bartling (1830) retained *Columellia* in Scrophulariaceae among "Genera incertae sedis." Sprengel (1830) supposed the affinity of the genus to be with Gesneriaceae. In 1839, Endlicher placed *Columellia* near Ebenaceae among "Genera Dubiae Affinitatis"; later (1841), he included it in his classis (order) Petalanthae (Primulaceae, Myrsinaceae, Sapotaceae, Ebenaceae, and Styracaceae) as a genus "Petalanthis affinis." Schnizlein (1843–1870) recommended an affinity with Saxifragaceae-Escallonioideae ("Escallonieen"), and particularly with the genera *Argophyllum* J. R. & G. Forst., *Brexia* Nor. ex Thou., and *Roussea* Smith. J. D. Hooker (1873, 1875) suggested referring the genus to Loganiaceae. Baillon (1888) included *Columellia* in Gesneriaceae as a representative of the monogeneric series Columellieae (between series Gesnereae and series Cyrtandreae). Hallier at first (1901) placed *Columellia* in Rubiaceae as an anomalous genus and later (1903) included it in Scrophulariaceae as questionably related to *Veronica* sect. HEBE Benth. of the tribe Leucophylleae. Finally (1908, 1910) he transferred it to Saxifragaceae-Philadelpheae. Herzog (1915) also regarded *Columellia* as a genus of Saxifragaceae.

Taxonomic position of Columelliaceae

David Don (1828), who founded the family Columelliaceae, considered it allied to Oleaceae ("Oleinae" and "Jasmineae") as well as to Styracaceae and Ebenaceae. Apparently following the suggestions of his brother, George Don (1838) showed Columelliaceae ("Columellieae") to contain three genera: *Columellia*, *Menodora* Humb. & Bonpl., and *Bolivaria* Cham. & Schlechtd. (= *Menodora* Humb. & Bonpl.). He placed the family between Oleinae and Jasmineaceae. Grisebach (1839) presumed a close relationship with Gentianaceae. Meisner (1836–1843) favored the affinity of Columelliaceae with Oleaceae. De Candolle (1839) assumed a close relationship with Gesneriaceae. Adrien de Jussieu (1848) placed Columelliaceae in Rubiales between Caprifoliaceae and Valerianaceae. Lindley (1835) put Columelliaceae in his alliance (order) Cinchonales (Rubiales) between Vacciniaceae and Cinchonaceae (Rubiaceae) with which families and Onagraceae he thought it related. He also presumed an affinity of Columelliaceae with Caprifoliaceae. Agardh (1858) suggested a close affinity of the family with Lythraceae ("Lawsoniae"). Basing his conclusions on the contorted anthers in both Columelliaceae and Cucurbitaceae, Clarke (1858) asserted that, ". . . if the nearest affinity of this family [Columelliaceae] is not with Cucurbitaceae, yet there is no other to which it more closely approaches. . . ." Following de Candolle, Bentham and Hooker (1876), and several of the more recent taxonomists — Fritsch 1894, Engler 1892 (unchanged in Melchior's 1964 edition of Engler's "Syllabus der Pflanzenfamilien"), Schlechter 1920, Wettstein 1935, and Pulle 1952 — placed Columelliaceae near Gesneriaceae. Fritsch emphasized the similarity with *Bellonia* L. (Gesneriaceae). Nevertheless, Wettstein stressed the continuing uncertainty of the systematic position of Columelliaceae. Warburg (1922) placed Columelliaceae near Gesneriaceae also; however, he noted: "Am natürlichsten dürfte die

Stellung bei den Rubiaceen sein." In 1959, Takhtajan allied Columelliaceae closely to Gesneriaceae, particularly with the genus *Ramonda* Rich. Here, and in his 1966 work, he stated that Columelliaceae is a derivative of Gesneriaceae. Hutchinson (1959) placed Columelliaceae in Personales with the families Scrophulariaceae, Acanthaceae, Gesneriaceae, Orobanchaceae, and Lentibulariaceae. Airy Shaw (in Willis 1966) stated: "Despite the sympetaly, slight zygomorphy and curious anthers [in Columelliaceae], probably related to *Escalloniac.* and *Hydrangeac.*; perhaps also to *Loganiac.*" In his recent conservative treatment of Saxifragaceae, Thorne (1968) treated Columelliaceae as a subfamily adjacent to Escallonioideae and Montinioideae. Columelliaceae is placed in Rosales by Cronquist (1968) near the Pittosporaceae and Grossulariaceae.

Anatomists have examined the microscopic structure of Columelliaceae in an attempt to establish its affinities with more certainty. Solereder (1899) was able to study the structure of *Columellia oblonga* Ruiz & Pavón ssp. *serrata* (Rusby) Brizicky (= *C. serrata* Rusby) and concluded that the occurrence of scalariform perforation plates and fibrous elements with conspicuous bordered pits in the secondary xylem precluded any close affinity with Gesneriaceae. Rather, he thought, Columelliaceae showed anatomical similarities to Saxifragaceae. Van Tieghem (1903), having several species of *Columellia* at his disposal, confirmed Solereder's anatomical observations, thus establishing the homogeneity of secondary xylem structure throughout the genus. However, van Tieghem believed Columelliaceae to be best placed in his alliance Rubiales near Rubiaceae. Metcalfe and Chalk (1950), having no further material at their disposal, repeated Solereder's findings. Erdtman (1952) stated that pollen morphology of Columelliaceae does not give any positive indications of the affinity of the family. He does remark, however, that "The following families have been mentioned as possibly related [to Columelliaceae]: Ebenaceae, Ericaceae, Gesneriaceae (the grains of *Bellonia* [Gesneriaceae] are not similar to those of *Columellia*!). . . ."

Columellia, or Columelliaceae, has been considered related to families of both Sympetalae and Choripetalae, to families with superior ovaries and to others with inferior ovaries. Some proposed relatives have stipules and others are exstipulate; some proposed relatives have opposite leaves and others have alternate leaves; some proposed related families are largely herbaceous and others are mostly woody. Among the taxa suggested as relatives, the following seem to predominate: The first proposals indicated Oleaceae; later the Ericaceae-Vaccinioideae and Rubiaceae were recommended; Scrophulariaceae appeared a few times in the literature during the early 19th century; but Gesneriaceae seemed most strongly defended in the late 19th and early 20th centuries. Although alliance with Saxifragaceae was suggested in the mid-19th century, it was not until the early 20th century and later that the proposal seemed to gain strength. Several other families have been proposed, though not as often as the foregoing: Ebenaceae, Styracaceae, Gentianaceae, Loganiaceae, Caprifoliaceae, and Onagraceae. Today, both the gesneriaceous and saxifragaceous hypotheses of relationship seem to have equal standing among plant taxonomists, although the most recent treatments favor alignment with saxifragaceous taxa. It is clear, though, that the variety of families proposed as relatives of *Columellia* (Columelliaceae) could not be much more diverse.

MATERIALS AND METHODS

In drawing comparisons between Columelliaceae and other families, it has been necessary for convenience and clarity to accept certain taxonomic delineations and judgements. This is especially important in referring to the Saxifragaceae which has been treated in different ways by different authors. Engler's (1928) treatment is the most detailed to date and his concept of the family is very broad. He divides Saxifragaceae into several subfamilies, namely, Penthoroideae, Saxifragoideae, Lepuropetaloideae, Parnassioideae, Tetracarpaeoideae, Pterostemonoideae, Iteoideae, Brexioideae, Kirengeshomoideae, Kanioideae, Baueroideae, Hydrangeoideae, Escallonioideae, Montinioideae, and Phyllonomoideae. Thorne's (1968) outline is very reminiscent of Engler's treatment. In our paper, when "Saxifragaceae, *sensu lato*," is employed, it is used in this broad Englerian sense.

Other taxonomists have chosen to disassemble the Englerian conglomerate into several smaller families; hence, Hutchinson (1967) treated Engler's subfamily Escallonioideae as the family Escalloniaceae and his subfamily Hydrangeoideae as the family Hydrangeaceae. Engler's tribe Philadelpheae of Hydrangeoideae is considered as Philadelphaceae by Hutchinson. The genus *Ribes* L. is part of the subfamily Saxifragoideae in Engler but Hutchinson treated it as the basis of the monogeneric family, Grossulariaceae. Cronquist (1968), similarly, has dissected Engler's Saxifragaceae. Because our comparisons among the vegetative parts of plants depend heavily on the information in Metcalfe and Chalk (1950), we have used their taxonomic designations for the Englerian subfamilies. The concept of Saxifragaceae employed by these two plant anatomists is wholly herbaceous, and the woody taxa in Engler's Saxifragaceae are relegated to other families, e.g., Escalloniaceae, Grossulariaceae, and Hydrangeaceae (including Hutchinson's Philadelphaceae). "Saxifragaceae, *sensu stricto*," as we have used it, refers to a strictly herbaceous family conforming to the sense of Metcalfe and Chalk.

Terminology used in the descriptions of xylem anatomy follows that prescribed by the Committee on Nomenclature of the International Association of Wood Anatomists (1957). Other terminology used in descriptions of anatomical structures is that in current use and deviations from common usage are explained where they occur.

TABLE 1 contains a detailed listing of specimens employed in the study of the vegetative anatomy of *Columellia*; materials used for comparative floral anatomy are cited in the text. Fluid-preserved material of about 30 flowers of *C. oblonga* ssp. *oblonga* was available from one of Továr's collections (*4033*, USM). All study specimens of wood, stems, leaves, and flowers (except for comparative floral material of *Escallonia* and *Carpodetus*), are supported by herbarium vouchers and their place of deposit is noted in TABLE 1 or in the text.

Methods of preparing specimens for study followed standard laboratory techniques. Woods were boiled in water to hydrate and stored in 70 percent ethanol prior to microtoming. Transverse, radial, and tangential sections of wood were stained with Heidenhain's iron-alum haematoxylin and counter-stained with safranin. Macerations of wood were prepared using Jeffrey's fluid. Clearing of leaves was carried out using Arnott's (1959) method involving 5 percent NaOH followed by a saturated aqueous solution of chloral hydrate. After washing in water, leaves were stained in aqueous safranin to accentuate vascular detail, dehydrated, and mounted on glass slides in Canada balsam. Transverse and paradermal sections of leaves were also prepared after embedding in paraffin. These were stained in Heidenhain's iron-alum haematoxylin and safranin. Nodal and petiolar anatomy were studied from hand-cut sections treated with phloroglucinol and concentrated HCl to differentiate the lignified tissues. Observations of floral anatomy were performed from serial microtome sections (transverse and longitudinal), cleared thick sections, and cleared whole flowers of *Columellia oblonga* ssp. *oblonga*. These preparations were made using familiar microtechnical methods from flowers fixed in formalin-acetic acid-alcohol.

ANATOMY

The flower

Transverse sections through the base of the *Columellia* gynoecium show two locules separated by a thick septum (FIG. 1, d, d^1). In successively more distal sections the placentas appear first as single lobes on each side of the septum (FIG. 1, e; FIG. 3), then as deeply two-lobed structures bearing many unitegmic ovules (FIG. 1, f). In still more distal sections there is an opening between the locules (FIG. 1, g, h), but the uppermost level of the ovary may again be divided by a complete septum (FIG. 2) through which the stylar canal enters the ovarian cavity.

If the stylar canal is followed distally its appearance in transverse section changes from that of a single cavity to that of a pair of tracts filled with pollen-transmitting tissue (FIG. 1, j, k). The pollen-transmitting tracts expand greatly below the two-lobed stigmatic surface, producing the unusual transectional effect shown in FIG. 4. The outer layers of gynoecial tissue, from the stylar base to the corolla, constitute a nectary of small cells with densely staining cytoplasm (FIG. 2).

Flowers of *Columellia* are devoid of unusual histologic features that can be used as taxonomic markers. The hypanthium, like the foliage, is

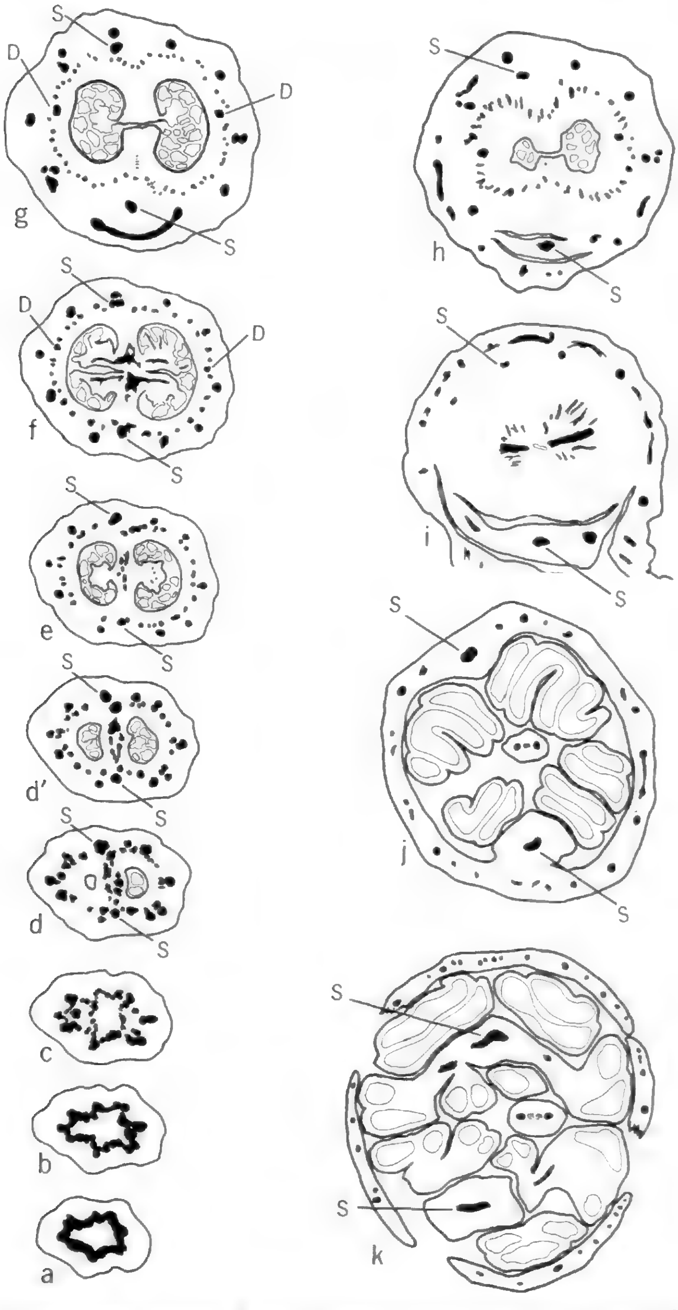
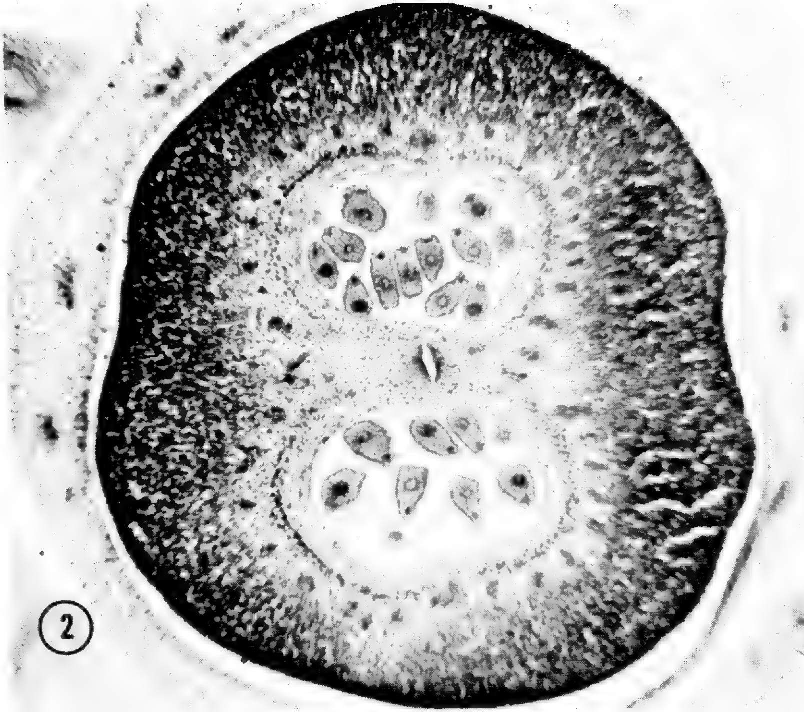


FIG. 1. *Columellia oblonga*, flower. Camera lucida drawings of selected transverse sections, arranged sequentially from pedicel (a) to upper part of flower (k). D, dorsal carpel bundles; S, stamen supply.

②



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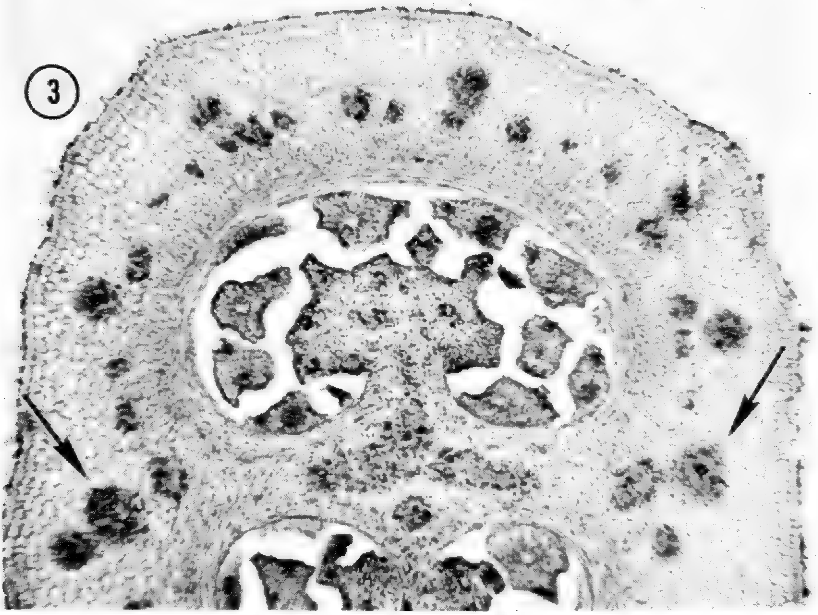

FIGS. 2 and 3. *Columellia oblonga*, flowers in transverse section. FIG. 2. Upper (free) part of gynoecium, showing nectary and upper ovarian septum, × 30. FIG. 3. Lower part of flower showing basal septum, arrangement of vascular bundles (cf. FIG. 1,e); arrows indicate bundles supplying the 2 stamens, × 60.

covered with simple, appressed trichomes. Floral tissues contain no conspicuous tannin cells or sclereids and no crystal inclusions except for a few scattered druses. The anthers dehisce with the aid of the familiar subepidermal banded layer (FIGS. 6, 7); moreover, the sporogenous portions, in spite of their peculiar external form, resemble in section the corresponding parts of ordinary four-locular anthers. The anther sacs, at least the young ones, are minutely glandular-hairy at the margins, the glandular trichomes being more or less club-shaped. The gynoecium contains a well-marked endocarp tissue, four to six cells deep on the dorsal side of the locule, gradually decreasing in thickness in the vicinity of the septum and the placentas. Cell walls of the endocarp are neither lignified nor greatly thickened in newly opened flowers, and there is no anatomical indication of a dehiscence line at this stage.

Floral vascular bundles, many of them amphicribral, diverge from a continuous cylinder in the pedicel (FIG. 1, a, b). Well below the base of the locules, the cylinder expands into the pattern shown in FIG. 1, c, with an inner portion of the vascular tissue directed to the septum and the placentas and an outer portion directed to other parts of the flower. A few sections above this level, and still below the locules, the outer portion separates into two series of traces, a gynoecial series and a series supplying perianth and stamens. With additional branching at even higher levels (FIG. 1, d, d^1, e), the gynoecial series contains as many as 20 bundles per carpel, and the other series (now outermost) contains about a dozen perianth traces plus two stamen traces. A stamen trace can be united for part of its length with the basal extension of a sepal midvein or it can be completely free of other bundles to the base of the flower. In either case, the position of the stamen traces is the same; they occupy roughly the same radius as the septum. The perianth traces, if followed distally, become the major veins of sepals and corolla lobes. As in many other kinds of flowers, there are lateral connections between these strands at the level where the calyx and corolla become free of the ovary wall, and minor strands diverge from the major ones within the perianth members. The vascular tissue of the stamen broadens within the filament (FIG. 1, k) and terminates in the connective with a great many short branches.

The vascular supply to the placentas rises through the septum in a massive and irregular column or plexus (FIG. 1, c–f). Branches to the ovules diverge from the plexus all through the placental region, but this portion of the vascular system does not continue above the placentas. The many outer gynoecial bundles, however, extend all the way to the base of the style (FIG. 1, g–i). Although the dorsal bundle is not easily distinguishable in sections through the lower half of the ovary, it is conspicuous in higher sections because of its proximity to the locule (FIG. 1, g, h). The dorsal bundle can be followed into the style, which it enters as a single well-defined strand. About a third of the way up the style, it divides into two or more strands, which subdivide further into many

TABLE 1.
Specimens of Columellia Examined

SPECIES	COLLECTOR	ORIGIN	VOUCHER	PARTS STUDIED *
lucida Danguy & Chermezon				
	André K–1444	Ecuador	F, GH	t
	André 4500	Ecuador	F, GH, NY	t
	Friedberg 240	Peru	US	l
	Mutis 2784	Colombia, *sine loco*	US	l
oblonga Ruiz & Pavón ssp. *oblonga*				
	Wurdack 1732	Peru	US	USw 32548, l
	Továr 4033	Peru	USM	USw, 36964, l, f
	Továr 3785	Peru	US	l
	Ruiz & Pavón 1/52	Peru	F	t
	Weberbauer 5584	Peru	F, GH, US	t, l
	Weberbauer 7791	Peru	A, F, MO, US	t, l
	Camp E–4461	Ecuador	GH, NY, Y, US	l
	Vargas 7408	Peru	US	l
	Cook & Gilbert 850	Peru	US	l
	Cook & Gilbert 1749	Peru	US	l
oblonga Ruiz & Pavón ssp. *sericea* (H.B.K.) Brizicky				
	Hitchcock 20846	Ecuador	GH, NY, US	l
	Rimbach 30	Ecuador	F, GH, Y	Yw 19496
	Rimbach 122	Ecuador	A, F, Y, US	Yw 22824, l

	Drew E–113	Ecuador	US	l
	Jameson *s.n.*	Ecuador	US 534794	l
	Jameson *s.n.*	Ecuador	US 534793	l
	Mille 44	Ecuador	A, GH, NY, US	l
	Mille 409	Ecuador	US	l
	Ownbey 2618	Ecuador	US	l
	Dodson & Thien 1067	Ecuador	US	l
	Asplund 7152	Ecuador	US	l
	Asplund 8003	Ecuador	US	l
	Wiggins 10351	Ecuador	US, DS	l
	Lehmann 4685	Ecuador	F, US	l
	Fosberg 21175	Colombia	US	l
oblonga Ruiz & Pavón ssp. *serrata* (Rusby) Brizicky				
	Bang 1172	Bolivia	US	l
obovata Ruiz & Pavón				
	Weberbauer 5482	Peru	F, GH, US	t, l
	Herrera 3451	Peru	F	t
	Velardo Nuñez 3309	Peru	US	t, l
	Továr 1266	Peru	US	l
	Dombey *s.n.*	Peru	US 1706475	l
	Dombey *s.n.*	Peru	US 1706480	l
	Vargas 7693	Peru	MO, US	l

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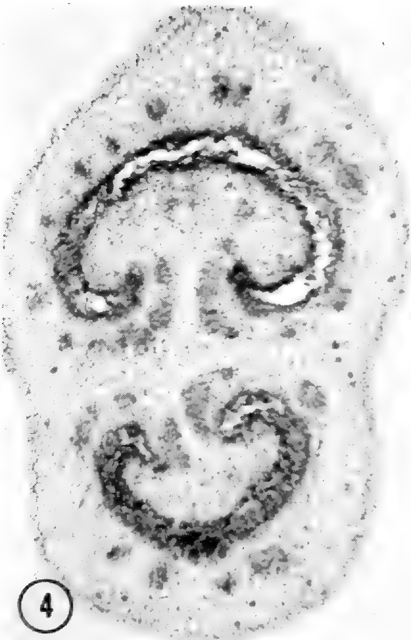
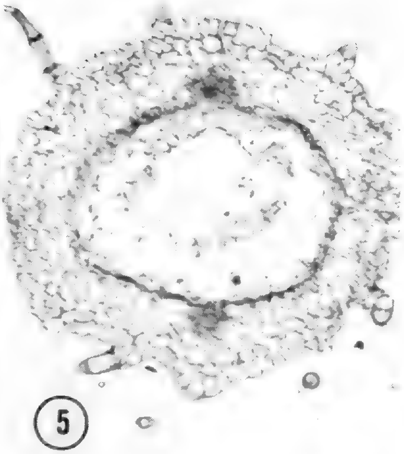
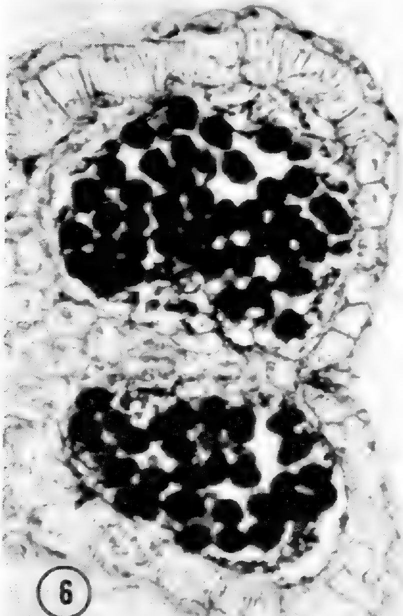
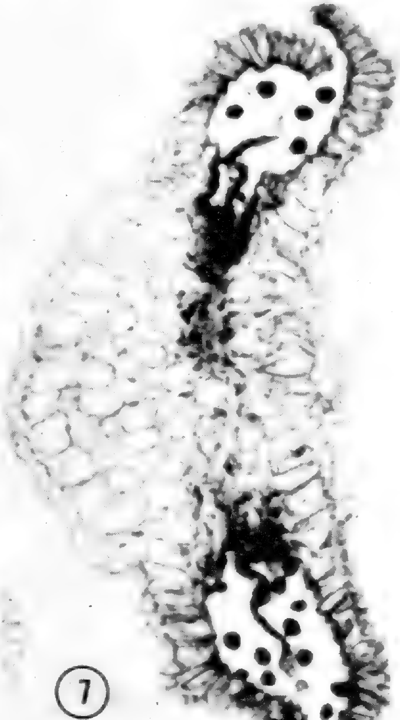
* l = leaf, w = wood, t = twig, f = flower; abbreviations of institutional wood collections follow Stern (1967) and Stern and Chambers (1960).

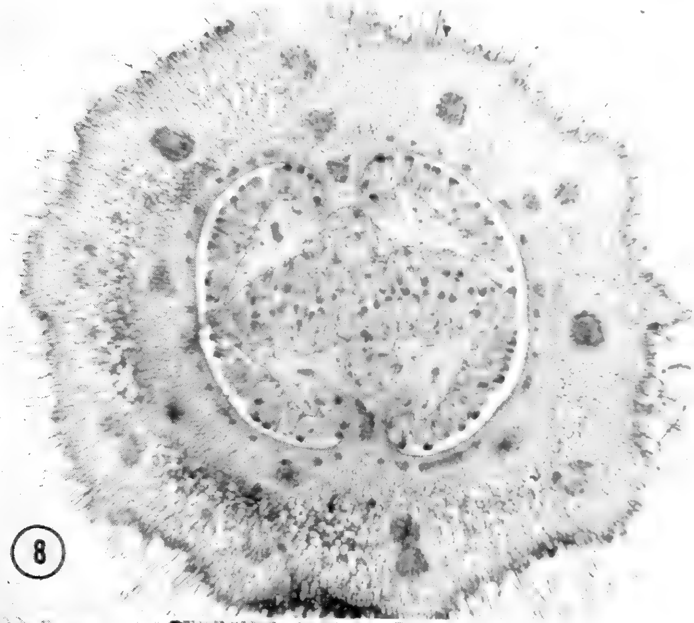








FIGS. 4–7. FIG. 4. *Columellia oblonga*, transverse section through upper part of style, × 55. FIG. 5. *Kohleria elegans* (Gesneriaceae), transverse section through upper part of style, × 66. FIGS. 6 and 7. *C. oblonga*, transverse sections of anthers before and after dehiscence. FIG. 6, × 125. FIG. 7, × 95.



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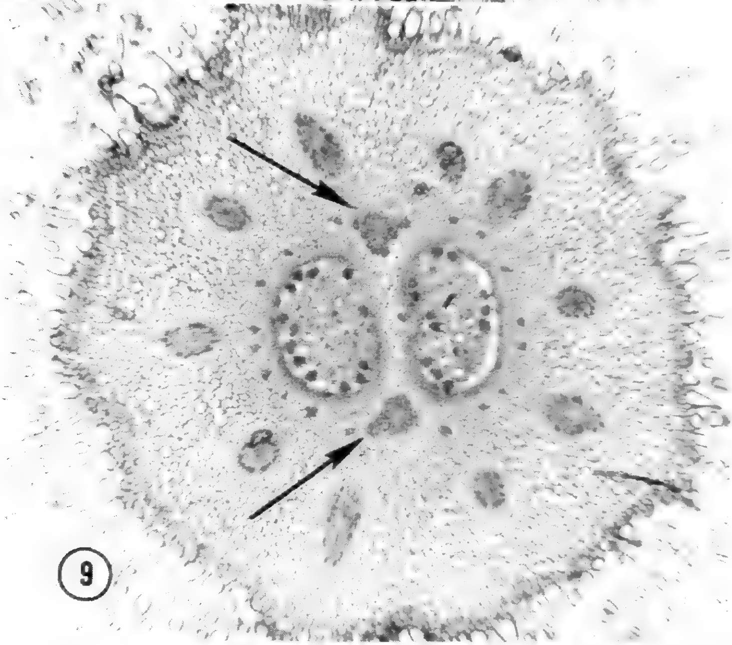

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FIGS. 8 and 9. *Kohleria elegans* (Gesneriaceae), transverse sections through lower part of flower. FIG. 8. Placental region, × 25. FIG. 9. Another flower, sectioned below placenta to show basal septum and ventral bundles (arrows), × 34.

strands just below the stigma. The remaining bundles of the gynoecium wall converge upon the dorsal at the base of the style (FIG. 1, i); however, they do not appear to merge with the dorsal, because it enters the style with its cross-sectional shape and dimensions unchanged.

The leaf and the node

Hairs on leaves of *Columellia* are thick walled and simple, tapering to the obtuse tip and slightly swollen or bulbous at the base (FIGS. 10, 11). Trichomes emanate from the center of saucer-shaped depressions in the lower epidermis. These are formed from several radially oriented cells each of which is thicker toward the periphery of the depression and thinner toward the center where the hair arises (FIGS. 10, 11).

The cuticle is thick and covers upper and lower epidermis. It is especially pronounced toward leaf margins and in the trichome-base depressions of the lower epidermis. It also covers all portions of hairs. The cuticle is strongly modified in the stomatal region; it covers the exposed surfaces of guard cells and it over-arches both the outer portion of the aperture producing a front cavity and the inner portion producing a back cavity (FIGS. 11, 12).

Stomata are restricted to the lower epidermis. The stomatal apparatus[2] is anomocytic (*sensu* Metcalfe and Chalk, 1950), i.e., the guard cells are surrounded by cells of varying number which are indistinguishable in form or position from the remainder of the epidermal cells (FIG. 10). Guard cell walls are thickened along the inner surface facing the spongy mesophyll and on the outer surface (FIGS. 11, 12). In paradermal view, guard cells are elongate-reniform (FIG. 10).

The lower epidermis is uniseriate; the upper epidermis is biseriate (FIGS. 11, 13, 15). Since developmental studies could not be conducted, it is not possible to determine if the inner layer is protodermal in origin or if it arose from the ground tissue. Inner cells of the biseriate upper epidermis are larger and conspicuously more rotund than those of the outer layer (FIGS. 13, 15). Leaves are dorsiventral and the mesophyll is divided into a biseriate, upper palisade layer and a lower spongy layer. In the thickish leaves of *Columellia lucida* and *C. obovata*, the transition between palisade and spongy mesophyll is not sharp. Furthermore, in these two species, there is a tendency for a lower palisade layer to be formed and an isobilateral condition (FIG. 15).

Leaves of all species of *Columellia* are glandular; in those species having serrate leaves, the tips of the teeth and the apical point are glandular; in species with entire leaves, the apex of the leaf may be glandular.

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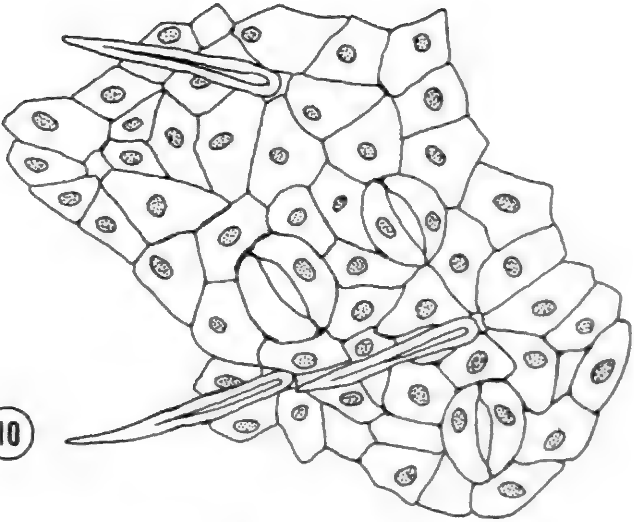
[2] Although Metcalfe and Chalk (1950), Fahn (1967), and Esau (1965) do not agree, the first author would prefer to use the term *stoma* (Gr. a mouth) in its restricted sense to mean the actual aperture or pore in the epidermis which is surrounded by the guard cells. The term *stomatal apparatus* is used here to mean the stoma, guard cells, and subsidiary (accessory) cells, if present. The maintenance of separate terms for the aperture and guard cells seems meritorious in that it provides for independent reference to each of these units and alleviates the possible redundant implications of referring to the "aperture of a stoma."



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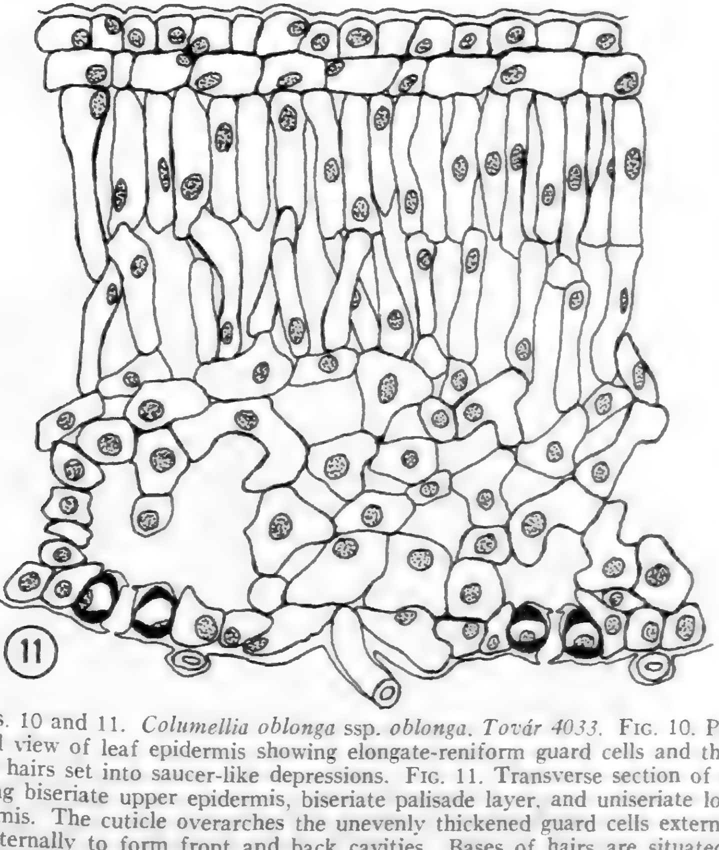

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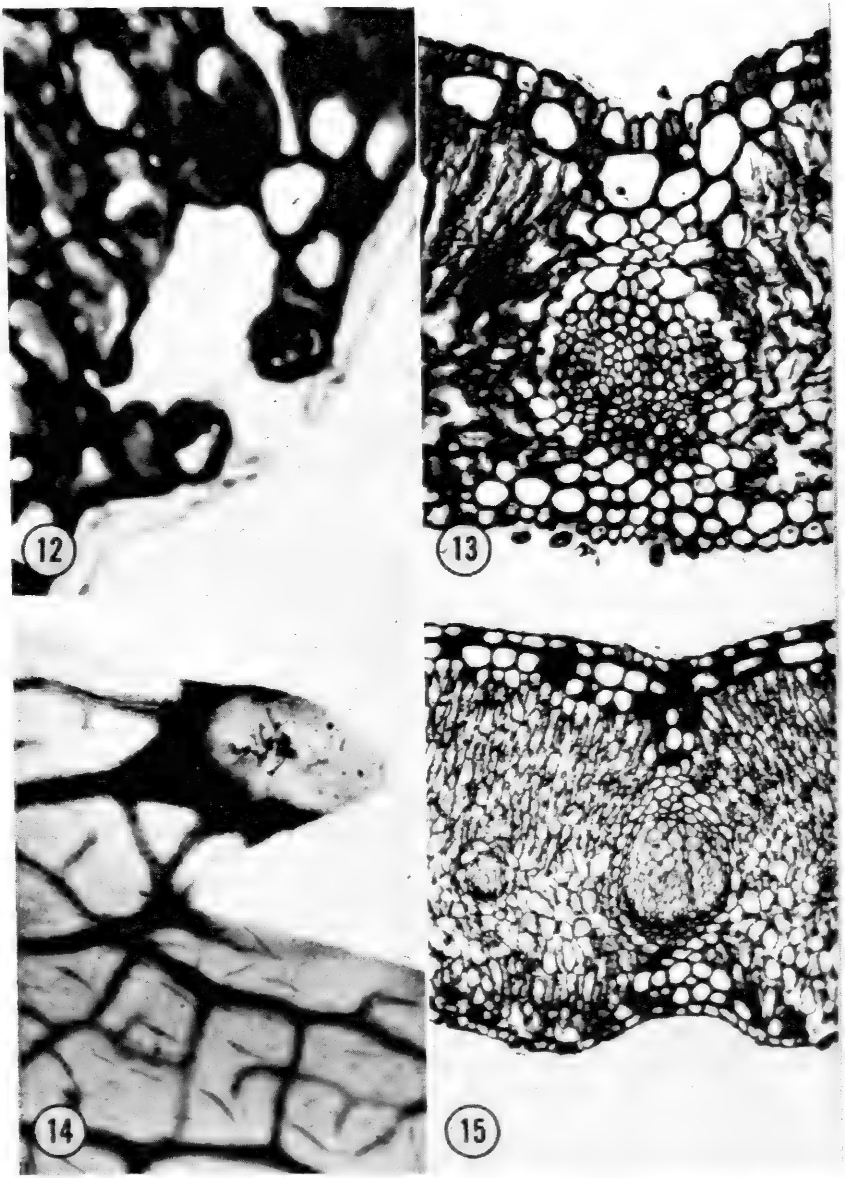
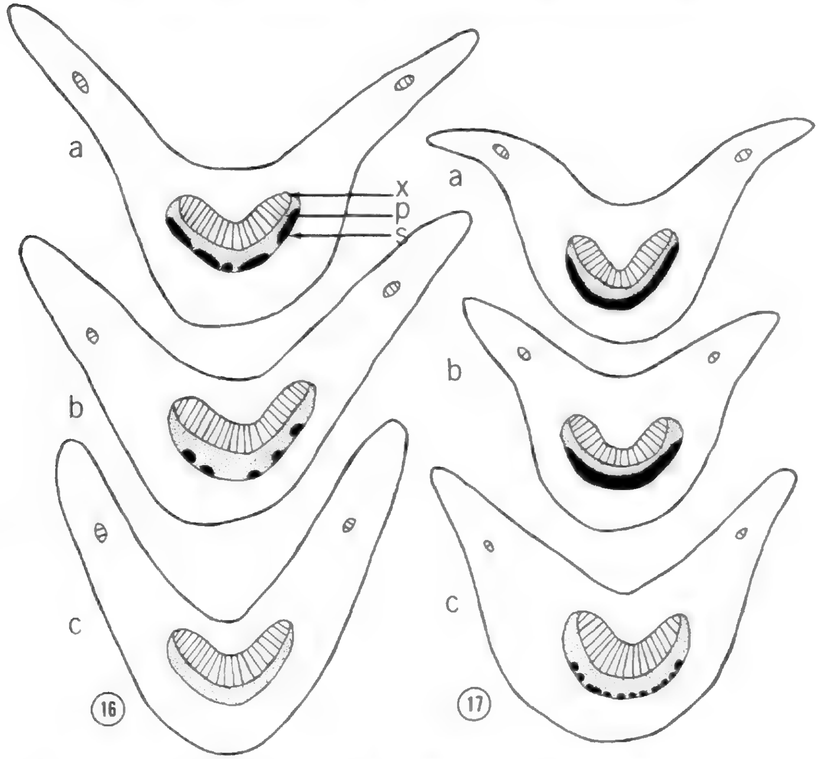
FIGS. 10 and 11. *Columellia oblonga* ssp. *oblonga*. *Továr 4033.* FIG. 10. Paradermal view of leaf epidermis showing elongate-reniform guard cells and thick-walled hairs set into saucer-like depressions. FIG. 11. Transverse section of leaf showing biseriate upper epidermis, biseriate palisade layer, and uniseriate lower epidermis. The cuticle overarches the unevenly thickened guard cells externally and internally to form front and back cavities. Bases of hairs are situated in saucer-like depressions of the lower epidermis.



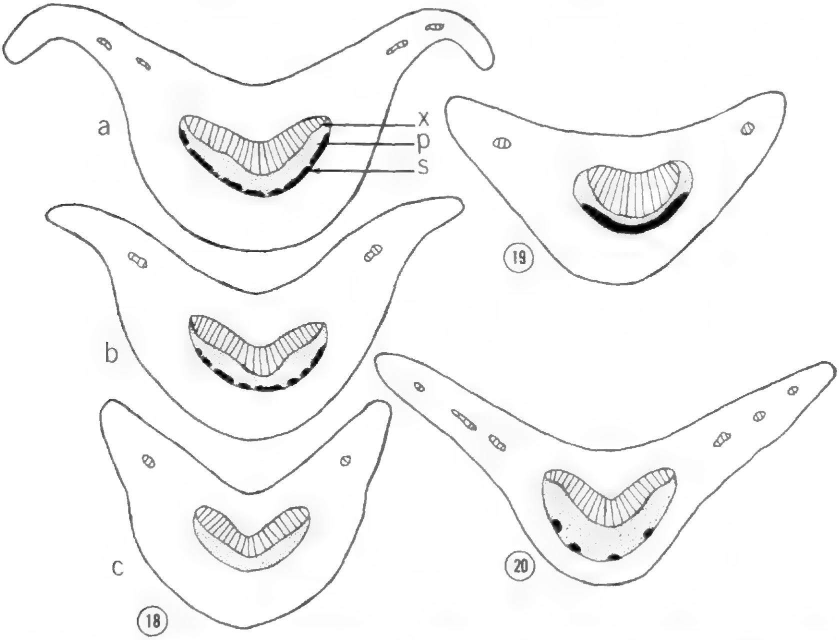
Figs. 12–15. Fig. 12. *Columellia lucida, Friedberg 240*, transverse section of lower epidermis of leaf showing thickened cuticle and overarching cuticular modification in association with stomatal apparatus, × 600. Fig. 13. *C. oblonga* ssp. *oblonga, Továr 4033*, transverse section through mid-vein of leaf showing biseriate upper epidermis, uniseriate lower epidermis, bundle sheath, and bundle sheath extensions, × 210. Fig. 14. *C. oblonga* ssp. *oblonga, Továr 3785*, cleared whole mount of leaf showing a single glandular serration; dark bodies in gland are fruiting structures of an aspergillous fungus, × 40. Fig. 15. *C. lucida, Friedberg 240*, transverse section through mid-vein of leaf showing biseriate upper epidermis, uniseriate lower epidermis, bundle sheath and bundle sheath extensions, tendency to development of a lower palisade layer, and abundance of thick-walled fibers in the vascular bundle, × 180.



FIGS. 16 and 17. Sectional series through petioles of *Columellia*, (a) being distal, (c) proximal, showing increasing distal development of sclerenchyma. FIG. 16. *C. oblonga* ssp. *sericea*, *Drew E-113*. FIG. 17. *C. oblonga* ssp. *oblonga*, *Cook & Gilbert 1749*. (x) xylem, (p) phloem, (s) sclerenchyma.

Glands are highly vascularized and massive (FIG. 14); proximally adjacent to the secretory epithelium is a cupulate reticulum of vascular elements. That the central portion of the gland contains a cavity is borne out by the occurrence there of aspergillous fruiting bodies in some specimens. Apices of glands are aperturate probably through schizogeny.

Vasculation of the petiole is characterized by a single collateral strand of conducting tissue varying from crescentiform to cupulate to almost semiterete in transverse section (FIGS. 16–20). Xylem is adaxial and phloem is abaxial. In all species examined, an abaxial sclerenchymatous region develops progressively from the proximal to the distal portion of the petiole (FIGS. 16–18). In specimens of *Columellia oblonga* ssp. *oblonga* (FIG. 17) and *C. lucida* (FIG. 19), a well-developed lunate layer completely subtends the phloem at the extreme distal end of the petiole; in specimens of other species (FIGS. 16, 18, 20) the sclerenchyma seems not to develop into more than a series of widely-spaced rods at this point. However, sections through the mid-vein of the lamina in *C. oblonga* ssp.



FIGS. 18–20. FIG. 18. *Columellia oblonga* ssp. *serrata*, *Bang 1172*, sectional series through petiole, (a) being distal, (c) proximal, showing increasing distal development of sclerenchyma. FIG. 19. *C. lucida*, *Friedberg 240*, distal section of petiole showing complete sclerenchymatous arc. FIG. 20. *C. obovata*, *Vargas 7693*, distal section of petiole showing sclerenchyma as an arc of rods at this point. (x) xylem, (p) phloem, (s) sclerenchyma.

sericea (*Drew E-113*), which shows a series of sclerenchymatous rods at the distal end of the petiole (FIG. 16, a), show a complete sclerenchymatous layer subtending the phloem. It is likely, therefore, that in the laminae of all species of *Columellia*, the mid-vein is supported by an abaxial layer of sclerenchyma. The central vascular strand of the petiole branches into a series of minor strands toward the base of the lamina (FIGS. 16–20).

In *Columellia oblonga* the mid-vein of the lamina is characterized by secondary growth and several layers of secondary xylem and phloem are produced (FIG. 13). In *C. lucida* and *C. obovata*, secondary growth is not pronounced; furthermore, in these species most of the xylem in the midrib and secondary veins consists of thick-walled fibers (FIG. 15). Bundle sheaths surround secondary veins in all species. Bundle sheath extensions (Wylie, 1952) reach upper and lower epidermises in *C. oblonga* (FIG. 13); in *C. lucida* and *C. obovata*, there are no bundle sheath extensions associated with the bundle sheaths of secondary veins.

The node in *Columellia* is unilacunar and a single trace emerges through each of the two opposite gaps in the vascular cylinder (FIG. 21).

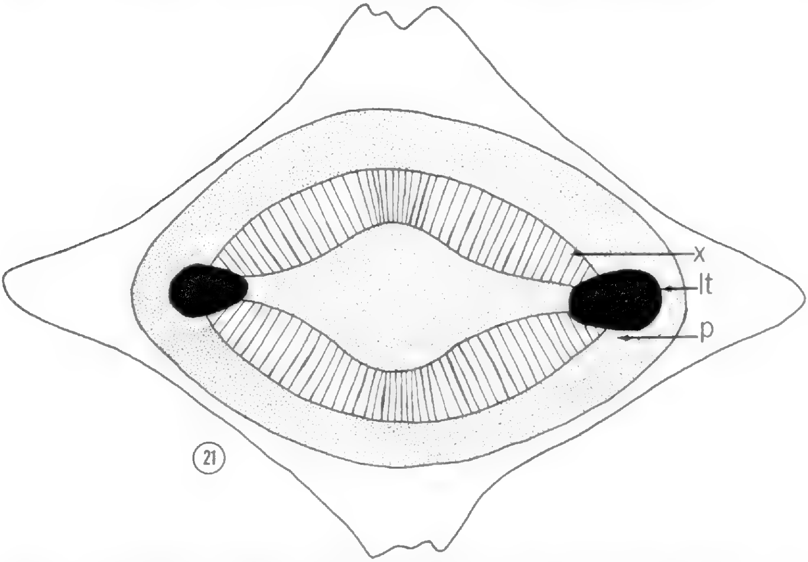


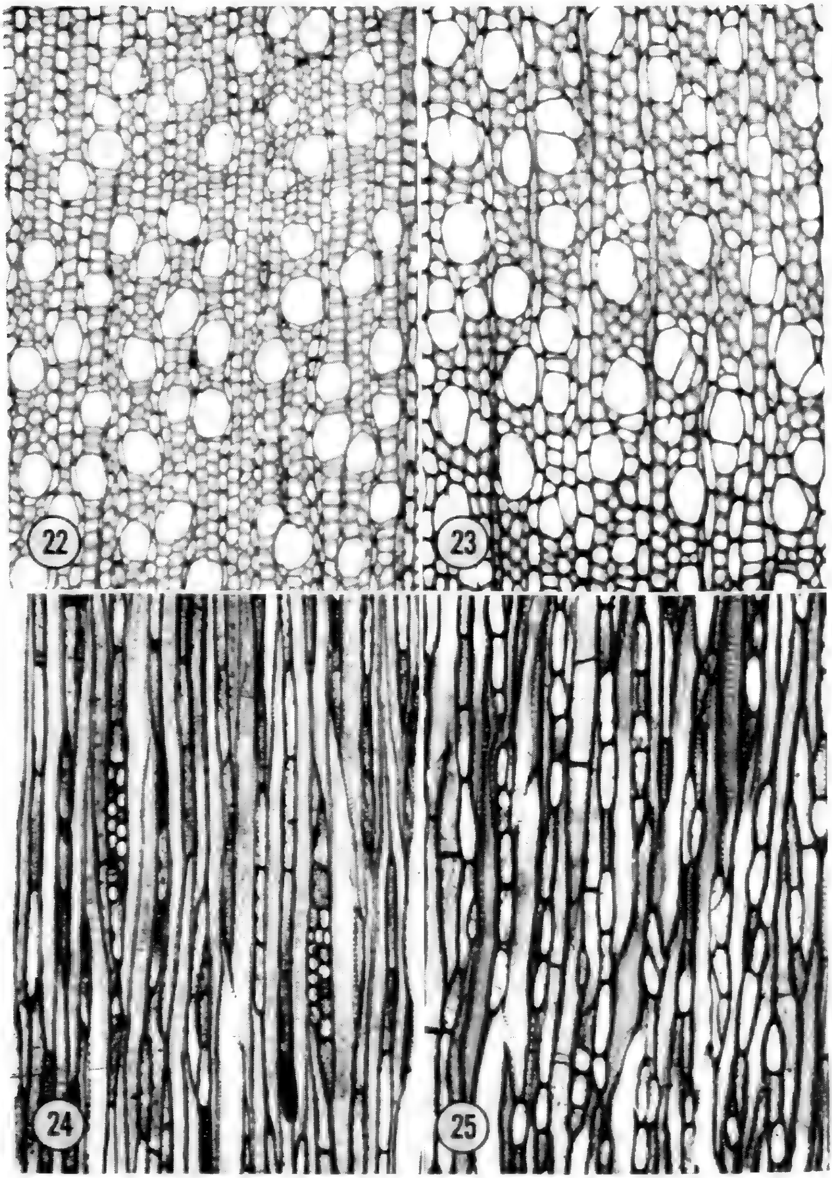
FIG. 21. Transverse section of stem illustrating the unilacunar node in *Columellia*; (x) xylem, (p) phloem, (lt) leaf trace.

The secondary xylem

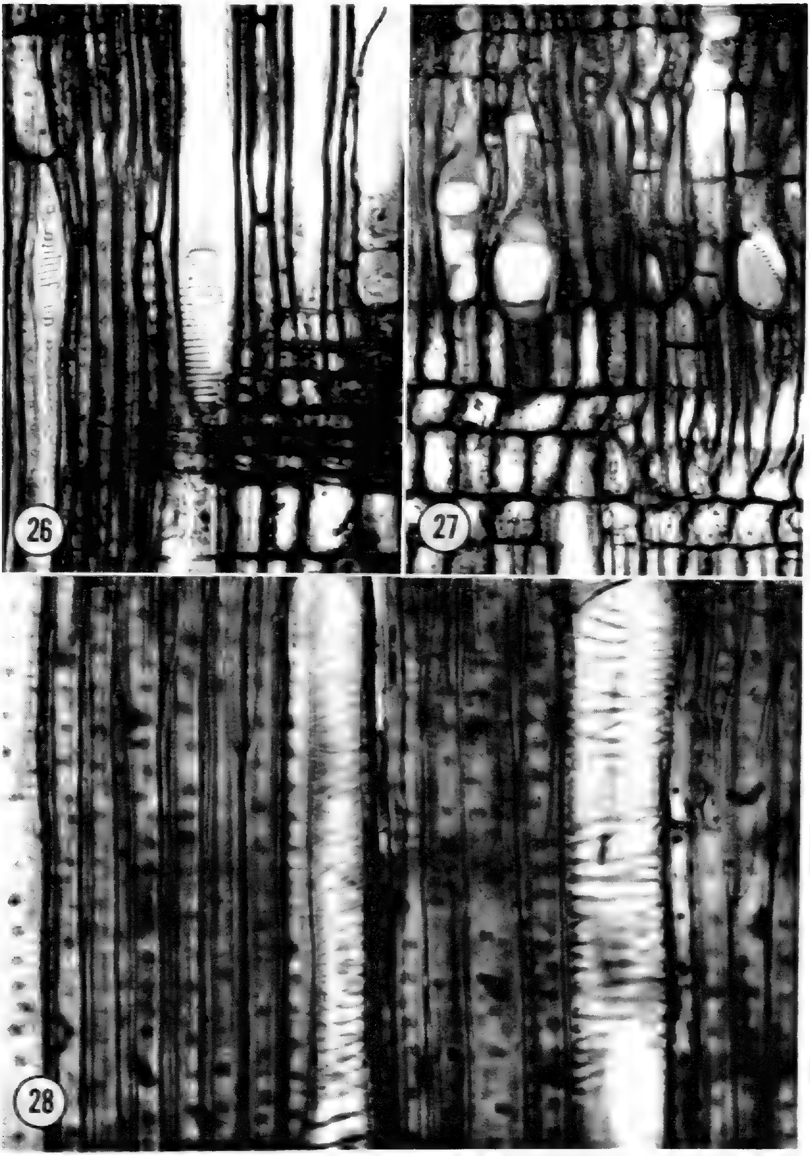
The wood of *Columellia* is generally without growth rings, although in the immature specimens of *C. obovata*, represented by *Weberbauer 5482* and *Nuñez 3309*, more or less sharply defined rings occur. However, both of these specimens show strong evidence of decay or disease and it is suspected that the growth rings are related to these conditions. All woods examined are diffuse-porous, the strictly solitary, uniformly-sized pores being distributed evenly across the transverse surface (FIG. 23). Vessel walls are thin and there are no tyloses. Pores are angular.

Data for measurements of vessel diameter, vessel element length, bars per scalariform perforation plate, tracheid length, and heights of vascular rays are presented in TABLE 2. Because both mature and immature wood were examined, measurements for each are separated in the table to provide a more meaningful basis for comparisons with xylem in other taxa.

Vessel elements are generally long and narrow although ligules as such are short and sometimes lacking. End wall angle ranges from 10° to 45°. Perforation plates are entirely scalariform (FIG. 27) and in some cases bars are so profusely branched they give the appearance of pits. Openings in scalariform perforation plates are completely bordered. Spiral thickenings occur in the cell walls of ligules throughout all species, being more prominent in some than in others. In specimens of *Columellia oblonga* ssp. *oblonga*, vaguely outlined spirals are seen in the body segment of vessel elements and they are strongly marked in the ligules; in *C. oblonga*



FIGS. 22–25. FIG. 22. *Escallonia myrtilloides*, *Rimbach 13*, Yw 16920, transverse section of xylem showing solitary distribution of angular pores, × 100. FIG. 23. *Columellia oblonga* ssp. *sericea*, *Rimbach 122*, transverse section of xylem showing solitary distribution of angular pores, and scanty vasicentric and diffuse axial parenchyma, × 100. FIG. 24. *E. myrtilloides*, tangential section of xylem with biseriate vascular rays and spiral thickenings in tracheids and vessels, × 100. FIG. 25. *C. oblonga* ssp. *sericea*, tangential section of xylem showing uniseriate vascular rays and tracheids, × 100.



FIGS. 26–28. FIG. 26. *Escallonia myrtilloides*, *Rimbach 13*, Yw 16920, radial section of xylem showing scalariform perforation plates, × 150. FIG. 27. *Columellia oblonga* ssp. *sericea*, *Rimbach 122*, radial section of xylem showing scalariform perforation plates, × 100. FIG. 28. *C. obovata*, *Weberbauer 5482*, longitudinal section of xylem showing spiral thickenings in vessels, × 500.

ssp. *sericea*, spirals are tenuous at best and appear only in ligular portions; in *C. lucida* spirals occur only in ligules; and in *C. obovata* spirals are conspicuous throughout the lengths of vessel elements (FIG. 28).

Intervascular pitting is generally absent owing to the solitary nature of vessels; however, a suggestion of intervascular pitting is sometimes present in the overlapping ends of superposed vessel elements. In these areas, the circular to elongate pits are sparse and irregularly scattered but there is a tendency toward the alternate arrangement.

Imperforate tracheary elements are tracheids, the pits in these cells being of the same order of magnitude as those which occur in the overlapping ligulate portions of vessel elements (FIG. 25). Pitting in tracheids is ordinarily uniseriate; less commonly two rows of pits are present, staggered alternately. Inner apertures of pits are elliptical, crossed in face view, and included within the pit border. Tracheid walls vary from very thin to thick.

Vascular rays are entirely uniseriate and comprise axially elongated or upright cells only (FIG. 25). These rays are homocellular and the ray tissue corresponds with Kribs' (1935) Heterogeneous Type III.

TABLE 2.

Summary of Xylem Anatomical Measurements in Columelliaceae

	MATURE [a]	IMMATURE [b]
VESSEL DIAMETER IN μ		
Average:	45	25
Range:	22–105	12–45
MFR [c]:	30–70	15–36
VESSEL ELEMENT LENGTH IN μ		
Average:	629	
Range:	308–1100	
MFR:	375–828	
BARS PER SCALARIFORM PERFORATION PLATE		
Average:	14	10
Range:	7–20	3–24
MFR:	11–16	6–17
TRACHEID LENGTH IN μ		
Average:	866	
Range:	378–1260	
MFR:	625–1110	
HEIGHT OF VASCULAR RAYS IN CELLS		
Range:	1–6	1–47+

[a] *Columellia oblonga* ssp. *oblonga, Továr 4033, Wurdack 1732. C. oblonga* ssp. *sericea, Rimbach 122* and *30.*

[b] *Columellia oblonga* ssp. *oblonga, Ruiz & Pavón 1/52; Weberbauer 5584* and *7791. C. lucida, André K–1444* and *4500. C. obovata, Weberbauer 5482, Herrera 3451.* Data from *Nuñez 3309*, a diseased specimen, are not included here.

[c] MFR = Most frequent range.

Axial xylem parenchyma is largely scanty vasicentric, a few isolated strands occurring about the vessels (Fig. 23). In addition a few strands were seen embedded within the groundmass of tracheids (diffuse parenchyma).

DISCUSSION

In view of the sympetalous corolla of *Columellia*, it is not surprising that taxonomists looked for its relationships among the sympetalous families, and especially those with inferior ovaries and opposite leaves. Among other features, the androecial peculiarities of *Columellia*, unmatched in any other known taxon, persuaded David Don to establish a separate family for this unusual group of plants. Time has shown him to have been correct in his assessment of the individuality of *Columellia*.

Evidence from gross morphology

There are such sharp differences in floral structure between Columelliaceae on one side, and Ebenaceae, Styracaceae, and Vacciniaceae on the other, that any consideration of close relationship is completely out of place. Oleaceae, with usually 2–4-merous flowers, 2 (–4) stamens with introrse, dorsifixed anthers, and superior ovaries with a few ovules situated on an axile placenta in each locule, can hardly be regarded as closely related to Columelliaceae. The mostly herbaceous Gentianaceae-Gentianoideae show some similarities with Columelliaceae in their cymose inflorescences, in the structure of ovaries and fruits (2-carpellate ovaries with numerous unitegmic, tenuinucellate ovules on parietal intrusive to axile placentas, septicidal capsules, small seeds, etc.), as well as in the possession of opposite, exstipulate leaves. They are markedly different, however, in their regular flowers; in the usually contorted aestivation of corolla lobes; in their usually dorsifixed, introrse anthers; and in their superior ovaries. Loganiaceae (excluding *Desfontainea* Ruiz & Pavón) differ from Columelliaceae in their usually stipulate leaves, regular flowers, and superior ovaries; in addition, in the subfamily Buddleioideae, the presence of glandular and stellate hairs is widespread. Some relationship with Scrophulariaceae and especially Gesneriaceae appears possible, but both families have highly specialized, mostly hypogynous flowers (only Gesnereae of Gesneriaceae, *sensu* Fritsch 1893, 1894, have semi-inferior or inferior ovaries). Some genera of Rubiaceae agree with Columelliaceae in floral structure (except for the non-reduced number of stamens) and opposite leaves, but they differ in the presence of stipules. A close relationship with Caprifoliaceae seems equally doubtful. The only genera of this family which are perhaps comparable with Columelliaceae in possessing multi-ovulate, 2-carpellate ovaries, are *Diervilla* Mill. and *Weigela* Thunb., genera apparently restricted to the temperate zones of North America and eastern Asia. The gross-morphological similarities between Lythraceae and Onagraceae and Columelliaceae are too scarce even to suggest a relationship. Within the saxifragaceous families —

Hydrangeaceae, Grossulariaceae, and Escalloniaceae — almost all the gross-morphological characters in *Columellia* may be found: frutescent and/or arborescent habit; opposite, exstipulate, often glandular-dentate leaves; 5-merous haplostemonous flowers (Escalloniaceae); sympetalous corolla (*Roussea* of Escalloniaceae); and semi-inferior or inferior, 2-carpellate ovaries with parietal intruding placentas bearing numerous, anatropous and apotropous, unitegmic, tenuinucellate ovules (Escalloniaceae and some genera of Hydrangeaceae). Septicidal capsules usually have numerous small endosperm-containing seeds (Hydrangeaceae and Escalloniaceae) with small embryos. Most of the features of *Columellia* are represented in the family Escalloniaceae. Although alternate leaves predominate in this family, opposite leaves are found in the genera *Grevea* Baill., *Roussea*, and *Polyosma* Blume. Other genera, as *Valdivia* Remy, have subopposite leaves.

Evidence from floral anatomy

It would not be practical, nor is it necessary, to attempt a detailed anatomical comparison of the *Columellia* flower to flowers of all the plant families with which *Columellia* has been allied. A brief commentary on the Cucurbitaceae seems to be in order, however, because androecial structure in that family has significance for the interpretation of the androecium in *Columellia*.

Clarke (1858) considered the stamens of *Columellia*, because of their contorted anthers, to be almost identical to those of many Cucurbitaceae. He interpreted the androecia of certain cucurbits — those with three appendages, one two-locular and two four-locular — as comprising two and a half stamens, an opinion shared by some other 19th century botanists. If this view were correct, the two-staminate androecium of *Columellia* would not seem greatly different. In more recent times, however, an alternative interpretation of such cucurbitaceous androecia has been confirmed again and again; that is, the two-sporangiate stamen is an entire one, and the four-sporangiate stamens are duplex appendages. Evidence for the more modern view is now overwhelming. It is derived from ontogeny; from vascular anatomy (the duplex stamens sometimes contain two well-defined bundles that are derived from two different petal traces); and from comparative studies of male, female, and bisexual flowers of many genera, some of them exhibiting transitional stages between the five-staminate condition and the "two and a half"-staminate condition. Reviews of the evidence are given by Miller (1929) and McLean (1947) and additional confirmation by Bhattacharjya (1954), Chakravarty (1958), and Quang (1963).

Although *Columellia* stamens are superficially similar to the duplex stamens of Cucurbitaceae, the vascular supply in *Columellia* is a solitary bundle. In transverse sections through the filament or the connective, the bundle is often very broad and may occasionally seem to have two xylem patches, but its appearance within the inferior part of the flower gives no hint of compound structure. Observing this, van Tieghem (1903) concluded that the two members of the *Columellia* androecium are solitary stamens, and most floral morphologists would accept his evidence. Thus, it can be argued rather convincingly that the evolutionary modification leading to the two-staminate condition in *Columellia* was a loss or "abortion" of stamens rather than any sort of phylogenetic union of stamens. The occasional occurrence of a third stamen in flowers of *Columellia*, reported by Brizicky (1961), supports this argument.

This reasoning might be thought to favor the relationship of *Columellia* to Gesneriaceae, because some gesneriads have one staminode — that is, an abortive stamen — accompanying four normal stamens, and in some other gesneriads there are only two stamens. In the latter case, as in *Columellia*, there are no staminodes. But the resemblance of *Columellia* to the gesneriads is not so close as this information would suggest, for in Gesneriaceae only genera with superior ovaries have the two-staminate androecium (Fritsch 1893, 1894).

A satisfactory anatomical comparison of the *Columellia* flower with gesneriaceous flowers is not yet possible because floral anatomy of the Gesneriaceae has never been investigated to any great extent. Comparative information is presently available only for flowers of a *Kohleria* hybrid, *K. amabilis* × *K. scladotydea* (Teeri, 1968), and for those of *Kohleria elegans* (Dcne.) Loes. (*H. E. Moore 8190*; US, BH). Serial sections of the latter were prepared from fluid-preserved material especially for this paper. Anatomically, flowers of the two gesneriads are much alike, and they have several characters in common with *Columellia*. For instance, the floral tissues are devoid of tannins, and general features of placentation and vasculation do not differ greatly from those of *Columellia*. In addition, both gesneriads have two-lobed placentas and many gynoecial strands (FIG. 8). On the other hand, there are differences in detail that may be important. The two gesneriads have no well-developed endocarp tissue, except for a single layer of transversely elongate cells adjoining the locule. The style is hollow for all of its length, with a single canal (FIG. 5). Floral trichomes are multicellular (but uniseriate). Vascular traces to the stamens are united with sepal traces for part of their passage through the inferior part of the flower, and the supply to the placentas is derived from two large septal bundles (duplex bundles representing paired heterocarpous ventrals; FIG. 9) in the septum. Of course, a major floral difference is that the anthers of the gesneriads are not contorted. Perhaps the most important difference aside from that is in the nectary: nectaries of Gesneriaceae are usually very well developed and deeply lobed or even divided into distinct appendages (Feldhofen 1933).

It is somewhat easier to compare flowers of *Columellia* with those of Rubiaceae because a detailed survey of floral anatomy in Rubiaceae is available (Rao, Ramarethinam, & Iyer 1964). Rubiaceae is a large family, rather diverse in floral structure; therefore, it is almost to be expected that some of the members would have characters in common with *Col-*

umellia. For instance, some Rubiaceae have separate vascular traces to calyx, corolla, androecium, and gynoecium. And in some genera (e.g., *Guettarda* L.) there are a great many gynoecial bundles. Placentation is often similar to that of *Columellia*, and many genera have an epigynous nectary resembling that of *Columellia*. A difference that strikes one immediately, when sectioned flowers of *Columellia* are compared with sections of rubiaceous flowers, is the absence of conspicuous tannins in the former. Floral tannins are rarely lacking in Rubiaceae. Another difference is that a single stylar canal seems to be of universal occurrence in the Rubiaceae. Furthermore, the peculiar androecial modification in *Columellia* has no counterpart among the rubiads.

Floral anatomy of the more easily obtained members of Saxifragaceae, *sensu lato*, is fairly well known through the investigations of many workers, including Palmatier (1943), Morf (1950), Dravitski (see Philipson, 1967), Gelius (1967), and Komar (1967). None of these studies has produced evidence to support Hallier's (1908, 1910) opinion that *Columellia* belongs with the Philadelpheae. In fact, ontogenetic observations on *Philadelphus* (Gelius, 1967) suggest that evolution has favored an increase in stamen number in this group. In some other genera of Philadelpheae, a reduction in the number of ovules has led to forms that bear little resemblance to *Columellia* (e.g., *Jamesia* Torr. & Gray, *Whipplea* Torr.). Schnizlein (1843–1870) proposed *Brexia* and *Roussea* as close allies of *Columellia*; however both *Brexia* and *Roussea* have superior ovaries with distinctly two-ranked ovules. *Argophyllum*, another genus mentioned by Schnizlein, is also very dissimilar to *Columellia*, for it has peculiar corolline ligules and T-shaped trichomes like its ally *Corokia* A. Cunn. (Eyde, 1966). If the relationships of *Columellia* are to be sought among the escallonioids, attention should be given to genera other than the aberrant *Argophyllum* and *Corokia*. *Berenice* Tul. can also be eliminated from consideration, because it has recently been transferred to Campanulaceae on anatomical and palynological grounds (Erdtman & Metcalfe, 1963). From the standpoint of floral anatomy, *Escallonia* Mutis ex L. f. is not as close to *Columellia* as might be indicated by other evidence. Tannins are abundant in floral tissues of *Escallonia* species and the floral trichomes frequently are multicellular with globular terminal portions; also, the gynoecial bundles are few and the ventral bundles commonly accompany the dorsals into the style. *Choristylis* Harv. has stamens united with corolla tube, but in other respects the flowers are unlike those of *Columellia*. One difference is that the gynoecial bundles are few; another is that the nectary is located on the lower part of the corolla tube. The latter character may be sufficiently important to remove *Choristylis* from its position adjoining *Forgesia* (Engler, 1928) and to place it elsewhere in the Saxifragaceae, *sensu lato*. (Agababyan 1964, links *Choristylis* with *Itea* on palynological evidence.) Flowers of *Forgesia* have rather massive multicellular trichomes; otherwise they are anatomically similar to *Columellia* flowers. To judge from our one sectioned herbarium flower, the gynoecial vasculature and the placentation approximate those of *Columellia*. The nectary, if there is one (it is not easy to tell from dried material), is part of the free portion of the gynoecium, and the androecium shows indications of reduction (abortive locules in some anthers). *Forgesia*, like many other Saxifragaceae, *sensu lato*, has free styles that could be viewed as a precursor to the two-canal structure of the *Columellia* style.[3]

In summarizing this section on floral anatomy, it must be conceded that the cited points of similarity and dissimilarity do not tell us much about the affinities of *Columellia*. The foregoing commentary includes no strong evidence against the proposed relationship with Gesneriaceae, nor does it include really firm evidence for such a relationship. The same can be said of the possible alliance with Rubiaceae or with the escallonioid group of Saxifragaceae, *sensu lato*. The reason for this is clear. All observed characters in the flowers of *Columellia* are widely distributed in many plant families, except for the contorted anthers. Ironically, the latter character does not help in placing *Columellia* because it has not been found in any other group of plants, the resemblance to anthers of certain cucurbits being demonstrably superficial.

Evidence from leaf anatomy

It does not appear possible to compare all features of the foliar anatomy of Columelliaceae with those of families reputed to be allied to it, since complete foliar surveys of these families are lacking from the literature. An original study of leaves in all these families is surely outside the scope of this investigation. Nevertheless, certain comparisons can be made.[4]

Leaves are dorsiventral in Gesneriaceae. Hairs are always multicellular and they are often situated on a pedestal. They may be glandular or non-glandular. A multiseriate hypodermis occurs in certain species. The stomatal apparatus is often very large and anisocytic. Vascular bundles in veins are not usually accompanied by sclerenchyma. Vasculation of the petiole is various and many genera show a single leaf trace; *Alloplectus* Mart., *Besleria* L., *Episcia* Mart., and others have three leaf traces and *Klugia notoniana* A. DC. shows a large number of separate strands. There is no "pericyclic" sclerenchyma associated with the petiolar vascular strand in Gesneriaceae. Gesneriaceous leaves differ markedly from those in Columelliaceae in their multicellular and glandular hairs, anisocytic stomatal apparatus, and lack of sclerenchyma associated with vascular tissue.

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[3] Observations on the floral anatomy of Escalloniaceae are based on serial sections prepared especially for this paper. Material was obtained from the following sources: *Escallonia*, fluid-preserved flowers from several cultivars growing in the Los Angeles State and County Arboretum, not vouchered; *Carpodetus serratus*, fluid-preserved flowers from plants cultivated at the University of Auckland, New Zealand, not vouchered; *Quintinia fawkneri*, pressed flowers, *L. J. Brass 4719*, US; *Choristylis shirensis*, pressed flowers, *Swynnerton 607*, US; *Forgesia borbonica*, pressed flowers, *de l'Isle 216*, US.

[4] Family circumscriptions follow those used by Metcalfe and Chalk (1950) for convenience in making comparisons.

Rubiaceous leaves are generally dorsiventral; centric and homogeneous leaf organization occur in a few species. Hairs may be unicellular, multicellular and uniseriate, tufted, and rarely peltate. A hypodermis occurs in many species. The stomatal apparatus is paracytic (rubiaceous) in most species, as might be expected. The petiolar vascular strand is usually shield shaped with more or less well-developed wings. There are also variously shaped median vascular strands, nearly always associated with smaller accessory bundles toward the wings. In such a large and anatomically diverse family as Rubiaceae, it is not surprising to find foliar resemblances to Columelliaceae. The only clear and consistent difference is the more or less ubiquitous occurrence of the paracytic stomatal apparatus in Rubiaceae.

Caprifoliaceae usually have dorsiventral leaves, but the palisade tissue is poorly developed in species of *Triosteum* L. and *Viburnum* L. Hairs may be glandular or non-glandular and unicellular, simple and multiseriate, tufted or stellate, and peltate. Glandular leaf teeth are present in some species. Stomatal organization is frequently anomocytic, but paracytic types occur in the same genera as anomocytic types. Except for *Diervilla*, a single layer of palisade mesophyll occurs; in *Sambucus* L. and *Viburnum*, cells of the palisade layer may have arms. The petiolar vasculation shows a considerable range of structure from a solitary, slightly crescentic bundle to an arc of 3–5 or more separate bundles to a closed vascular cylinder. The anomocytic stomatal apparatus and solitary petiolar strand in Caprifoliaceae are similar to Columelliaceae, but the paracytic stomatal apparatus, single-layered palisade mesophyll, and multistrand and cylindrical vasculation of the petiole, which also occur in some species of Caprifoliaceae, are very different from the situation in Columelliaceae.

Leaves in Saxifragaceae, *sensu stricto*, are dorsiventral and isobilateral. Hairs are glandular and non-glandular and these may be simple, uniseriate and multicellular; shaggy; and multiseriate. Stomatal organization is anomocytic and sometimes subsidiary cells, smaller than neighboring epidermal cells, are evident. The mesophyll in some species of *Saxifraga* L. is undifferentiated, and in species where it is differentiated, the palisade segment may range from 1 to 7 cells deep. Hydathodes are of common occurrence. Petiolar vasculation is distinctive, especially in *Saxifraga* where one concentric bundle or one hemi-concentric bundle may occur. In other species of *Saxifraga*, there are three such bundles, each with its own endodermis. Some Saxifragaceae have the usual collateral bundles. but these may be scattered. The herbaceous Saxifragaceae resemble Columelliaceae in the presence of an anomocytic stomatal apparatus, apparently modified in some taxa; but the undifferentiated mesophyll in some species of *Saxifraga* and multilayered palisade tissues in others, are very different from the condition in *Columellia*. Petiolar vasculation in Saxifragaceae bears little resemblance to that in Columelliaceae.

Leaves in Grossulariaceae are dorsiventral and bear unicellular and also glandular hairs. Pairs of small, circular guard cells are characteristic. The petiole is characterized by three separate vascular strands at the base which fuse distally to produce a single crescentiform strand all supported by sclerenchyma in the "pericyclic" region. The specialized, small circular guard cells vary from those in Columelliaceae but the abaxial sclerenchyma associated with the petiolar bundle also occurs in Columelliaceae. The proximally triple vascular strand differs from the condition in Columelliaceae.

All leaves in Escalloniaceae are dorsiventral. In *Escallonia*, foliar hairs are thick-walled and unicellular; in *Abrophyllum* Hook.f., hairs are glandular with unicellular heads; in some species of *Escallonia* hairs are glandular-shaggy with multiseriate stalks; in *Quintinia* A. DC. peltate hairs occur; and T-shaped hairs occur in *Argophyllum*. Stomatal organization is variable and pairs of nearly circular, small guard cells, resembling those in Grossulariaceae, occur in *Escallonia*, *Itea* L., and other genera; the stomatal apparatus in *Quintinia* is paracytic; and the stomatal apparatus in *Brexia* is characterized by a double front cavity. A 1–3-layered upper hypodermis occurs in species of *Argophyllum*, *Carpodetus*, *Escallonia*, and other genera. A single-layered palisade mesophyll is present in two genera. Three vascular bundles enter the base of the petiole in *Escallonia*, but in *E. macrantha* Wedd. (= *E. polifolia* Hook.) and *E. rubra* (Ruiz & Pavón) Pers., a single crescentiform petiolar bundle with accessory strands is present. Apparently there is no abaxial sclerenchyma present in *Escallonia*. *Brexia* appears unique, for besides the abaxial, crescentiform vascular strand in the petiole, there is also a small cylinder of xylem in the medullary region and two abaxial xylem cylinders. Certain similarities between Columelliaceae and Escalloniaceae occur: unicellular, thick-walled hairs; presence of a hypodermis; and a single petiolar vascular strand in at least two species of *Escallonia*. However, there are also marked differences and Escalloniaceae show glandular and multicellular hairs, grossulariaceous stomatal organization, and a triple vascular condition in petioles of most species of *Escallonia*.

Hydrangeaceous leaves are dorsiventral. Hairs are various with long, unicellular trichomes in *Jamesia*; tufted trichomes in *Broussaisia* Gaudich. and *Pileostegia* Hook. f. & Thoms.; and stellate, calcified, and unicellular types in *Deutzia* Thunb. Glandular leaf teeth occur in *Decumaria* L., *Deutzia*, and *Philadelphus*. A hypodermis occurs in *Broussaisia* and in species of *Hydrangea*, and the epidermis contains some horizontally divided cells in *Carpenteria* Torr. The stomatal organization is paracytic in species of *Dichroa* Lour. and *Hydrangea* L. and anomocytic in *Philadelphus*. Palisade mesophyll is uniseriate in *Deutzia* and *Philadelphus*. The petiolar vascular strand differs throughout the family: It is single and crescent-shaped in species of *Deutzia*, *Jamesia*, *Philadelphus*, *Hydrangea*, and *Pileostegia*; petioles of *Decumaria sinensis* Oliv., *Dichroa febrifuga* Lour., and *Hydrangea petiolaris* Sieb. & Zucc. are characterized by a main abaxial arc with several flat adaxial bundles between the ends.

Additional strands are present in other species, including medullary bundles. Although some foliar similarities exist between some taxa of Hydrangeaceae and Columelliaceae — unicellular hairs, glandular leaf teeth, hypodermis, anomocytic stomatal organization, and arcuate petiolar vascular supply — the differences are equally clear. Multicellular and tufted hairs, paracytic stomatal organization, and multistranded petiolar vascular supply occur in Hydrangeaceae.

The remaining plant families which have at one time or another been suggested as near relatives of Columelliaceae or *Columellia* — Scrophulariaceae, Ebenaceae, Loganiaceae, Oleaceae, Lythraceae, Vacciniaceae, Ericaceae, Gentianaceae, and Onagraceae — present a wide array of foliar anatomical features, some similar and others different from Columelliaceae. As should be apparent from the brief comparative summary above, no family presents a consistent foliar pattern which is similar enough in most respects to that in Columelliaceae to convince the critical botanist that leaf anatomy is a key to understanding the relationships of the family. To be sure, this is probably related to the lack of thorough anatomical investigation in those taxa reputedly related to Columelliaceae, but as the situation stands now, foliar anatomy is at its best equivocal in pointing the way to the relationships of Columelliaceae.

Evidence from nodal anatomy

According to Sinnott's (1914) survey of the nodal condition among seed plants, all members of the Tubiflorae, which include Scrophulariaceae and Gesneriaceae, are unilacunar. However, three or five gaps are typical for *Cyrtandra* J. R. & G. Forst. (Gesneriaceae). Onagraceae, Ericaceae, Ebenaceae, Oleaceae, Gentianaceae, Loganiaceae, and Rubiaceae, are also characterized by unilacunar nodes. In addition, some members of Gentianaceae are multilacunar and some Rubiaceae are trilacunar. Caprifoliaceae are generally tri- and sometimes pentalacunar. Cucurbitaceae are all trilacunar. Rosales, which include Saxifragaceae (treated in the broad Englerian sense by Sinnott), are said to be mostly trilacunar although five gaps occur in Brunelliaceae and in a few Saxifragaceae, Rosaceae, and Leguminosae. Platanaceae exhibit seven gaps.

Plant orders are remarkably constant with respect to their nodal conditions but Sinnott recognized that nodal anatomy is only one character, that nodal structure is not always invariable, and that further study will necessitate changes in his outline. In 1955, Marsden and Bailey presented their penetrating analysis of the node and interpretation of the primitive nodal condition. In contrast to Sinnott's hypothesis that the trilacunar condition is basic and primitive, Marsden and Bailey provided evidence to indicate that the unilacunar, two-trace condition is ancestral and they indicated possible means for deriving both the unilacunar, single-trace condition and the trilacunar, triple-trace condition directly from it. Furthermore, they hypothesized that the unilacunar node could give rise to the trilacunar node through amplification, much as Sinnott derived the multilacunar form from the trilacunar.

Takhtajan's (1964) scheme of nodal evolution is similar to that of Sinnott in that he accepted the primitiveness of the trilacunar node. However, the median lacuna has a double trace: "Thus, from all of these data one can conclude, it seems to me, that the node with three or more lacunae (FIG. 9) is the primary type of node in angiosperms. At present, it is impossible to determine more accurately the initial nodal type in angiosperms."

Because of the studies of Marsden and Bailey, it is apparent that a reassessment of the taxonomic value of nodal anatomy, as exemplified by Sinnott's treatment, is very much in order. The derivation of the unilacunar, one-trace condition in Columelliaceae, rather than the condition itself, is the key to taxonomic understanding. This is also true of the nodal configuration in all putative relatives. We cannot say that Columelliaceae is unrelated to saxifragaceous families because these are largely characterized by trilacunar nodes, nor can we assign the relationship of Columelliaceae to those families with unilacunar nodes, if we agree with Marsden and Bailey that, "Structures which appear to be similar at the nodal level may not be truly homologous, and conversely differences which seem outstanding at the nodal level may acquire a different significance where comprehensive developmental studies at successive levels of the stem and leaf are made."

Evidence from xylem anatomy [5]

A brief recapitulation of the salient features in the xylem anatomy of Columelliaceae is in order here: perforation plates scalariform; pore distribution exclusively solitary; intervascular pitting usually absent, except tending to alternate in regions of ligular overlap between superposed vessel elements; axial parenchyma vasicentric scanty; vascular rays exclusively uniseriate consisting solely of upright cells; spiral thickenings present in walls of vessel elements; and imperforate tracheary elements are tracheids.

Gesneriaceae all have simple perforations in vessel elements. However, vestigial bars were noted in perforation plates of *Solenophora calycosa* Donn. Smith. In all woods examined, pores are solitary, in radial multiples, and in clusters except in *Solenophora* sp. (Yw 22822) where no clusters were observed. Intervascular pitting is exclusively alternate, except in *Solenophora calycosa* where transitional pitting was also seen. Axial parenchyma distribution is various; however, it is paratracheal except for *Drymonia spectabilis* (H.B.K.) Mart., *Rhytidophyllum crenulatum* DC., and *Solenophora calycosa*, in which diffuse parenchyma occurs. In most species the vasicentric parenchyma is scanty; vasicentric parenchyma is abundant, however, in *Columnea purpurata* Hanst., *Cyrtandra oenobar-*

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[5] Anatomical data presented in this section are based on original observations in Gesneriaceae, Grossulariaceae, Hydrangeaceae, and Escalloniaceae. Microscope slides examined were from the Yale (Yw) and Smithsonian (USw) wood collections. Data from other families are from the literature. For convenience in making comparisons, families are considered as circumscribed in Metcalfe and Chalk (1950).

bata H. Mann, *C. spathacea* A. C. Smith, and *Gesneria* sp. (Yw 16832). In *Drymonia* sp. (Yw 17724), aliform and aliform-confluent parenchyma occurs. Vascular rays are absent in *Besleria* spp. (Yw 12217, 12225). In *Columnea purpurata* rays are 1 to 3 cells wide and in *Solenophora calycosa*, rays are mostly uni- and biseriate. In all other species investigated, rays are multiseriate. Rays are homocellular consisting solely of upright cells in *Drymonia spectabilis*, *Columnea purpurata*, *Rhytidophyllum crenulatum*, *R. tomentosum* (L.) Mart., and *Rhytidophyllum* sp. (Yw 20017). Heterocellular rays occur in *Cyrtandra oenobarbata*, *C. spathacea*, *Gesneria* sp. (Yw 16832), *Drymonia* sp. (Yw 17724), *Solenophora calycosa*, and *Solenophora* sp. There are no spiral thickenings in vessels of Gesneriaceae. Imperforate tracheary elements are various: septate elements occur in *Besleria* spp., *Gesneria* sp., *Drymonia spectabilis*, *Columnea purpurata*, *Rhytidophyllum crenulatum*, *R. tomentosum*, *Solenophora calycosa*, and *Solenophora* sp. Only *Cyrtandra* did not show septate imperforate tracheary elements. *Drymonia spectabilis* exhibits only fiber-tracheids and *Gesneria* sp., *Drymonia* sp., *Rhytidophyllum crenulatum*, and *Solenophora* sp. show only libriform wood fibers. All other species investigated show both fiber-tracheids and libriform wood fibers.

Except for the common occurrence of vasicentric scanty axial parenchyma in Gesneriaceae and Columelliaceae, the wood anatomy of these two families is very different. Perforation plates in Columelliaceae are scalariform; in Gesneriaceae they are simple. Pore distribution is strictly solitary in Columelliaceae; in Gesneriaceae it is solitary and in radial multiples and clusters in most of the species studied. Intervascular pitting is virtually absent in Columelliaceae because of the independent distribution of vessels; in Gesneriaceae it is alternate. All species of Columelliaceae have vascular rays; in Gesneriaceae, *Besleria* lacks vascular rays. Vascular rays are uniseriate in Columelliaceae; in Gesneriaceae all species have vascular rays more than one cell wide. Vascular rays contain only upright cells in Columelliaceae; in Gesneriaceae species may show both heterocellular rays and homocellular rays with upright cells. Spiral thickenings are present in the vessels of Columelliaceae; in Gesneriaceae, vessels lack spiral thickenings. In Columelliaceae all imperforate tracheary elements are tracheids; in Gesneriaceae both fiber-tracheids and libriform wood fibers occur, but no tracheids.

Grossulariaceae have scalariform perforations in vessel elements, but some simple perforations were also observed. Pores are solitary, in radial multiples, and in clusters. Growth rings are pronounced and the wood is ring porous. Intervascular pitting is transitional and scalariform. Axial parenchyma is absent. Vascular rays are multiseriate, broad, and heterocellular. Sheath cells are of common occurrence in the rays. Spiral thickenings are absent from vessel walls. Imperforate elements are septate tracheids and in *Ribes viscosissimum* Pursh, fiber-tracheids were also recorded.

The presence of scalariform perforations and tracheids seems to provide the only common anatomical features between Grossulariaceae and Columelliaceae. Solitary, radial multiple, and clustered pores; ring porosity; broad, heterocellular vascular rays; septate imperforate tracheary elements; and the absence of axial parenchyma in the wood of Grossulariaceae are rather distinct anatomical characteristics which differ from Columelliaceae.

Perforation plates in vessel elements of Hydrangeaceae are scalariform.[6] Pores are exclusively solitary in *Broussaisia arguta* Gaudich., *B. pellucida* Gaudich., *Fendlera rupicola* A. Gray, and *Philadelphus* sp. (Yw 11845). In *Deutzia vilmorinae* Lemoine & D. Bois, *Hydrangea panamensis* Standley, and *Philadelphus coronarius* L., pores are solitary and in radial multiples. *Hydrangea bretschneideri* Dipp. and *Dichroa febrifuga* show pores in solitary, radial multiple, and clustered dispositions. Intervascular pitting is generally absent in *Broussaisia arguta*, *B. pellucida*, and *Fendlera rupicola*. However, in the overlapping vessel ligules of *Broussaisia arguta*, scalariform pitting was seen, whereas in this position *Fendlera rupicola* shows a tendency to alternate intervascular pitting. In *Philadelphus coronarius*, intervascular pitting is transitional; in *Philadelphus* sp., pitting is alternate with some opposite. Pitting in vessel walls of *Deutzia vilmorinae*, *Hydrangea bretschneideri*, and *H. panamensis* is scalariform. Vessel walls in *Dichroa febrifuga* show both transitional and scalariform pitting. Axial xylem parenchyma is diffuse and vasicentric scanty in all species studied. No axial parenchyma was observed in *Fendlera rupicola* and *Hydrangea bretschneideri*. In all species studied, homocellular uniseriate rays were present in which cells are upright. These occur in conjunction with other heterocellular rays, two or more cells wide. Rays up to 8-cells wide occur in *Broussaisia pellucida*. *Deutzia vilmorinae*, *Fendlera rupicola*, and *Hydrangea bretschneideri* have only uni- and biseriate rays. Sheath cells are common in species with wide rays. In *Deutzia vilmorinae*, scalariformly perforated ray cells occur. Tenuous spiral thickenings occur in the cell walls of vessels and tracheids of *Fendlera rupicola*; in *Philadelphus coronarius* and *Philadelphus* sp., spirals occur in tracheids. Imperforate tracheary elements in *Fendlera rupicola*, *Hydrangea bretschneideri*, *Philadelphus coronarius*, and *Philadelphus* sp., are exclusively tracheids. In *Broussaisia arguta*, *B. pellucida*, and *Dichroa febrifuga*, both tracheids and fiber-tracheids appear. *Deutzia vilmorinae* and *Hydrangea panamensis* show only fiber-tracheids. Imperforate tracheary elements are septate in *Hydrangea panamensis* and *Dichroa febrifuga*.

There are several similarities between the woods of some species of Hydrangeaceae and Columelliaceae: scalariform perforation plates, exclusively solitary pores and concomitant absence of intervascular pitting, a tendency to alternate intervascular pitting, and tracheids. Axial xylem parenchyma is vasicentric scanty in Columelliaceae with some diffuse; in

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[6] Metcalfe and Chalk (1950) report simple perforation plates in *Deutzia glabrata* Kom. and in some species of *Philadelphus*.

all Hydrangeaceae studied, where axial xylem parenchyma was present, it it vasicentric scanty and some strands were diffusely arranged. On the other hand, there are also pronounced anatomical differences between these families: Pores are exclusively solitary in Columelliaceae; in several species of Hydrangeaceae pores are in both solitary and other arrangements. Intervascular pitting tends toward alternate in Columelliaceae; in Hydrangeaceae scalariform and transitional intervascular pitting occur in several species. All species of Columelliaceae show axial parenchyma; several species of Hydrangeaceae lack this tissue. In Columelliaceae, vascular rays are all uniseriate and homocellular; all Hydrangeaceae have uniseriate rays plus rays which are two or more cells wide and heterocellular. Imperforate tracheary elements in Columelliaceae are tracheids; some species of Hydrangeaceae show both tracheids and fiber-tracheids, while other species have only fiber-tracheids.

Perforation plates in Escalloniaceae are exclusively scalariform except in *Brexia*, where plates are mostly simple, and in *Kania* Schlechter,[7] where they are exclusively simple. All Escalloniaceae have solitary pores; in *Escallonia floribunda* H.B.K., *E. fonkii* Phil., and *E. myrtilloides* L.f., pores are exclusively solitary. In *E. pulverulenta* (Ruiz & Pavón) Pers., *E. revoluta* (Ruiz & Pavón) Pers., *E. rubra* (Ruiz & Pavón) Pers., and *E. tortuosa* H.B.K., pores are also in radial multiples. Pores are solitary and in radial multiples in *Brexia madagascariensis* Thou. ex Ker-Gawl., *Itea* sp. (Yw 20142), *Quintinia acutifolia* T. Kirk, *Q. serrata* A. Cunn., and *Q. sieberi* A. DC. In *Quintinia*, however, multiples are rare but tangentially oriented groups of pores are conspicuous. Solitary, radial multiple, and clustered dispositions are seen in *Anopterus glandulosus* Labill., *Argophyllum ellipticum* Labill., and in all *Polyosma* species studied. Intervascular pitting is sparse in *Quintinia acutifolia* and *Q. serrata*; pitting in *Q. sieberi* is alternate with a tendency to opposite. In those species of *Escallonia* with exclusively solitary pore distribution, the widely overlapping vessel ligules provide areas of intervascular communication showing alternate intervascular pitting. Species of *Escallonia* with radial pore multiples show alternate intervascular pitting. Alternate intervascular pitting also occurs in *Anopterus macleayanus* F. Muell., *Argophyllum ellipticum*, *Brexia madagascariensis*, *Itea* sp., and in all *Polyosma* species studied except *P. integrifolia* Blume and *P. serrulata* Blume which have exclusively opposite pitting. In addition to alternate intervascular pitting, *Anopterus macleayanus* and *Escallonia floribunda* show transitional pitting. *Anopterus glandulosus* only has transitional intervascular pitting. In addition to alternate pitting, *Itea* sp. shows transitional and scalariform pitting. All species of *Polyosma* with alternate intervascular pitting also show opposite pitting. Escalloniaceae are characterized by apotracheal axial parenchyma and all species studied show either a diffuse and/or

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[7] Erdtman and Metcalfe (1963) have assigned this genus to Myrtaceae on anatomical and palynological grounds. Their evidence is so strong, that *Kania* will not be considered further in this discussion.

diffuse-in-aggregates pattern. In *Escallonia revoluta*, *E. rubra*, all species of *Polyosma*, and *Quintinia sieberi*, both diffuse and diffuse-in-aggregates patterns occur. In *Anopterus glandulosus*, *Escallonia myrtilloides*, *E. tortuosa*, *Itea* sp., *Quintinia acutifolia*, and *Q. serrata*, only diffuse axial parenchyma was observed. Parenchyma in *Brexia madagascariensis* consists of multiseriate bands. Short uniseriate bands occur in *Escallonia floribunda*, in addition to the diffuse-in-aggregates pattern. Axial parenchyma is absent in *Argophyllum ellipticum*. All species of Escalloniaceae have some uniseriate rays, although none was observed in *Anopterus glandulosus* where rays are exclusively multiseriate. All species have some heterocellular rays except for *Brexia madagascariensis*. The following species has uni- and biseriate rays only: *Anopterus macleayanus*, *Brexia madagascariensis*, *Escallonia myrtilloides*, and *E. tortuosa*. All other species studied have both uniseriate rays and rays which are two or more cells wide. Vascular rays are exclusively heterocellular in *Anopterus glandulosus*, *A. macleayanus*, *Argophyllum ellipticum*, and *Escallonia floribunda*. Rays in *Brexia madagascariensis* are homocellular and cells are upright. In the following species, multiseriate and biseriate rays are heterocellular and uniseriate rays are homocellular containing only upright cells: *Escallonia fonkii*, *E. myrtilloides*, *E. pulverulenta*, *E. revoluta*, *E. rubra*, *E. tortuosa*, *Itea* sp., and all species of *Polyosma* and *Quintinia*. Species with wide multiseriate rays commonly exhibit sheath cells. Spiral thickenings occur in walls of vessels in *Escallonia floribunda*, *E. myrtilloides*, *E. rubra*, and *E. tortuosa*. In *E. myrtilloides* and *E. tortuosa*, spiral thickenings also occur in tracheid walls. Only tracheids occur in *Anopterus glandulosus*, *Escallonia floribunda*, *E. myrtilloides*, *E. revoluta*, *E. rubra*, *E. tortuosa*, *Polyosma cunninghamii* Benn., and *Quintinia*. Both tracheids and fiber-tracheids occur in *Anopterus macleayanus*, *Escallonia pulverulenta*, and *Itea* sp. *Argophyllum ellipticum*, *Brexia madagascariensis*, *Escallonia fonkii*, *Polyosma cambodiana* Gagn. (?), *P. ilicifolia* Blume, *P. integrifolia*, *P. mutabilis* Blume, and *P. serrulata*, exhibit only fiber-tracheids. Septate fiber-tracheids appear in *Argophyllum ellipticum*.

The xylem anatomical similarities between species of Escalloniaceae and Columelliaceae are striking: exclusively scalariform perforation plates (except in *Brexia*), exclusively solitary pore distribution (in some species of *Escallonia* and in *Polyosma cunninghamii*), spiral thickenings in vessels (in some species of *Escallonia*), and exclusively tracheids (in *Anopterus glandulosus*, in some species of *Escallonia*, *Polyosma cunninghamii*, and *Quintinia*). The only major anatomical differences between these two families are the presence of vascular rays which are two or more cells wide and exclusively apotracheal axial parenchyma in all Escalloniaceae. Among the species studied, the xylem anatomy of *Escallonia myrtilloides* can hardly be distinguished from that of Columelliaceae, except for the biseriate condition of some of the rays and exclusively diffuse axial parenchyma in the former (cf. FIGS. 22 and 23, 24 and 25, 26 and 27).

Among the remaining families which have been suggested as close relatives of Columelliaceae — Ebenaceae, Styracaceae, Gentianaceae, Loganiaceae, Caprifoliaceae, Rubiaceae, Onagraceae, Oleaceae, Vacciniaceae, and Scrophulariaceae — xylem anatomy provides serious bases for comparison only with Styracaceae, Caprifoliaceae, and Vacciniaceae. Styracaceae typically show scalariform perforation plates and uniseriate, homocellular vascular rays in some species; some Caprifoliaceae have scalariform and simple perforation plates, spiral thickenings in vessels, and imperforate tracheary elements with distinctly bordered pits; and most Vacciniaceae have scalariform or scalariform and simple perforations and imperforate tracheary elements with distinctly bordered pits. Ebenaceae, Loganiaceae, Rubiaceae, Onagraceae, Oleaceae, and Scrophulariaceae, are characterized by simple perforations. In addition, Gentianaceae-Gentianoideae universally possess internal phloem and medullary vascular bundles; Loganiaceae-Loganioideae are characterized by included phloem; and Onagraceae have internal phloem in the axis and a few genera show included phloem. These dispositions of phloem are very specialized and are ordinarily indicative of close relationship within specific taxa, sometimes on an ordinal basis (e.g., internal phloem in families of Myrtales).

CONCLUSION

In reviewing the foregoing presentations of evidence and discussions, it is clearly impossible to assemble an array of data from each form of evidence presented — gross morphology, floral anatomy, foliar anatomy, nodal anatomy, and xylem anatomy — which would affirm unequivocally the relationships of Columelliaceae with any one of the several families to which it has been allied. The similarities in gross morphology of flowers and fruits among many families of various alliances probably indicates parallel evolution rather than close genetic relationship. The evolutionary development which has culminated in *Columellia* has proceeded in such a manner that the complex of its characteristics is different from any known taxon today. What baffles us now baffled our predecessors and it is time to admit once and for all that Columelliaceae is a unique plant family, probably with no really close living relatives. The clearest line of evidence for the possible relationships of Columelliaceae is provided by xylem anatomy and it appears not too far from reality to assert that this family belongs in the great saxifragaceous assemblage with the Escalloniaceae, Hydrangeaceae, and Grossulariaceae. Data from gross morphology, floral anatomy, palynology, etc., at least do not contradict this probability. Perhaps its nearest relatives are in the Escalloniaceae. If there was a common saxifragaceous ancestor, phylogenetic departure must have occurred long ago, for transitional forms seem to have been lost in the development of the modern plants of which this taxon is composed. Evidence from xylem anatomy seems equally persuasive in negating an alliance with any other family or group of families. Unfortunately, data from cytotaxonomy, embryology, and biochemistry, which might be helpful in resolving our somewhat equivocal stand, are not available for *Columellia*.

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NOTES ON THE DISTRIBUTION AND HABITAT OF COLUMELLIA

GEORGE K. BRIZICKY AND WILLIAM L. STERN

IN THE COURSE of an investigation on the taxonomic position of Columelliaceae, the authors had the opportunity to examine additional herbarium material of *Columellia* which was unavailable to Brizicky when he compiled his "Synopsis" of the genus (Jour. Arnold Arb. **42**: 363–372. 1961). This material documents range extensions for the genus and for three of the species beyond those indicated in the "Synopsis." The authors believe that the publication of these extensions, and of additional collections not reported heretofore, will be of some interest to Neotropical botanists.

The range of *Columellia* Ruiz & Pavón, as it is known at present (FIG. 1), extends from southwestern Colombia southward to Ecuador, Peru (as far south as the departments of Cuzco, Urubamba, and Apurimac), and to the "yungas" of western Bolivia. Extensions of the ranges of species and additional collections are cited below.

Columellia oblonga Ruiz & Pavón.

DISTRIBUTION: southern Colombia, Ecuador, Peru, and western Bolivia.

Columellia oblonga subsp. **oblonga.**

Peru. AMAZONAS: prov. Chachapoyas, middle eastern Calla-Calla slopes, near kms. 415–418 of Leimebamba-Balsas road, elev. 2900–3150 m., *J. Wurdack 1732* (US, A), Aug. 20, 1962. HUANCAVELICA: prov. Tayacaja, Ampurco, entre Salcabamba y Surcubamba, bosque perennifolio, alt. 3000 m., *O. Továr 3785* (US), Apr. 19, 1962; alrededores de Huachocolpa, Valle del Mantaro, monte perennifolio, suelo arcilloso, nombre vulgar "yurac-chachas," alt. 2800–2900 m., *O. Továr 4033* (USM), Apr. 16, 1963.

Some leaves in *Wurdack 1732* are almost entire, approaching subspecies *sericea* in this character. This is not surprising, since the occurrence of specimens transitional between subspecies *oblonga* and subspecies *sericea* in that geographical area had already been reported in the "Synopsis."

Columellia oblonga subsp. **sericea** (H.B.K.) Brizicky.

Colombia. NARIÑO: Cordillera Occidental, upper east slope of Volcán Gualcalá, 18 km. east of Piedrancha, páramo on steep slope, vegetation chiefly grass and *Espeletia*, alt. 3500–3600 m., *F. R. Fosberg 21175* (US), Oct. 5, 1943.

This collection by Fosberg is the first documented report of the species and the subspecies from Colombia. Pubescence on the lower side of leaves is less dense and the hairs are shorter than is typical for this subspecies.

Ecuador. IMBABURA: Cordillera Occidental, along trail to Piñan, slope of Volcán de Cotacachi, common near edge of páramo, alt. 10,400 ft., *W. B. Drew*

FIG. 1. Northwestern South America illustrating known range of *Columellia*. 1, *C. oblonga* subsp. *sericea*; 2. *C. obovata*; 3, *C. oblonga* subsp. *serrata*; 4. *C. oblonga* subsp. *oblonga*; 5. *C. lucida*; 6, *C. subsessilis*.

E-113 (US), Mar. 14, 1944; ridge along trail above Taminanga, southwest of Volcán de Cotacachi, elev. 10,500 ft., *M. Ownbey 2618* (US), Dec. 1, 1943.

PICHINCHA: between Quito and Santo Domingo de los Colorados, km. 20, alt. 3400 m., *C. H. Dodson & L. B. Thien 1067* (US), Oct. 22, 1961.

Drew notes that the plant is medicinal and is locally called "turbata." Many leaves in *Drew E–113* and in *Ownbey 2618* are toothed with one to five teeth on each side of the leaf, below the apex.

Columellia lucida Danguy & Chermezon.

DISTRIBUTION: southwestern Colombia, Ecuador, and northern Peru. Occurrence of this species in Colombia and Peru has not been reported previously.

Colombia: *sine loco, Mutis "Cestrum, 175"* (US). The arbitrary number assigned by E. P. Killip to this collection is *2784*. The exact locality of collection is unknown; however, the vicinity of Ibagué or of Mariquita in the Cordillera Central may be considered as possible regions for Mutis's gathering [Hernandez de Alba, G. 1958. Diario de observaciones José Celestino Mutis (1760–1790). Tomo II. Instituto Colombiano de Cultura Hispanica. Bogotá. (*Cestrum*, pp. 51, 136–137)].

Peru. PIURA: prov. Huancabamba, Talanco Huaca, cerca á Huancabamba, monte bajo, alt. 3300 m., *C. Friedberg 240* (US), June 14, 1961. This specimen compares extremely well with the original description of *C. lucida*.

Columellia obovata Ruiz & Pavón.

DISTRIBUTION: Peru.

Peru. HUANCAVELICA: prov. Huancavelica, Huando [Mantaro Valley], entre Conaica y Huancavelica, estepa de gramíneas con arbustos dispersos, alt. 3650 m., *O. Továr 1266* (US), Apr. 6, 1953. APURIMAC: prov. Aymaraes, valley of Río Colcachaca at Cotarusi-Colca, ca. 1 km. above junction with Río Chalhuanca, ca. 15 km. (air) south of Chalhuanca, alt. ca. 3000–3100 m., *H. H. & C. M. Iltis, D. & V. Ugent 547* (US), Dec. 16, 1962.

These two collections document extensions of the range of this species in Peru. *Továr 1266* is represented by a branchlet with rather small, entire, apparently young leaves.

No taxonomic changes within the genus are indicated through our study of this additional material. It is still true, unfortunately, that our knowledge of the infrageneric taxa is incomplete owing to the relative sparsity of collections. Data from cytology would be extremely useful in resolving questions of infraspecific taxa.

At our request, Dr. Oscar D. Továr, Herbario San Marcos, Museo de Historia Natural, Lima, made and transmitted observations on the habitat of *Columellia* based on his collections (*4033*) of plants of *C. oblonga* subsp. *oblonga*: This subspecies is more or less frequent in the area of collection. The habitat is a subtropical, evergreen low forest called in Peru, "Ceja de la montaña." However, it is a little dry in comparison with the true "Ceja de la montaña" vegetation. The altitudinal distribution (of this vegetation?) is between 2600 and 3300 meters. The soil is more or less "humid," and rich in humus. Unfortunately, there are no annual records of temperature and rainfall kept for this region. The climate is temperate and on April 16, 1963, the minimum temperature was 10°C. and the maximum temperature was 24°C., in the shade. *C. oblonga* subsp. *oblonga* in this area grows with species of *Phenax*, Melastomataceae, *Befaria* and other Ericaceae, *Embothrium*, *Weinmannia*, *Desfontainea*, *Centropogon*, *Seemannia*, *Manettia*, *Rubus*, *Clusia*, and *Hesperomeles ferruginea*, as well as with other species.

Columellia obovata, represented by *Továr 1266*, is found in a different habitat from *C. oblonga* subsp. *oblonga*. The soil is drier and the vegetation is dominated by low, deciduous shrubs and other plants including species of *Baccharis*, *Minthostachys*, *Alonsoa*, *Calceolaria*, and *Monnina salicifolia*. Továr remarks that *C. obovata* is very rare in the Mantaro Valley zone and that at the time of collection, only this single specimen was seen.

The specimen of *Columellia obovata* collected by the Iltises and Ugents (*547*) is recorded from steep, very rocky (calcareous) south facing slopes with many cereus and opuntia cacti, bromeliads, few trees (escallonias) with *Tillandsia usneoides*, many shrubs, all heavily grazed.

Camp's notes on his collection (*E–4461*) of *Columellia oblonga* subsp. *oblonga* contain fairly complete data on the manner of growth and habitat of this plant in Ecuador (prov. Azuay, near Sevilla de Oro, elev. 8000–9000 ft.) — "This species flowers when quite young, specimens seen in the region in full flower and only about 1 m. high; it is fairly abundant on cut-over and burned areas which are regenerating (possibly from root-sprouts) where it might be taken for a shrub; also seen in forested areas, the tree easily detectable by the irregular contour of the trunk and the shreddy bark, one patriarch seen along this same quebrada at about 8,000 ft. elev. with a trunk diam. of nearly 2 m. (the top broken out of this tree and so no estimate can be given of maximum height)."

From the reports above, it appears that both *Columellia oblonga* subsp. *oblonga* and *C. obovata* are able to thrive under fairly harsh conditions imposed by burning, heavy grazing, and occasional drought. At least *C. oblonga* subsp. *oblonga* seems also to do well in forested areas and probably has the capacity to regenerate following fires, possibly by root sprouts. Like so many woody plants which can exist successfully under disturbed conditions, *C. oblonga* subsp. *oblonga* appears to be paedogenetic.

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THE ECOLOGY OF AN ELFIN FOREST IN PUERTO RICO, 3. HILLTOP AND FOREST INFLUENCES ON THE MICROCLIMATE OF PICO DEL OESTE

HAROLD W. BAYNTON

A GENERAL DESCRIPTION of the geography and microclimate of Pico del Oeste is given in earlier reports in this series (Howard, 1968; Baynton, 1968). This report gives a more detailed analysis of both diurnal variations, and the differences above and below the canopy for rain and wind. The collection of cloud water is also described and its significance is discussed.

INSTRUMENTATION

A wind-driven generator was installed on top of a 20-foot tower to provide 12-v power for recording a number of meteorological events. The tower also supported an anemometer and a wind vane about 8 feet above the forest, and a tipping-bucket rain gage at tree top (see *fig. 2*, p. 420, Baynton 1968). A second anemometer was mounted within the forest about 6.5 feet above ground (see *fig. 7*, p. 425, Baynton 1968).

Rain below the forest was measured by means of a tipping-bucket gage of special design. Instead of the conventional round collector, a teflon-lined trough of equal projected area but 125 inches long and 0.9 inches wide was used in order to average out variations in the density of the canopy. Teflon was chosen because of its non-wetting characteristic. With the collector set at a slope of 10 degrees, entering drops move quickly to the exit funnel and thence to the tipping bucket.

Collection of cloud water was undertaken in order to evaluate the relative importance to the overall water budget of water impinging upon the trees from the cloud. FIGURE 1 is a photograph of the collector. Two layers of aluminum shadescreen, shown by the Pineapple Research Institute of Hawaii to be superior for this purpose (Ekern, 1964), were supported on a redwood frame, and laced together with brass wire at the bottom. A brass trough below the shadescreen carried the water through an orifice to a standard tipping-bucket collector. Calibration of the bucket in place on Pico del Oeste yielded 18.93 milliliters/bucket tip, which, when combined with the area of the collecting screen, yielded a calibration constant of 50.4 milliliters per square meter (ml/m^2) of cross section. This was rounded off to 50 ml/m^2.

The cloud-water collector was built to fit inside the thermometer shelter in order to exclude rain from the collected water. The location of the

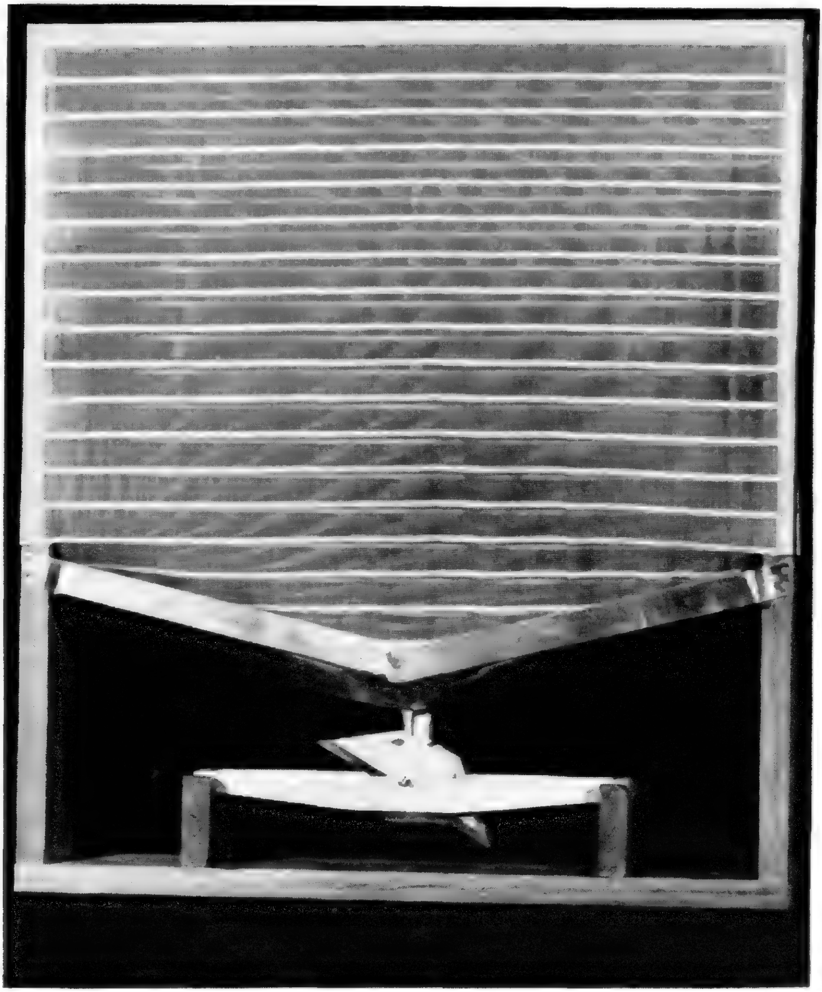

Fig. 1. Cloud-water collector.

thermometer shelter was just above the canopy (see *fig. 1*, p. 420, Baynton 1968) and the cloud-water collector was inside the shelter with its collecting surface approximately at right angles to the prevailing wind (see *fig. 3*, p. 421, Baynton 1968).

Each mile of wind passing an anemometer caused a switch closure that was recorded on a 20-pen event recorder and a 10-digit impulse printer set to print out and rezero at 1-hour intervals. The recorder and printer are shown in Figure 2. Each hundredth inch of rain collected by a tipping-bucket gage caused a switch closure that was recorded on the event recorder, and entered on the impulse printer. Each tenth and

FIG. 2. From left to right the instruments are: event recorder, impulse printer, and accumulating counters. The counters registered total rainfall and wind direction.

whole inch of rain were also recorded by the event recorder to provide for better resolution of the data during heavy rain. As the study progressed and equipment deteriorated, the redundancy of the two records minimized gaps in the records of wind and rain. Each bucket tip in the cloud-water collector, equal to 50 milliliters of cloud water per square meter of collecting surface, caused a switch closure that was recorded by another pen of the 20-pen event recorder.

RESULTS

Rainfall. Various factors may affect the rainfall of Pico del Oeste. It is near enough to the sea to respond to tropical maritime influences. Kraus (1963) found that maritime precipitation is significantly more frequent at night; Alaka (1964) reports the widely held belief that precipitation is suppressed during midday over the tropical oceans. The peak is also far enough inland to be affected by convective showers, high enough to experience orographic rainfall, and of course subject to synoptic scale weather disturbances. These assorted conflicting influences explain why an analysis of the diurnal variation of rainfall showed three maxima and three minima, all of uncertain significance.

However, when the frequency of occurrence of rain and the intensity of the actual rainfall occurrences were analyzed separately a clear picture emerged as shown in FIGURE 3. Rainfall was almost twice as frequent at

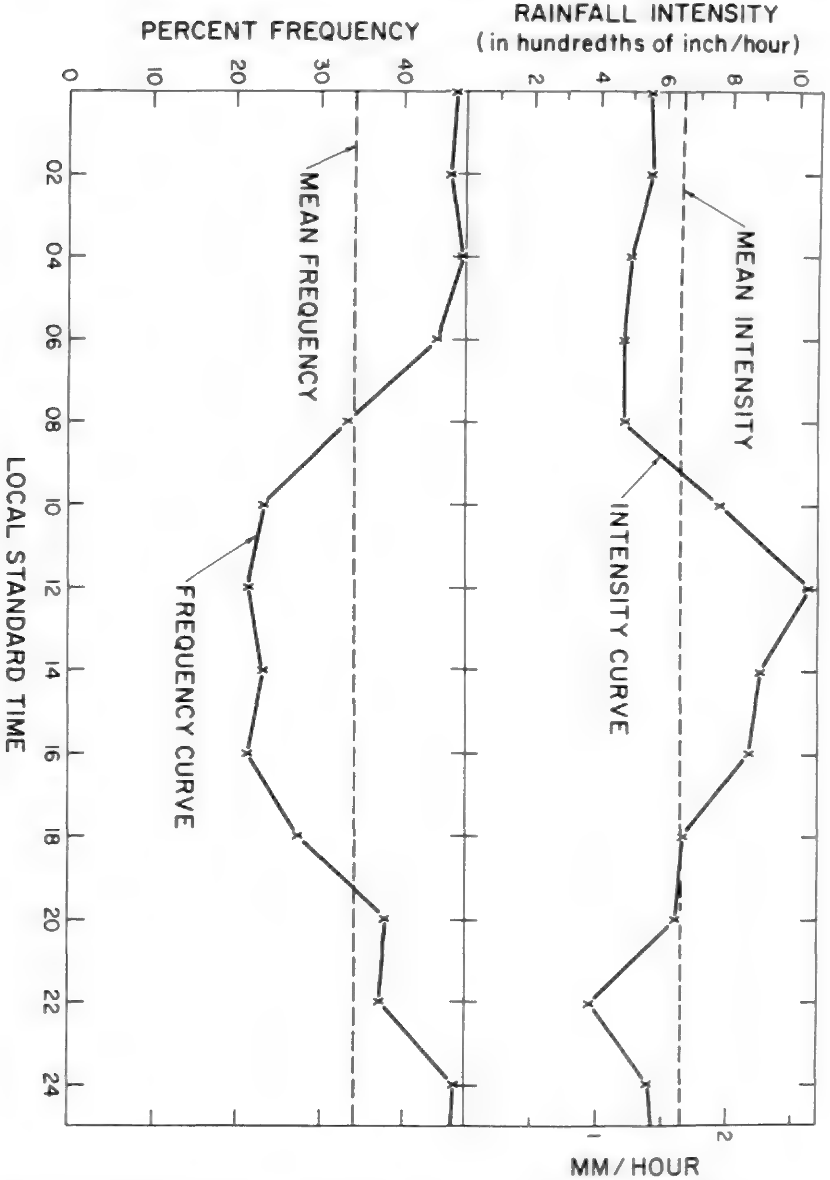

FIG. 3. A representation of the diurnal variation of intensity and frequency of rainfall occurrences.

night as in the day, whereas daytime rains were almost twice as heavy as nighttime rains. Presumably daytime rains are predominantly convective, while nighttime rains are orographic.

The effect of the forest on rainfall rate is illustrated in FIGURE 4 where the 1-minute accumulations of rainfall above and below the forest are compared for a typical shower. During an 11-minute interval 0.54 inches of rain fell above the forest. Within a minute the rain began below the forest, continued for 12 minutes and totalled 0.38 inches. The forest acts like a filter, delaying the onset of rain at ground level, lessening the peaks and smoothing the variations of intensity, and prolonging the rain slightly as it drips from the leaves.

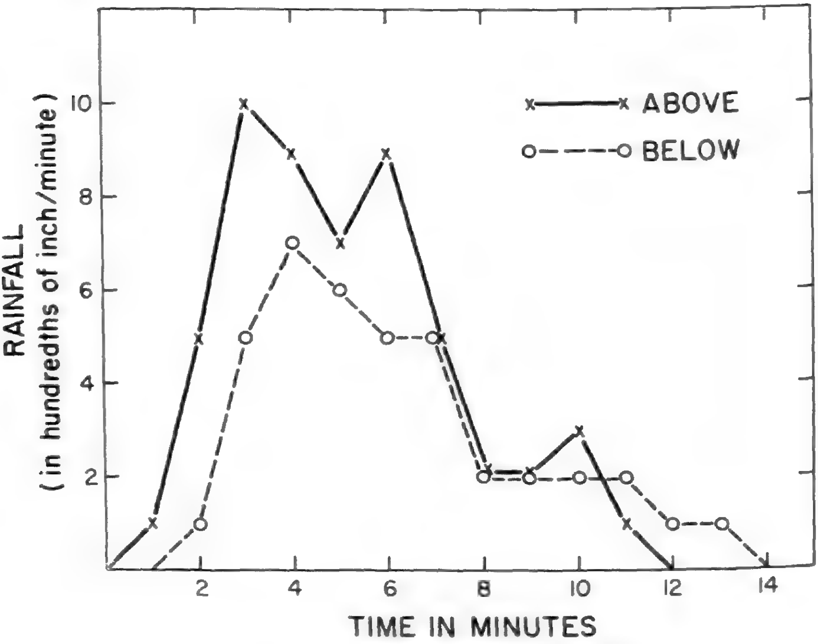

FIG. 4. A representation of the rainfall rate above and below the forest *versus* time, near noon, 20 July 1966.

The rain above that is not caught by the lower rain gage has either been intercepted by the trees or has reached the ground by means of the trunks. Hydrologists define interception as that portion of precipitation that never reaches the ground either as rain or trunk flow. This relationship is expressed in the simple continuity equation:

$$\text{Rain Below} = \text{Rain Above} - \text{Trunk Flow} - \text{Interception} \qquad (1)$$

Wisler and Brater (1959) point out that after the initial wetting of the leaves, branches, and trunks of trees, the interception rate becomes equal to the evaporation rate from those surfaces. Since Pico del Oeste is usually shrouded in fog it follows that the interception rate is usually zero and that trunk flow must account for almost all of the difference between rain above and below the forest. This result contrasts with the rather large interception and small trunk flow reported by Clegg (1963) in much taller stands at lower elevations in the Luquillo Mountains.

Rainfall below the forest as a function of rainfall above was analyzed by standard regression techniques. One hundred and twenty-four rains were selected for the analysis. Each had the property that it was preceded by a 6-hour drying period as shown by the hygrograph trace. Thus part of each rain was used in wetting the foliage. The balance either ran down the trunks or dripped through. Using the notation X = rain above the forest in inches, Y = rain below the forest in inches, the analysis yielded:

$$Y = 0.768X - 0.034$$

with a correlation coefficient of 0.99 between X and Y.

A correction was dictated by slight differences in the volume of water required to tip the buckets in the two gages. The design value is 18.5 ml. Calibration of the two gages in place gave 18.5 for the upper gage and 18.9 for the lower gage. Appropriate adjustment leads to the final result:

$$Y = 0.786X - 0.035$$

On rewriting the equation in the form:

$$Y = X - 0.214X - 0.035$$

and comparing it to equation (1) we can identify trunk flow as 21.4 percent of the rain above and interception as 0.035 inches. Clegg cites other investigators as setting trunk flow no higher than 10 percent of the total rainfall. The explanation for large trunk flow on Pico del Oeste is undoubtedly found in the unusually high number of stems, a feature of this forest that is well illustrated in FIGURE 5.

The interception figure of 0.035 inches implies that the vegetation over each square meter of ground is able to store 886 ml/m^2. Studies of the U.S. Forest Service reported by Wisler and Brater indicate storage capacities of about 0.14 inch for hardwoods and 0.23 inch for pines in North Carolina. Storage in the cloud forest of Pico del Oeste would be expected to be very much less since it is only 10 to 12 feet high. It should be noted that, for rains occurring when the forest is already thoroughly wet, the relationship between rain below and above simplifies to

$$Y = 0.786X$$

Cloud Water. The difficulty with all cloud water studies is to relate the observations of a collecting device to the amount of water that the foliage itself extracts from the cloud. Although the same difficulty besets the interpretation of the data collected on Pico del Oeste, different lines of argument support the conclusion that cloud-water is of secondary importance in this region of abundant rain. In the first place, cloud water is not a means of sustaining the forest during drouth since cloud-free periods coincide with rainless periods. Secondly, four distinct analyses, each of which by itself is imprecise, give very similar results.

FIRST ANALYSIS. The cloud-water sampler was in service for 258 days during the year from June 1966 to May 1967. By extrapolating the data

FIG. 5. A view of the elfin forest illustrating the great number of stems in its composition.

to a full year the annual total of cloud water is estimated at 325 liters/square meters (l/m^2). Since 1 mm. of rain is the same as 1 l/m^2, the annual rainfall total of 453 cm. may be expressed as 4530 l/m^2. Although the unit cross section is in a vertical plane for cloud water and in a horizontal plane for rain, no adjustment is needed for trees such as those on Pico del Oeste that present about equal cross sections on horizontal and vertical planes. Moreover the wind speed through the thermometer shelter housing the cloud-water collector was found to be nearly the same as the wind in the forest halfway to the top, namely 17.6 and 16 percent, respectively, of the 20-foot wind. Deferring for the moment any discussion of differences in the collection efficiency of the aluminum shadescreen and the foliage, and differences in the sampling period, the data imply that cloud water is only 7.2 percent of rain water.

SECOND ANALYSIS. Another approach was based on a 1,000-hour period from 18 July to 29 August 1966. Since cloud water intercepted by the trees contributes to rain measured below the forest, the record of the 20-pen event-recorder was examined for occurrences of rain below the forest without rain above. The event of interest, "rain below without rain above," was defined as no rain above during the three hours including the hours preceding and following an occurrence of rain below. Any run of three hours without rain above the forest is a possible occurrence of the event of interest. There were 324 possible occurrences and only 15 observed occurrences. During the 1,000 hours the total rainfall below the forest was 15.83 inches. Of that total 0.15 inch occurred without rain above and must therefore be attributed to cloud water. Additional cloud water is also collected during rain but the exact amount cannot be determined. Again the implication is that cloud water is only a small fraction of rain water.

THIRD ANALYSIS. The 15 cases were then examined in detail in an attempt to relate the observed cloud water collection to the observed rainfall below the forest. The approach was to count the number of tips of the cloud-water collector during the time for 0.01 inch of rain to accumulate in the below-canopy rain gage. The data are summarized in TABLE 1. The entry for August 19 is suspect because of the long accumulation time indicating that the foliage must have dried out and had to be rewetted before the process of foliage drip could resume. The same might be true for August 16. The analysis is imprecise because in many cases some rain fell during the accumulation time. Omitting August 19 the mean is 5.4 units of cloud water per 0.01 inch of rain below the forest.

Earlier it was shown that 78.6 percent of rainfall drips through when the foliage is wet and the same will be true for cloud water. Thus the collection of $\frac{18.9}{18.5} \times 0.01$ inch[1] or 259 ml/m^2 of water below the canopy

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[1] $\frac{(18.9)}{(18.5)}$ is the correction factor that accounts for 18.9 ml. being the actual volume of water to tip the bucket rather than the design volume of 18.5 ml.

during a rainless period results from the collection of $\frac{259}{0.786} = 330$ ml/m^2 of cloud water by the foliage. During the same period this analysis shows that 5.4 (50) = 270 ml/m^2 of water were collected by the cloud-water detector. Therefore, the foliage is 1.2 (i.e. 330/270) times as efficient as the cloud-water collector.

TABLE 1. **For fifteen occurrences of 0.01 inch rain below the forest without rain above, the amount of cloud water collected during the accumulation time, and the accumulation time.**

Date		Amount cloud water during accumulation time	Accumulation time for 0.01 inch rain below	
July	29	8.1 units *	4 hours	11 min
	30	9.6	3	37
Aug.	2	6.6	4	50
	2	5.4	4	30
	5	5.0	3	12
	5	1.2	1	40
	7	1.4	3	12
	9	7.3	3	43
	11	2.5	3	9
	13	4.2	5	14
	13	4.0	4	54
	14	5.5	4	17
	16	10.0	11	8
	19	16.5	24	39
	22	5.0	3	10

* One unit, or bucket tip, equals 50 ml/m^2.

FOURTH ANALYSIS. The main shortcoming of the third analysis was the truncation error associated with the collection of rain and cloud water in discrete steps of a bucket. It appeared possible to sharpen the analysis by replacing the tipping buckets with bottles and measuring exact volumes of water collected by the two rain gages and the cloud-water collector under personally observed weather conditions. The fourth analysis summarizes the results of this approach carried out in December of 1967.

Five separate attempts were made to collect rain and cloud water under known boundary conditions. When the data were analysed, errors in experimental technique became evident. Generally there was doubt about the boundary conditions. No interpretation of the first attempt was possible because it became apparent that the foliage was neither fully wet nor fully dry. Another error in technique may be illustrated by the analysis of the data collected on 9 December.

The collecting of water began at 9:55 a.m., immediately after a moderate shower, and continued until 4 p.m. The error in technique was that the sampling began so soon after the shower that its effect was still being felt as drip from the foliage. The collected water was equivalent to 3227 ml/m^2 of rain above the canopy, 2746 ml/m^2 below the canopy, and only 70 ml/m^2 of cloud water. Because the foliage was always fully wet the relationship

$$Y = 0.786X$$

should apply where $Y = 2746\ ml/m^2$. But because of the faulty technique, we have

$X = \text{Rain Above} + (\text{Cloud Water})\ E + \triangle R$, with E being the ratio between the collecting efficiency of the vegetation and the cloud-water collector, and $\triangle R$ being the unknown amount of rain above the canopy immediately before 9:55 that is in the process of getting to the ground via trunks and drip-through. Substituting both Y and X in the equation gives:

$$2746 = 0.786\ (3227 + 70E + \triangle R)$$

whence:

$$E = 3.82 - 0.014\ \triangle R$$

We conclude therefore that E is less than 3.82 since $\triangle R$ is not zero, but that is all we can say.

Two of the attempts were for periods that began with dry foliage, i.e. no liquid water attached to plant surfaces. The collections in the three gages should therefore be related by:

$$Y = 0.786X - 886$$

where the units of X and Y are ml/m^2 so that 886 replaces 0.035 in the original equation because each hundredth of an inch of rain = 254 ml/m^2.

Between 4:35 p.m. December 7 and 1 p.m. December 8 the amounts collected were 3570 ml/m^2 of rain above, 2004 ml/m^2 below, and 16 ml/m^2 of cloud water. With so little cloud water the equation is too sensitive to slight errors in the collected amounts above and below to permit estimates of E, the relative collecting efficiency of the vegetation. We can, however, get independent estimates of the Y-intercept, 886, by substituting $E = 1.2$, the value obtained earlier or $E < 3.82$,[2] the upper limit. These choices of E yield a Y-intercept = 817 and <850.

Conditions were also dry on the peak at 11:45 a.m. December 3 when collections were begun. By 3:45 p.m. December 4 the amounts were 1936 ml/m^2 of rain above, 906 ml/m^2 below, and only 22 ml/m^2 of cloud water. Setting $E = 1.2$ and <3.82 gave values of 637 and <682 for the Y-intercept. The average of these two trials was 727 for $E = 1.2$ and <766 for $E < 3.82$, providing fair confirmation of the value, 886, obtained from the regression equation.

One attempt combined enough cloud water with light rain to permit an estimate of E, the relative collecting efficiency of the forest. Between

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[2] $<$ is the symbol for "is less than."

4:30 p.m. on December 2 and 11:20 a.m. on December 3 the observed collections were 2128 ml/m² of rain above, 310 ml/m² of cloud water, and 1151 ml/m² of rain below. On December 2 the peak had been clear for four hours during the day but had fogged in shortly before 4:30 p.m.

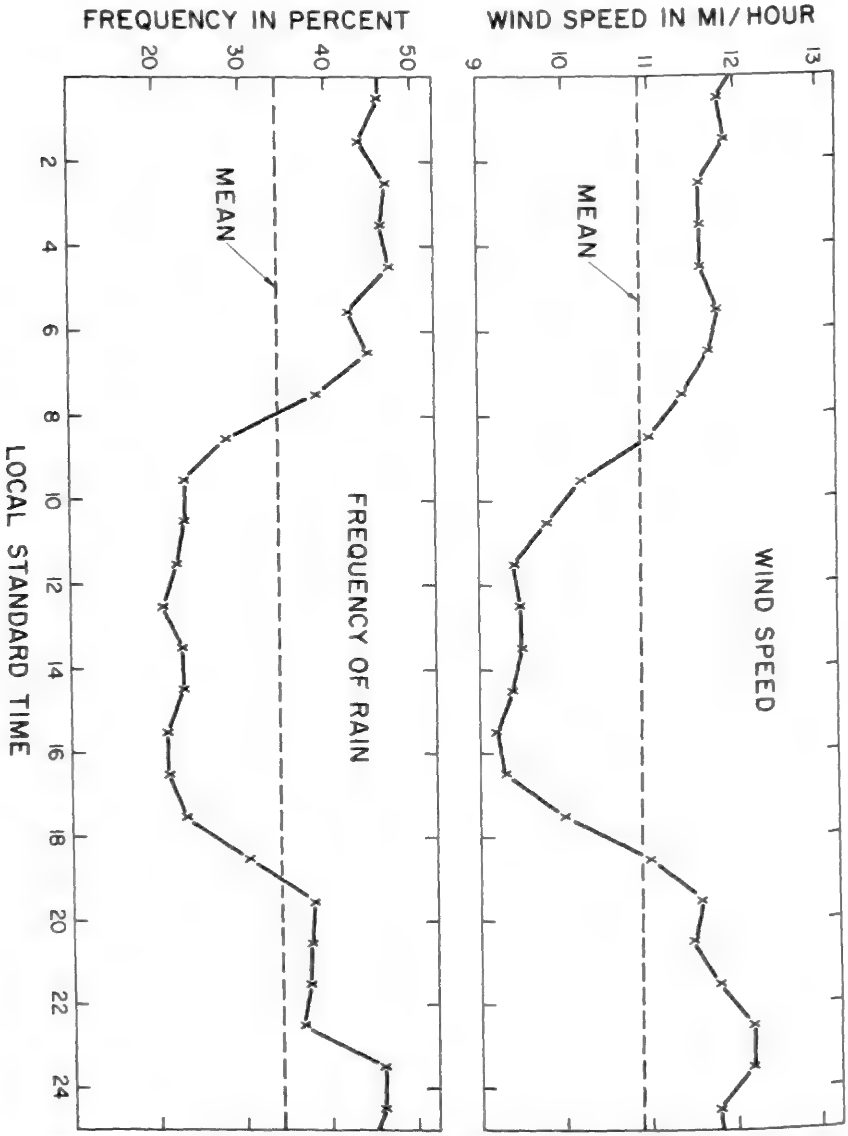

FIG. 6. A graphic comparison of the diurnal variations of wind speed and frequency of rain.

Presumably the forest was substantially, but not fully, dry. Substitution in the regression equation gives:

$$1151 = 0.786\ (2128 + 310\,E) - 886,$$

from which E = 1.5 or slightly less since the constant, 886, is for fully dry foliage.

While not providing the hoped for "acid test," the fourth analysis confirms that the foliage is only slightly more efficient than the cloud-water collector and that its storage capacity is substantially less than that reported for other forests.

Correcting the first analysis for the greater collecting efficiency of the foliage, we have annual cloud water of 1.2 (325) = 390 l/m^2, which is 8.6 percent of the annual rainfall. Although this amount is relatively unimportant to the water budget of Pico del Oeste it is equal to the normal annual precipitation for Denver, Colorado.

Wind Speed. The diurnal variation of wind speed above the forest is shown in the upper half of FIGURE 6. The data were for a month with little daytime clearing, August, and a month with considerable daytime clearing, October. Both months showed the same pattern and were therefore combined. For comparison the diurnal variation of rainfall frequency is included in FIGURE 6. The night maximum and day minimum show the influence of convection. During the daytime there is a downward flux of mo-

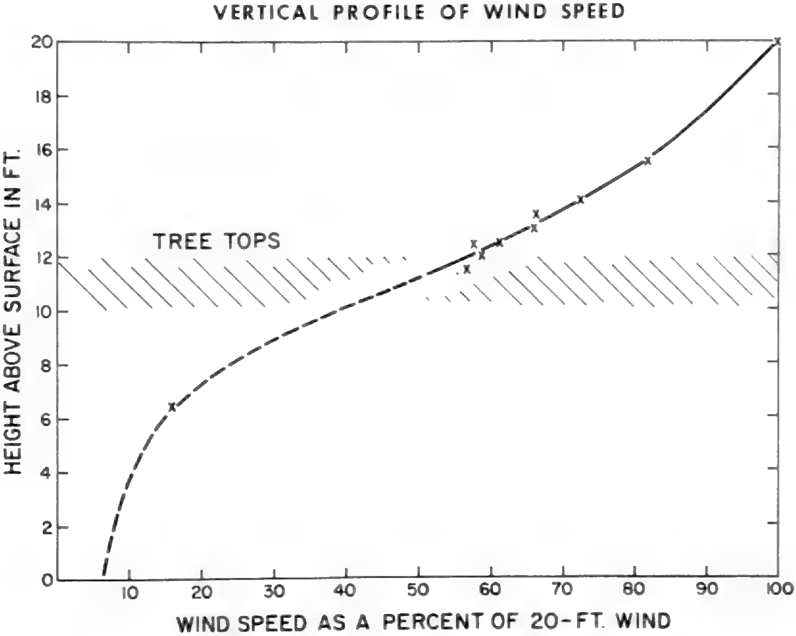

FIG. 7. A vertical profile of wind speed.

mentum below the mountain top and a consequent decrease in wind speed. The same anomalous cycle has been reported on towers several hundred feet above flat ground.

The almost identical cycle of rainfall frequency supports the interpretation that the frequent nighttime rains are mainly orographic, and that daytime rains are mainly convective.

The vertical profile of wind speed above and below the tree tops was investigated by installing a sensitive Casella anemometer at various heights on the tower. Wind speed averaged over an hour was expressed as a percent of the 20-foot wind. The results are presented in FIGURE 7. Additional points below the tree tops might modify that portion of the curve.

SUMMARY

Rainfall on Pico del Oeste, although twice as frequent by night, is only half as intense as during the day. Rain is mainly orographic by night and convective by day.

Trunk flow accounts for 21 percent of the rainfall.

The canopy has a storage capacity equal to a depth of 0.035 inches or 886 ml/m^2.

On the average, water extracted from the clouds by the foliage is slightly less than 10 per cent of rainfall.

Winds are strongest at night and weakest during the afternoon.

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THE ECOLOGY OF AN ELFIN FOREST IN PUERTO RICO, 4. TRANSPIRATION RATES AND TEMPERATURES OF LEAVES IN COOL HUMID ENVIRONMENT[1]

David M. Gates

The purpose of the studies reported here is to contribute some understanding of the adaptation, growth, and behavior of plants in the mist forest at the top of Pico del Oeste, Luquillo Mountains, Puerto Rico.

The primary influence of climate on a plant is through the transfer of energy. All physiological processes consume energy. Biochemical reactions are temperature dependent and some are light dependent. The vitality of a plant depends on its temperature and its energy content. If a plant is too warm, its vital processes slow down; and above certain temperatures many physiological processes stop and denaturation of proteins occurs. If a plant is too cool, its vital processes slow down. The plant will not survive below certain temperatures. Most plants grow best at an optimum temperature.

The energy content of a plant determines its temperature. Several factors affect the energy exchanged between a plant and its surroundings. The significant environmental factors are radiation, air temperature, wind and humidity. In order for these factors to be translated into their effect on the plant, they must be expressed as energy flow. The incident radiation is a specific amount of energy. The air temperature and wind speed are translated into energy flow by the concept of convection. The humidity of the air affects the energy exchange for a leaf by means of the transpirational cooling. The leaf temperature and transpiration rate are dependent variables which are functions of the four independent variables: radiation, air temperature, wind, and humidity. Therefore, it is seen that one must deal with a six-dimensional problem. This is complicated, but there is no choice. It is not valid to ask for the influence of air temperature on transpiration rate without specifying the values of all other variables simultaneously. It is this simultaneity of factors which makes ecological problems complex.

Energy Exchange

A leaf absorbs an amount of radiation which is designated Q_{abs} in cal cm^{-2} min^{-1}. The absorbed radiation is the sum of absorbed direct sun-

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light, scattered skylight, reflected light, and emitted thermal radiation from ground, vegetation, and atmosphere. The leaf absorbs each incident stream of radiation according to the absorptivity of its surface and the leaf orientation. This is discussed by Gates (1968a) in detail. The leaf consumes a very small fraction, maybe one or two percent, of the absorbed radiation in photosynthesis. The major portion of the absorbed radiation is lost by radiation emitted from the leaf surface, by convection and by transpiration. The energy budget for the leaf is given as follows:

$$Q_{abs} = \epsilon \, \sigma \, T_l^4 + k\left(\frac{V}{D}\right)^{1/2} (T_l - T_a) + L\,\frac{{}_s d_l(T_l) - \text{r.h.}\ {}_s d_a(T_a)}{r_l + r_a} \tag{1}$$

where ϵ is the emissivity of the leaf surface, σ is the Stefan-Boltzmann radiation constant, k is a constant, V is the wind speed in cm sec^{-1}, D the width of the leaf in cm, T_l and T_a the leaf and air temperatures respectively, L the latent heat of vaporization of water (580 cal gm^{-1} at 30°C), ${}_s d_l$ (T_l) and ${}_s d_a(T_a)$ the saturation vapor densities at the leaf and air temperatures respectively, r.h. the relative humidity of the air, and r_l and r_a the diffusion resistance of the stomatal pathway and adhering boundary layer of air on the leaf surface respectively. The value of r_a is inversely proportional to the wind speed and proportional to the leaf size. These factors are discussed more thoroughly by Gates (1968b). The energy budget is balanced by the leaf temperature adjusting to a value such that the energy into the leaf equals the energy out from the leaf. The leaf does this automatically for any conditions. We must use a computer to solve Eqn. (1) for the temperature and transpiration rate for any set of conditions.

Climate of Pico del Oeste

The purpose here is to make a reasonable estimate of the transpiration rate of the plants at the summit of Pico del Oeste, Luquillo Mountains, Puerto Rico. In order to estimate transpiration rate one needs to know the climate to get values of radiation, air temperature, wind speed, and humidity. The climate of El Yunque Mountain in the Luquillo Mountains is reported by Briscoe (1966) and for Pico del Oeste meteorological observations are reported by Baynton (1968) and by Howard (1968). The climate of the peak is generally wet with frequent rain and mist, windy, temperate, and of low illumination. Table 1 summarizes the climate and is an approximate indication of the conditions expected. The mean wind speed at tree top level on the peak is 14 mph. The incident global radiation on a horizontal surface has a maximum value of 0.8 cal cm^{-2} min^{-1} on the peak as compared with 1.3 cal cm^{-2} min^{-1} at San Juan. There is no question that the peak has a low light level as the result of the persistent cloud cover. Briscoe's measurements for El Yunque show it to have a mean wind speed of 13 mph and a mean relative humidity of 98 percent. The maximum radiation at noon on El Yunque was 0.8 cal cm^{-2} min^{-1}, with a minimum of about 0.3 cal cm^{-2} min^{-1}.

LEAF TEMPERATURES AND TRANSPIRATION

The temperatures of the leaves of several plants growing on the summit of Pico del Oeste were measured on 7 and 8 January 1968, using a portable infrared radiometer. A detailed description of this infrared thermometer is given by Gates (1968c). The infrared thermometer senses the radiation emitted by a leaf and from the blackbody radiation law converts the response to the surface temperature of the leaf. Temperature readings are accurate to 0.3°C. Air temperature was measured with a dial thermometer and the wind speed with a hand held anemometer. The forest on the summit is dominated by *Tabebuia rigida* and *Ocotea spathulata*. The leaves of these plants are approximately 6 to 8 cm. in width.

The Q_{abs} is estimated at 0.57 cal cm^{-2} min^{-1}. The relative humidity of the air was about 85 per cent. By use of the energy budget, Eqn. (1), the relationship between transpiration rate and leaf temperature as a function of humidity and internal diffusion resistance for leaves of 6×8 cm. dimension, at an air temperature of 17°C and a wind speed of 100 cm sec^{-1} (2.2 mph) is shown in FIG. 1. It is possible to read from the graph the expected transpiration rate, if the leaf temperature is known. Assuming an internal resistance for the leaf of 5 cm sec^{-1}, it is anticipated that the leaves of the canopy would transpire about 1.5×10^{-5} gm cm^{-2} sec^{-1}, as shown by point A in FIG. 1.

The canopy then became illuminated with an increased amount of sunshine to give an amount of absorbed radiation of about 0.62 cal cm^{-2} min^{-1}. These conditions are represented by point B in FIG. 1. The leaf temperature was measured to be 18°C and the transpiration rate is 3.5×10^{-5} gm cm^{-2} min^{-1}. A few moments later the canopy was illuminated with more sunshine as the clouds thinned and the leaf temperature became 21°C. The conditions for the leaf are represented now by point C in FIG. 1, which indicates the transpiration rate as 6.3×10^{-5} gm cm^{-2} min^{-1} at an absorbed radiation of about 0.78 cal cm^{-2} min^{-1}. Since the internal diffusion resistance of the leaves of the canopy was not measured, it is possible that it was different than 5 sec cm^{-1}. Since the leaves were highly sclerophyllic, it is likely that the internal resistance was not less than 5 sec cm^{-1}. It may have been greater than 5 sec cm^{-1}. If it were 10 cm sec^{-1}, the transpiration rates would have been cut in half and the points referred to would be shown by a, b, and c respectively.

TRANSPIRATION RATE

A more accurate way to measure the transpiration rate of the leaves of the canopy is to sever a leaf, mount it side by side with an attached leaf and measure the temperature difference of the two leaves. If this is done, it is possible to use the energy budget computation to determine the transpiration rate of the attached leaf. On the basis that the severed leaf closes its stomates within about 15 minutes but that it absorbs the same amount of radiation as the attached leaf, one can read from FIGURE 1 the

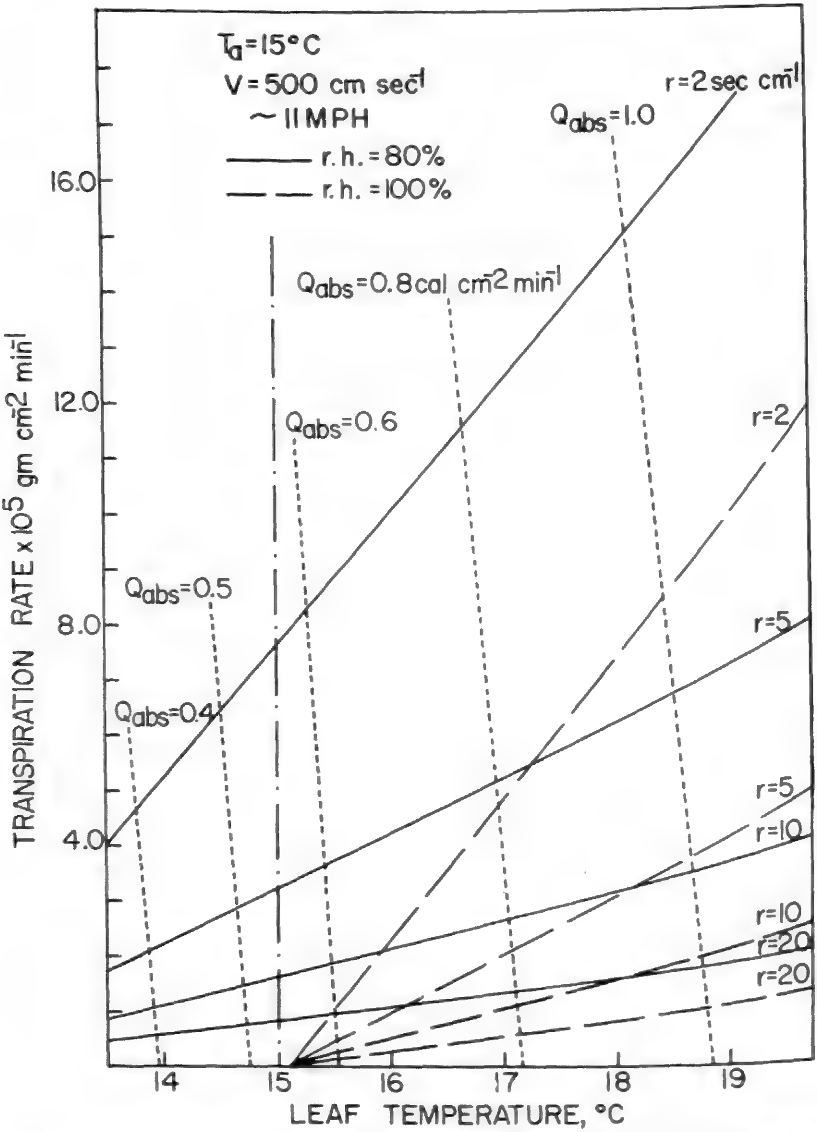

FIG. 1. Transpiration rate and leaf temperature as a function of the absorbed radiation, relative humidity, and internal diffusion resistance for leaves of dimension 6 × 10 cm. at an air temperature of 17°C and wind speed of 100 cm sec^{-1}.

transpiration rate corresponding to a measured temperature difference between the two leaves. When the radiation absorbed was about 0.8 cal cm^{-2} min^{-1}, achieved by direct sun incident on the leaf through a break in the clouds, and the wind speed was 2.5 mph, the temperature difference between a severed and an attached leaf was 0.8°C. According to

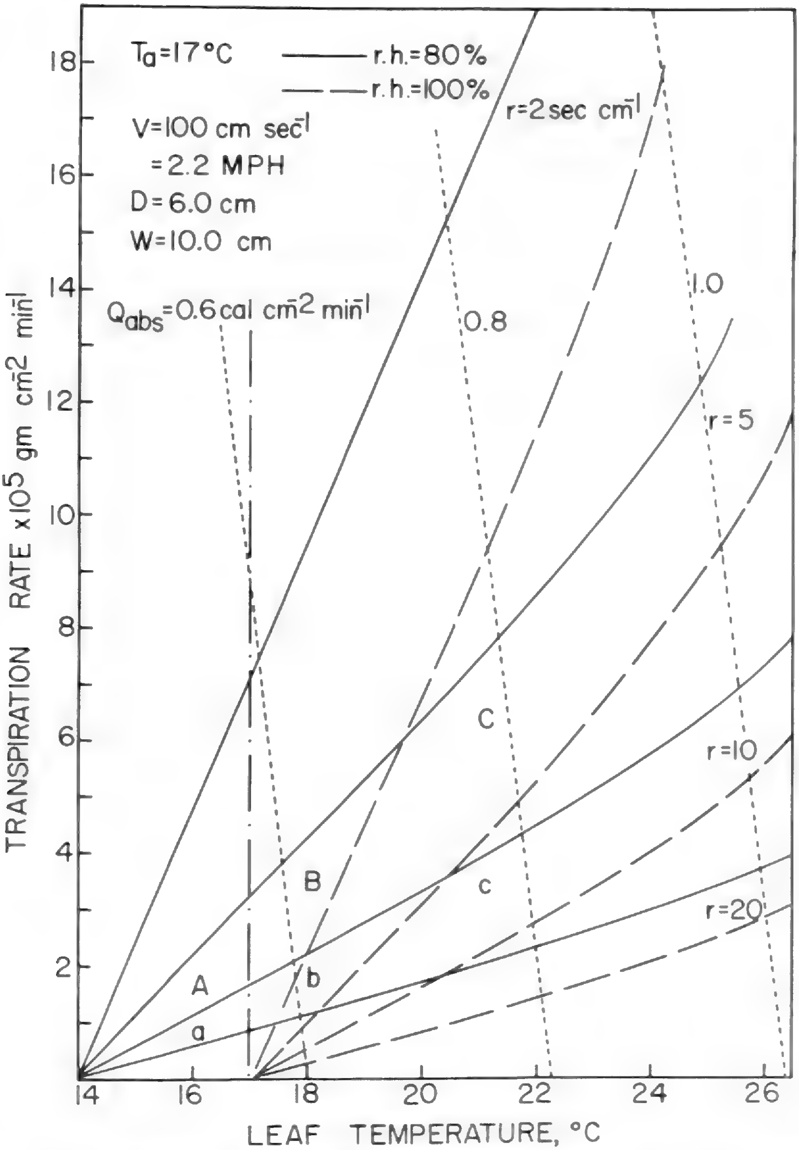

FIG. 2. Transpiration rate and leaf temperature as a function of the absorbed radiation, relative humidity, and internal diffusion resistance for leaves of dimension 6 × 10 cm. at an air temperature of 15°C and a wind speed of 500 cm sec^{-1}.

FIGURE 1, the transpiration rate was about 6.3×10^{-5} gm cm^{-2} min^{-1}, a position just to right of C. This would confirm the estimate that the internal resistance of the leaf was about 5 sec cm^{-1}.

CONSEQUENCES FOR AVERAGE CONDITIONS

If the wind speed increases to 11 mph and the air temperature is 15°C, then the relationship between transpiration rate and leaf temperature is shown in FIGURE 2. Once again it is evident that for Q_{abs} between 0.5 and 0.8 cal cm^{-2} min^{-1} and relative humidities of 80 to 100 percent, the leaves of the canopy do transpire. These transpiration rates are very low compared with more normal or frequent conditions when transpiration rates will exceed 10^{-4} gm cm^{-2} min^{-1}. The values for the forest on Pico del Oeste were low, but not zero by any means.

The leaf temperatures of the plants on Pico del Oeste probably never drop below 59°F (15°C) nor become warmer than 77°F (25°C). These temperatures are probably slightly below optimum for these sub-tropical species as concerns their photosynthesis and growth. Optimum temperature for these plants may be 30 to 35°C, but we do not really know. If they are at suboptimum in temperature, it would reduce their growth rate only slightly. On the other hand, if the light level is very much suboptimal then photosynthesis is strongly reduced. At the light levels measured to occur on the peak, it would appear that about half the maximum photosynthesis occurs for *Ocotea* and *Tabebuia*. In the absence of specific measurements of the photosynthetic rate as a function of leaf temperature and light intensity, it must be admitted that this is only conjectural.

TABLE 1. **Summary of climate data for Pico del Oeste**

	July	August	September
Max. Temp. °F	69.2	70.4	70.7
Min. Temp. °F	66.3	66.9	66.0
Rel. Hum. %	94.6	91.5	84.4
Min. Rel. Hum. %	83	72	65

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THE ECOLOGY OF AN ELFIN FOREST IN PUERTO RICO, 5. CHROMOSOME NUMBERS OF SOME FLOWERING PLANTS

LORIN I. NEVLING, JR.

ONE OBJECTIVE of this elfin-forest study was to obtain chromosome counts for as many of the species of flowering plants growing on the research site as practicable.[1] The purpose was to evaluate any relationship which might be found to exist between chromosomal level and adaptation to an extreme habitat (in terms of climate). Although it has been stated in previous papers in this series that the environment of Pico del Oeste is a fairly rigorous one for the investigators, it is harder to obtain direct evidence that it is difficult for the plants as well. In some respects, such as temperature and perhaps rainfall, the environment may be excellent for the promotion of plant growth but in others, such as low light quantities, it must be considered rigorous. Perhaps the best evidence, although indirect, is furnished by the relatively small number of angiosperm species represented in the flora. The absence of certain well-developed tropical families may be additional evidence. We believe Pico del Oeste is a type of ecological extreme and is one in which few species are capable of extended persistence. Several weedy species were introduced accidentally into the research site and it will be of considerable interest to determine the duration of their survival. All species now represented in the flora may not be equally adapted to the prevailing environmental conditions and those which are not may be the same ones which appear to be having difficulty in maintaining a regular cycle of sexual reproduction.

Fixation of bud material was with a fresh mixture of three parts absolute ethyl alcohol and one part glacial acetic acid although in special cases this was modified to six parts alcohol, three parts chloroform and one part glacial acetic acid. Buds were rinsed and hydrated to 95 percent ethyl alcohol after 12 to 24 hours, except with the Rubiaceae where fixation was limited to 15 minutes. The material was then refrigerated until transported to Cambridge by air. A standard squash technique utilizing aceto-carmine stain was used for staining pollen-mother-cell divisions. In

[1] This note could not have been as nearly complete without the devoted talents of Mrs. Lily M. Rüdenberg who is responsible for some of the original counts and for verification of others. I am very grateful for her interest and persistence in handling some of the difficult material. Acknowledgment is made to the National Science Foundation for a grant to Richard A. Howard (GB: 3975) which directly supported the major portion of this study. I am especially grateful to Mr. Joseph B. Martinson for providing facilities and generous hospitality on numerous pleasant occasions in Puerto Rico.

those instances where it was necessary to examine mitotic material (greenhouse grown in Jamaica Plain) several pre-fixatives were used and the root tips were stained by the feulgen technique.

Obtaining chromosome counts proved to be a difficult and frustrating undertaking for a variety of practical as well as technical reasons. Among the former the most important being the variety of personnel who prepared flower buds for subsequent staining and examination. In general it does not seem to be possible to impress strongly enough the necessity of working within the tight perimeters necessary for successful fixation during periods of active meiosis. We suspect that our chief problem in this regard was timing in connection with hours of sunshine. The number of sunlight hours being so few that there was a "desperation" attempt to fix material as soon as the sun appeared and thus to avoid the possibility of not obtaining material. Too often this proved totally unsatisfactory and as an alternative we employed a notebook containing fixation information, including proper bud size, time of day, etc., for individual species. Ordinarily, we would not consider it appropriate to present this type of information and we do so in the present report only in the hope that it may be of some use in another study.

The technical failures are more difficult to assess. There is little question that working with a variety of unfamiliar groups is an inefficient method. Under these circumstances it is difficult, if not impossible, to work out the subtleties of technique often necessary in some plant groups. Two of our more interesting failures are presented in the belief that often more is learned in failure than in instant success. One such failure was *Marcgravia sintenisii* Urban, in which we did not obtain meiotic or countable mitotic figures in spite of repeated attempts. We also examined material of a related species kindly sent to us by our friend Dr. Ding Hou of the Rijksherbarium, Leiden. As we failed with this species, too, we are now inclined to believe that the fault lies with the technique. Meiosis occurs when the flower buds are very small and this adds measurably to the difficulty. Partly as a result of these failures, *M. sintenisii* was kept under careful observation and we have been able to gather some information about its reproductive biology. This data will be reported in detail at a later date.

Another instance in which results were not obtained was from *Tabebuia rigida* Urban, a conspicuous and very distinct species of the Bignoniaceae. It is one of the dominant trees of the elfin forest in the Luquillo range. Observation over several years indicates that this magenta-flowered species is in bloom in all months of the year. There is no indication of increased flowering (i.e., a flowering peak) during any specific part of the year. Individual flowers open between 8 and 8:30 A.M. when most of them are visited by bananaquits (*Coereba flaveola*). These birds approach the flower from the rear and with a quick thrust of the bill split the corolla tube lengthwise from the base in order to obtain the nectar contained within. Most flowers are damaged in this way by 9:30 A.M. While the general floral morphology would seem to indicate a long-tongued pollinator, no such pollinators were observed visiting the flowers. More important, not a single fruit of this species matured on the research site during the entire course of the study. Several attempts to hand pollinate flowers yielded no fruit set. Lack of fruiting was attributed, at first, to the bird damage, but when cytological investigation was stymied another answer had to be sought. In spite of repeated attempts, with varied fixation schedules, no meiotic figures were obtained. Pollen stainability tests (cotton blue in lactophenol) were variably low on both fresh and herbarium material. It is our conjecture that meiosis proceeds properly to form fertile pollen only when certain environmental conditions, possibly pertaining to sunlight, are met. It is my estimate that five or more days of sunlight are necessary for proper pollen development: it should be noted that a half-dozen consecutive days of continuous sunshine would be a rare event on Pico del Oeste. The phenomenon of the correlation of weather (in contrast to climate) to a biological system is poorly known but an intimate relationship may be found to exist in this case. All indications point to irregular sexual reproduction in *Tabebuia rigida*, and further that the time lapse between periods of sexual reproduction may be of considerable length. In view of the semi-dominance of *T. rigida* on the Pico this consistent lack of sexual reproduction is of considerable import. The amount of vegetative reproduction is difficult to assay, and although it is not easy to propagate by cuttings under greenhouse conditions, the significance of vegetative reproduction cannot be underestimated.

The positive results of this portion of the investigation are presented below in tabular form. Voucher collection numbers (in italics) are given for all counts reported here for the first time, all of which are based on material from Pico del Oeste unless indicated otherwise in appropriate footnotes. Voucher specimens are deposited in the herbarium of the Arnold Arboretum (A). Where ranges of numbers are given these are not meant to be actual ranges but only an indication to assist future workers. No information about their chromosome numbers is known to me for those species which are not included in the following list.

GRAMINEAE
Ichnanthus pallens (Sw.) Munro. $2n = 40$ (*Nevling 347*)[2]

CYPERACEAE
Eleocharis yunquensis Britton. $2n = 10$ (*Howard & Nevling 15996*) [2]

ARACEAE
Anthurium dominicense Schott. $n = 15$ (*Howard 16179*) [2]

DIOSCOREACEAE
Rajania cordata L. $2n = 36$ [8]

ORCHIDACEAE
Dilomilis montana (Sw.) Summerhayes. $n = 21$ (*Nevling & Evans 131*) [2]

CHLORANTHACEAE
Hedyosmum arborescens Sw. $n = 8$ [3]; $2n = 16$ (*Howard & Nevling 15995*) [2]

MORACEAE

Cecropia peltata L. $n = 14$ (*Howard & Nevling 16934*)[2]; $2n = 26$ [4]; $2n = 28$ [5]

URTICACEAE

Pilea krugii Urban. $n = 12$ (*Evans 229*) [2]

Pilea yunquensis (Urban) Britt. & Wils. $2n = 24$ (*Howard & Nevling 15975*) [2]

LAURACEAE

Ocotea spathulata Mez. $n = 12$ (*Dodd & Appenzeller 25*) [2]

MELIACEAE

Trichilia pallida Sw. $2n = 48$–52 (*Nevling 348*) [2]

AQUIFOLIACEAE

Ilex sintenisii (Urb.) Britt. $n = 20$ (*Evans 139*) [2]

OCHNACEAE

Sauvagesia erecta L. $2n = 38$ (*Nevling 349*) [2]

THEACEAE

Cleyera albopunctata (Griseb.) Krug & Urb. $2n =$ ca. 25 (*Howard & Nevling 15960*) [2]

MELASTOMATACEAE

Mecranium amygdalinum (Desr.) C. Wright ex Sauv. $n = 12$ (*Howard & Nevling 15960*) [2]

Miconia foveolata Cogn. $n = 17$ (*Howard et al. 16164*) [2]

Miconia pachyphylla Cogn. $2n =$ ca. 34 (*Howard et al. 16178*) [2]

ERICACEAE

Gonocalyx portoricensis (Urb.) A. C. Smith. $n = 23$ or 24, $2n = 46$ or 48 (*Howard & Nevling 15958*) [2]

Hornemannia racemosa Vahl. $2n =$ ca. 38 (*Howard 16058*) [2]

MYRSINACEAE

Grammadenia sintenisii (Urb.) Mez. $n = 23$ (*Howard et al. 16158*) [2]

Wallenia yunquensis (Urb.) Mez. $n = 21$ (*Howard & Nevling 15959*) [2]

SYMPLOCACEAE

Symplocos micrantha Krug & Urb. $n = 12$ (*Evans 138*) [2]

OLEACEAE

Haenianthus salicifolius Griseb. var. *obovatus* (Krug & Urb.) Knobl. $n = 20$ (*Howard & Nevling 16933*) [2]

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[2] Original count.

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CONVOLVULACEAE

Ipomoea repanda Jacq. $n = 15$ (*Howard & Nevling 15511*)[2]; $2n = 30$ (*Howard & Nevling 16003*)[2]

GESNERIACEAE

Alloplectus ambiguus Urb. $n = 18$[6]

Gesneria sintenisii Urb. $n = 7$ (*Dodd & Appenzeller 23*)[2]

ACANTHACEAE

Justicia martinsoniana Howard. $n = 14$ (*Evans 26*)[2]; $2n = 28$ (*Nevling 350*)[2]

RUBIACEAE

Psychotria guadalupensis (DC.) Howard. $n = 22$ (*Dodd & Appenzeller 19*)[2]

CAMPANULACEAE

Lobelia portoricensis (Vatke) Urb. $n = 7$ (*Howard & Nevling 15978*)[7]

COMPOSITAE

Mikania pachyphylla Urb. $n = 17–20$ (*Evans 50*)[2]; $2n = 34–38$ (*Howard & Nevling 15987*)[2]

Of the 51 genera of flowering plants represented on the research site, published chromosome counts are readily available for only 28 of them; for the remaining 23 genera I have not located published counts. The counts presented above represent the first definite counts, as far as I am aware, for the following genera: *Ichnanthus*, *Dilomilis*, *Ocotea*, *Sauvagesia*, *Mecranium*, *Miconia*, *Grammadenia*, *Wallenia*, and *Haenianthus*.

Previously published chromosome counts are available for only five of the species under investigation (cited in footnotes). In general, where published counts are available for other species of the same genera represented on the site and where a range of haploid numbers has been reported, our species tend to be on the low end of the range. This might be best illustrated by some examples: reported haploid numbers in *Eleocharis* are 5, 9, 10, 16, 18, 20, 23–*E. yunquensis* has a haploid number of 10; in *Anthurium* haploid numbers are 15, 16, 17, 22, 28, and multiples thereof–*A. dominicense* has a haploid number of 15; in *Pilea* haploid numbers are 12 or 24–our species are $n = 12$ and $2n = 24$ respectively; in *Ipomoea* the haploid numbers are 15 or multiples thereof–in *I. repanda* $n = 15$; in *Justicia* the haploid numbers are 13, 14, 15, 16, 17, and 19–in *J. martinsoniana* the haploid number is 14; in *Lobelia* haploid numbers are 7 or multiples–in *L. portoricensis* the haploid number is 7. There are four notable exceptions to this pattern. In *Ilex* ($n = 18$ or 20) and *Psychotria* ($n = 11$ or 22) our species have the larger number. The two other exceptions are *Gesneria* and *Symplocos* where I am reporting haploid numbers lower than those previously reported for either genus. There have been some speculations recently that plants growing under adverse or extreme conditions often have a high percentage of polyploid species. On the basis of our studies to date, our plants do not seem to fit this pattern. Considerable work remains to be done and it is only at the time of completion that a truly balanced opinion can be presented.

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THE GENERA OF SENECIONEAE IN THE SOUTHEASTERN UNITED STATES [1]

BERYL SIMPSON VUILLEUMIER

Tribe SENECIONEAE Cassini, Jour. Phys. Chim. Hist. Nat. Arts **88:** 196. 1819.[2]

Subtribe **Senecioninae** Dumortier, Fl. Belg. Prodr. 65. 1827.

Involucre composed of either a single series of bracts or two series with the outer in the form of supernumerary bractlets [or in a few genera multiseriate]. Anthers terminally appendaged, truncate at the base, or with short auriculate tails. Style branches of perfect florets truncate, obtuse, penicillate, or with a conical appendage, often with a distinct crown of hairs at the base of the appendage, or the appendage more elongate and papillate.

The Senecioninae are the only subtribe of the Senecioneae (of four, Bentham & Hooker, or three, Hoffmann) represented in the southeastern United States. In our treatment it is necessary to deal not only with *Senecio* L., perhaps the largest genus of flowering plants, but also with several of the satellite groups surrounding it. Most of these segregates are small, but seem to form natural groups usually distinguishable by a number of characters (cf. *Ligularia* L., *Emilia* Cass., *Cacalia* L., *Gynura* Cass., *Cineraria* L., *Erechtites* Raf., *Kleinia* Miller). *Senecio* itself, and three of these groups, *Emilia*, *Cacalia*, and *Erechtites* occur in the southeastern United States.

Various authors have considered these assemblages either as subgenera or sections of *Senecio* or as distinct genera. Bentham & Hooker maintained *Gynura* and *Emilia* but united *Cacalia* with *Senecio*. Baillon con-

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[1] Prepared for a generic flora of the southeastern United States, a project of the Arnold Arboretum made possible through the support of the National Science Foundation and under the direction of Carroll E. Wood, Jr. The scheme and terminology follow that outlined at the beginning of the series (Jour. Arnold Arb. **39**: 296–346. 1958). As in previous treatments, the area includes North and South Carolina, Georgia, Florida, Alabama, Mississippi, Tennessee, Arkansas, and Louisiana.

I wish to thank C. E. Wood, Jr., for advice and suggestions; R. W. Long and D. B. Ward for distributional information; R. W. Pippen for advice and suggestions concerning the treatment of *Cacalia*; A. Cronquist for reading and commenting on the manuscript; and members of the staff of the New York Botanical Garden for their hospitality on several occasions. I am also indebted to the late G. K. Brizicky for the translation of material in Russian.

[2] The tribes of the Compositae in the southeastern United States have been treated by Solbrig (Jour. Arnold Arb. **44**: 436–461. 1963). The reader should consult this work for additional information (e.g., familial and tribal descriptions, notes, and references) not included here.

sidered *Cacalia*, *Erechtites*, *Gynura*, and *Emilia* to be sections of *Senecio*, whereas Hoffmann gave *Erechtites*, *Gynura*, and *Cacalia* generic status and made *Emilia* a subgenus of *Senecio*. Muschler, in his treatment of the African species of *Senecio*, placed *Gynura* and *Emilia* in synonymy, but Greenman, dealing with the North and Central American senecios, considered these two genera distinct from *Senecio*.

At present, the acceptance or rejection of these taxa as independent genera depends primarily on the weight given to stylar characters. Thus, the question is essentially one of rank rather than affinity. For clarification of the generic nomenclature, ease of discussion, and historical reasons (cf. Torrey & Gray, Fl. N. Am.; Gleason, New Britt. & Brown Illus. Fl. Northeast. U.S.; Fernald, Gray's Man., ed. 8; Small, Man. Southeast. Fl.) the segregates of *Senecio* in our area are treated here as genera. It is, however, fully realized that, with the exception of *Arnica* L., none of the genera included is clearly set off morphologically from *Senecio*, that they frequently show transitions to *Senecio* in different parts of their ranges, and that evolutionarily they represent imperfectly isolated offshoots from a senecionid stock.

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KEY TO GENERA OF SENECIONEAE IN THE SOUTHEASTERN UNITED STATES

A. Heads radiate, or if discoid, the style branches truncate and only slightly penicillate; florets yellow (white or purple in *Senecio Rugelia* Gray).
  B. Leaves opposite; carpellate florets in two series; pappus uniseriate; style branches of perfect florets slightly acute with a brushlike tip of papillose hairs (penicillate). .... 1. *Arnica*.
  B. Leaves alternate; carpellate florets, if present, in a single series; pappus multiseriate; style branches of perfect florets truncate and more or less penicillate. .... 2. *Senecio*.
A. Heads discoid; style branches always with a terminal appendage; florets white, purple, reddish, or if yellow-orange, the style branches exceedingly long and covered with papillose hairs.
  C. Florets white or whitish (pinkish in some *Cacalia*); style branches with a short conical appendage which has no hairs at the base or only a semicircular crown of hairs.
    D. Leaves palmately nerved or pinnately nerved and hastate; corollas deeply 5-parted; all florets perfect. .... 3. *Cacalia*.
    D. Leaves pinnately nerved, oblanceolate to lanceolate, irregularly lobed; corollas shallowly 5-toothed; outer florets of head carpellate. .... 4. *Erechtites*.
  C. Florets lavender, red, or yellow-orange; style branches either with a long conical appendage surrounded by a circle of hairs or elongate and penicillate.
    E. Involucre of a single series of bracts; florets purple or flame colored; style branches with a conical appendage surrounded by a circle of hairs. .... 5. *Emilia*.
    E. Involucre with an outer series of supernumerary bracts; florets yellow-orange; style branches elongate and penicillate. .... [*Gynura*.][3]

1. **Arnica** Linnaeus, Sp. Pl. **2**: 884. 1753; Gen. Pl. ed. 5. 376. 1754.

Perennial herbs to 90 cm. tall arising from an erect and simple [or creeping and branched] rhizome covered with fibrous roots [or scales, or naked] and the remains of last year's leaf bases. Flowering stems herbaceous, bearing 2 or 3 [1–3 or 5–10] pairs of opposite, ovate to suborbi-

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[3] Although included in J. K. Small's *Manual of the Southeastern Flora, Gynura* Cass. has apparently not survived as an escaped herb. I have seen only two specimens, presumably those on which Small based his inclusion of *Gynura,* which seem to have been noncultivated (both were Florida: Palm Beach Co., Delray. Pineland. May 12, 1922. *J. K. Small 10497* [NY]). According to Dr. R. W. Long, there are no records of naturalized *Gynura* in Florida at the University of South Florida, and Dr. D. B. Ward has indicated that the University of Florida has only three specimens, all of which are from cultivation. In his "Compositae of South Florida" (Quart. Jour. Florida Acad. Sci. **14**: 189. 1951), R. B. Ledin listed *Gynura aurantiaca* (Blume) DC. only as a cultivated species. The genus is nevertheless included in the key, and a number of pertinent references are among those for the subtribe.

cular [lanceolate] sessile [petiolate] leaves with multicellular filiform and/or glandular hairs. Inflorescence cymose (appearing paniculate in ours) of 1–30 campanulate, radiate, monochromatic heads, each with a ring of hairs at the top of the peduncle beneath the head. Involucre of 2 series of essentially equal herbaceous, lanceolate bracts with a variable pubescence; receptacle convex, fimbrillate. Florets dimorphic; pappus white or straw colored, setose; ray florets carpellate [occasionally with 5 staminodia], the corolla with a 3-toothed ligule, yellow or orange; disc florets perfect, the corolla goblet shaped [tubular], yellow or orange; anthers of disc florets yellow [purple] with a lanceolate terminal appendage and short auricles at the base; style branches of perfect florets slightly flattened, with penicillate tips of long papillae. Achenes cylindrical with a ring at the base, surface with glandular hairs [or glabrous, or with both glandular and double hairs], shorter and broader in the ray florets than in the disc florets. LECTOTYPE SPECIES: *A. montana* L.; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. 3: 533. 1913. (Name of uncertain origin, possibly either from Greek, *ptarmica*, goose-tongue, or *amicur*, friend, because the plant is used medicinally.) — LEOPARD'S BANE, WOLF'S BANE.

A genus of some 32 species in five subgenera (Maguire), represented in the southeastern United States only by *Arnica acaulis* (Walt.) BSP., $2n = 38$, of subg. ARNICA. This species reaches farther south than any other in the genus, occurring from southern Pennsylvania and Delaware in damp areas of the open pine forest of the Atlantic Coastal Plain to northern Florida. Other species of *Arnica* occur in quite different habitats in the tundra and mountains of higher latitudes. Three other species enter the eastern United States far to the north of our area: *A. lonchophylla* Greene subsp. *arnoglossa* (Greene) Maguire (subg. ARCTICA Maguire) in northern Minnesota, *A. cordifolia* Hook. (subg. AUSTROMONTANA Maguire) on the Keweenaw Peninsula of Michigan, and *A. lanceolata* Nutt. (subg. CHAMISSONIS Maguire) in the high mountains of Maine, New Hampshire, and New York. The remaining species are concentrated in northwestern North America but some are distributed in other boreal areas. However, only the polymorphic *A. alpina* (L.) Olin (subg. ARCTICA), considered the basal species of the genus by Maguire, is completely circumboreal. One of its six subspecies, *A. alpina* subsp. *tomentosa* (Macoun) Maguire, dips down the Rocky Mountains into Montana.

Our species, *Arnica acaulis*, shows a disjunct relationship with the northern European *A. montana* L., $2n = 38$, the only other member of subg. ARNICA (cf. Maguire). *Arnica acaulis* is not closely related to any of the other 30 species found in North America and is easily distinguished from them by its short, upright, unbranched rhizome covered with fibrous roots.

The generic affinities of *Arnica* seem to be rather obscure. Cassini tentatively placed the genus in his "Tagetinae" with a group of genera now considered to belong in the Heliantheae. Bentham first placed it in the

Senecioneae, remarking that, morphologically, it was not very close to *Senecio* L. but approached *Doronicum* L. in several characters. James Small also mentioned morphological similarities to *Doronicum*, but thought that "a relationship of *Arnica* with *Tussilago* L." (p. 284) was confirmed by the presence in *Tussilago* of faradiol, a sterol related to the arnidol found in *Arnica*.

Maguire supposed a North American origin for the genus since all five of the subgenera (except subg. ARNICA) are found in northwestern North America and the species there show few specializations compared with more peripheral species. A chromosome number report of $2n = 10$ (the lowest in the genus) for the northwestern American *Arnica longifolia* D. C. Eaton bolstered this view, but this count has subsequently been shown to be incorrect; $2n = 76$ (also reported as $2n = 60$) is now accepted as the correct count.

Chromosome numbers now known for more than half the species (representing all subgenera) include $2n = 38, 57, 60, 69, 76, 90 \pm 6, 95 \pm 4$, and ca. 97. These counts combined with other evidence prompted Ornduff *et al.* to postulate a base chromosome number of 19.

The occurrence of apomixis has complicated both the counting of chromosomes and the delimitation of species in *Arnica*. Afzelius first reported apomixis in three species in which there was no meiosis, no tetrad formation, and the production of the embryo sac directly from the megaspore mother-cell (apparently in both the ray and the disc florets). Recently, Baker listed autonomous apomixis for five additional species and the possibility of pseudogamy in two others. Four different species and the subspecies of two others which he investigated showed normal sexual reproduction. All species with a diploid number of 38 studied thus far are sexually normal; those with higher numbers (with one exception) are apomictic. Yet, a number of the species studied by Ornduff *et al.*, including several with a diploid number of ca. 38, exhibited irregularities in pollen meiosis.

Stamen irritability,[4] or the reaction of the stamens and/or style to a stimulus when the floret is touched, was reported in *Arnica alpina* by Small.

Several species (*Arnica montana* L., *A. fulgens* Pursh, *A. sororia* Greene, and *A. cordifolia* Hook.) have chemicals useful in medicine. The heads are collected and dried, the florets removed and ground, and a tincture prepared from the powder. This liquid is used externally for cuts, bruises, and sprains, but can cause severe dermatitis. Small internal doses are used as a respiratory, nervous, and digestive system stimulant, diuretic, and purgative, but large doses can lead to central nervous system disturbances, vascular collapse, and even death.

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[4] Stamen irritability is discussed by James Small in his Chapter III (see subtribal references). Two basic kinds are involved: that in which the style is exserted when the floret is touched, thus forcing out the pollen, and that which results in a contraction of anther filaments which tilts the floret toward the stimulus. Some species have florets capable of tilting in only limited directions. In *Arnica*, the anther tube (and consequently the floret) is capable of moving in any direction.

Historically, extracts have been made from either the dried rhizomes or the flowering heads, but only the heads are now used. The active principle is arnicin (apparently $C_{20}H_{70}O_4$), a yellow hygroscopic substance soluble in organic solvents and alkalies.

In this connection it should be noted that Hess found an intensely yellow-colored hygroscopic compound in the basal cells of the double hairs[5] of *Arnica montana* achenes. Thus the substance used medicinally by man is possibly utilized in the plant for water absorption (and perhaps also as a deterrent to grazing animals). Interestingly, our species, *A. acaulis*, has no double hairs on the achenes and also has never been used for medical purposes.

The attractiveness of the large showy heads and the "alpine" habit of numerous species of *Arnica* have led to the cultivation of about a dozen taxa (see Dress).

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2. **Senecio** Linnaeus, Sp. Pl. 2: 866. 1753; Gen. Pl. ed. 5. 373. 1754.

Caulescent perennial or annual herbs [shrubs, trees, or vines] with glabrous, tomentose, or villous stems and leaves. Leaves basal and/or alternate, entire, dentate, lobate, or pinnately parted; decreasing in size up the stem, the cauline often notably different from the basal ones. Inflorescence corymbiform [or monocephalous]. Involucre cylindrical or

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[5] Hess has studied in detail the morphology of the hairs of the achenes of numerous species of the Compositae representing all of the tribes. The hairs he calls double hairs (Zwillingshaare) consist of two more or less isometric basal cells which are surmounted by two perpendicular elongate and connate hair cells. The basal cells act as pulvini sensitive to water and raise the hair cells when absorption takes place. Numerous elaborations and/or reductions of this basic type of double hair have occurred in different species and genera of the family. (Cf. *Senecio*.)

hemispherical, composed of a single row [rarely more] of erect, usually free, flat [keeled], green bracts; supernumerary bracts sometimes present; receptacle slightly convex [flat], naked, foveolate. Florets dimorphic (perfect and carpellate) or all tubular and perfect; pappus setose-capillary, soft, white; ray florets, when present, carpellate, in a single outer series,[6] the corolla with an irregularly toothed ligule, yellow; disc florets perfect, the corolla tubular, shortly 5-fid, yellow to orange (rarely white or light purple), the anthers with terminal appendages and truncate bases; pollen spherical, more or less spiny, prominently tricolporate (cf. Greenman); style branches of perfect florets truncate (to penicillate) or with a short, pointed apex. Achenes subterete, 5–10-nerved, variously pubescent. LECTOTYPE SPECIES: *S. vulgaris* L.; see Cassini, Dict. Sci. Nat. **48**: 454. 1827. (Name Latin, applied to groundsel, *S. vulgaris*; derived from *senex*, old man, referring to the soft, white pappus which suggests the beard of an old man). — RAGWORT, GROUNDSEL.

An ubiquitous genus, possibly the largest of the flowering plants, estimates varying from 900 (Bentham & Hooker) to 3000 (Cabrera) species. There has been no treatment of the entire genus since that of De Candolle (1838) in which he divided the genus into several "series" based on geographical distribution. Most authors have arbitrarily accepted this treatment as a basis and have worked within one geographical area (e.g., Muschler, Africa; Cufodontis, northern Eurasia; Cabrera, Chile; Greenman, North and Central America). Greenman placed the North and Central American species in 21 sections; five sections (some of which are not very distinct) with eleven species occur in the Southeast and four introduced and 15 native species are known from the eastern United States as a whole.

The European section SENECIO (§ *Annui* Hoffm.), composed of weedy annual herbs, is represented in our area only by the now almost cosmopolitan *S. vulgaris* L., $2n = 40$, which differs from our other species in its annual habit and uniformly discoid heads of yellow flowers. Two species of sect. SANGUISORBOIDEI Greenman, characterized by the perennial habit of its species and the more or less glabrous, once or more pinnately parted leaves, occur in the Southeast. *Senecio glabellus* Poir., $2n = 46$, is wide ranging in wet habitats from Mexico eastward to Florida and north to Oklahoma, Kansas, Missouri, Illinois, Indiana, Kentucky, Tennessee, and North Carolina, whereas *S. Millefolium* Torr. & Gray (including *S. Memmingeri* Britton), with basal leaves two or three times pinnate, is restricted to rocks and cliffs in a few counties in the mountains of southwestern Virginia, western North and South Carolina, and northernmost Georgia. The remainder of the species of this section are found predominantly in the uplands of Mexico and Central America.

Most of our species fall into sect. AUREI Rydb., which is composed of

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[6] The presence of ray florets in normally radiate species is not an absolute character. The number of ray florets is also subject to great variation, mainly according to the number of involucral bracts.

perennial, usually glabrous herbs with petiolate simple or lyrately parted basal leaves and cauline leaves reduced upward. Six of the 22 species of this group reach our area: *S. aureus* L. (including *S. gracilis* Pursh), $2n = 44$; *S. Robbinsii* Oakes ex Rusby, $2n = 46$; *S. obovatus* Muhl. (including *S. rotundus* (Britton) Small), $2n = 40$; *S. Smallii* Britton, $2n = 44$; *S. pauperculus* Michx. var. *Crawfordii* (Britton) T. M. Barkley; and *S. plattensis* Nutt. *Senecio aureus*, *S. Robbinsii*, and *S. pauperculus* var. *Crawfordii* all frequent moist to wet meadows and bogs, *S. obovatus* and *S. plattensis* prefer drier areas, and *S. Smallii* grows primarily in fields, roadsides, and open woods. *Senecio Robbinsii* occurs in the Southeast only as a remarkably disjunct population on Roan Mountain (Tennessee-North Carolina border) with the principal populations located far to the north in the mountains of New York and New England and in adjacent Canada.

Many of these species commonly hybridize where their ranges and habitats overlap, which often makes identification of intermediate plants difficult. However, hybrids are usually restricted to "hybrid" habitats and do not seem to swamp out the parental species. The species of sect. AUREI, their ecology, natural history, and evolution, have been thoroughly discussed by Barkley.

Members of sect. TOMENTOSI Rydb. differ from those of sect. AUREI primarily in a tendency toward being permanently tomentose. The majority of the species are centered in the Rocky Mountains, but the range of the type species, *Senecio tomentosus* Michx. (including the glabrous-leaved f. *alabamensis* (Britton) Fern.; *S. alabamensis* Britton), $2n = 46$, stretches across the country in weedy areas from Arkansas and Texas to Florida and north to southern New Jersey. Hybrids between *S. tomentosus* and *S. aureus* are fairly common (Barkley), and the hybrid of *S. tomentosus* and *S. Smallii* also occurs. The latter has been studied cytologically (in the first meiotic division $2n = 21$–22 bivalents and 1–3 univalents). This evidence and other studies of Barkley have shown that some of the sections used by Greenman are artificial and should possibly be abandoned. In the southwestern United States (Colorado, New Mexico, Texas) hybrids are formed between *S. mutabilis* Greenm. (sect. TOMENTOSI) and *S. neomexicanus* Gray (sect. TOMENTOSI), *S. mutabilis* and *S. multilobatus* Torr. & Gray (sect. LOBATI Rydb.), and between *S. mutabilis* and *S. tridenticulus* Rydb. (sect. AUREI). An earlier study had already indicated that the species of the *S. multilobatus* group belonged in an integrated complex with species formerly considered to belong to sects. BOLANDERANI Greenm., LOBATI, and AUREI. (See also the cytological data of Ornduff *et al.*, 1967.)

The last section, RUGELIA (Shuttlew. ex Chapm.) Greenm., contains only the unique *Senecio Rugelia* Gray (*Rugelia nudicaulis* Shuttlew. ex Chapm.), winterwell, $2n = 56$, a perennial herb with alternate, undivided leaves and large, nodding discoid heads of white or light purple florets in a simple corymbose raceme. This species grows in partial shade in cool woods (usually of *Picea rubens* Sarg. and/or *Abies Fraseri* (Pursh) Lindl.) at high elevations (ca. 1300 m.) in the Smoky Mountains of western North Carolina and eastern Tennessee. On the basis of both the morphology and the chromosome number, Ornduff *et al.* have reiterated that this species should be removed from *Senecio.*

Considering the size of the genus, relatively few studies have been made on its embryology, cytology, and anatomy. Palmblad (1965) and Ornduff *et al.* (1967) have recently added much new cytological information and discussed some of the possible significance of chromosome numbers within the genus, but too many species have still not been counted to allow decisions concerning the genus as a whole. Gustafsson reported no apomixis in the species of *Senecio* he examined, a finding corroborated on other species by Afzelius and Haskell. The breeding system in the few cases studied appears to be one of facultative outbreeding with occasional inbreeding (Knuth, Haskell). Hauman postulated that the arborescent senecios (sect. ARBOREI Hoffm.) of Africa are all obligate inbreeders.

Anatomical studies have been made most extensively on the African arborescent species of *Senecio* (cf. Hare). Recent comparative work by Carlquist with numerous other senecionid species has shown little correlation between wood anatomy and the classical infratribal taxonomy, apparently because in the Senecioneae stem anatomy is easily modified under different environmental conditions. Yet within *Senecio* itself, Carlquist found that clustering of species on the basis of wood anatomy was, in some cases, consistent with groupings based on other morphological criteria. Hare and Carlquist concur that the woody members of the Senecioneae are derived from herbaceous ancestors and that the stem structure of *Senecio* is advanced in comparison with other genera.

A recent study by Drury & Watson on some of the Eurasian sections of *Senecio* has revealed that the leaf and achenial hairs, pappus types, and the kinds of ovarian crystals — when carefully and critically examined — provide useful taxonomic characters. They call for a reassessment of many characters usually superficially examined in species of the Compositae and imply that the use of these characters might help in producing a more natural classification of such troublesome genera as *Senecio.*

The specialized anatomy of the achenial double hairs of *Senecio vulgaris* (see footnote 5 under *Arnica*) has been described by Macloskie and J. Small and that of several other species of *Senecio* by Hess. The basal cells, as in the double hairs of most Compositae, act as pulvini sensitive to moisture. In several species of this genus, the two hair cells are further specialized and are filled with a spiral tongue of a mucilaginous substance which is extruded when pressure due to water absorption forces the hair cells to separate. Apparently, the mucilage sticks the achenes to soil particles and thus helps to insure germination.

Alkaloids reported in at least 75 species (cf. Willaman & Schubert) undoubtedly account for the medicinal use of various species of *Senecio.*

In the United States, only *S. aureus* was extensively used, the leaves first being dried, then steeped in water, and the liquid used as a stimulant, diuretic, and uterine tonic. The last use of this brew by North American Indian women led to the common name of squaw-weed. In other parts of the world, shoots and leaves of several species are eaten raw or cooked. Some species (especially those of *Cineraria* L., if this genus is merged with *Senecio*) are cultivated as ornamentals.

Much attention has been directed toward *Senecio* and the Senecioneae because of the writings of James Small, who attempted to prove in an elaborate series of papers (1917–1919) that *Senecio* was the ancestral genus of the Compositae. His theory has, however, been dismissed by most workers with only a partial explanation. It thus seems worth noting here that four general concepts, now considered to be erroneous, lay at the base of his argument: (1) derivation of the Compositae from the Campanulaceae subfam. Lobelioideae; (2) acceptance of the now refuted Age and Area hypothesis of Willis; (3) the uplift of the Andes in the early Cretaceous; (4) belief in the doctrine of evolution by saltation. As a consequence of these tenets, Small proposed that the ancestral pre-Composite had a woody habit, a zygomorphic bilabiate corolla, and united anthers (free anthers are now considered primitive);[7] that *Senecio*, the largest and most widespread genus of the family was naturally the oldest; that the uplift of the Andes in the Cretaceous (rather than in the Pliocene-Pleistocene as is now accepted) gave the genus ample time to spread around the world; and finally, that evolution by saltation, combined with this (presumed) early Andean uplift created a situation in which the lobelioid pre-Composite evolved and radiated as the Andes rose and thereby created a plexus of species able to migrate throughout the world.

Small also had a number of ideas concerning morphology which reinforced his conviction that *Senecio* was the ancestral Composite:

1. The pappus was developed from a structure that was morphologically a hair. Consequently, a fine capillary pappus (as is found in *Senecio*) should be primitive. The pappus now considered by most taxonomists to be the ancestral type is composed of broad, flat bristles resembling the lobes of the calyx, from which it is thought to be derived.

2. The inflorescence of the pre-Composite was an umbel with all of the pedicellar bracts except the outermost series already suppressed. Further reduction would have resulted in a head with a flat or convex naked receptacle and, correspondingly, a uniseriate involucre. Additional series of receptacular or involucral bracts would be produced by the abortion of florets in the head. Although it is still debated whether the primitive Composite possessed an umbel or a panicle, most authors now accept Bentham's view that receptacular bracts and a multiseriate involucre are unspecialized. A uniseriate involucre and a naked receptacle, as in *Senecio*, are now considered to be advanced reductions.

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[7] See Cronquist (1955) for a discussion of the evolution of the Compositae and an enumeration of characters considered to be unspecialized in the family.

3. Through a series of drawings, Small showed how all the types of style branches now found in the Compositae could be derived from the flat, truncated style arms of *Senecio*. Similarly, he derived all the anther types from the senecionid type with its terminal appendage and tailless base. Yet, since this kind of hypothetical derivation from a selected prototype can be made using almost any form (except for the obviously highly modified ones) as a starting point, it really has little biological meaning.

4. Several corolla characters in *Senecio* were also suggested by Small as primitive. Yellow, for example, was considered the "unspecialized" flower color. Bilabiate corollas found in the ray florets of some species of *Senecio* were deemed unspecialized because they were like those of *Lobelia*. Although yellow may be a basic flower color in the Compositae, the tubular corolla is now believed to be primitive and to have given rise to both the bilabiate and the ligulate corolla (cf. Koch).

5. The chromosomal evidence available to Small suggested that five was the base number for *Senecio*. More recent evidence, however, indicates that ten is actually the base number for the genus (Ornduff *et al.*).

In spite of these mistaken ideas about *Senecio*, Small's studies provide one of the most complete comparative morphological surveys ever made on the Compositae. Even without the bibliographies and summaries of previous work, his research is an indispensable reference on *Senecio* and the Compositae in general.

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3. **Cacalia** Linnaeus, Sp. Pl. 2: 834. 1753; Gen. Pl. ed. 5. 362. 1754.

Tall caulescent herbs arising from a rosette of alternate, petiolate, spathulate, ovate, reniform, or hastate, entire, undulate, crenate, or toothed [or lobed] basal leaves; stem leaves petiolate or sessile, decreasing in size toward the inflorescence. Inflorescence a compound cyme of numerous campanulate discoid heads with cylindrical or campanulate involucres composed of a single series of herbaceous, lanceolate, winged or flat bracts (sometimes with an outer series of supernumerary bracteoles); receptacle flat, naked, or with a fleshy projection in the center. Florets monomorphic, perfect; pappus capillary, white; corolla deeply 5-cleft, white, cream, or pinkish; anthers with terminal appendages and obtuse bases; style branches truncate or with short conical [or elongate in some Mexican species] appendages. Achenes fusiform to cylindrical with a variable number of ribs, smooth. (*Synosma* Raf. ex Britton & Brown, 1898 [*Hasteola* Raf. ex Pojark., 1960, nom. superfluum]; including *Arnoglossum* Raf., 1817 [*Mesadenia* Raf., 1838, nom. superfluum].) LECTOTYPE SPECIES: *C. hastata* L., largely typified by the removal of the original species to other genera; see Miller, Gard. Dict. Abr. ed. 4. 1754; De Candolle, Prodr. **6**: 327. 1838; Kitamura, Mem. Coll. Sci. Kyoto Univ. B. **16**: 170. 1942; Shinners, Field Lab. **18**: 79. 1950; Pojarkova, Fl. URSS **26**: 684. 1961.[8] (Name from Greek, *kakalia*, a name given by Dioscorides to a plant believed to be a *Tussilago*.) — INDIAN PLANTAIN.

A genus of perhaps 40 species distributed from eastern Europe to eastern Asia, in eastern North America, Mexico, and Central America, and in South America along the Andes southward to Bolivia. The Mexican species were referred to *Psacalium* Cass., *Odontotrichium* Zucc., and *Pericalia* Rydb. by Rydberg (1924) and recently to these plus *Digitacalia* Pippen by Pippen (1968). Some Asiatic species have been removed to *Syneilesis* Maxim. and *Miricacalia* Kitamura. Nine species distinctly divisible into two sections occur in the southeastern United States. Section CACALIA (treated as the genus *Synosma* by Small and by Britton & Brown, ed. 2) is represented only by *Cacalia suaveolens* L., $2n = 40$, which occurs in moist woods from Massachusetts to Minnesota, southward to Missouri, Tennessee, and western North Carolina. Morphologically, it is distinct from all the other eastern North American species in having hastate leaves with pinnate venation, large heads with 12–15 involucral bracts (plus a ring of bracteoles), a naked receptacle, and numerous florets.[9] Its affinities lie with the Eurasian *C. hastata* L., $2n =$

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[8] The typification of *Cacalia* will be discussed in a subsequent paper. Rydberg (1924), Cuatrecasas (1960), and Pippen (1968), contrary to the course followed here, have maintained that *Cacalia* should be typified by *C. alpina* L., which was removed from *Cacalia* as the type species of *Adenostyles* Cass. This choice restricts the name to a genus of four or five species of Central Europe.

[9] I have seen one atavistic specimen of *Cacalia suaveolens* (*Moore, Rosendahl & Haff 19883*, GH) with all normal leaves except for one reniform, palmately veined basal leaf. Moreover, the character of the fleshy projection in the center of the receptacle of sect. CONOPHORA and its absence in sect. CACALIA does not seem to be absolute. Some specimens of various species of sect. CONOPHORA seem to lack the fleshy growth.

60, and its Asiatic relatives rather than with any other North American species.

The seven other species in the Southeast form a closely knit distinctive group (cf. Pippen) which constitutes sect. CONOPHORA DC. (*Arnoglossum* Raf., *Mesadenia* Raf.). All are morphologically similar in having palmately nerved leaves, five involucral bracts, a fleshy projection in the center of the receptacle, and five florets.[9] *Cacalia Muhlenbergii* (Sch.-Bip.) Fern. (*C. reniformis* Muhl.), $2n = 50$, occurs in woodlands from New Jersey and Pennsylvania, west to Minnesota and south to Missouri, Alabama, and Georgia. *Cacalia lanceolata* Nutt. var. *lanceolata*, $2n = 56$, occurs in moist to wet habitats from eastern Texas and Louisiana to Florida, northward into southeastern North Carolina, and *C. lanceolata* var. *Eliottii* (Harper) Kral & Godfrey (*M. Eliottii* Harper, *C. Elliottii* (Harper) Shinners) [10] occurs from peninsular Florida northward into South Carolina. *Cacalia diversifolia* Torr. & Gray also occurs in swampy areas of southern Georgia and northern Florida, westward to Louisiana, and *C. floridana* Gray is endemic to the dry, sandy oak and pine woods of central and northern Florida. *Cacalia atriplicifolia* L., $2n = 50, 52, 54, 56$, and *C. tuberosa* Nutt. (probably including *C. plantaginea* (Raf.) Shinners), $2n = 54$, are wide ranging: the former in dry woodlands from New York to Minnesota and Nebraska, south to Oklahoma, and east to Mississippi, Alabama, and Georgia, and the latter in damp prairies from Ontario to Minnesota, south to Oklahoma and Texas. The last species of this section, *C. sulcata* Fern., is restricted to sandy bogs in southern Georgia and western Florida.

Within the North American species, evidence supports the distinctiveness of the two sections, but the inclusion of both into one genus. The morphological differences between the two groups of species are reinforced by differences in germination. Three species of sect. CONOPHORA which have been investigated (*Cacalia tuberosa*, *C. atriplicifolia*, and *C. Muhlenbergii*) have achenes which need four days to two weeks for germination and cotyledons which are strongly curved upon emergence. In contrast, *C. suaveolens* (sect. CACALIA) needs only 48 hours for germination and the cotyledons are only slightly curved when they emerge. Afzelius reported the infrequent occurrence of two embryo sacs in ovules of *C. suaveolens*, each formed from a separate megaspore mother-cell. In one sac, the egg apparatus was invariably crushed but the antipodals were normal,

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[10] The placement of *Cacalia ovata* Walt. is at present uncertain. This taxon, presumably distinguishable from *C. lanceolata* by its ovate, rather than lanceolate, leaves occurs from South Carolina to Florida. Apparently (cf. J. K. Small and Kral & Godfrey) all specimens referred by Chapman to this species are synonymous with *C. Elliottii* (Harper) Shinners (= *C. lanceolata* var. *Elliottii* (Harper) Kral & Godfrey). *Cacalia* is not represented in Walter's herbarium (BM; photocopy, GH), and Walter's short description (Fl. Carol. 196. 1788) is hardly diagnostic. If *C. ovata* and *C. Elliottii* are eventually considered to be synonymous and if the present taxonomic treatment is followed, *C. lanceolata* var. *Elliottii* becomes *C. ovata* var. *ovata*, and *C. lanceolata* var. *lanceolata* will require under *C. ovata* a new combination based on the oldest legitimate varietal epithet (if available).

while in the other, the egg apparatus appeared normal, but the antipodals were crushed. Greene later reported that good seeds of *C. suaveolens* were difficult to find, and Wadmond stated that it was impossible to locate viable seed of *C. Muhlenbergii.* These two observations suggest a similar sort of meiotic irregularity in *C. Muhlenbergii.*

Another feature which links the Southeastern American species (sect. CONOPHORA) and the Asiatic species (sect. CACALIA) is the presence of the same type of asexual reproduction. Kral & Godfrey reported, as a general phenomenon in the Florida species, the production of lateral rosettes which become disconnected from the parent plant by disintegration of the connecting stolons. Liubarsky described the same phenomenon in greater detail for several Russian species. Two Japanese species, *Cacalia auriculata* DC. var. *bulbifera* Koidz. and *C. farfarifolia* Sieb. & Zucc., produce bulbils in the leaf axils (cf. Ohwi).

Within sect. CONOPHORA, the species are very similar morphologically, seemingly closely related, and apparently rather removed from other species in the genus. Hybrids within this section appear to be rare, however. The only natural hybrid reported, that between *Cacalia atriplicifolia* and *C. Muhlenbergii* (also produced artificially by Coleman), was exceedingly sterile (2–9 per cent pollen staining and no seed set).

Generically, *Cacalia* is ill defined from *Senecio* L. and its satellite genera. Originally, Linnaeus included in *Cacalia* the herbaceous perennials treated here (and other species) and a group of shrubby African plants now considered to constitute either the genus *Kleinia* Mill. or *Senecio* subg. *Kleinia* (Mill.) Hoffm. Bentham placed both the herbaceous and the shrubby groups in *Senecio*, while Hoffmann separated the two, retaining the herbaceous species as *Cacalia* and referring the species of *Kleinia* to *Senecio.* In opposition to Hoffmann's treatment, however, large and solitary crystals of calcium oxalate (rather rare in the Compositae according to Metcalfe & Chalk) have been found in both *Cacalia* and *Senecio* subg. *Kleinia*.

Chromosome numbers of the 27 species reported as *Cacalia* are $2n = 40$, 50, 52, 54, 56, 58, 60, 70, and 120. The 16 counts recently reported by Pippen as species of the segregate genera *Digiticalia*, *Odontotrichum*, *Pericalia*, and *Psacalium* are all $2n = 60$, with the exception of that for *O. Palmeri* which is $2n =$ ca. 50. Ornduff *et al.* (1967) suggest that the basic chromosome numbers in *Cacalia* are 20 and 30 and that other numbers have been derived by aneuploid reduction from $n = 30$. More chromosome counts and further study of the generic limits of *Cacalia* on a worldwide basis undoubtedly are needed.

It seems possible, especially in view of the morphological continuity with *Senecio* in Africa, that the genus is of Old World origin, but Liubarsky's postulation of an origin in the region of the upper Amur River is highly questionable.

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4. **Erechtites** Rafinesque, Fl. Ludov. 65. 1817.

Robust annual [perennial] caulescent herbs with fibrous roots and alternate, toothed or parted, glabrous or pubescent leaves. Inflorescence a "panicle" or cyme of numerous heads, each with a basally swollen involucre composed of a single series of narrow lanceolate scabrous bracts often surrounded by a series of supernumerary bracteoles; receptacle flat, alveolate or fimbrillate. Florets monomorphic and perfect [or in some cases florets dimorphic, the ray florets then carpellate with filiform 4–5-parted corollas]; pappus thin, white, soft, copious; corolla tubular, regular, 5-toothed, whitish or yellowish; anthers with obtuse bases; style branches of perfect florets with a terminal appendage of fused papillose hairs surrounded at the base by a semicircular crown of collecting hairs (cf. Belcher). Achenes oblong to linear in outline, more or less 10[–20]-ribbed, glabrous. (*Erechtites* sensu Bentham & Hooker and Hoffmann, in part.) TYPE SPECIES: *E. praealta* Raf. = *E. hieracifolia* (L.) Raf. ex DC. (Name from Greek, *Erechthites*, a name given by Dioscorides to a species of *Senecio*.) — FIREWEED, PILEWORT.

Two sections with five species native to the Americas (*sensu* Belcher) and adventive in the Pacific region, Asia, and Europe. One wide-ranging species, *Erechtites hieracifolia* (L.) Raf. ex DC., of sect. ERECHTITES (§ *Hieracifoliae* Belcher), occurs in weedy habitats in the southeastern United States.

Erechtites usually has been distinguished from *Senecio* and its allies by its two to several series of outer carpellate florets with filiform, eligulate corollas. Belcher, however, narrowed the genus to include only New World species which possess what he considers the diagnostic feature of the genus: style branches with an appendage of fused papillose hairs with a semicircular crown of collecting hairs at its base. He returned several Australian and Indonesian species traditionally included in *Erechtites* to *Senecio* and placed five New Guinean species (one population in New South Wales) in *Arrhenechthites* Mattfeld. The characters used to separate *Arrhenechthites* from *Erechtites* include the presence of functionally staminate disc florets and reduced, astigmatic (and thereby without the critical character of Belcher's *Erechtites*) style branches. In view of the obvious correlation between sterile (abortive) ovaries and reduced stigmas, the question arises as to whether these species are not simply inbreeders derived from the outbreeding American species. Also, the chromosome number of *Senecio* (*Erechtites*) *minimus* Poir., the only Old World species counted, has a diploid count of $2n = 60$, less like the most common number in *Senecio*, $2n = 40$, than *E. hieracifolia* with $2n = 40$. Regardless of which circumscription is used, the taxonomy of our species is unchanged.

Our species, *Erechtites hieracifolia*, has three varieties, two of which are now widely distributed weeds. Varietas *hieracifolia* (including vars. *intermedia* Fern. and *praealta* (Raf.) Fern.) occurs naturally from Canada southward through the Greater Antilles. It is distinguishable from the other varieties by its short bracteoles less than 1/4 the length of the involucre and by its 10-ribbed achene. It has been introduced into Hawaii and Europe. Varietas *megalocarpa* (Fern.) Cronq. (*E. megalocarpa* Fern.), separable from var. *hieracifolia* in its much larger receptacle (twice as wide) and its 16–20-ribbed achene, is endemic to sandy coastal habitats from southeastern Massachusetts to New Jersey. Belcher's suggestion that the plants may be tetraploids derived from var. *hieracifolia* seems not to have been tested. The third variety, var. *cacalioides* (Fisch. ex Spreng.) Griseb., is found in Central America, the Lesser Antilles, and South America to Argentina, and is now established as a weed in Asia. It differs from the other two varieties in its longer bracteoles with multicellular hairs (instead of being glabrous or bearing unicellular hairs). Intermediates between this and var. *hieracifolia* occur in the West Indies.

The success with which *Erechtites hieracifolia* has managed to colonize new areas is apparently due to its adaptability to new environmental conditions and to its easily dispersed achenes. Ridley listed it as one of the first plants to recolonize Krakatau after the volcanic eruption of 1883.

Although this species is usually an annual herb, Carlquist has examined a Hawaiian specimen over six feet tall which had secondary xylem. The change from the annual habit in the Hawaiian population has occurred, Carlquist postulated, because plants on oceanic islands are "released" from the selection pressures of a cyclical climate. However, there must be some positive selection for woodiness on islands (see also Carlquist, 1965).

In Brazil, the leaves of *Erechtites hieracifolia* (and of *E. valerianifolia* (Wolf) DC.) are cooked with palm oil (Corrêa), and Ochse reports that in the East Indies the upper leaves, called "lalab," are eaten raw or steamed with rice and are rumored to be beneficial for nursing mothers.

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5. **Emilia** Cassini, Bull. Sci. Soc. Philom. Paris III. **1817**: 68. 1817.

Annual or perennial caulescent herbs arising from a rosette of lyrate-pinnatifid or spathulate, dentate [entire], glabrous or glaucous leaves. Stem leaves alternate, dentate or lyrately lobed, decreasing in size toward the lax corymbose inflorescence [plants sometimes monocephalous] of discoid heads. Involucre tubular, often swollen at the base, composed of a single row of lanceolate slightly scarious bracts; receptacle flat, naked. Florets perfect; pappus setose, soft, white or purplish; corollas tubular, shortly 5-fid, lavendar [white] or red; anthers truncate at the base; style branches terete with penicillate appendages surrounded by a ring of hairs. Achenes 5-angled, truncate at both ends. TYPE SPECIES: *Cacalia sagittata* Vahl, nom. illegit. = *Emilia javanica* (Burm.) C. B. Robinson. (Derivation of name not explained but apparently from the French proper name Émilie.) — CUPID'S PAINTBRUSH.

A genus of about five species native to the Tropics of Africa and the Far East. Two weedy species, *Emilia sonchifolia* (L.) DC. ex Wight, $2n = 10$, and *E. javanica* (Burm.) C. B. Robinson (*E. coccinea* (Sims) G. Don in Sweet, *E. sagittata* (Vahl) DC., *E. flammea* Cass.), $2n = 20$, are naturalized in disturbed and weedy habitats in the warmer parts of peninsular Florida, where the latter is more frequently encountered. Both are also rather widely naturalized in the West Indies, Central America, northern South America, and Brazil.

The application of the names of these two species has been the source of much confusion. There has never been any doubt that there are two entities: one a species with lyrate-pinnatifid lower leaves, small heads, lavender (rarely white) corollas which barely exceed the involucre, lavender anthers and styles, and white pollen; the other with ovate-spathulate dentate leaves, carmine corollas which extend conspicuously beyond the involucre, orange anthers and styles, and bright yellow pollen. The first species is *Emilia sonchifolia*, and the other long has been known as *E. sagittata* in the Old World and *E. coccinea* in the New. When Cassini described *Emilia* he listed *Cacalia sagittata* Willd. as type species. Willdenow, in turn, referred to *Cacalia sagittata* Vahl, excluding the synonym *Hieracium javanicum* Burman. Because Willdenow excluded the synonym (Vahl's inclusion of this earlier legitimate name as a synonym made the name *Cacalia sagittata* superfluous) and because the type specimens of

Vahl's and Burman's names had not been examined, it has been assumed that two different taxa were involved. However, Mattfeld (1929) established that Vahl's type belongs to the large-headed, red-flowered species, and Fosberg (1966) finally located the Burman type and reported that it, also, was this species. Since Burman's is the oldest legitimate name available, it must replace the other names now used. That Cassini had the showy red-flowered species in mind when he described the genus *Emilia* is evidenced by his changing the name of the type species to *E. flammea* (nom. illegit.).

The two species apparently do not interbreed in nature, and attempts to produce artificial hybrids (cf. Lee) have failed, indicating that a sterility barrier (as well as the difference in chromosome number) is involved. The two species are not only incompatible, but also have different mechanisms of reproduction (at least in Jamaica): *Emilia sonchifolia* is an obligate inbreeder, while *E. javanica* is outbreeding.

The genus seems to be a natural group of species closely related to, but distinct from, *Senecio* L. Three of the five species counted have a chromosome number of $2n = 10$, and the other two have $2n = 20$. The species with five pairs of chromosomes are annuals apparently derived from less specialized species with $2n = 20$ (cf. Ornduff *et al.*).

The genus has no true commercial value, although *Emilia javanica* is sometimes used in tropical areas as an ornamental. Baldwin mentioned that the plants were eaten in the Far East, but not in the New World.

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ASPECTS OF THE COMPLEX NODAL ANATOMY OF THE DIOSCOREACEAE [1]

EDWARD S. AYENSU

THIS PAPER IS AN ATTEMPT to explain how the vascular tissue of two successive internodes maintains continuity in the complex nodal structure between them in stems of the Dioscoreaceae, especially in the genera *Dioscorea* and *Tamus*. Because of the economic importance of this family early emphasis (Mason, 1926) was placed on the relation between structure and function. This led physiologists to take a look at the anatomy before they had a full knowledge of how food substances are translocated in the plant.

The Dioscoreaceae is a monocotyledonous family which is distributed throughout the tropics and subtropics of the world. It is, by all standards, one of the most economically important foodstuffs in the diet of most tropical peoples (cf. Coursey, 1967). Attention has recently been focused on this family, especially the genus *Dioscorea*, because a precursor of cortisone and other related steroidal drugs is derived from the tubers of some species.

The unique anatomy of the nodes of the stems of the Dioscoreaceae was brought to attention by Mason (1926) when he studied the rate of sugar transport in *Dioscorea alata* L. Earlier, Falkenberg (1876) had called the glomerulus of the node an imperfect knot in his study of *D. villosa* L. Mason noted that the phloem was of a markedly abnormal type. He further observed that the sieve tubes of the successive internodes did not join with each other directly but through a glomerulus which was composed of a great number of oblong thin-walled parenchymatous cells, each with a distinct nucleus, running fairly parallel with each other. Behnke (1965a) questioned the presence of nuclei in the glomerulus cells. Present studies show that nuclei occur at certain stages in the ontogeny of these cells (FIG. 2).

In his study of the ontogeny of the stem of *Tamus communis* L., Burkill (1949) disproved Mason's claim that glomeruli were absent from the nodes of *T. communis*. Present studies reveal that glomeruli are certainly present in the nodes of *Tamus* (FIG. 12) and, although they cannot be easily overlooked, it should be emphasized that the glomeruli in this genus are not so pronounced as those of most species of *Dioscorea* (FIGS. 4–11).

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[1] A full account of the vegetative anatomy of the Dioscoreaceae will be included in the *Anatomy of the Monocotyledons. Dioscoreales*, ed. C. R. Metcalfe, Oxford University Press.

Happ (1950) wrote his thesis on the nodes of the Dioscoreaceae but a copy is not available to me. However, a comment on it appeared in Braun's (1957) work. Essentially, Happ investigated by means of serial sections the interlacing of the xylem-phloem glomeruli in the vascular system of the node.

Brouwer (1953) published his account of the arrangement of the vascular bundles in the nodes of Dioscoreaceae and presented a diagram of the elements of the node. Brouwer concluded that the sieve tubes of two successive internodes were connected in the following manner: sieve tubes, funiculus cells, bast tubulus cells, glomerulus cells, bast tubulus cells, funiculus cells, and sieve tubes. Brouwer, following Mason (1926), concluded that the phloem-glomerulus cells were (a) densely filled with cytoplasm; (b) with a persistent nucleus with nucleolus; and (c) without sieve areas.

A comprehensive study of the nodal anatomy of *Dioscorea batatas* Decne. and *Tamus communis* was conducted by Braun (1957). He concluded that (a) the xylem-glomerulus consists of very numerous short tracheids of various sizes, the orientation of which is difficult to trace; (b) the phloem-glomerulus, which is divided into several partial glomeruli, is composed of a new type of translocatory cell, called phloem-glomerulus cells; and (c) the phloem-glomerulus cells possess thin walls without sieve pores and without visible pitting; they are distinguished from parenchyma cells by their lack of starch. Behnke's (1965c) electron microscopic studies show that sieve areas are, in fact, present in the phloem-glomerulus cells.

The present study, involving more species than were available to earlier investigators, essentially supports and extends their conclusions.

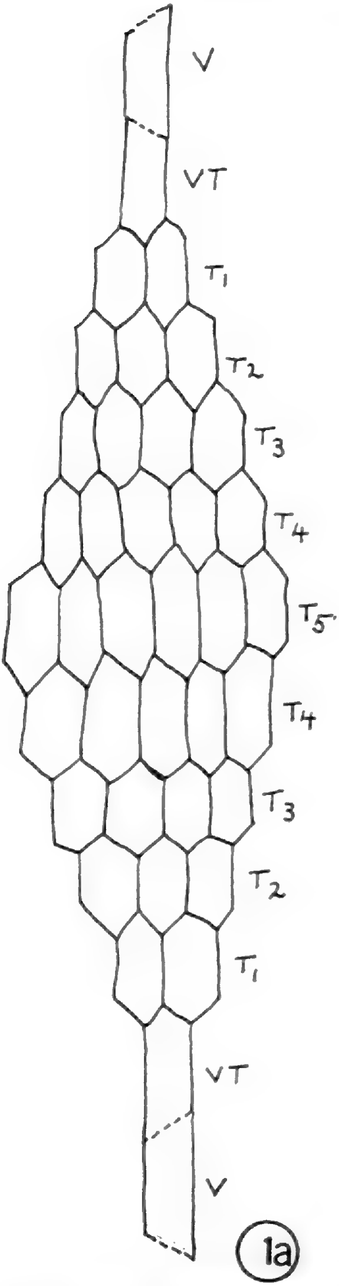
MATERIALS AND METHODS

My observations are based on 180 specimens of 112 species. A complete list and citations are given elsewhere (Ayensu, 1966).

Most of the specimens examined were fluid-preserved in formalin acetic alcohol. Microscopic details were studied in serial sections at 10μ, and those produced on a sliding microtome usually at 16μ. Depending upon the nature of some specimens, sections were cut up to 90μ. The sections were stained in safranin and counterstained with Delafield's haematoxylin followed by conventional differentiation, dehydration, clearing in xylene, and mounting in Canada balsam.

NODAL ANATOMY

As pointed out in an earlier paper (Ayensu, 1965), the vascular strands between the petiole and the stem at the nodes of many species of Dioscoreaceae are highly distinctive and are believed to be unique in the family. Longitudinal serial sections of the node reveal two groups of interlacing vascular elements, each forming a plexus close to the petiole insertion.



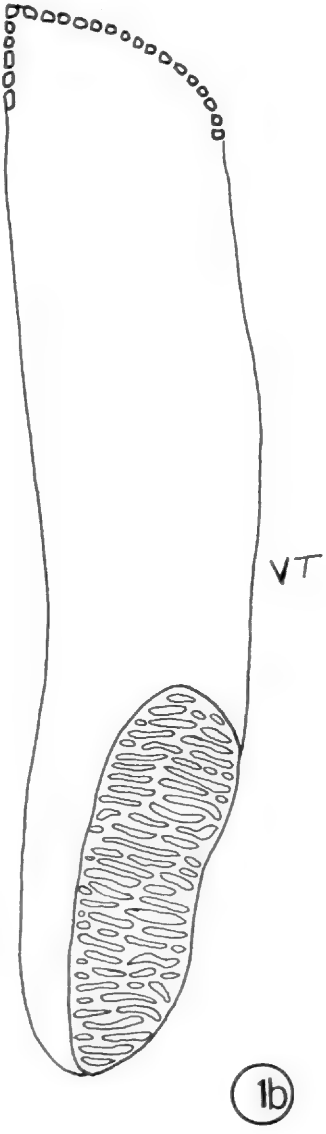


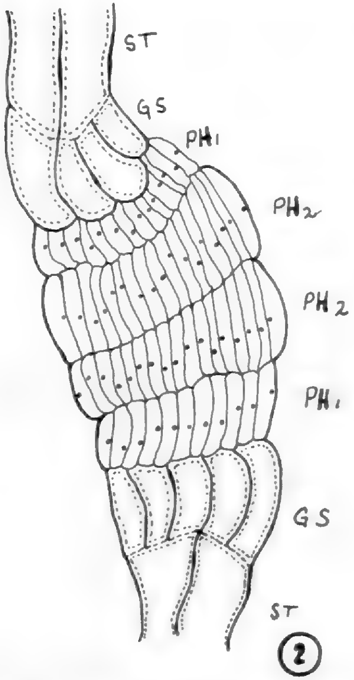
FIG. 1a (LEFT). Schematic diagram illustrating the arrangement of the elements of xylem-glomerulus in the nodal region of stems of *Dioscorea* and *Tamus*.

FIG. 1b (RIGHT). Vessel-like tracheid showing a reticulate perforation plate (lower) and bordered pits (upper).

Xylem-glomerulus. Serial sections and macerations reveal that the mature xylem glomerulus is mainly composed of short tracheids of variable shape closely fitted together, thus resembling the distinct parts of a composite jig-saw puzzle. These peculiar tracheids are confined to the node and have large bordered pits. Presumably in the internodes water moves freely from vessel element to vessel element through the scalariform perforation plates. Exactly how materials are translocated through the nodal region is not clearly understood.

The phyllotaxy determines the width of the glomerulus in the nodes. In the species having simple, alternate leaves, a single glomerulus occupies about one-third of the area of the node. In an opposite (or decussate) arrangement, the glomerulus occupies about two-thirds of the nodal area. In species that exhibit a whorled arrangement, the glomerulus occupies almost all the nodal area.

The tracheids vary in width and length within species. The widths varying from 40μ to 110μ, and lengths from 80μ to 260μ have been recorded for different species. These tracheids are closely fitted together, and have numerous pit-pairs on their common walls. The exact pathway of the contiguous tracheids between successive internodes is very complicated and variable within a species. (See FIGS. 4–12.) Longitudinal



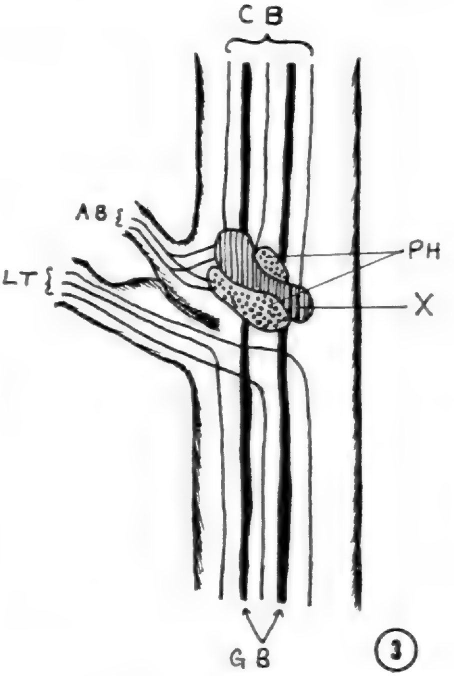


FIG. 2 (LEFT). Schematic diagram of the phloem glomerulus.

FIG. 3 (RIGHT). Schematic representation of the stem showing the relationship of and the position of the xylem and phloem glomeruli in the region of the leaf insertion.

sections and macerations of the node give a partial elucidation of the complicated sequence of the tissue structures. As Braun (1957) interpreted *D. batatas* and *Tamus communis*, a vessel just about to enter a node is attached to 1, 2, or 3 cells which Braun referred to as "vessel-like tracheids." The end wall of the vessel-like tracheid (VT) facing the vessel (v) has a reticulate perforation plate, while the other end wall has bordered pits (FIGS. 1a, b). The elements that constitute the bulk of the xylem-glomerulus lie between the vessel-like tracheids. The tracheids of the first group (T_1) are closely fitted to those of the second group (T_2) and to other successive tracheid groups, thus establishing the normal communication between them. The lengths of the tracheids vary from one node to the other within a species. In this respect variation in tracheid length does not have any taxonomic value. Those of the first few groups ($T_1 — T_3$) are shorter than those of T_4 and T_5. It is also observed that the tracheid groups increase in number from T_1 to T_5, presumably for enlarging the water conducting tissues in the node. The surface area of the water conducting tissues is further increased by the complex arrangement of many xylem-glomeruli at a node. Each glomerulus is S-shaped and longitudinally orientated. A xylem-glomerulus diagram (FIG. 1) is presented for the sake of simplicity, but the full complexity of it is demonstrated by FIGS. 4–12.

Phloem-glomerulus. The construction of the phloem-glomerulus (FIG. 2) follows essentially the scheme presented for the xylem-glomerulus (FIG. 1). The phloem-glomerulus is made up of what Braun (1957) named "glomerulus sieve-tubes" (GS). Earlier, the same tissues had been called "funiculus cells" by Brouwer (1953) and "funnel-cells" by Mason (1926). Recently, Behnke (1965a) has called the same tissues "connecting sieve-tubes." Essentially, these tissues are composed of somewhat funnel-shaped, thin-walled cells having numerous small simple pits at the end walls adjoining the PH. They differ from ordinary sieve tubes in the presence of sieve plates only at the end adjoining the sieve tubes. The glomerulus sieve-tubes adjoin the cells that make up the bulk of the phloem glomerulus. These cells were designated "phloem-glomerulus cells" of the first (PH_1), second (PH_2), and third (PH_3) orders by Braun (1957). Similar cells had earlier been called "bast tubulus" and "glomerulus cells" for PH_1 and PH_2 orders, respectively, by Brouwer (1953). PH_1 and PH_2 had also been called "Nodal sieve-tubes" and "Nodal sieve-elements" respectively by Behnke (1965a). The PH_3 of Braun may actually be the over-lapping ends of PH_2 and PH_21.

The phloem-glomerulus cells vary in length, and as was observed in the case of the xylem-glomerulus, some of the cells of the phloem groups are shorter than others. In this case, the cells of the PH_1 order vary from 20μ to 60μ in length, while those of PH_2 vary from 60μ to 140μ.

The cells of PH_1 and PH_2 have thin walls (about 1μ thick) with simple pits that can hardly be seen with a light microscope. Whether the walls are interconnected by cytoplasmic threads (plasmodesmata) or by any other mechanism has not been demonstrated with the light microscope. Dr. Behnke of Bonn University informed me that his electron microscope studies show that plasmodesmata are indeed present in the cells of PH_1 and PH_2. His recent publications (Behnke, 1965a, b, c) support his findings. It is, however, certain that these phloem cells are specialized and differ from sieve tubes and sieve cells of ordinary phloem tissue. Microchemical tests reveal the absence of starch-grains from the phloem-glomerulus cells; the surrounding parenchyma cells possess starch. The histochemistry of the phloem will have to await critical studies.

Cleared and stained portions of young and old stems reveal that at the node (FIG. 3) three major vascular bundles (LT) enter the petiole from the stem through the node without joining other vascular bundles, coming through the underlying internode as peripheral vascular bundles. These leaf-trace bundles are V-shaped.

The vascular bundles of the stem axis lying in front of the point of entry of the leaf traces, and those of the inner and outer circles become enlarged and join to form the xylem and phloem glomeruli (X, PH). These glomeruli lie obliquely above each leaf insertion at the same height as the axillary bud (AB). Opposite the outer circle of the vascular bundles in the internode they appear somewhat towards the outside and project into the base of the axillary bud or the lateral shoot. Five cauline vascular bundles leave a glomerulus into the internode above (CB), but only two enter it from below (GB). The latter are the characteristic large vascular bundles which are arranged in the gaps between the three leaf-trace bundles, which lie on the inside of the stem furrows. Hence the five cauline vascular bundles forming the circle are made up of the two vascular bundles from the glomerulus (GB) and the three vascular bundles of the leaf-trace (LT).

The vascular bundles of the axillary buds come from the glomerulus directly. Just after they leave the glomerulus, each divides into two (an upper xylem branch and a lower phloem branch), which come from the upper and lower regions of the glomerulus respectively. Occasionally the lower phloem branch subdivides into two with one establishing itself above the xylem branch.

DISCUSSION

The structure of the xylem and phloem glomeruli in the nodes of the Dioscoreaceae seems to be unique amongst the monocotyledons. Futhermore, the presence of tracheids and the distinct type of sieve elements in the node has considerable implications regarding the evolutionary history of these tissues in the angiosperms.

The anatomical studies of the xylem by Bailey and Tupper (1918) showed that the most logical phylogenetic sequence is the derivation of vessels from tracheids in the angiosperms. Cheadle (1943) working with the xylem of monocotyledons confirmed Bailey's work. In the light of the above theory it is interesting to examine the developmental aspects of the tracheal elements in the node of the Dioscoreaceae. The bulk of the xylem glomerulus is made up of tracheids which are considered primitive in the phylogenetic sense. Similarly, the cells of the phloem glomerulus are considered to be of a relatively primitive type (cf. Braun, 1957, and the papers he quotes).

It is significant that such a difference can occur in a stem with primitive structures in the nodes and more advanced structures in the internodes. Bailey (1956) stated that "It is now clearly demonstrated that evolutionary modification of the xylem of stems and roots is *not necessarily* closely synchronized with phylogenetic trends in the specialization of the angiospermic flower. Either trend of evolution may be accelerated or retarded in relation to the other." The above can be extended with a statement that vessel development in an individual part of an organ can be delayed or advanced within that particular part as demonstrated in the node and internode of the Dioscoreaceae respectively.

This study demonstrates that in the midst of the complex nodal vascular system lies an orderly and systematic mechanism that permits the transport of assimilatory materials through the stems of the Dioscoreaceae. However, any attempt to gain full understanding of the exact pathway, and therefore, the movement of material through the phloem glomerulus must first confirm the present observations which are based on a reconstruction from serial microtome sections. A more reliable understanding of the pathway will hopefully be gained when the writer is able to study the vascular system of the Dioscoreaceae using the motion-picture analysis technique employed by Zimmermann and Tomlinson (1965, 1967).

The complexity of the phloem glomerulus in the Dioscoreaceae raises some fundamental questions about the current hypotheses on transport mechanisms in plants. Esau, Currier and Cheadle (1957) summarized the hypotheses as (a) mass or pressure flow; (b) mass flow together with activities of parenchyma cells associated with the phloem that account for the turgor gradients necessary for mass flow; (c) transport of solutes in the sieve tube along protoplasmic interfaces; (d) accelerated solute movements in sieve tubes resulting apparently from some special kind of cytoplasmic movement or flow; (e) independent solute movement resulting from one or more as yet unknown active transfer processes that occur in the sieve element cytoplasm.

The unique anatomical characteristics of the phloem glomerulus in this family seem to suggest that perhaps more than one of the above methods is responsible for the movement of assimilatory substances in the Dioscoreaceae. Arisz's (1952) suggestion that every substance moves its own way, and that different mechanisms may be involved in translocation should be considered in the light of the anatomical variation in the phloem of this family.

Although I have no proof as to the exact function of the phloem glomerulus, it seems likely that rapid translocation is achieved by the numerous cells that form the bulk of the nodal region.

SUMMARY

The complex nodal anatomy which is unique and basically uniform in the Dioscoreaceae, especially in *Dioscorea* and *Tamus*, is described. The width of the two masses of tissues referred to as glomeruli is correlated with the phyllotaxy in each species. The xylem-glomerulus is composed of numerous short tracheids of various sizes and shapes which are closely fitted together. The phloem glomerulus, whose construction is essentially that of the xylem-glomerulus, consists of thin-walled cells without visible pitting and sieve areas. Because of the presence of primitive xylem and phloem structures in the nodes in contrast to more advanced structures in the internodes, it is postulated that vessel development in an individual part of an organ can be delayed or advanced within that particular part as shown in the node and internode of the Dioscoreaceae respectively. The peculiar nature of the vascular bundle glomeruli is presumed to have some effect on the rate of fluid transport in the stem. It is suggested that another technique, such as the motion-picture analysis method, should be employed to study further the nodal structure and its relation to translocation.

ACKNOWLEDGMENTS

I am very grateful to Drs. P. B. Tomlinson, R. H. Eyde, and H. Robinson for reading the manuscript.

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EXPLANATION OF PLATES

FIGS. 4–12. Longitudinal sections of the stem nodal region illustrating the complexity of the xylem and phloem glomeruli, × 80.

PLATE I

FIG. 4. *Dioscorea hirtiflora* Benth., showing an example of the meeting point between the phloem glomerulus cells (PH_2) of the second order, and a transverse section of a sieve tube (ST).

FIG. 5. *Dioscorea discolor* Kunth, interlacing of xylem glomerulus cells. Arrow points to a transverse section of a vessel (V) just entering the node.

PLATE II

FIG. 6. *Dioscorea schimperiana* Hochst., exhibiting general orientation of xylem and phloem glomeruli. Vessel element (V); phloem glomerulus of the first (PH_1) and second (PH_2) orders. Xylem glomerulus cells (XG), phloem glomerulus cells (PHG).

FIG. 7. *Dioscorea multiflora* Mart., showing a vessel element (V) and xylem glomerulus cells (XG).

PLATE III

FIG. 8. *Dioscorea luzonensis* Schauer, showing transverse sections of phloem glomerulus cells (PHG).

FIG. 9. *Dioscorea composita* Hemsl. (*D. tepinapensis* Uline ex Knuth). Arrows pointing to vessel (V), vessel-tracheid (VT) and xylem glomerulus in transverse section (XG).

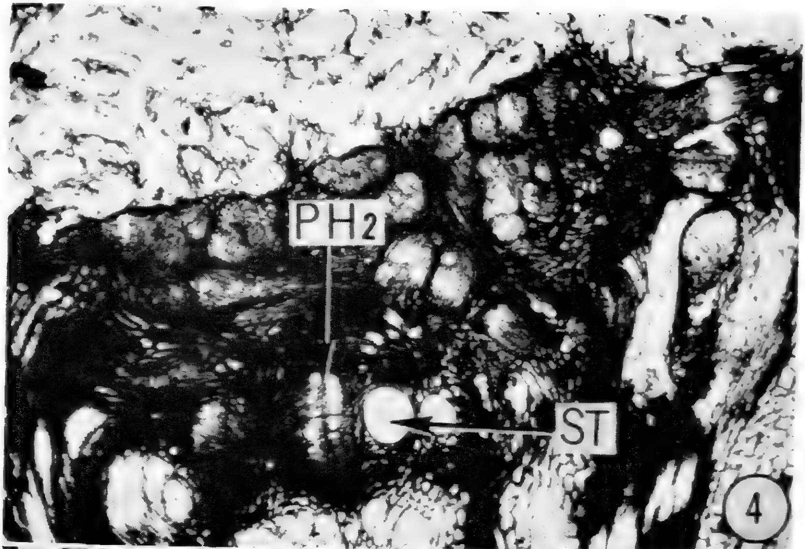
PLATE IV

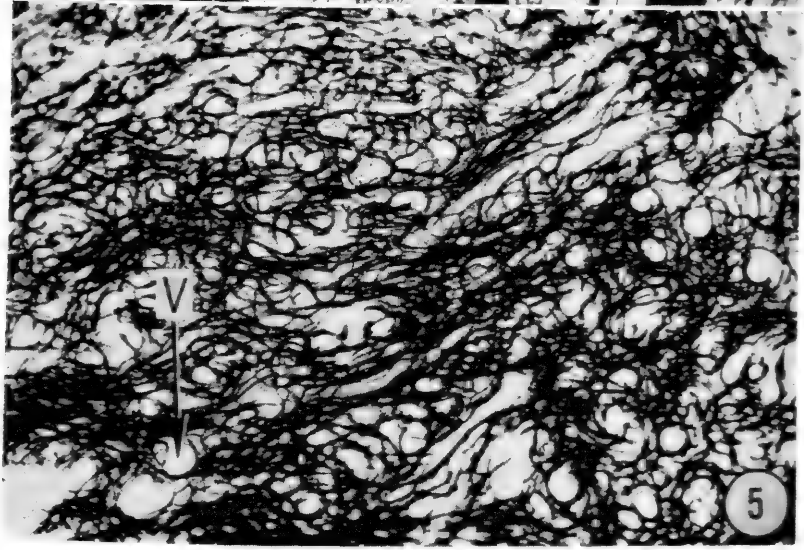
FIG. 10. *Dioscorea pentaphylla* L., end plates of a vessel-tracheid (VT) and a vessel element (V).

FIG. 11. *Dioscorea dregeana* (Kunth) Th. Dur. & Schinz, end plate of vessel-tracheid (VT) and phloem glomerulus cells (PHG).

PLATE V

FIG. 12. *Tamus communis* L., exhibiting the presence of xylem (XG) and phloem (PHG) glomeruli.





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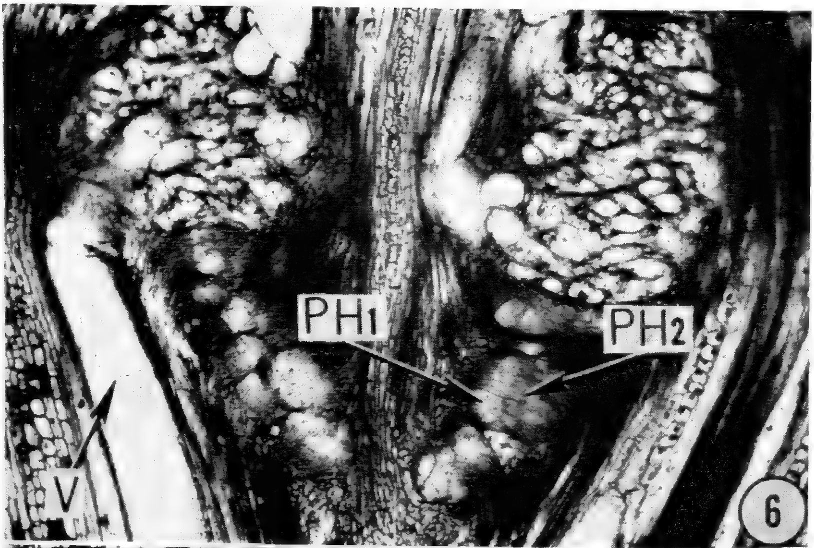

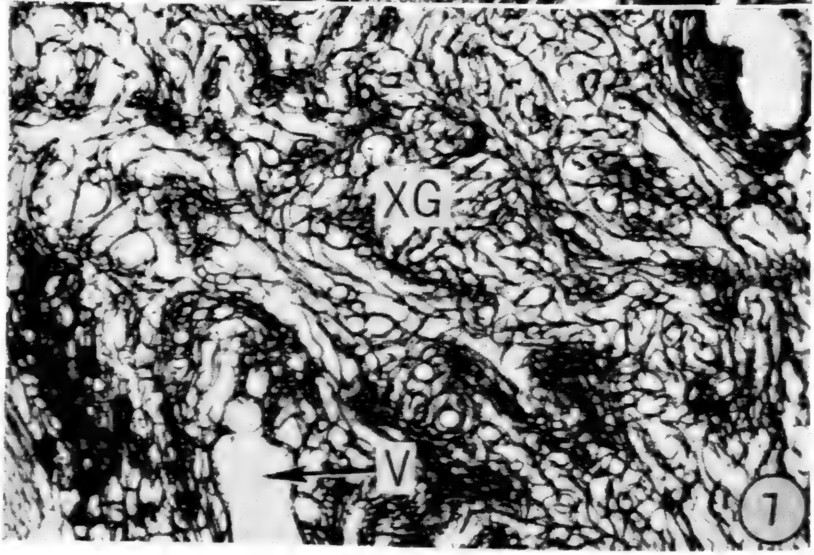

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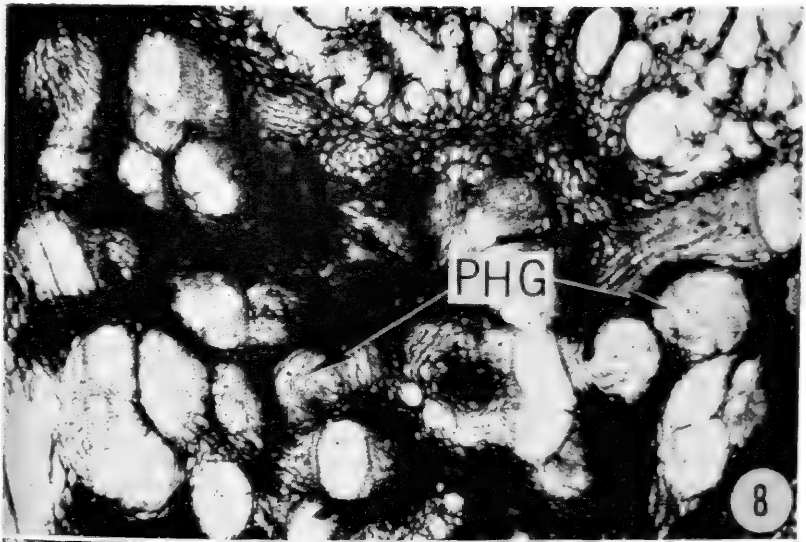

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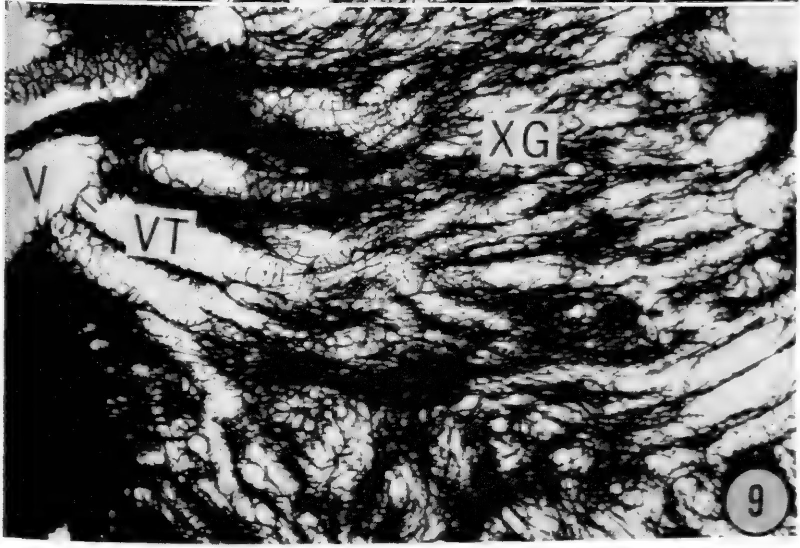

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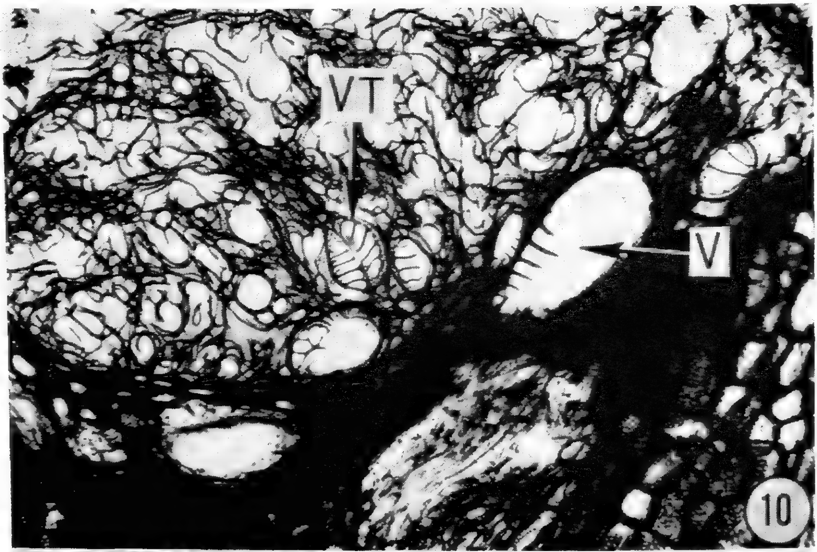

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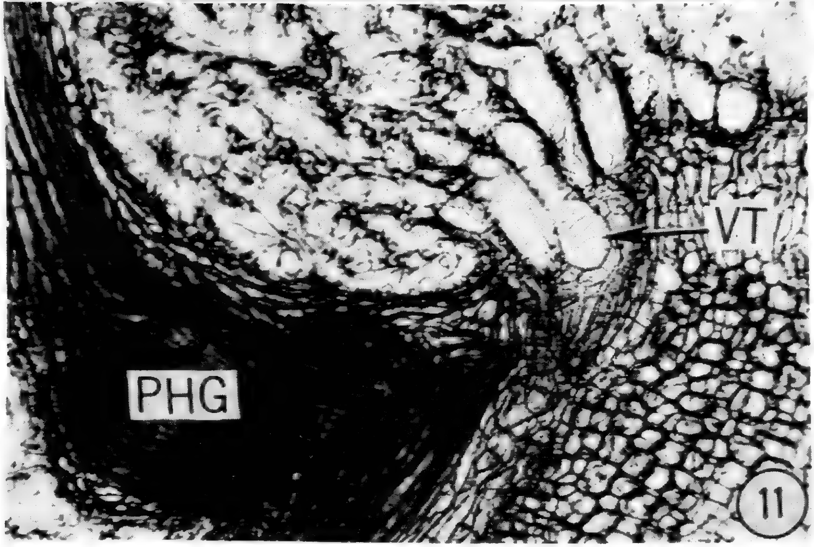

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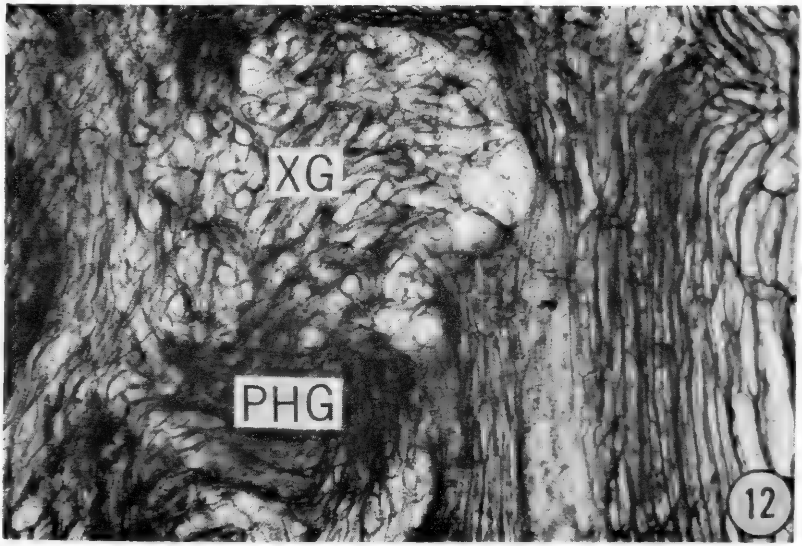

AYENSU, DIOSCOREACEAE

ANATOMY OF THE PALM RHAPIS EXCELSA, VII. FLOWERS *

N. W. UHL, L. O. MORROW, AND H. E. MOORE, JR.

THE GENUS *Rhapis* is one of a group of six genera in the subfamily Coryphoideae centered in the southeastern United States (*Rhapidophyllum*) and southeastern Asia (*Liberbaileya, Maxburretia, Trachycarpus, Rhapis*) with a Mediterranean outlier (*Chamaerops*). These genera are notable for complete apocarpy coupled with an apparently specialized inflorescence (relative to the subfamily as a whole), polygamy or dioecism, and slight to marked morphological distinction between staminate and pistillate flowers. Among them, *Rhapis* appears to be most highly specialized in having greater dissimilarity between staminate and pistillate flowers and a gamophyllous corolla.

That perfect flowers may sometimes occur is suggested by the formation of apparently normal seed on an isolated pistillate plant at Cornell University and further by the comments of Tomlinson and Zimmermann (1968). In young stages of pistillate flowers, anthers appear normal but in the mature flowers they are small and do not normally contain pollen. There is a basic similarity between staminate and pistillate flowers in young stages. Differences — functional versus abortive carpels and anthers and elongate staminate corolla tube — are obvious only in later and mature stages. The nature of most palms makes morphogenetic experimentation difficult. *Rhapis*, however, is a small palm (Zimmermann & Tomlinson, 1965) and readily grown in the tropics and subtropics or as a pot plant in greenhouses. When the present anatomical series is complete, it may prove an excellent subject for studies of development and morphogenetic experiments on different aspects of flowering. The purpose of this paper is to describe the anatomy of the two morphological types of flowers in order to continue the anatomical series on *Rhapis*, to add to a survey of floral anatomy in palms, and to provide the basis for further work.

MATERIAL AND METHODS

A partial description of the floral anatomy of *Rhapis* was previously prepared by one of us (Morrow, 1965) from collections vouchered by

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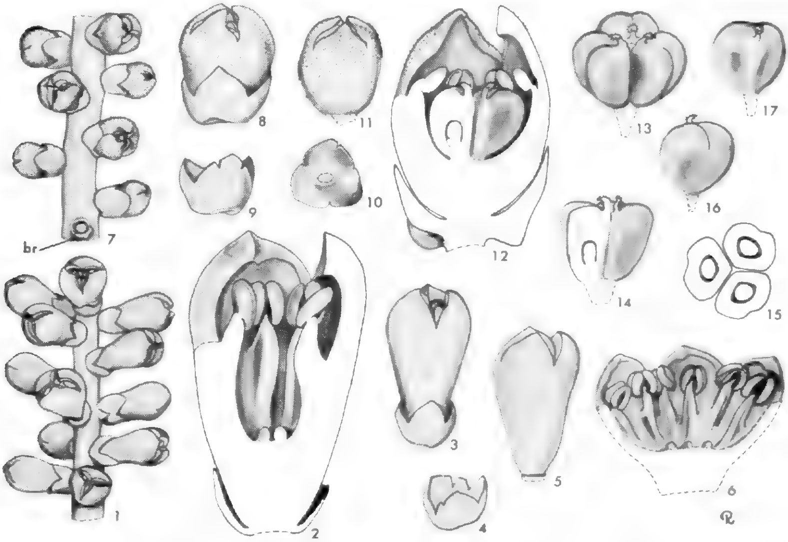
* This study was undertaken at the request of and in collaboration with Drs. P. B. Tomlinson and M. H. Zimmermann. We would like to thank them for this invitation and their interest in the work which has been supported by National Science Foundation Grants G–18770, GB–3528. Previous papers in this series have appeared in Jour. Arnold Arb. volumes 46 (1965), 47 (1966), 48 (1967), and 49 (1968).

Read 701 and *774*. Further study of this material and of new collections (*Moore & Uhl 9561, 9562*) has resulted in the more complete description presented in this paper. Staminate and pistillate flowers (*Moore & Uhl 9561, 9562*) at anthesis were cleared and sectioned as described previously (Uhl, 1966). Serial sections were studied in polarized light and by cinematography (Zimmermann & Tomlinson, 1965), a technique we are finding most useful for analyzing flowers where many bundles are present.

RACHILLAE

As described in a previous paper of this series (Tomlinson & Zimmermann, 1968), both staminate and pistillate inflorescences of *Rhapis* are small panicles with up to three orders of branching. Bract to branch relationship, although somewhat obscured by adnation, reveals a simple monopodial system similar to that described for *Nannorrhops ritchiana* (Tomlinson & Moore, 1968). Flowers are inserted in irregular spirals (FIGS. 1, 7) on branches of the first, second or third orders and on the terminal part of the main axis, these axes being rachillae as defined by Tomlinson and Moore (1968).



FIGS. 1–17. FIG. 1, portion of staminate rachilla, × 2; FIG. 2, staminate flower in vertical section, × 8; FIG. 3, staminate flower, × 4; FIG. 4, staminate calyx, × 4; FIG. 5, staminate flower, calyx removed, × 4; FIG. 6, staminate flower expanded, × 4; FIG. 7, portion of pistillate rachilla, × 2; FIG. 8, pistillate flower, × 4; FIG. 9, pistillate calyx, exterior view, × 4; FIG. 10, pistillate calyx, interior view, × 4; FIG. 11, pistillate flower, calyx removed, × 4; FIG. 12, pistillate flower, vertical section, × 8; FIG. 13, gynoecium, × 8; FIG. 14, gynoecium, vertical section, × 8; FIG. 15, carpels in transection, × 8; FIG. 16, one carpel, dorsal view, × 8; FIG. 17, one carpel, ventral view, × 8. DETAILS: br, bractlet.

Pistillate inflorescences (FIG. 7) have fewer, commonly shorter branches than staminate, with flowers more widely spaced (1–2 mm. apart). In staminate inflorescences (FIG. 1), third order branches are more common, often longer, and flowers are more crowded (0.5–1 mm. apart), sometimes opposite, or in pairs. Many more flowers are produced in a staminate than in a pistillate inflorescence (TABLE 1).

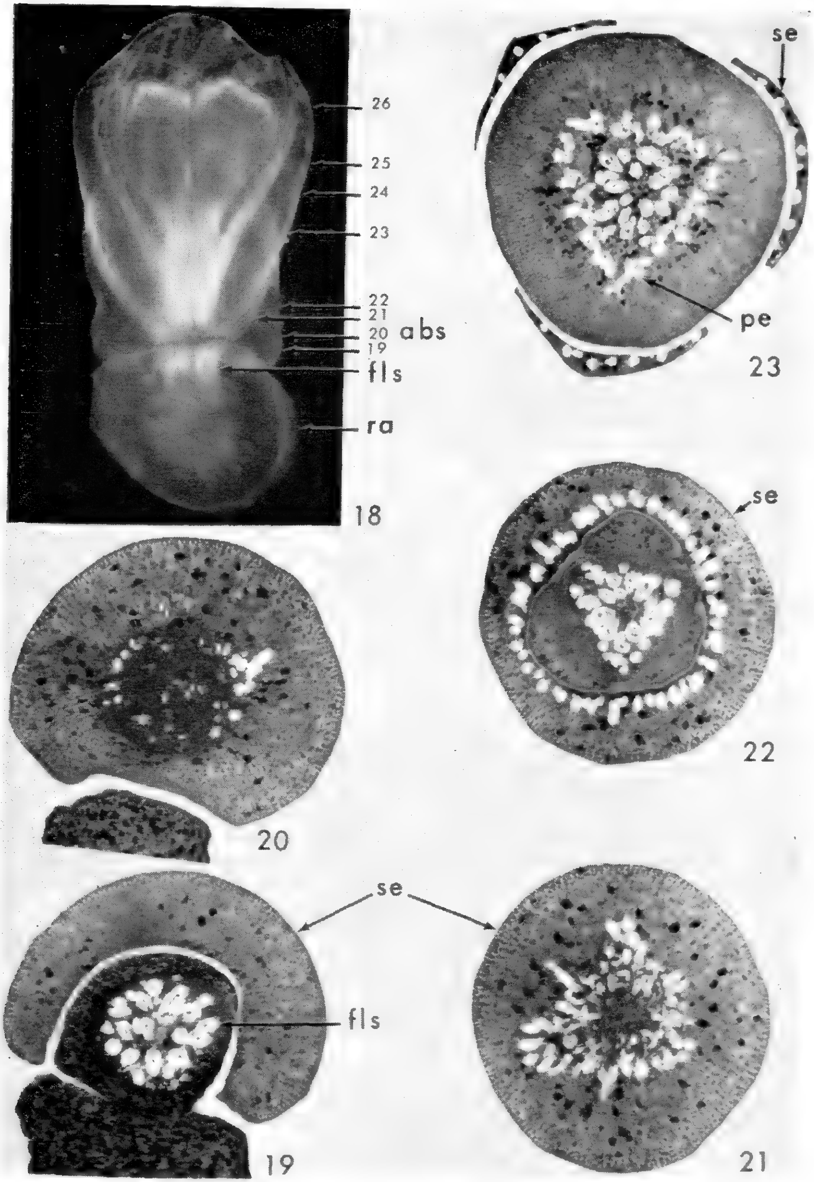
Anatomy. Anatomically all rachillae are similar. Epidermal cells are small with rounded to slightly papillose outer walls. A thin cuticle is present. The cortex is moderately wide and of unspecialized parenchyma cells which increase in diameter centripetally. Some of the cells contain tannins. The vascular complement consists of both large and small bundles. Each larger bundle has one or two large vessels, a single phloem strand, and a fibrous sheath four to five cells wide next to the phloem and two to three cells wide next to the xylem. Smaller bundles have fewer vascular elements; a few may contain only a phloem strand or be completely fibrous. In general these axes differ from the main axis in having less lignified ground tissue and fewer cortical fibrous strands.

There is a definite arrangement and orientation of axial bundles in rachillae of many palms. In *Rhapis*, a transection of a rachilla at any level shows some large central bundles, one or two peripheral groups of smaller bundles, and some scattered fibrous or very small vascular bundles in the inner cortex. This configuration is easily explained in terms of origin of bundles to the flowers.

Slightly below and opposite a floral insertion, six to ten axis bundles branch (FIG. 18, fls) to form the bundles supplying the flower. A single axial strand may produce one to four small branches in close vertical succession or in a horizontal plane. Commonly the vertical derivative continues as an axial bundle; however all branches of a bundle may become floral traces. The peripheral clusters of small bundles are traces to higher flowers; consequently, the number of small bundles varies depending on the proximity to a floral insertion.

One or two axis bundles as well as branches from many others extend directly into each flower. The total number of bundles in a rachilla is thus progressively reduced distally (TABLE 1). Bundles in the axis branch frequently, providing the numerous traces to flowers. Absolute numbers of bundles are difficult to determine because bundles branch frequently, the levels at which bundles are counted cannot be considered perfectly comparable, and fibrous sheaths of main strands and branches are often confluent. Mere vigor or order of the branch may also affect the number of bundles in a rachilla. However, the number of bundles in floral stalks and organs seems to vary within definite limits. Approximately 6 to 9 bundles are present in staminate floral stalks below the abscission zone, and a larger number (20–25) in pistillate floral stalks.

Rachillae are not terminated by flowers. In pistillate branches a rounded or pointed projection of the axis extends beyond the flower; some 14 to 16 vascular bundles are present in this reduced tip. Staminate



FIGS. 18–23. Pistillate flower. FIG. 18, cleared half of a pistillate flower, × 10; levels of succeeding figures (19–26) indicated by the appropriate numbers; FIG. 19, transection of the floral stalk, × 18, level 19 in FIG. 18; FIG. 20, transection through abscission zone, × 18; FIG. 21, transection at level of origin of sepal traces, × 18; FIG. 22, transection at level of origin of petal traces, × 18; FIG. 23, transection showing distal parts of sepals, petal traces form outer triangular group of bundles, × 18. DETAILS: abs, abscission zone; fls, floral stalk; pe, petal traces; se, sepal; ra, rachilla.

rachillae usually end less abruptly, one to seven abortive flowers being present. Bracts subtending these abortive flowers are more prominent than bracts of normal flowers, which are often obscured as the axis and flower increase in size. A difference in growth patterns is suggested in the two types of inflorescences. More branches and more flowers per branch are formed in staminate inflorescences, suggesting that factors affecting branch and floral initiation are more active and that cessation of growth is less abrupt.

TABLE I. **Flowers and Bundles per cm. of Length in Rachillae**

1 cm. intervals, base to apex	Pistillate rachilla		Staminate rachilla	
	bundles/cm.	flowers/cm.	bundles/cm.	flowers/cm.
base	50		42	
1	43	4	36	3
2	40	5	35	7
3	40	4	35	10
4	39	4	31	9
5	31	3	28	15
6	16	1	28	12
7	16		26	13
9			19	14
10			12	13
11			5	7 abortive

PISTILLATE FLOWER

Bracts. Each pistillate flower is subtended by a bractlet (FIG. 7, br). Bractlets subtending basal flowers on rachillae may be larger than bractlets of distal flowers which are usually small, crowded between the flower and the axis, and apparent only when flowers are detached (FIG. 7). A small trace, originating as a branch of an axis bundle, is usually present in the bractlet. One or more floral traces may originate from the same stelar bundle from which the trace to the bractlet diverged at a lower level.

Morphology (FIGS. 7–17). Although considerable connation and adnation are present in floral organs, a 3–3–6–3 floral plan is obvious both morphologically and anatomically. Sepals of pistillate flowers (FIGS. 8, 9, 10) are connate forming a shallow parenchymatous cup about 1 mm. high with three pointed lobes 1–1.5 mm. long. The three petals (FIG. 11) are also connate for approximately 3 mm., above which the free lobes are briefly imbricate and then valvate reaching an additional length of 1–2 mm. The staminodes (FIG. 12) resemble the stamens in staminate flowers but are smaller. The filaments are linear, adnate to the petal tube for 1 mm., and free above that for about 0.5 mm. In the material studied the reduced anthers did not produce pollen.

The three separate carpels (FIG. 13) are wedge-shaped with flat ventral sides and rounded and grooved dorsal sides (FIGS. 13, 16). Each carpel has a distinct stalk which is fused with the petal-staminode tube for a very short distance basally (FIG. 24). A locule with a single basal ovule occupies the lower half of the carpel (FIGS. 12, 14). Distally the style is wide; the upper part is distended abaxially and converges abruptly toward the ventrally situated, conduplicate, tube-shaped stigma (FIG. 28). Thus the styles of these carpels are enlarged and are also histologically specialized, as described below.

A single, hemianatropous ovule with a large funicular aril is attached basally in the ventral angle of the locule (FIG. 27). There are two integuments which are free for about 1/3 the length of the ovule. The outer integument is six to seven cells wide and increases to about nine cell layers around the micropyle. The inner integument consists of two cell layers and is widened to three to four cells around the micropyle to form a short beak. The inner layer of the inner integument is specialized as an integumentary tapetum.

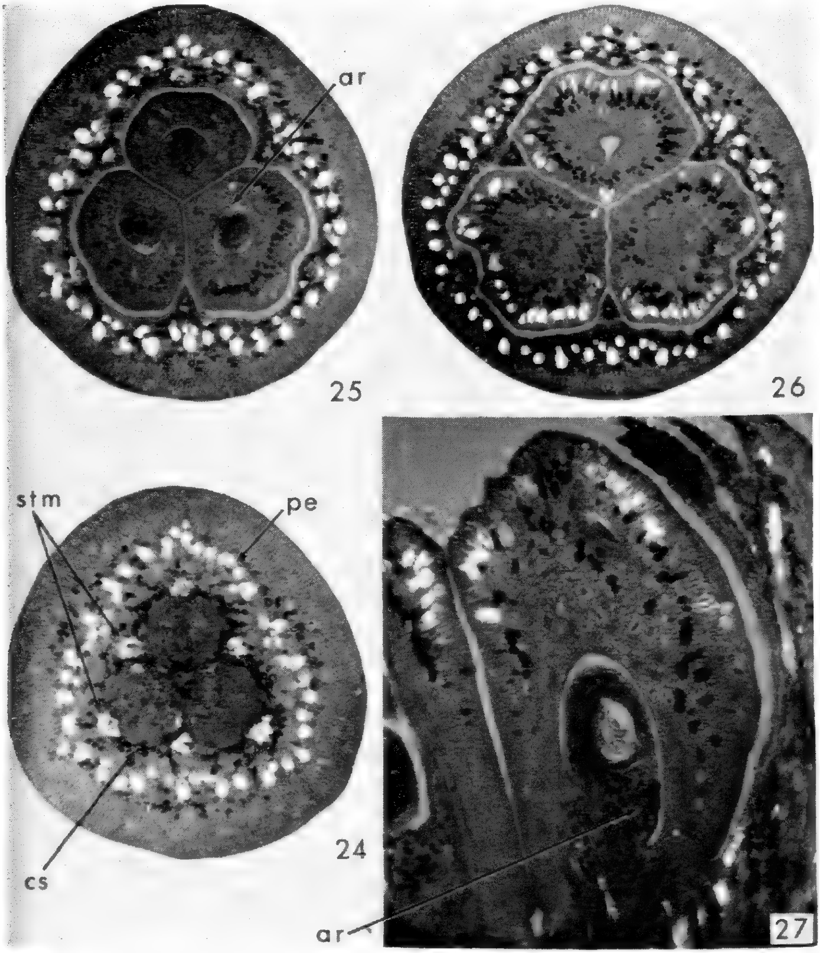
Anatomy (FIGS. 18–32). Pistillate flowers appear to be sessile (FIG. 7). Anatomically, however, a very short stalk with a distinct group of floral traces, can be recognized (FIG. 19). As explained above, the majority of the bundles of the floral axis originate as branches from strands in the rachilla, one or two of which also extend directly into the flower without branching. The number of bundles supplying the pistillate flower (FIG. 19) is about 23

An abscission zone forms a characteristic feature of floral stalks of both staminate and pistillate flowers (FIG. 18, abs). This zone is distinguished by the absence of fibrous bundle sheaths and by smaller ground parenchyma cells (FIG. 20) through which bundles can be followed.

Generally, in palm flowers, even when organs are connate, the origin of their traces indicates a spiral insertion. This is not apparent in the sepals or petals of *Rhapis*. Directly above the abscission zone, most bundles of the floral axis branch at about the same level (FIG. 21) to form about 30 sepal traces. The origin and horizontal divergence of so many bundles at one level results in a collar-like complex in which inner bundles extend radially between outer strands and some lateral fusion of bundles occurs (FIG. 21). Individual bundles may be followed through this complex. FIGURE 38 is a radial plot of a single major bundle of the floral axis. The sepal trace (se 1) originating from this bundle branches to form three other sepal traces (FIG. 39, se 2, se 3, se 4) and these bundles in turn branch forming the continuing vertical bundles VB 2, VB 3, and VB 4. Smaller (minor) bundles of the floral axis may produce only a single sepal trace or extend directly into the sepal.

Above the sepal complex about 30 vertical bundles form a central group (FIG. 22). Some 30 to 40 petal traces diverge at an acute upward angle (30° to 40°) from these as opposed to a near 90° angle of divergence for sepal traces (FIG. 18). Smaller vertical bundles (FIG. 39, VB 2 and

VB 3) may extend directly into a petal without branching. Most petal traces, at the level of their origin, contain phloem only and fibrous sheaths of main bundles and branches are often confluent (FIG. 23, pe). At higher levels where traces are separate, a few scalariform xylem elements are present. Sclerenchymatic sheaths of petal traces are thinner walled than those of sepal traces. As in the sepals, a few lateral bundles may branch and a median and two lateral veins extend into each petal tip.



FIGS. 24–27. Pistillate flower, continued. FIG. 24, transection through stalks of the three carpels, outer ring of bundles are petal traces, inner six large bundles supply staminodes, all bundles in carpel bases are provascular, × 18; FIG. 25, transection through petal-staminode tube and three carpels at level of funicular attachments, × 18; FIG. 26, transection showing petal-staminode tube and expanded styles of carpels, × 18; FIG. 27, longitudinal section of one carpel, × 35. DETAILS: ar, aril; cs, carpel stipe; pe, petal trace; stm, staminode trace.

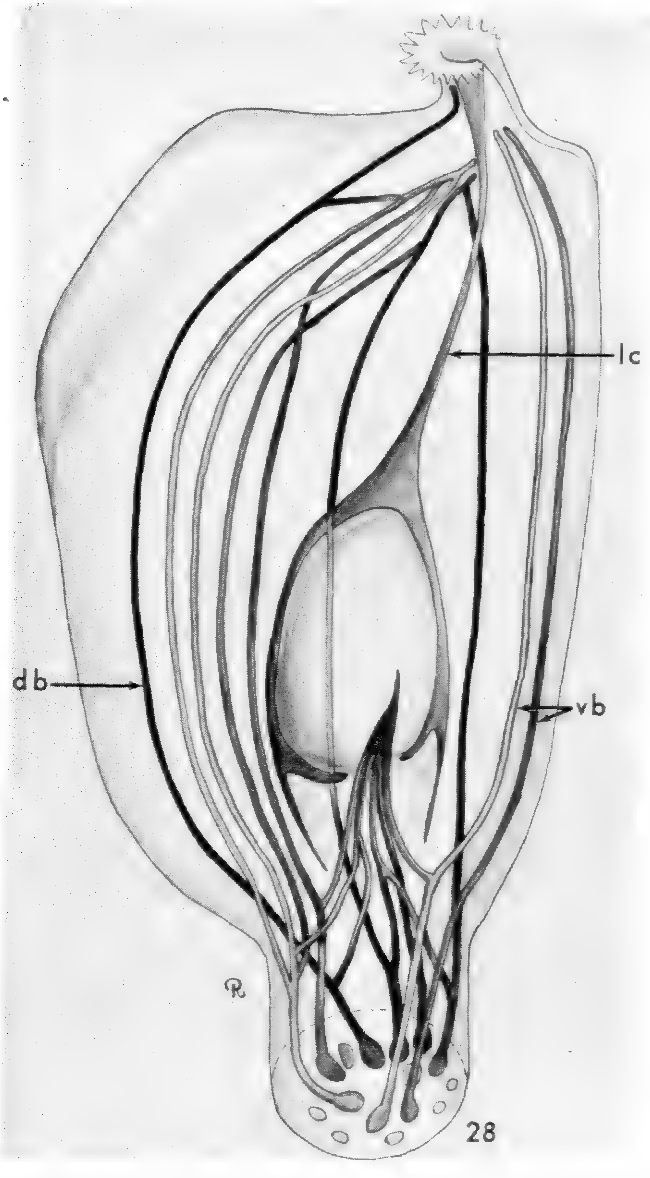
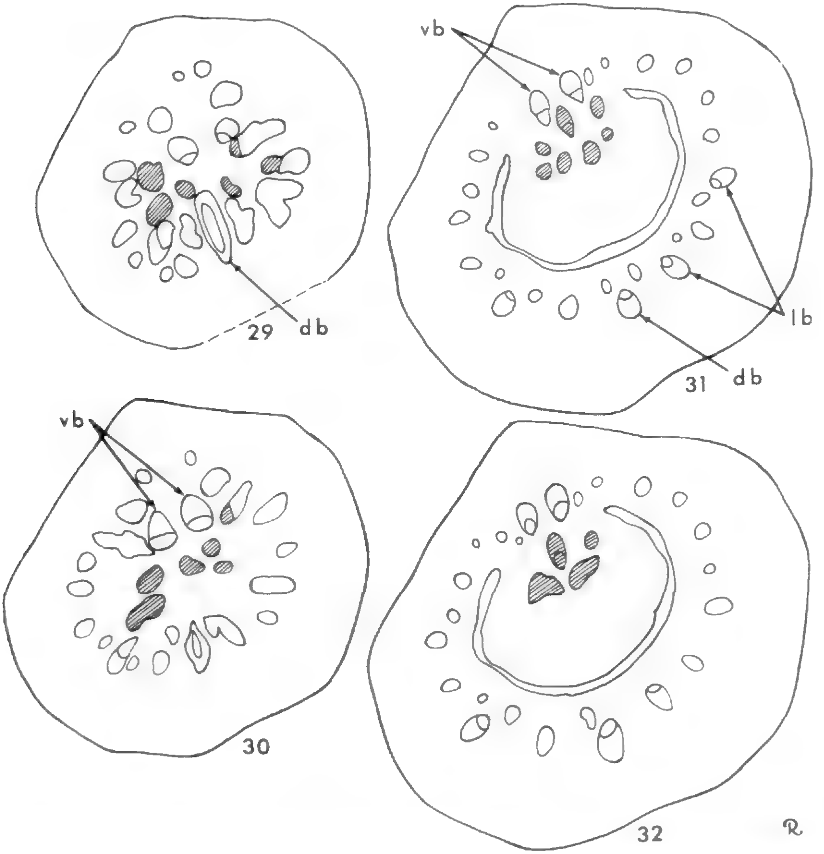


FIG. 28. Three dimensional drawing of one carpel to show vascular supply. Dorsal and ventral bundles labeled, remaining are lateral bundles. Seven lateral bundles are not completed for clarity, × ca. 50. For details see FIGS. 29–32.

About 20 relatively large receptacular bundles, each with a complete fibrous sheath (FIG. 23, central bundles) are present above the origin of the petal traces. Just above this level, considerable reorientation and branching of strands takes place. Traces to staminodes (FIG. 24, stm) are formed, often as a central branch of a trifurcating receptacular bundle. Traces to antisepalous staminodes diverge at a slightly lower level than those to the antipetalous ones. The remaining bundles become oriented into three groups, one group representing the supply to each carpel.

Fibrous bundle sheaths extend as far as the stalk of each carpel but are absent in the carpel base where all bundles are procambial. Three or four of the bundles in each carpel base are larger than the remainder and possess xylem elements which are birefringent. The central of these larger strands extends across the carpel base and distally around the locule to the base of the stigma (FIG. 28, db). Two of the other larger strands remain in ventral positions (FIGS. 28, 29–32, vb). Thus a dorsal



FIGS. 29–32. Series of transections through the base of one carpel drawn with Wild M20 research microscope and drawing tube, to show origin of ovular supply. Ovule traces shaded, bundles with birefringent xylem shown divided, × 60. DETAILS: db, dorsal bundle; lb, lateral bundle; lc, locular canal; vb, ventral bundle.

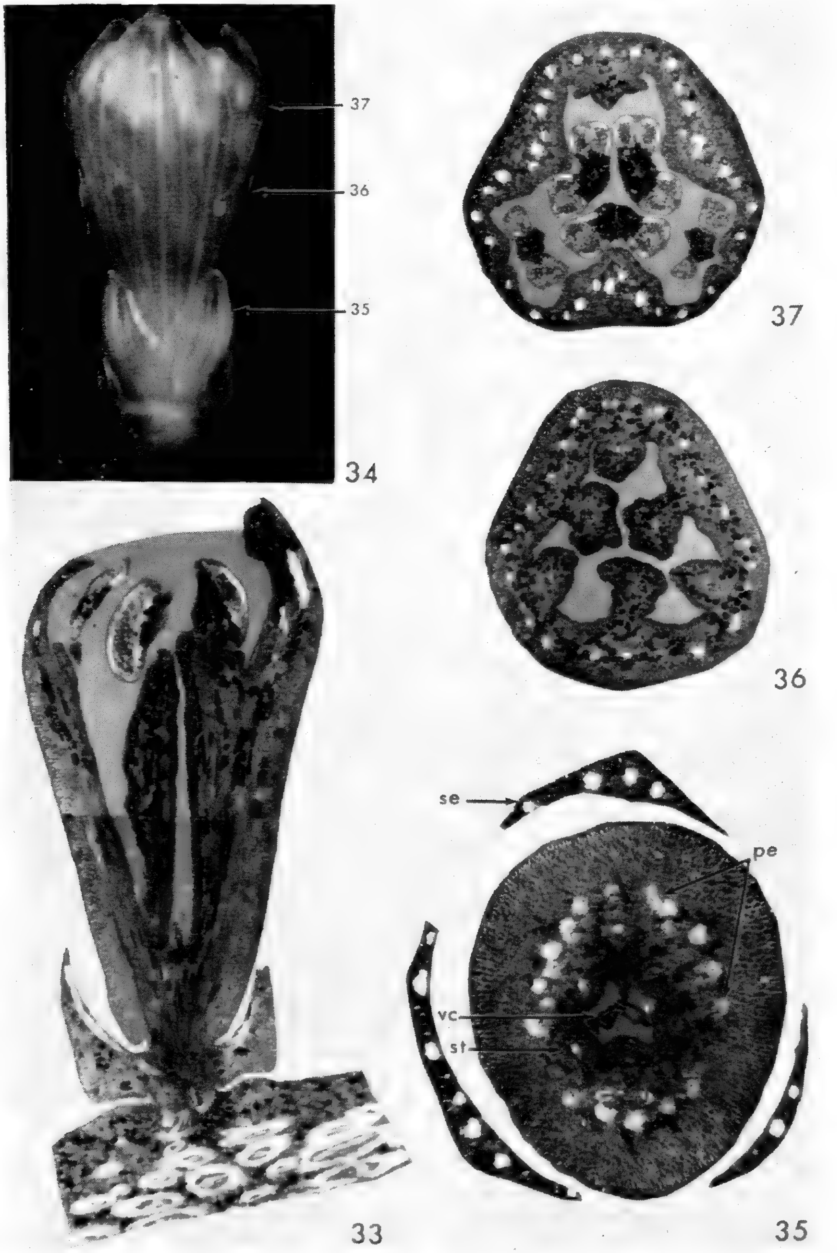
and two ventral bundles can be recognized by size, position, and maturity (FIGS. 29–32). Remaining strands form the 20 to 24 lateral bundles present in an irregular ring in the carpel wall (FIGS. 31, 32). Four of these are larger and more mature (FIGS. 31, 32, lb). Some lateral bundles fuse with others near their upper limits, the major ones extending toward the locular canal (FIG. 28). The ventrals extend slightly higher and the dorsal ends just below the stigma (FIG. 28).

The origin of the vascular supply to ovules varies in palms (Uhl, unpublished). In *Rhapis*, a branch from the dorsal bundle, a branch from each of four or five lateral bundles, and a branch from one ventral bundle form a group of strands (FIGS. 29–32) which extends into the funiculus (FIG. 28). These strands fuse near the chalaza and the resulting large bundle ends near the base of the outer integument. A similar pattern for the origin of ovule traces has been observed in *Trachycarpus* and *Corypha*. Angiosperm taxa with more than one trace to the ovule and with traces derived from dorsal and ventral carpellary bundles are not frequent. Such taxa occur in groups usually considered to be primitive, as Magnoliaceae (Canright, 1960) and Nymphaeaceae (Moseley, 1961).

STAMINATE FLOWER

Morphology (FIGS. 1–6). A comparison of staminate and pistillate flowers shows both differences and similarities. Bractlets are alike in both types of inflorescence. Sepals in the two flowers (FIGS. 3, 4) are also similar in shape and size; those of staminate flowers are perhaps slightly less fleshy. Petals are about the same length (4–5 mm.) and are 2/3 to 3/4 connate (FIGS. 3, 5). In staminate flowers, however, the petal tube is definitely obovoid or clavate and much less fleshy than that in pistillate flowers (cf. FIGS. 8 and 11 with 3 and 5). The diameter of the petal tube immediately below the free lobes is approximately 2 mm. in staminate flowers and 3 mm. in pistillate flowers. Staminate petals are valvate and often incompletely connate, a groove of varying depths showing the limits of each petal. In pistillate flowers, however, the petal-tube is smooth and free lobes are briefly imbricate. Filaments (FIG. 6) are wider in stamens than in staminodes and bear well-developed, latrorse anthers with dark, tannin-containing connectives (FIGS. 33, 37). Three very tiny vestigial carpels are present (FIGS. 33, 35, vc).

Anatomy (FIGS. 33–37). The origin of traces to floral organs is similar to that described for pistillate flowers except that in some organs fewer bundles are present. The number of traces to sepals is approximately six to eight (FIGS. 34, 35). Petals receive only three, four, or five bundles (FIG. 35) as opposed to eight to ten in pistillate flowers. Major petal traces also branch more frequently in pistillate flowers. Thus there are many more bundles in petals of pistillate than in those of staminate flowers (cf. FIGS. 25 and 26 with 36 and 37). The traces to stamens originate in two groups of three and are large, sometimes double vascular



FIGS. 33–37. Staminate flower. FIG. 33, longitudinal section. × 18; FIG. 34, cleared staminate flower, levels of FIGURES 35–37 indicated by the appropriate numbers. × 10; FIG. 35, transection through base of flower, × 35; FIG. 36, transection through petal-stamen tube, × 18; FIG. 37, transection of distal part of flower, ×18. DETAILS: pe, petal traces; se, sepal; st, stamen trace; vc, vestigial carpel.

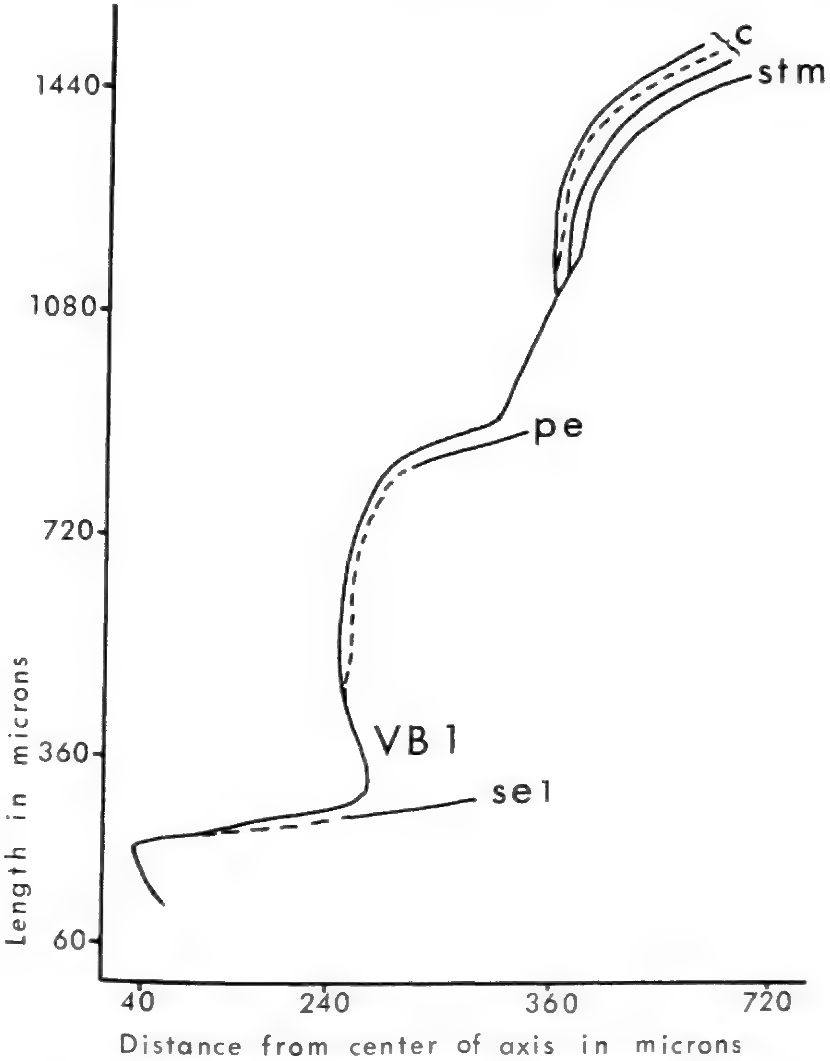


FIG. 38. Diagram of the radial path of a major bundle of the floral axis. DETAILS: c, carpel traces; pe, petal trace; se, sepal trace; stm, staminode trace; VB 1, continuing vertical bundle. Dotted lines indicate where fibrous bundle sheaths are confluent.

bundles. About three strands remain in the floral receptacle above the origin of the stamen traces. These disappear just below the vestigial carpels.

Histology. Histological features in floral organs are sometimes diagnostic in palms (Uhl, unpublished). In *Rhapis*, tannins are present randomly in sepals and filaments, near the adaxial surfaces of petals and in all cells of connectives. Fibrous bundle caps are lacking in receptacular, lower petal, and stamen bundles of staminate flowers; in carpels; and in abscission zones of both flowers. It is perhaps significant that there are few, if any, crystals in fleshy sepal bases and petal tubes. The abaxially distended styles are histologically the most specialized parts of the flowers, containing raphides, tannin cells in radial rows, and distal, cap-like layers of sclereids (FIG. 26).

DISCUSSION

Comparison with vegetative organs. Emphasis in this series on *Rhapis* has been on vascular pathways throughout the plant. Careful analysis of the flowers shows continuity of bundles from those of the

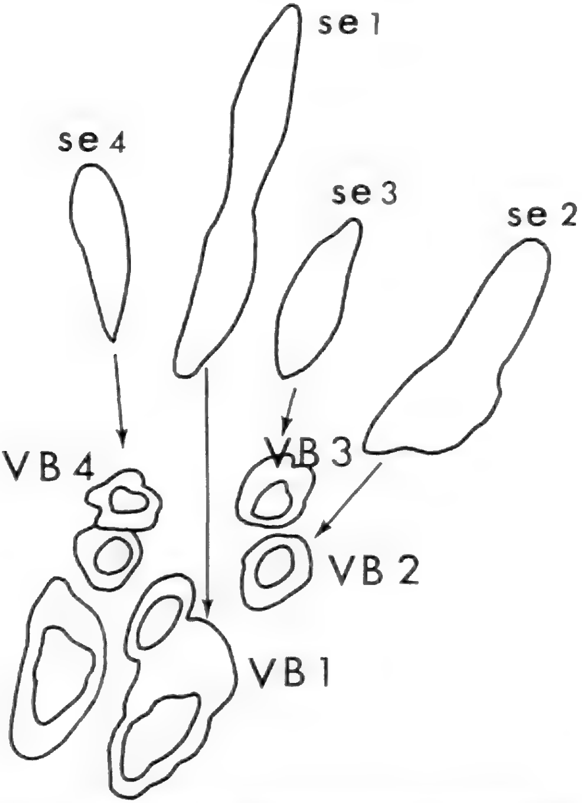


FIG. 39. Part of a transection, drawn with the Wild M20 research microscope and drawing tube, to show the continuation of the sepal trace (se 1) diagrammed in FIG. 38; se 2, se 3, and se 4 are sepal traces derived as branches of se 1. Each of these branches to form a continuing vertical bundle (VB 2, VB 3, and VB 4) as indicated, × 125.

rachilla to the ovule or stamen. The pattern of origin is a simple one. Bundles of the floral axis, derived as branches of rachilla bundles, branch in turn at appropriate levels to provide traces to sepals, petals, staminodes or stamens, and carpels.

This vascular continuity throughout *Rhapis*, which is now completed in the description of floral vasculature, shows a similar pattern throughout every kind of axis on the plant (e.g. seedling, aërial axis, rhizome, inflorescence axis, rachilla, and pedicel). The same principle of vascular organization is expressed in the flower, but it is somewhat more difficult to recognize here than in the vegetative organs because the floral axis is condensed and the lateral organs are small. Nevertheless we may say that the divergence of traces to sepals, petals, and staminodes or stamens, involving axial continuity, is comparable to the departure of leaf traces in rhizome and aërial stem (Tomlinson & Zimmermann, 1966; Zimmermann & Tomlinson, 1965). This is most obvious when an individual bundle is followed through the floral axis. The radial path resulting from such an analysis is presented diagrammatically in FIGURE 38. In addition very short bundles, which may be interpreted as bridges (Zimmermann & Tomlinson, 1965), often link diverging traces with bundles of the receptacular system. More detailed comparison of floral and vegetative vascular pathways must await a more complete understanding of monocotyledonous vascular development.

Comparison with other palms. Among coryphoid palms, *Rhapis* may be considered intermediate in specialization. The connation in sepals and petals and corresponding derivation of sepal and petal traces in whorls are evidences of specialization, as is also the adnation of stamens and staminodes to the petal tube. Several features of the carpel are noteworthy. Completely free, stipitate, spirally inserted carpels are considered primitive in palms and angiosperms. However, the large dorsally extended styles and completely closed ventral sutures of *Rhapis* indicate specialization. The orientation of the ovule is intermediate between the primitive anatropous and the most advanced orthotropous position. The multiple derivation of traces to the ovule from the dorsal, several laterals, and a ventral carpellary bundle suggests laminar placentation (Eames, 1961) and may be a basic pattern in palms. In a preceding paper of this series it was stated that *Rhapis* has a relatively specialized inflorescence (Tomlinson & Zimmermann, 1968). Similarly it may be said that among the Coryphoideae the flowers are relatively specialized.

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GLYCOSMIS PENTAPHYLLA (RUTACEAE) AND RELATED INDIAN TAXA

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THE PUBLICATION of a new series, *Limonia arborea*, by Roxburgh (Pl. Coromandel. **1**: 60. *t. 85.* 1798) and his providing the plant which he believed to be "*Limonia pentaphylla* Retz." (Roxb. *loc. cit. t. 84*) with a detailed description and illustration, as well as the subsequent discovery of the authentic type specimen of *Limonia pentaphylla* Retz. by Tanaka (Bot. Not. **1928**: 156–160. 1928), has led to some controversy in the nomenclature of these two species now included in the genus *Glycosmis*. In the interest of clarity, relevant parts of the earlier works are reviewed in brief.

Tanaka (*loc. cit.*) pointed out that *Limonia pentaphylla* Retz. is conspecific with *Limonia arborea* Roxb. and is entirely different from the plant treated by Roxburgh as "*Limonia pentaphylla* Retz." He therefore treated *Glycosmis arborea* (Roxb.) Correa (= *Limonia arborea* Roxb.) as a synonym of *Glycosmis pentaphylla* (Retz.) Correa (= *Limonia pentaphylla* Retz.), and in *Botaniska Notiser* (**1928**: 159. 1928) proposed *Glycosmis mauritiana* (Lam.) Tanaka (= *Limonia mauritiana* Lam.) for the plant erroneously treated by Roxburgh as "*Limonia pentaphylla* Retz."

Narayanswami (Rec. Bot. Surv. India **14**(2): 26. 1941) did not agree with Tanaka's view and maintained *Limonia pentaphylla* Retz. and *Limonia arborea* Roxb. as distinct from each other; accordingly the correct names in the genus *Glycosmis* should be *G. pentaphylla* (Retz.) Correa and *G. arborea* (Roxb.) Correa, respectively. Brizicky (Jour. Arnold Arb. **43**: 88. 1962) upheld Tanaka's view on the conspecificity of *Limonia pentaphylla* Retz. and *Limonia arborea* Roxb. and remarked, "Narayanswami (1941), apparently having overlooked Tanaka's article on the type of Retzius' species, came to the conclusion . . . that Tanaka's interpretation of *L. pentaphylla* was entirely incorrect . . ." Brizicky also pointed out that De Candolle (Prodr. **1**: 538. 1824), instead of Correa (Ann. Mus. Hist. Nat. Paris **6**: 386. 1805), should be assigned the authorship of these two binomials, *G. pentaphylla* and *G. arborea,* since De Candolle made these combinations for the first time in the sense of the *Code.* However, Brizicky's conclusion on their nomenclature is untenable, not being in accordance with the existing *Code.* Brizicky (*loc. cit.*, p. 87) is of the opinion that ". . . . . . *Glycosmis pentaphylla* DC. was based on the plant identified and illustrated by Roxburgh as '*Limonia pentaphylla* Retzius' and only questionably on Retzius' species

('*G. pentaphylla, . . . Limonia pentaphylla* Retz. obs. 5. p. 24? Roxb. cor. 1. t. 84.')." Brizicky (*loc. cit.*, p. 89) further argues, "Then *Glycosmis pentaphylla* DC., based on Roxburgh's plant, not on that of Retzius, must be regarded not as a new combination, but as a new name in *Glycosmis* for the species for which Tanaka later (1928b) created the combination *G. mauritiana* (Lam.) Tanaka . . . Since *G. pentaphylla* DC. cannot be applied to Retzius' *Limonia pentaphylla*, the next available name for the latter species is *Glycosmis arborea* (Roxb.) DC." In treating *Glycosmis pentaphylla* as a new name and not as a new combination Brizicky was probably applying the provisions of Art. 72. However, this article is not operative in this case; it is clear from Roxburgh's treatment of "*Limonia pentaphylla* Retz." that he was not describing a new species under a homonymous name, but was only misidentifying Retzius' plant. Thus, the question of De Candolle's basing the binomial *G. pentaphylla* on "Roxburgh's plant — *Limonia pentaphylla*" does not arise. Moreover, De Candolle, in making the transfer (Prodr. **1**: 538. 1824), gave a direct reference to Retzius' plant, though with a question mark, ". . . . . . *Limonia pentaphylla* Retz. obs. 5. p. 24? Roxb. cor. l. t. 84." It is evident from above that De Candolle was not certain about the identity of the two plants involved in the confusion. Hence, Brizicky's argument for treating the binomial *Glycosmis pentaphylla* as a new name cannot be accepted.[1] Article 55 (par. 2) of the *International Code of Botanical Nomenclature* (ed. 1966) clearly states, "When, on transference to another genus, the specific epithet has been applied erroneously in its new position to a different species, the new combination must be retained for the species

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[1] Dr. Brizicky, who died on June 15, 1968, saw an earlier but hardly different version of this paper and, on May 4, 1968, set down the comments which follow. These comments were duly communicated to the authors of this paper, who are still not agreeable to the arguments placed by Dr. Brizicky.

"The authors of this paper believe that my view of *Glycosmis pentaphylla* DC. as a new name, rather than combination, is untenable from the standpoint of the Code, so they regard *G. pentaphylla* DC. as a new combination based on *Limonia pentaphylla* Retzius. They find evidence for this in the fact that 'De Candolle, while making transfer, gave a direct reference to Retzius' plant, "*Limonia pentaphylla* Retz. Obs. 5. p. 24?. . ."' Curiously, though, applying the Code mechanically [Art. 55?], the authors disregard the question mark which follows the complete citation of Retzius' specific name and which expresses De Candolle's doubt of the conspecificity of Retzius' species with *Glycosmis pentaphylla*. This expression of taxonomic doubt indicates rather clearly that De Candolle could not and did not base his *G. pentaphylla* either nomenclaturally on Retzius' binomial or taxonomically on Retzius' species, which he knew only from a brief description, and that he questioned its conspecificity with *G. pentaphylla*. There seems to be no article in the Code directly referable to this situation, but, how can a serious botanist deliberately publish a new combination based nomenclaturally on one and taxonomically on another, supposedly different, species? Least of all can such a combination be expected from one of the founders of the rules of botanical nomenclature.

"Although neither prescribed nor required by the Code, the knowledge of the taxon which is being transferred and an at least reasonable certainty that the taxon, the epithet of which is used as basionym, is really identical or conspecific (convarietal, congeneric, etc.) with that for which a new combination is made, are *a priori* presumed to be possessed by a taxonomist who publishes a new combination, new status, to which the epithet was originally applied, and must be attributed to the author who first published it." *Glycosmis pentaphylla* (Retz.) DC., therefore, must be retained as a new combination based on *L. pentaphylla* Retz. The nomenclature of the relevant taxa follows:

Glycosmis pentaphylla (Retz.) DC. Prodr. **1**: 538. 1824, quoad basionym; Tanaka, Jour. Indian Bot. Soc. **16**: 229. 1937.

Limonia pentaphylla Retz. Obs. Bot. **5**: 24. 1789.
Limonia arborea Roxb. Pl. Coromandel. **1**: 60. *t. 85.* 1798.
G. arborea (Roxb.) DC. Prodr. **1**: 538. 1824; Narayanswami, Rec. Bot. Surv. India **14**(*2*): 20. 1941; Brizicky, Jour. Arnold Arb. **43**: 90. 1962.

Glycosmis pentaphylla var. **linearifoliola** Tanaka, Jour. Indian Bot. Soc. **16**: 230. 1937, *"linearifoliolis."*

G. arborea var. *linearifoliola* (Tanaka) Narayanswami, Rec. Bot. Surv. India **14**(*2*): 26. 1941, *"linearifoliolata."*

Glycosmis mauritiana (Lam.) Tanaka, Bot. Not. **1928**: 159. [4 Apr.] 1928; Bull. Soc. Bot. France **75**: 708. [12 Oct.] 1928; Jour. Indian Bot. Soc. **16**: 229. 1937; Brizicky, Jour. Arnold Arb. **43**: 90. 1962, excl. syn. *G. pentaphylla* DC.

Limonia mauritiana Lam. Encycl. Méthod. Bot. **3**: 517. 1792.
Limonia pentaphylla auct. non Retz.: Roxb. Pl. Coromandel. **1**: 60. *t. 84.* 1798.
G. pentaphylla sensu Narayanswami, Rec. Bot. Surv. India **14**(*2*): 12. 1941, excl. syn. *L. pentaphylla* Retz.

Tanaka proposed this combination in a manuscript sent to the *Bulletin de la Société Botanique de France* on January 13, 1928. In a subsequent paper sent to *Botaniska Notiser* on February 18, 1928, he referred to his

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etc. There certainly have been cases when because of unavailability of the types and/or of misinterpretation of some taxa the new combinations turned out to have been made for taxa different from those for which they were intended. However, in all these cases the authors of the combinations sincerely believed that their taxa and those the epithets of which were taken as basionyms were identical (conspecific, convarietal, etc.). Apparently, there are so few, if any, combinations which are based on the epithets of doubtfully conspecific taxa that there has been no necessity to mention them in the Code, and the solution of those cases has been left to the good sense of botanists.

"Thus, since De Candolle himself indicated that *Limonia pentaphylla* Retz. was doubtfully conspecific with *Glycosmis pentaphylla* and might therefore not be taken as basionym, there is no reason to regard *Glycosmis pentaphylla* as a new combination based on *Limonia pentaphylla* Retz. On the contrary, *Glycosmis pentaphylla*, identified with and based on the plant described and illustrated by Roxburgh (Pl. Coromandel. 1: *pl. 84.* 1891) under the misapplied name '*Limonia pentaphylla* Retz.,' certainly was a new name for Roxburgh's plant, and is typified by the *pl. 84* of Pl. Coromandel. 1. 1891. This certainly is not the only case when a name strongly suggesting a combination was not that, but a new name. Thus, A. Gray took *Malvastrum*, the name of De Candolle's section of *Malva* L., as the name of his genus without having based the genus on De Candolle's section." — GEORGE K. BRIZICKY proposed combination "*Glycosmis mauritiana* (Lamk.) Tanaka in Bull. Soc. Bot. France" with basionym and a few more synonyms; but this latter paper appeared in print first. Tanaka's awareness of this changed situation is evident from his subsequent citation in the *Journal of Botany* (**68**: 226. 1930).

Glycosmis mauritiana var. **andamanensis** (Narayanswami) Mitra & Subr., comb. nov.

G. pentaphylla var. *andamanensis* Narayanswami, Rec. Bot. Surv. India **14**(2): 16. 1941.

Publication of *Glycosmis mauritiana* var. *andamanensis* Tanaka (Jour. Indian Bot. Soc. **16**: 229. 1937) was not valid, for a Latin description was not given.

Glycosmis mauritiana var. **insularis** (Kurz) Tanaka, Jour. Indian Bot. Soc. **16**: 229. 1937.

G. arborea var. *insularis* Kurz, Jour. Bot. **14**: 38. 1876, *pro parte*.
G. pentaphylla var. *insularis* (Kurz) Narayanswami, Rec. Bot. Surv. India **14**(1): 20. 1941.

Glycosmis mauritiana var. **fuscescens** (Kurz) Mitra & Subr., comb. nov.

G. trifoliata var. *fuscescens* Kurz, Jour. Bot. II. **5**: 37. 1876.
G. pentaphylla var. *fuscescens* (Kurz) Narayanswami, Rec. Bot. Surv. India **14**(2): 20. 1941.

We could examine only one sheet present at CAL (*King's Collector* 1884, *acc. no.* 74984) from which the diagram given by Narayanswami (*loc. cit.* page 21, *fig. 5*) was drawn. We agree with Narayanswami in treating this as a distinct variety.

Glycosmis cymosa var. **linearifoliola** (Tanaka) Mitra & Subr., comb. nov.

G. cyanocarpa var. *linearifoliola* Tanaka, Jour. Indian Bot. Soc. **16**: 229. 1937, "*linearifoliolis*."
G. cymosa var. *changsillana* Narayanswami, Rec. Bot. Surv. India **14**(2): 32. 1941.

DOUBTFUL TAXON

Glycosmis pentaphylla var. **latifolia** (Kurz) Narayanswami, Rec. Bot. Surv. India **14**(2): 20. 1941.

We are doubtful whether this plant needs a distinct rank. The lone sheet examined at CAL (*Helfer 525*, *acc. no.* 74981) has only two twigs mounted on it, the inflorescence being altogether lost. The leaf character of the right-hand specimen appears to be that of the *Glycosmis mauritiana* var. *andamanensis* while the left-hand one is closer to *G. mauritiana* var. *insularis*.

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VASCULAR ANATOMY OF MONOCOTYLEDONS WITH SECONDARY GROWTH — AN INTRODUCTION

P. B. TOMLINSON AND M. H. ZIMMERMANN

ARBORESCENT PLANTS with secondary growth from a vascular cambium represent a small minority of monocotyledons. Nevertheless their significance is out of proportion to their abundance because they exhibit a growth habit comparable to that of familiar dicotyledonous and gymnospermous trees. Monocotyledonous secondary vascular tissue, however, unlike that of other trees, includes discrete vascular bundles.

Earlier botanists in their study of palms and other arborescent monocotyledons devoted considerable attention to those few forms with secondary vascular tissues and it is largely on the efforts of these nineteenth-century anatomists that our present knowledge is based. It was therefore inevitable that in our own studies of palms we should follow this earlier tradition and turn our attention to monocotyledons with secondary growth, especially as we had found that early work on the vascular system of monocotyledons had been incomplete and furthermore had become misrepresented in modern textbooks (Tomlinson & Zimmermann, 1966).

In the present article we review the vascular anatomy of monocotyledons with secondary growth in order to provide the background for our observations which will be published separately. Such a lengthy and independent introduction is justifiable because few botanists have first-hand familiarity with these plants and the literature about them is old and not readily available. Nevertheless our introductory review is necessarily very selective, because the early literature is extensive and some of it is no longer very informative. We have largely cited those articles which contributed significantly to knowledge about these plants. Reviews of the subject do already exist. Those by Cordemoy (1894) and Cheadle (1937) are lengthy. Cheadle's paper is relatively recent and accessible, but it is restricted to a study of small tissue samples. General organization, growth habits, and overall distribution of vascular tissues are not discussed in it. This is somewhat in contrast to the approach adopted by earlier generations, as indicated by Cordemoy's review, and reflects the way in which anatomists have lost sight of the plant as a functioning whole in their preoccupation with histological detail. It is with the object of re-instating the approaches of botanists concerned with overall aspects of growth and construction that our own studies have been undertaken.

TAXONOMIC DISTRIBUTION

The occurrence of aborescent genera in certain families of monocotyledons which possess secondary vascular tissues is indicated in Table 1. We treat these genera in a very broad sense but appreciate that some, notably *Yucca* (e.g. Trelease, 1902) have been subdivided. Two systems of classification are compared, that of various authors in Engler and Prantl (1930) and that of Hutchinson (1959) in order to emphasize that the taxonomic distribution of these plants is far from certain. We do not intend to discuss the evolutionary relationship between arborescent and herbaceous monocotyledons, but we suggest that anatomical investigation is likely to contribute significantly to a resolution of these problems. Of the listed genera, *Beaucarnea*, *Cordyline*, *Dasylirion*, *Dracaena*, and *Yucca* consist of species ranging in size from trees to shrubs and rhizomatous herbs. The genus *Aloë* is predominantly herbaceous, but includes a few aborescent

Table 1. **Taxonomic distribution of larger monocotyledons with secondary vascular tissues.**

Engler and Prantl	Representative genera	Hutchinson
Amaryllidaceae		Agavaceae
subfamily Agavoideae	*Agave*, *Furcraea*	tribe Agaveae
Liliaceae		
subfamily Dracaenoideae		
tribe Yucceae	*Yucca*	tribe Yucceae
tribe Nolineae	*Beaucarnea* (*Nolina*) *Dasylirion*	tribe Nolineae
tribe Dracaeneae	*Cordyline*, *Dracaena* (*Pleomele*)	tribe Dracaeneae
subfamily Asphodeloideae		Liliaceae
tribe Aloineae	*Aloë*	tribe Aloineae
tribe Lomandreae	*Lomandra*, *Xanthorrhoea*	Xanthorrhoeaceae
tribe Calectasieae	*Kingia*	
Iridaceae		Iridaceae
subtribe Aristeinae	*Aristea* (*Nivenia*), *Klattia*, *Witsenia*	tribe Aristeae

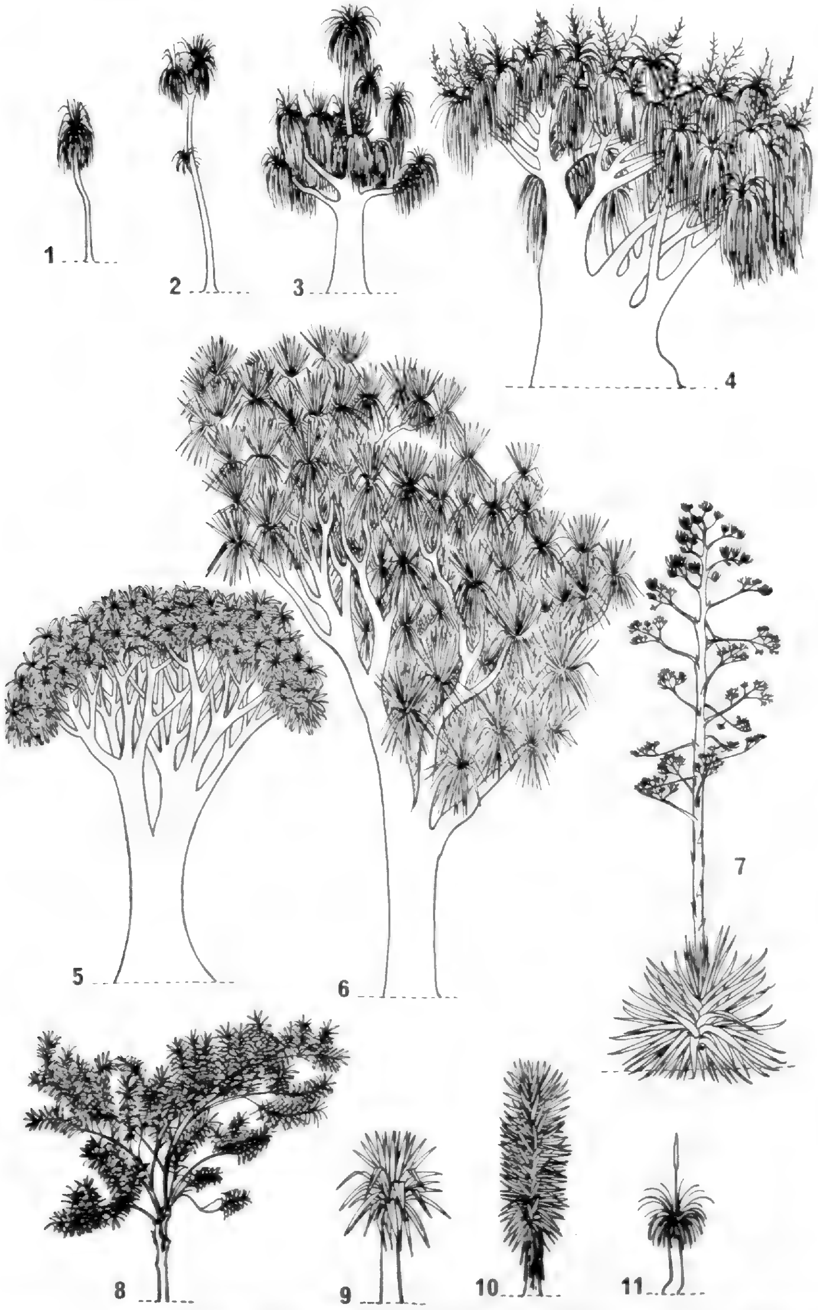
species, notably *A. bainesii* and *A. dichotoma*. *Agave* and *Furcraea* do not really fit a strict definition of a tree although some species achieve massive proportions. The same seems true of the Xanthorrhoeaceae although there is little information about their size, growth habit, and the extent of secondary tissue except in the work of Floresta (1902). The iridaceous genera are listed, although they are little more than shrubs, because secondary tissue is extensive and has been well described (e.g. Adamson, 1926; Scott & Brebner, 1893). On the other hand, we have omitted many monocotyledons which possess a limited amount of secondary growth but are otherwise essentially herbaceous. These include a number of genera in the Liliaceae, like *Aphyllanthes, Veratrum* and others in Hutchinson's Agavaceae. Fleshy rhizomes with secondary tissues, as in the Dioscoreaceae, are also disregarded. Vascular tissue which is by definition secondary may be quite common in other, unrelated, herbaceous monocotyledonous families [e.g. Bromeliaceae, Krauss (1948); Musaceae, Skutch (1932); Zingiberaceae, Chakraverti (1939)] where it seems to be associated with root insertion. However, before any major evolutionary significance can be attached to secondary cambial activity, we must attempt to understand it from a developmental point of view.

MORPHOLOGY

Growth habits (FIGS. 1–11). Growth form is quite diverse although it can be seen to depend on a common pattern of development. Leaves are linear, usually rigid, often thick and fleshy. They are rarely distinctly petiolate as in some smaller species of *Cordyline* and *Dracaena*. Axes are made up of short, often very congested internodes. In slow-growing plants this results in the characteristic terminal tufts of leaves or, if the main axis is very much shortened, in the basal rosette which characterizes the *Agave*-habit (FIG. 7). Branching is usually sparse; the reason for this is discussed below. In *Agave* and *Furcraea* the vegetative axis may be unbranched so that the plant is monocarpic. Otherwise the rosette in these plants is propagated by basal and usually stoloniferous suckers. Stoloniferous shoots are not usually present in other genera but they are common in herbaceous relatives (e.g. *Sansevieria*). The habit of most arborescent monocotyledons is quite tree-like, and some may even be mistaken for a dicotyledonous tree by a superficial observer, as noted by Wright (1901). However, some species of *Dracaena*, especially those in its segregate genus *Pleomele*, look more like shrubs with their much-branched crown and fine twigs (FIG. 8).

It is evident that shoot diameter on a single plant is not entirely dependent on the amount of secondary growth. In smaller and much branched species variation in crown diameter is considerable and seems related to the vigor of the shoot. Basal, erect shoots are thickest and most vigorous; distal horizontal shoots are narrow and least vigorous. We have noted a range in primary shoot diameter of 6 to 30 mm. in *Pleomele*.

Some of the simpler growth forms can be looked upon as juvenile stages



FIGS. 1–11. Growth habits in arborescent monocotyledons with secondary thickening (all to approximately same scale). FIGS. 1–4. *Beaucarnea recurvata.*

in the development of the larger forms, which are fixed permanently. Development of a large *Beaucarnea* (FIGS. 1–4), for example, begins with a rapidly growing main axis which remains unbranched for several years. Leaves may be long persistent so that they clothe the axis of quite tall specimens. Many species of *Yucca* do not develop much beyond this stage (FIG. 10). A link between the specialized rosette of *Agave* and this juvenile habit is provided by a number of species of both *Agave* and *Furcraea* with relatively tall stems (e.g. *F. longaeva* illustrated in Engler & Prantl (1930) p. 419). Otherwise, normal development of the tree form continues with branching, the loss of leaves from the older stem parts, thickening of the base of the stem, and development of a fissured bark. The evolutionary relation between ontogeny and phylogeny is suggested by *Cordyline* in New Zealand. *Cordyline indivisa* can be equated with the unbranched juvenile stage of *C. australis* (FIG. 9) and in turn the low rosette of *C. pumilio* with a younger stage still.

A disproportionate thickening of the base of the stem characterizes mature plants (FIGS. 4, 5, 13) and has probably led to some exaggerated statements about their longevity. Speculations about possible great age have particularly centered around *Dracaena draco*. The early literature about this is summarized in the paper of Wossidlo (1868). Perhaps the most famous individual tree in this respect was the specimen of *Dracaena draco* of Orotava on Teneriffe, described by Alexander von Humboldt (1850). Its historical record goes back to the fifteenth century. But estimates that it dated back to the period of the building of the pyramids (4,500 years) are probably exaggerations, especially in view of the known rate of growth of *Dracaena reflexa* (Wright, 1901). In 1799 the famous tree of Orotava had reached a height of about 70 feet and a circumference of 48 feet at the base of the trunk. A hurricane destroyed it in 1821. There is no certain method of telling the age of a specimen in the absence of planting data. A more meaningful time scale is given by a specimen of *Beaucarnea recurvata* (FIG. 13) in Fairchild Tropical Garden which is 25 feet high, 19 feet in circumference at a height of 2 feet and yet is known to be not more than 50 years old. Rates of growth otherwise appear not to have been determined for any of these plants.

Inflorescences are always terminal. On unbranched axes they are large and very conspicuous as in *Yucca* and Xanthorrhoeaceae (FIG. 11) and even on young specimens of *Beaucarnea*. They reach massive proportions in *Agave* and *Furcraea*. In the much-branched forms flowering is usually simultaneous on all or most distal shoots and renders the tree very conspicuous. In temperate species flowering is seasonal as in *Cordyline*

Plants of successive ages to show development of massive trunk. 1, Unbranched sapling 5–6 years old. 2–3, Early development of branch system in older stages. 4, Mature specimen in flower. Flowering begins in saplings of the size shown in FIG. 1. and with it is initiated branching. 5, *Aloë dichotoma*. 6, *Cordyline australis*. 7, *Agave* sp. 8, *Pleomele* (*Dracaena*) *reflexa*. 9, *Cordyline indivisa*. 10, *Yucca aloifolia*. 11, *Xanthorrhoea quadrangulata*.

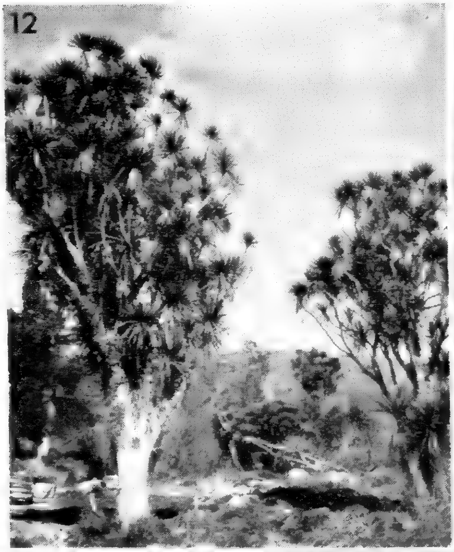


FIG. 12. Specimens of *Cordyline australis*, growing in their natural habitat near Owhango, New Zealand.

FIG. 13. *Beaucarnea recurvata*, specimen about 50 years of age, at the Fairchild Tropical Garden in Miami, Florida.

FIG. 14. *Dracaena fragrans*. Outgrowth of branches from dormant axillary buds after decapitation.

FIG. 15. *Pleomele reflexa*. Outgrowth of branches from dormant axillary buds on the upper side of a leaning stem.

australis in New Zealand. Tropical and sub-tropical species may flower more than once each year. In general, however, there is little information about phenology and rates of growth of these plants.

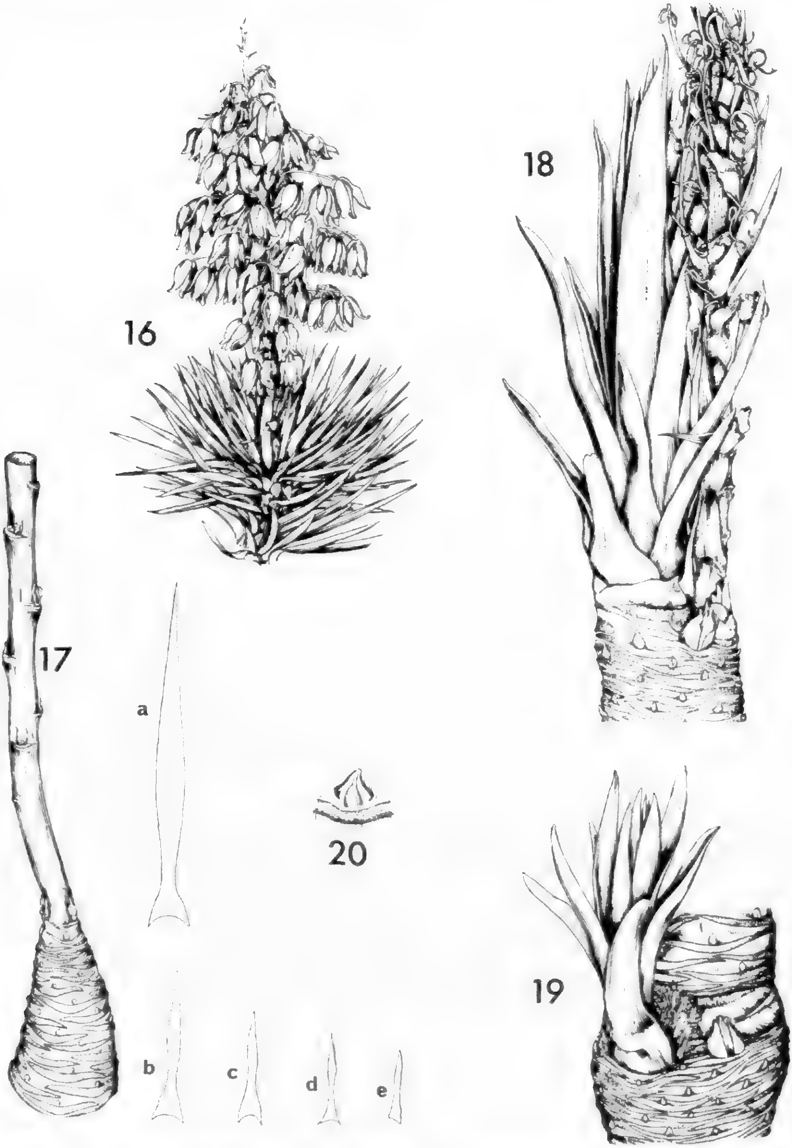
Growth of axes seems to be continuous. At least it is not of a periodic kind which involves resting buds protected by bud scales. Axes are always evergreen. Infrequent branching, which characterizes most monocotyledonous trees, is related to this continuous growth as will be suggested below.

Buds. In most groups each leaf subtends a minute bud (Fig. 17) which is strongly inhibited and very inconspicuous. It is either embedded in the stem tissue or enveloped by the prophyll (Fig. 20). Vegetative axillary buds are regularly present in *Dracaena* and related genera but their occurrence is less regular in *Aloë* (Schoute, 1903). Palms are in strong contrast because here the leaf axils in the mature vegetative phase of development are without vegetative buds (Tomlinson, 1964). However, there is no constant correlation between the presence of vegetative axillary buds and the development of secondary tissues. In Pandanaceae, with no secondary growth, axillary buds are present.

Sympodial branching below inflorescence (Figs. 16–20). With the exception of the palms branching is normally sympodial in woody monocotyledons, regardless of whether they have secondary vascular tissue or not (Schoute, 1903, 1918). The sequence of events is quite obvious. The terminal shoot meristem is transformed from vegetative to reproductive, and a terminal inflorescence is produced (Figs. 16, 17). This inflorescence eventually dies, and the inhibition of one or more buds in the axils of foliage leaves immediately below the terminal inflorescence is thus released (Fig. 18). If only one of these buds grows out it replaces the parent axis, pushing the inflorescence aside (Fig. 19). In this way sympodia are developed, segmented by the scars of pseudolateral, but originally terminal, inflorescences. Each unit of the sympodium is a lateral branch from the parent axis. When more than one lateral bud grows out, the sympodium forks and in this way a "dichotomy" may be simulated although the remains of the terminal inflorescence above the fork can always be found. Schoute (1903) described this pseudo-dichotomy in careful detail but his observations have been largely overlooked. For example one finds recent reports which refer to this type of branching as a "true dichotomy" in order to provide "evidence" for very fanciful evolutionary theories (e.g. Meeuse, 1961; 1965 and elsewhere).

Although the morphology of this sympodial branching is otherwise well understood, there has been no anatomical investigation of the way in which continuity of vascular tissue beneath branch and parent axis is developed. We shall consider this aspect in a later article.

Branching in the absence of flowering. Apical dominance of terminal over lateral buds is obviously very strong during normal growth of the axis. Since growth is seemingly continuous, no branches develop. Flowering and the ultimate death of the reproductive shoot releases apical dominance and enables one or more lateral buds to grow out. This happens at more or less regular intervals. In addition to this mechanism



FIGS. 16–20. Sympodial branching after flowering in *Yucca aloifolia*. 16, Habit of a flowering plant, × 1/10. 17, Defoliated flowering stem to show the reduction in diameter throughout the transition from vegetative to inflorescence axis, × 1/3, a–e showing the gradual reduction of leaf size, × 1/5. 18, Outgrowing axillary bud has pushed the dead inflorescence to the right, × 1/3. [Note that several axillary buds began to grow out but were later inhibited by the one which became dominant.] 19, A much later stage with the sympodial branch fully grown and the inflorescence weathered away (between two partially grown lateral buds), × 1/3. 20, Dormant axillary bud, × 1.

release of apical dominance may occur in other ways. One or more buds are usually released when a shoot is accidentally or experimentally decapitated (FIG. 14). Buds may also grow out of the upper side of the leaning stem in the absence of decapitation (FIG. 15). These phenomena may be explained according to familiar theories of the redistribution of growth regulators (Münch, 1938; Thimann, 1964). Similarly, release of buds at the base of old stems produces sucker shoots. It is likely that all these types of branching result from the same physiological cause.

PRIMARY VASCULAR STRUCTURE

The serious study of monocotyledonous anatomy began in the early nineteenth century and was largely stimulated by the theory of the "endogenous" growth as against the "exogenous" growth of dicotyledons. This theory seems to have originated with Daubenton (see Branner, 1884) and was elaborated by Desfontaines (1798). It owed much of its initial success to De Candolle (1813) who adopted it as a basis for distinguishing the two main classes of Angiosperms. The earliest work centered on arborescent forms, notably the palms, because as von Mohl emphasized, "the characters of the Monocotyledons are most clearly exhibited in them." The woody Liliiflorae, with secondary growth were given as much attention as monocotyledons without secondary growth. Attempts were made to equate these two types in developmental terms, but the resultant theorizing is now largely of historical interest. Investigations of this period are significant because they provided some reliable factual information, and also established the major taxa in which secondary tissue was to be found. Contributors of this period included Dupetit-Thouars (1809) and Mirbel (1809).

The theory of endogenous growth was effectively demolished by von Mohl (1824) when he described the overall course of bundles in the palm stem and indicated the regular way in which bundles cross over in a manner which could not be accounted for by endogenous growth. The process of demolition was completed by Meneghini (1836) and Mirbel (1843) who essentially confirmed von Mohl's observations. In a subsequent study of *Dracaena draco* Mirbel (1845) came to the conclusion that the growth of this plant was exogenous.

A paradox which has resulted from our modern understanding of vascular development in monocotyledons (e.g. Zimmermann & Tomlinson, 1968) is that we could easily reinstate, in a somewhat modified sense, the concept of "endogenous growth" of the primary vascular system of monocotyledons, and contrast it with the "exogenous growth" of dicotyledons, and the secondary vascular tissue of monocotyledons.

Von Mohl thought that the lower ends of vascular bundles in palms were reduced to narrow peripheral fibrous strands. We have referred to this basic error in detail elsewhere (Tomlinson & Zimmermann, 1966). He noted that the distribution of primary bundles in *Dracaena* was of the palm type and regarded the secondary bundles as the basipetal continuation of the lower ends of the primary ones. Meneghini (1836) disputed this point with von Mohl who re-examined the matter in 1849. He was to refer to it once more (von Mohl, 1858) but the question was never really settled, as we now know the primary vascular anatomy had not been completely analyzed at the time and the explanations offered simply compounded existing errors. One of our first tasks in continuing this study will be to describe the primary vascular anatomy of *Dracaena* and show how it is indeed like a palm, but according to our modern understanding (Zimmermann & Tomlinson, 1969).

SECONDARY VASCULAR STRUCTURE (FIGS. 21, 22)

Information about the anatomy of secondary vascular tissue is available in a series of articles from Millardet (1865) and Wossidlo (1868) to Cheadle (1937). The secondary tissue consists of vascular bundles embedded in ground parenchyma. The original radial alignment of cambial derivatives is readily lost, except in stems with a high proportion of parenchyma to bundles. Cordemoy (1893) who was concerned with the function of this tissue noted that the ground parenchyma commonly contains calcium oxalate deposits in the form of raphides and other crystalline inclusions, frequently starch and sometimes oils. He further distinguished between stems in which the secondary ground tissue was lignified and thick-walled and those in which it was not. The latter situation is most characteristic of underground organs, as in rhizomes of Dioscoreaceae.

Individual vascular bundles are usually amphivasal, with a peripheral series of long overlapping tracheids surrounding a central phloem strand. The development of these tracheids in relation to other cells of the conducting strands will be discussed in further detail below. The xylem also includes short parenchyma cells. Phloem also includes short parenchyma cells and sieve-tube elements which have simple sieve plates on more or less transverse end walls. Russow (1882) concluded that these sieve tubes functioned indefinitely because the amount of callose in them did not change with the age of the bundle. In this presumed ability to function indefinitely these sieve tubes recall those of palms (Parthasarathy & Tomlinson, 1967). The bundles anastomose extensively, mostly in the tangential direction. Continuity with the primary vascular tissues is effected by short bridges which link with the leaf traces as described below.

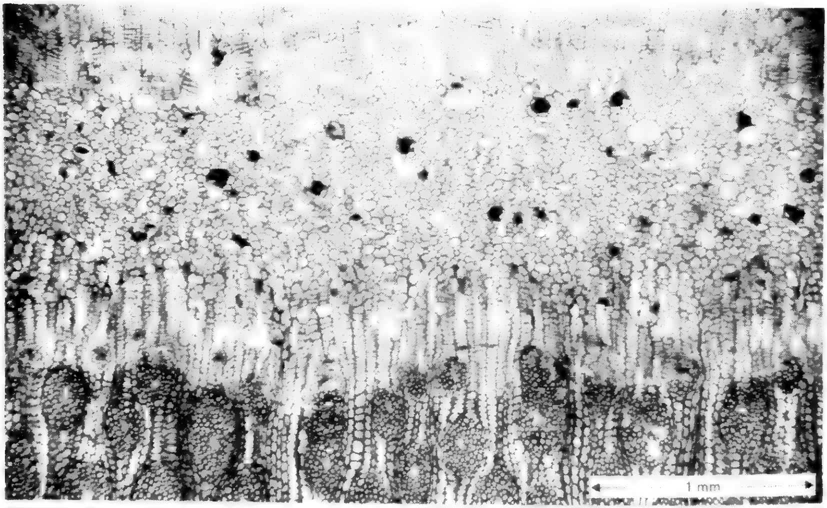
Indistinct growth rings have been recorded by a number of observers (FIG. 23) (e.g. Floresta, 1902; Lindinger, 1909). Chamberlain (1921) was not the first to record this phenomenon, as he claimed. The rings are often more conspicuous to the naked eye than they are under the microscope and seem to be the result of a tendency for bundles to be arranged in tangential rows together with slight variation in cell size and the amount of wall thickening in successive layers. Whether growth rings are related to fluctuations in shoot growth or not is not known.

Formation of secondary vascular tissue (FIG. 21). Mirbel (1843) recognized the essential features of the *Dracaena* cambium, as a meristematic zone which continually produces secondary vascular bundles. Later authors like Karsten (1847), Schacht (1852), and Nägeli (1858) were most concerned with theories about the equivalence of secondary vascular meristems in monocotyledons and dicotyledons, but the little information they produced was largely superseded by the more complete observations of later investigators.

The work of Röseler (1889) was the first detailed attempt to account for the process of division in the cambium and the way in which secondary vascular bundles differentiate from the derivatives. It was by no means the first of such investigations but it set a much higher standard than previous ones. It had become common knowledge, for example, that the tracheids in the secondary bundles are much longer than the cambial initials and their derivatives, whereas other elements of the bundle, like sieve-tube elements, phloem and xylem parenchyma are of the same length. Most early authorities assumed that the tracheids achieved their length by growth of a single derivative and that no cell fusion was involved. Krabbe (1886), for example, used these tracheids in *Dracaena* as an example in his work on sliding growth. Nevertheless these observations were disputed by a number of observers, notably by Kny (1886), who was of the opinion that no elongation of cambial derivatives was involved, but rather that the so-called tracheids were actually short vessels produced by the fusion of a longitudinal file of cells. The background to this controversy has been reviewed by Scott and Brebner (1893). Röseler (1889) re-instated the original concept on a firm basis by examining macerated material in which he demonstrated stages in the elongation of future tracheids. Another method he used, which involved counting the number of cells in transverse sections of the vascular bundle at different stages of development, proved to be less successful because, as Scott and Brebner emphasize, there is no fixed point at which counting could begin. Sliding growth evidently begins before cell division has ceased. It is also a matter of observation that the innermost tracheids at one level in any bundle are mature whereas outermost cells are still elongating or even dividing (FIG. 21). In addition the number of cells in a bundle varies and it is impossible to observe the same bundle at different stages of development.

The dispute was finally settled by Scott and Brebner themselves who confirmed Röseler's conclusions with various kinds of observations in spite of the fact that Scott (1889) himself had earlier supported Kny's opinion. They also suggested that the interpretation of other workers had resulted from a failure to distinguish carefully between developing tracheids and young sieve tubes in which nuclear breakdown simulates early stages in cell fusion. All subsequent investigators have found no cause to doubt Röseler's observations (cf. Cheadle, 1937).

Cambial division (FIG. 21). Most of our knowledge of the actual process of division in the cambial region is the result of a detailed study by Schoute (1902). He came to the conclusion that the meristem is at



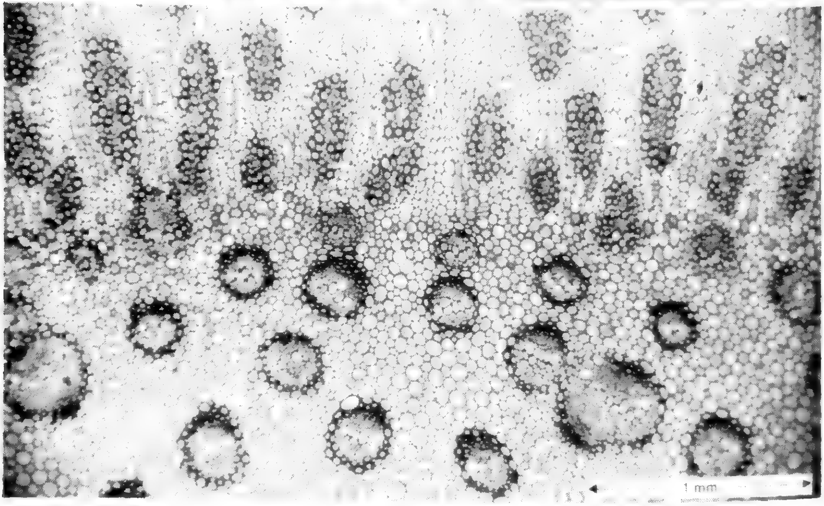


FIG. 21 (ABOVE). *Cordyline indivisa*, the mountain cabbage tree of New Zealand. Transverse section of stem at the periphery of the secondary tissue to show etagen cambium and stages in development of vascular bundles. A cork cambium, originating in the cortical parenchyma produces outer bark. (From Tomlinson & Zimmermann, 1967).

FIG. 22 (BELOW). *Dracaena hawaiensis*. Transverse section showing the boundary between primary (collateral bundles at bottom of picture) and secondary tissue (amphivasal bundles amidst radially-seriated parenchyma at top of picture). (From Tomlinson & Zimmermann, 1967).

first tiered (Etagenmeristem) and involves a succession of tangential longitudinal divisions in parenchyma resulting in radially-seriated derivatives. The innermost derivatives become incorporated in the secondary tissue whereas divisions are repeated in outer derivatives. Some of the outermost derivatives may remain undivided and form a "secondary cortex," the extent of this tissue being determined by the vigor of the cambium according to Cordemoy. This type of activity may only be a temporary stage in development of the cambium and Schoute compared it with the early stages in the establishment of the interfascicular cambium in dicotyledons. Subsequently a true "initial" cambium, more like that of dicotyledons, is established in which divisions are said to be confined to a single series of initials. At this later stage derivatives are now added more consistently on the outside as the parenchymatous secondary cortex. In *Beaucarnea*, for example, Hausmann (1908) concluded that the same meristem was distally an etagen meristem, but proximally an initial meristem. Cheadle (1937) essentially concurred with these observations and added some comments on variation in shape of the cambial initials. He was the first to publish photographs of the cambium in tangential view, although tangential illustrations had been provided earlier, as in the drawings by Millardet (1865). It should be noted, however, that our understanding of divisions in this cambium is largely based on a study of the plane of insertion of new cell walls rather than by observation of nuclear divisions. In addition, in Schoute's account it is hard to distinguish theoretical inference from direct observation. It is clear that there is still a great deal to be learned about this monocotyledonous cambium from cytological studies. We must agree with Cheadle when he says "neither the exact location nor a convincing description of the cambial initials could be found in the literature."

Distribution of cambial activity in the tree. Shoot growth and cambial activity are correlated, but not in a very straightforward way, as our future discussion will reveal. Young, unbranched stems of *Dracaena draco* may have a slight obconical form which may be repeated in the distal branches of older trees. It is more usual, however, for the basal part of the main trunk to be much thicker than distal parts. This is of obvious adaptive significance as it makes for mechanical stability. This pronounced basal thickening is entirely due to secondary growth. The disproportionate bulbous expansion of the base of the stem to which it leads has already been described. We do not know what is responsible for the initiation of cambial activity in the primary shoot and how cambial activity is maintained. However, there is strong external evidence that distal branching and the outgrowth of new laterals is a stimulus to cambial activity below. In *Dracaena fragrans*, for example, we have observed that secondary vascular tissue is always present immediately below each new unit of the sympodium, and it is often discontinuous below so that the segmented appearance of the stem caused by sympodial growth is enhanced by a variation in stem thickness. A discontinuous distribution of secondary tissue in *Dracaena* roots as observed by Scott and Brebner may also be recalled. This situation will be discussed in detail in a later paper; it is of considerable functional significance. It is equally clear, however, that secondary thickening occurs in the absence of branching as in seedling axes, although Dupetit-Thouars (1809) had initially suggested such a dependence between branching and secondary growth, a suggestion soon corrected (e.g. Wossidlo 1868, p. 25).

Although we have, as yet, little precise information about cambial activity in monocotyledons, the similarity of the phenomenon with that in conifers and dicotyledons is striking. Discontinuous cambial activity is known, for example, in very long roots of some dicotyledonous trees (Wilson, 1964). Another striking similarity is the asymmetric distribution of cambial activity in a leaning stem. Near Cape Sabal, in the Everglades National Park, the authors found a specimen of *Yucca aloifolia* which evidently had been thrown down by a hurricane a few years earlier. From the time of displacement the new shoot grew vertically again, but the displaced older part of stem remained in a leaning position. Transverse sections of the vertical part of the stem showed quite symmetrical arrangement of the secondary tissue, while on the leaning portion secondary growth had been quite asymmetric (diameter of primary stem 50 mm., radius of secondary tissue on upper side 8 mm., lower side 25 mm.).

On the other hand "reaction wood" has not been described for monocotyledons even in studies which have specifically been concerned with its distribution (Scurfield, 1964). This reflects the marked histological difference between monocotyledonous and dicotyledonous woods (Tomlinson & Zimmermann, 1967). Axes in these woody monocotyledons seem to be righted by re-orientation of the crown through unequal distribution of primary growth.

SECONDARY THICKENING IN ROOTS (FIGS. 24, 25)

It is known from the observations of many investigators (but see especially Lindinger, 1906) that in the roots of arborescent monocotyledons secondary thickening occurs only in *Dracaena.* However, from what is known about the method of insertion of adventitious roots in woody monocotyledons (and this knowledge is still based on the early account by Mangin (1882)) a limited amount of secondary thickening may occur in roots close to their insertion. This is nevertheless a matter for conjecture.

In *Dracaena*, all observers have noted that the secondary tissue in the root is identical in structure and origin with that in the stem. A major point of disagreement, however, has been the site of origin of the cambium which produces the tissue. Most early authors (e.g. Strasburger, 1884; Morot, 1885) recorded this as being the pericycle, although cambial activity could spread into the cortex via rupture of the endodermis. Others (e.g. Lindinger, 1906) recorded an exclusively cortical origin for the cambium. Scott and Brebner (1893) recorded both possibilities, together with a mixed condition where secondary growth began in the pericycle but then continued in a cambium formed in the cortex. In some instances all three conditions could be demonstrated in a single section (FIGS. 24, 25). They also made the very significant observation that secondary tissues are

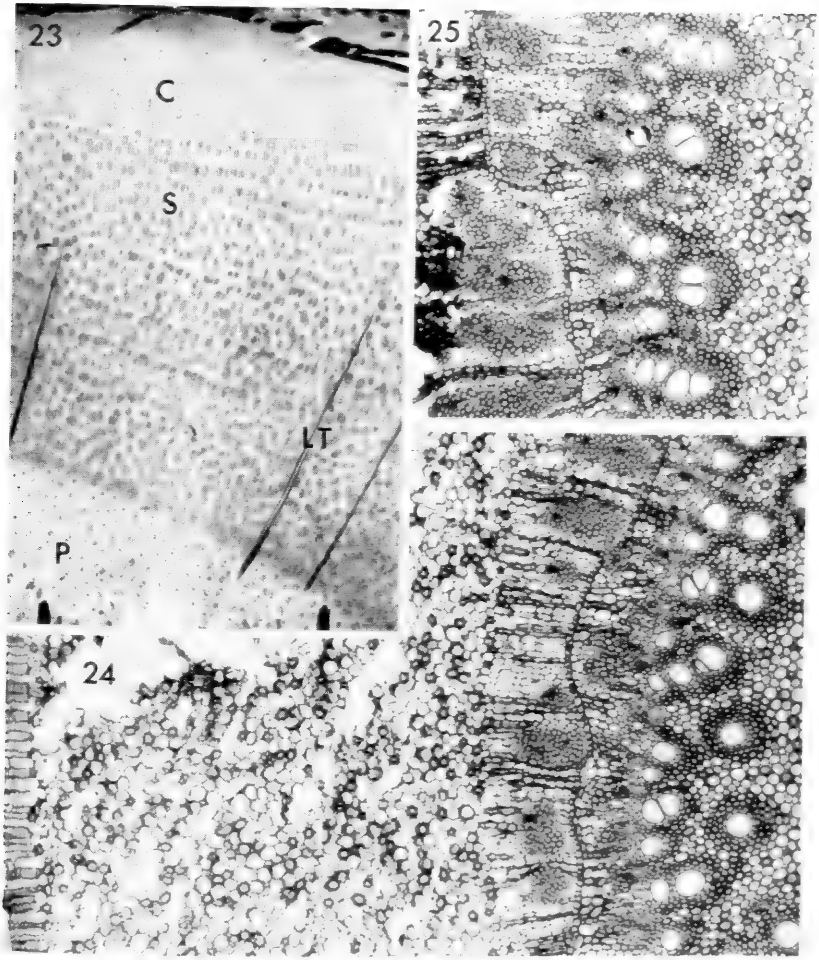


FIG. 23. *Yucca aloifolia*. Transverse section of stem at very low magnification. × 3.8, showing some primary (P) and secondary (S) tissue. Growth rings are evident in the secondary tissue particularly if the illustration is viewed from a distance. Cambium at C. Leaf traces (LT) traversing stem radially.

FIGS. 24, 25. *Dracaena fragrans*, transverse section of root. × 33. A small amount of secondary tissue is present. [Note the position of endodermis showing that cambial activity began in places inside it, in other places outside of it.]

always thickest in the region of insertion of lateral roots, and suggested that secondary thickening is initiated in this region.

It is quite obvious that the somewhat conflicting observations of different workers have a rational explanation in terms of growth and the factors which influence cambial development and activity. The problem has to be studied by following the origin and subsequent growth of adventitious roots in seedlings of different age, as Wright (1901) suggested. Wright also made the observation that the cambium originates in the pericycle of the very short hypocotyl, thence spreading upward into the stem and downward into the root. Further observations of this kind are needed to establish a clear understanding of secondary growth in roots of *Dracaena*.

THE RELATION OF PRIMARY TO SECONDARY GROWTH

The earlier studies on growth and development of these monocotyledons were carried out at a time when the understanding of plant growth in general was at a very primitive stage. It was also inevitable that theories of plant growth were dominated by concepts derived from studies of dicotyledons, and some of the earliest interpretations of monocotyledonous growth made unfortunate comparisons between monocotyledons and dicotyledons. To this early period belong a series of studies concerned with the relation between the secondary "thickening ring" and the meristematic tissues of the shoot apex proper as in the investigations of Karsten (1847), Schacht (1852), Nägeli (1858) and Sanio (1863). It seems that these studies were based on examination of single sections cut in transverse and longitudinal planes and that no attempt was made to trace the distribution of developing vascular bundles and the 3-dimensional relation between primary and secondary growth. We will show in a later article that this kind of investigation is crucial to the understanding of this relation.

One of the features of arborescent monocotyledons which captured the interest of earlier workers was the apparent continuity between the secondary meristem and the meristematic tissues of the crown. Some authors considered these two meristems to be discontinuous (e.g. Scott & Brebner, 1893). This discontinuity is also implied by Millardet (1865) who gave measurements of the distance below the apex at which the secondary meristem could be first recognized. This varied from as little as 3 mm. in *Yucca aloifolia* to as much as 22 cm. in *Dracaena marginata*. On the other hand many authors regarded the two meristems as continuous (e.g. Wossidlo, 1868; Lindinger, 1908). Hausmann (1908) reviewed the extensive literature on this topic and himself supported the latter point of view, concluding in fact that the distinction between the two meristems was rather artificial. In a developmental sense this is true, because establishment and activity of secondary tissue is dependent upon growth of the primary meristem. Nevertheless, earlier authors have often adopted a very dogmatic point of view, largely in an effort to establish whether the secondary meristem originated in tissue which had completed its maturation or not, and was therefore, *by definition*, truly "secondary."

A similar dogmatic preoccupation which is also largely a semantic one, was with the level, in a radial direction, at which divisions which initiated the secondary meristem occurred. The problem was to decide whether there was a region in the monocotyledonous stem, to which the term "pericycle" could be given. This is entirely an artificial concept, since in most monocotyledonous stems, cortex and central cylinder each ends where the other begins. A true understanding of the development of that region of the stem in dicotyledons for which the older term "pericycle" was devised has been forthcoming only in recent years (Blyth, 1958). The term pericycle has no application in monocotyledonous stems (Carano, 1910).

In terms of the overall distribution of the monocotyledonous cambium, one factual error does deserve comment. Röseler (1889) and apparently some earlier authors stated that the cambium does not extend into the leafy zone of the shoot. This is manifestly so untrue a generalization, whatever may have been the situation in the material on which it was based, that it is not surprising that it was soon corrected (e.g. by Cordemoy, 1894). The presence of functioning leaves, the traces of which must cross the cambium and secondary tissues, does raise interesting physiological and developmental questions to which we will return in a later article.

One reason for the conflicting reports on these topics which appears in the literature was that many authors failed to appreciate the variability in the time of appearance of the cambium and its vigor, which in turn seems largely to depend on the vigor of the shoot. We have already commented upon the variation in vigor expressed in the different diameters of shoots in one plant. This variation extends to the secondary cambium and may depend largely on the type of shoot. Seedling axes, for example, initially produce secondary tissue very actively. This activity declines on distal branches. Newly released buds, either below inflorescences or decapitated shoots, are dependent on an active production of secondary tissue in the early stages of growth in order to establish vascular continuity with the parent axis. In view of this variation it is not surprising that reports by early authors conflict, since they are probably based on comparison of shoots in different positions and of differing vigor.

COMPARATIVE INVESTIGATIONS

A few authors have been concerned with the relation between those monocotyledons with secondary growth and those without. Notable are Mangin (1882) and Petersen (1893). Chouard (1936) was concerned with the same topic, but his interpretations of monocotyledonous growth are not easy to comprehend. Petersen studied a number of monocotyledons which together represented a wide variety of families and growth forms. He came to the conclusion that in the group as a whole there was a continuous series with all intermediate steps, from those, like the orchids with no trace of a secondary meristem, via those in which one is briefly active, as in the Bromeliaceae, to the continually active cambium of *Dracaena* which permits unlimited growth.

Mangin (1882), on the other hand, was concerned with the way in which adventitious roots develop and establish vascular continuity with the conducting tissues of the parent axis. Adventitious roots arise in a meristematic region (couche dictyogène) between cortex and central cylinder. This meristem also gives rise to a plexus of vascular tissue (réseau radicifère) which connects conducting tissues of root and stem.

The extent of this plexus varies in different kinds of monocotyledons. Mangin considered that in some arborescent monocotyledons, like *Agave*, this meristematic region remains active throughout the life of the plant. In others, like *Dracaena* and *Yucca*, the root meristem is replaced by the secondary meristem. When more is known about the factors which stimulate and maintain an active cambium in monocotyledons it will be possible to approach the topic on a comparative base. Nevertheless Mangin's contribution to anatomical literature remains a notable one.

CONCLUSIONS

It is obvious from the previous pages that a reappraisal of this subject from first principles is needed. We hope to present in future articles the results of studies which to a large part resolve much of the conflicting literature. In particular we will describe the course and developmental pattern of the primary vascular bundles, the constructional relation between primary and secondary vascular bundles and demonstrate how the initiation and activity of the secondary meristem is dependent upon shoot growth. These will be related to growth of the shoot system as a whole.

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ASPECTS OF REPRODUCTION IN SAURAUIA

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THE GENUS *Saurauia* is a widespread tropical member of the Actinidiaceae with representatives in both the Old and the New World. The American range of distribution extends from Central Mexico to southern Bolivia, through Andean South America. According to a recent study by Hunter (1966), 22 species occur in Mexico and Central America, and my present study indicates that 49 species are represented in South America. The genus is not represented in the West Indies, and there are no records of its occurrence in the Guianas or Brazil.

During the course of field work in southern Colombia in 1965, I observed that some individuals of *Saurauia tomentosa* (H.B.K.) Sprengel have flowers with sessile stigmas, in contrast to the flowers with long styles (5–7 mm.) of individuals commonly held to be characteristic of the species. Later herbarium studies indicated that several other South American species are similar to *S. tomentosa* in this respect.

To be certain that such a phenomenon had not previously been described in *Saurauia*, I have searched the literature and found that nothing conclusive has ever been published. There are several references, however, to the reproductive system of *Saurauia*. Gilg (1895) and Gilg and Werdermann (1925) described the flowers of *Saurauia* as hermaphroditic to polygamo-dioecious. Brown (1935), who observed the flowering pattern of *S. subspinosa* Anthony, an Asiatic species, noted that the ovary development in this species lags behind the development of the anthers by about five days, suggesting that cross-pollination may be dominant. Hunter (1966) mentioned that some species in Mexico and Central America have flowers with "aborted" pistils. Killip (Jour. Wash. Acad. Sci. **16**: 570. 1926) referred to the flowers of *S. micayensis* Killip as unisexual, while Benoist (Bull. Soc. Bot. France **80**: 334. 1933) described the flowers of his *S. hypomalla* as staminate.

A few field workers have noted the existence of "male" and "female" plants in some species of *Saurauia*. Lorenzo Uribe Uribe, for example, noted the peculiarity in *S. isoxanthotricha* Busc. (L. Uribe U.'s collection number *4802*): "Este pie, que crecía cerca a mí No. 4801, no tenía sino flores femeninas." (This tree, which grew close to my No. 4801, had only female flowers.)

The flowers of *Saurauia* are borne in a thyrsiform inflorescence, consisting of a peduncle, rachis, and axillary scorpioid cymes arising in a spiral pattern. Each cyme is borne in the axil of a bract. The flowers are

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[1] The author is currently engaged in the revision of the South American species of *Saurauia*.

actinomorphic, pedicellate, each subtended by a bract and two lateral bracteoles; basically, the flowers are pentamerous and are usually described as bisexual or hermaphroditic. To the best of my knowledge, there is no true "male" or "female" plant; in other words, there is no true sexual dioecism in *Saurauia*.

The observations discussed in this paper were made to obtain more conclusive evidence about the reproductive system and its operations, and to suggest the implications for evolution in the South American species of *Saurauia*. This paper is the basis for more detailed studies on the breeding systems of the group which are in progress.

MATERIALS AND METHODS

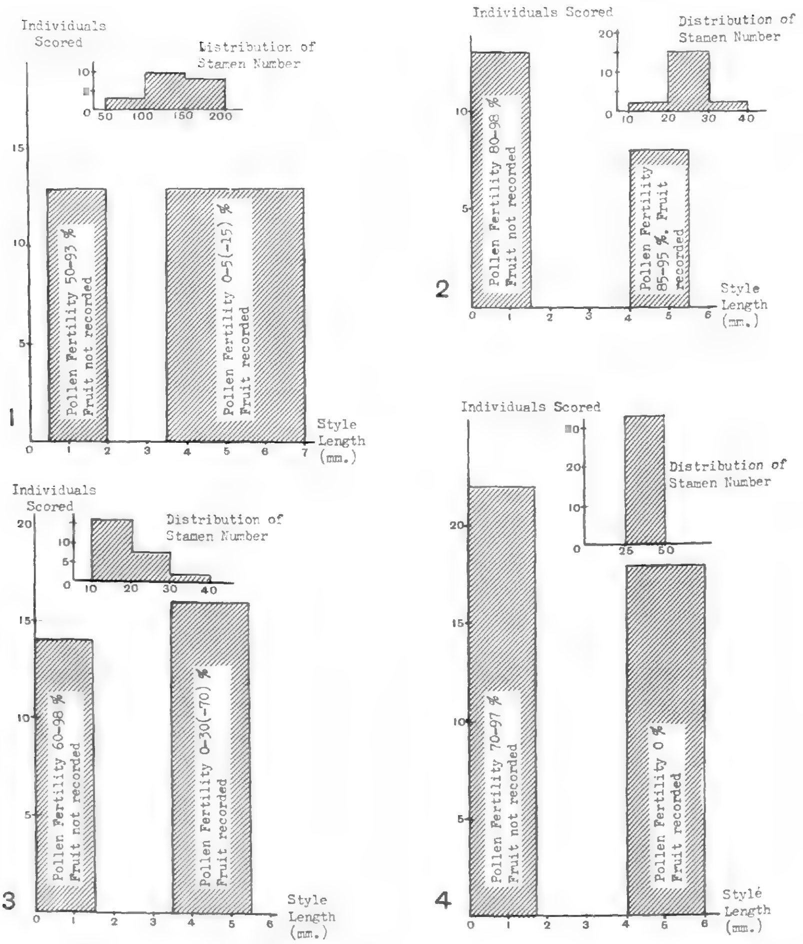
The present investigation has been based primarily upon data obtained from herbarium specimens. Initially, the work consisted simply of sorting specimens with reproductive parts into long- and short-(obsolete-) styled groups. The next step was examination of the pollen grains (their morphology, size, and fertility) of individuals in each of the two groups. Pollen fertility count was obtained either from open flowers or from mature flower buds. The best results were obtained by boiling the flowers or flower buds (sufficiently mature) to obtain the anthers for maceration. Boiling restores the dried material to a natural texture, which makes dissection and measurement of the floral parts more accurate. The pollen grains were mounted in glycerine jelly and stained with cotton blue dissolved in water. All pollen fertility counts reported here were obtained by using a Wild M20 phase contrast microscope, with bright-field illumination with or without a green filter. Percentage numbers were based upon a count of between 100 and 500 pollen grains on a single preparation. From two to five samples were prepared from one individual.

Stamen counts were made for taxonomic purposes. More important to this study, however, was to ascertain whether or not stamen number has any significant relation to floral dimorphism. All counts were made by boiling the (mature) flower buds, since counts based upon open flowers may be inaccurate, as some stamens may have aborted or others may have been broken and fallen during the process of drying and handling.

Measurements of style length were made mainly from open flowers and/or fruits, since the styles are persistent in *Saurauia*. Style length is not reduced much by drying, so boiling was only occasionally necessary. When neither open flowers nor fruits were available, measurement was made from the mature flower buds. This is a valid and reliable substitute, as will be obvious from the following discussions.

OBSERVATIONS

Analysis of data. I have examined all species from South America for my taxonomic revision, but, due to lack of data, only species with sufficient representation are included here for discussion. These are *Sau-*

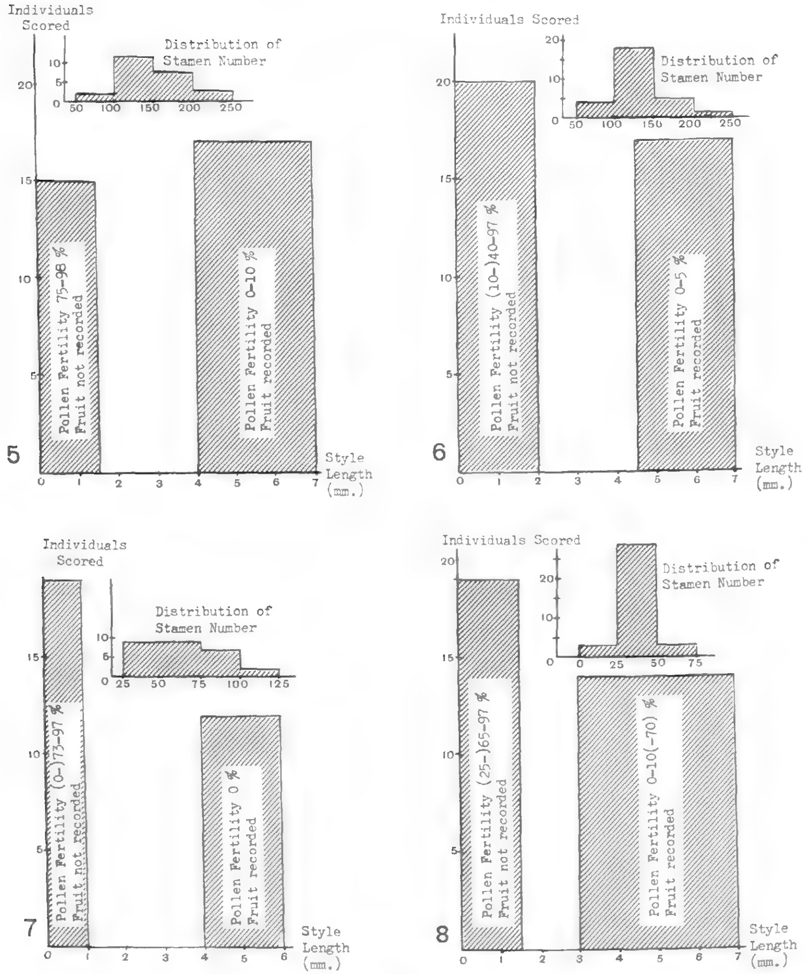


FIGURES 1–4. Graphic representation of the distribution of long- and short-styled forms represented by herbarium collections, together with histogram distribution of the stamen numbers. FIG. 1, *Saurauia tomentosa* (H.B.K.) Spreng.; FIG. 2, *S. omichlophila* R. E. Schult.; FIG. 3, *S. putumayonis* R. E. Schult.; FIG. 4, *S. ursina* Tr. & Pl. Sample examined for each species consists of short- and long-styled forms in more or less equal numbers.

rauia bullosa Wawra, ***S. brachybotrys*** Turczaninow, ***S. excelsa*** Willdenow, ***S. Humboldtiana*** Buscalioni, ***S. tomentosa*** (H.B.K.) Sprengel, ***S. omichlophila*** R. E. Schultes, ***S. putumayonis*** R. E. Schultes, and ***S. ursina*** Triana & Planchon. Data for each species, such as presented in TABLE 1 for *S. bullosa*, and in TABLE 2 for *S. omichlophila*, have been converted into graphs, FIGS. 1–8. Of the eight species, seven show a definite correlation between low pollen fertility (or absolute pollen sterility and a long-

Table 1. Saurauia bullosa Wawra

Collector	Fl. buds or Fls.	Pollen Fertility (%)	Style Length (mm.)	Stamen Number	Fruit	Collecting Date	Altitude (m.)
Soejarto 496	–	—	5.5	—	+	Aug.	2900
Soejarto 1504	–	—	6	—	+	Aug.	3000
Soejarto 1533	–	—	6.5	—	+	Aug.	2700
Soejarto 1472	+	0	5	160	–	Aug.	3100
Soejarto 1336	–	—	7	—	+	Aug.	2900
Soejarto 495	+	0	6	115	+	Aug.	2900
Soejarto 1015	+	0	5	127	+	July	3200
Soejarto 1478	+	0	5.5	220	–	Aug.	2900
Soejarto 1595	+	0	7	160	–	Sept.	3000
Soejarto 500	+	0	5	125	–	Aug.	2900
Cuatrecasas 20805	+	0	6	100	+	Apr.	3100
Cuatrecasas 20414	+	1	4.5	85	–	March	3200
Cuatrecasas 23316	+	2	5	70	–	Nov.	3000
Jorge Castro 78	+	0	5	140	–	Apr.	3400
L. Uribe Uribe 5278	+	0	5.5	100	+	July	3000
Ynes Mexia 7599	+	10	5	140	–	Aug.	3000
Soejarto 1496	+	75	0	175	–	Aug.	3100
Soejarto 1435	+	80	0	225	–	Aug.	3100
Soejarto 1484	+	85	0	150	–	Aug.	3000
Soejarto 1491	+	93	0	164	–	Aug.	3000
Soejarto 1045	+	80	0	150	–	July	3600
Soejarto 1508	+	92	0	127	–	Aug.	3000
Soejarto 1474	+	88	0	149	–	Aug.	3000
Soejarto 1335	+	40	0	240	–	Aug.	3200
Soejarto 1473	+	96	0	145	–	Aug.	3000
Fajardo G. 81	+	96	0	125	–	Apr.	3400
I. F. Holton 23	+	97	0	—	–	Jan.	3000
Cuatrecasas 20997	+	98	1	145	–	Apr.	3000
Hitchcock 20888	+	—	1.5	150	–	Aug.	3400
L. Uribe Uribe 5328	+	90	0	160	–	July	3100



FIGURES 5–8. Graphic representation of the distribution of long- and short-styled forms represented by herbarium collections, together with histogram distribution of the stamen numbers. FIG. 5, *Saurauia bullosa* Wawra; FIG. 6, *S. brachybotrys* Turcz.; FIG. 7, *S. Humboldtiana* Busc.; FIG. 8, *S. excelsa* Willd. Sample examined for each species consists of short- and long-styled forms in more or less equal numbers.

styled condition, and between high pollen fertility and a short-(obsolete-) styled condition. This correlation breaks down in *S. omichlophila*, where both long- and short-styled plants have high pollen fertility. Plants of each type occur in approximately equal numbers within a sampling collection of each species, which may reflect the distribution in the natural populations. Another significant correlation is that specimens bearing fruits have been recorded only from plants with long styles. This is certainly not mere coincidence, since all eight species discussed here (and many others for which statistics are not included) show this condition throughout. Morphological examinations from free hand sections of advanced ovaries in short-styled flowers show that these are aborted and they simply "do not grow" (PLATE II, FIG. 19). In long-styled flowers fruiting is accompanied by good seed set, except in several individuals where seed set is poor, notably in *Soejarto 1043* (*S. tomentosa*).

Short or long condition of the styles is not in any way correlated with high or low number of the stamens. As is obvious from FIGS. 1–8, and from TABLES 1 and 2, the distribution of the stamen number is continuous throughout the population, regardless of the style length. From the measurements of flower parts (data not included here), it also appears that a short- or long-styled condition is not correlated with the size of the flowers.

From field observations and from herbarium records, there is no indication of any particular flowering and fruiting season among the South American species of *Saurauia*. Flowering is usually associated with the wet months of the year. In most species, however, flowering and fruiting are continuous throughout the year, although fruiting is recorded in the herbarium collections (at least, in the eight species under discussion) only from February through October.

Pollen grains (PLATE I). All eight species have 3-colporate pollen, which is oblate spheroidal (cf. also Erdtman, 1952). Several individuals of *S. excelsa* have 3-colpate, prolate pollen grains. Most of the South American species that I have examined have oblate spheroidal pollen grains, although occasional prolate pollen is also present. No single pollen shape is restricted to a particular species. This condition applies only to fertile pollen grains, where the cell content stains uniformly with cotton blue and appears light to dark blue with bright-field illumination. The cell wall is smooth, with no observable wall sculpturing (at least with the present processing technique). The (fertile) pollen grains are binucleate at the time of anthesis (PLATE I, FIG. 14; cf. also Brewbaker, 1967); the generative cell is ellipsoidal or spindle-shaped, and the vegetative cell is roundish. The vegetative cell usually does not take acetocarmine stain so well as the generative cell. The binucleate condition of the grains may be seen (with cotton blue stain) in a sufficiently mature flower bud, prior to anthesis, and *it is assumed that this condition indicates that the pollen is fertile.*

The sterile pollen grains, on the other hand, have no fixed shape or any orientation. They may be lenticular, roundish or simply irregular in shape, but, lacking contents, do not stain. The cell wall usually is shrivelled. Some roundish pollen grains have minute dark granules within.

The size of the pollen varies, and no serious attempt has been made to measure size variation species by species. I am convinced, however, that pollen size is not taxonomically significant. Pollen size variation is always present in any preparation from a single plant, and size variation between species is very slight. According to Erdtman (loc. cit.) the pollen size of *S. Prainiana* Busc. from Perú is 18.5 × 20 microns (oblate spheroidal), and that of a species from Bolivia identified as *S. brachybotrys* Turcz. (probably a misidentification, since *S. brachybotrys* occurs only in southwestern Colombia) is 19 × 15 microns (subprolate). According to my rather crude measurements, fertile pollen grains vary in diameter from 15 to 25 microns, and sterile grains vary in diameter from 10 to 30 microns. There are no visible differences between fertile pollen grains from a short-styled plant and those from a long-styled plant; nor between sterile pollen grains from a long-styled and from a short-styled plant.

Androecium and gynoecium (PLATE II). There is no pollen dimorphism in *Saurauia*, in the sense of two types of pollen grains differing morphologically and correlated with floral dimorphism. The correlation in most cases is straightforward: *long styles* and *low pollen fertility* (*absolute sterility*) vs. *short styles* and *high pollen fertility*. The term *long* used here is relative, depending on the individual species involved. Species with large flowers (3–5 cm. in diameter), such as *S. bullosa* and *S. tomentosa*, have *long styles* 5–7 mm. long, and *short styles* 1–2.5 mm. long, whereas species with smaller flowers (0.5–1 cm. in diameter), such as *S. pseudoleucocarpa* Busc. and *S. micayensis* Killip, have *long styles* 3–5 mm. long, and *short styles* 0.5–1 mm. long. Styles less than 0.5 mm. long are considered to be obsolete.

The ovary of the American species of *Saurauia* is mostly five-carpellate, but in some species, e.g. *S. yasicae* Loes., *S. peruviana* Busc., and *S. leucocarpa* Schlecht. may be three- to five-carpellate or, in *Saurauia* sp. (a new species from Bolivia to be described by me), five- to seven-carpellate. Each style of the long-styled flower is surmounted by a capitate stigma. The stigmatic surface is either roundish or cordate (1–2 mm. broad in *S. bullosa*), covered by minute papillae. The size of the stigma — and for that matter of all other floral parts — varies with the size of the flower. At the time of anthesis, the stigmas turn dark brown and become sticky. This condition lasts, in *S. bullosa*, for four to seven days. On the other hand, the styles of a short-styled flower are tipped by simple stigmas which are non-papillate, and according to my field observations, there is no change in color or stickiness during anthesis.

Pollination. It appears from field observations that pollination in *Saurauia* is promiscuous. Most flowers have persistent green sepals and white petals (free for most of their length, but coherent at the base, falling as a unit with the stamens[2]). Occasionally, some species (e.g. *S. isoxanthotricha* Busc.) have both white and pink flowers, but I have never seen species with only pink flowers.[3] The stamens, with white filament and

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[2] As a result, flowers examined after anthesis are often described as "unisexual."

[3] *S. Conzattii* Busc. from Mexico has red, beautiful flowers (Schultes, personal comm.).

yellow anthers, characteristically form a yellow clump at the center of the corolla. The anthers consist of two thecae, versatile and extrorse at the time of anthesis; the point of attachment of the filament is at the junction of the two thecae, which fork in most cases about two-thirds the distance from the (embryonic) base. The versatile anthers and the pale, morphologically unspecialized flowers represent, in a way, an adaptation for wind pollination.[4] There is no definite nectary present in the flower, but nectar-secreting tissue is found inside at the base of the corolla, partly hidden by the stamens (cf. Brown, 1935); also, most flowers have a faint, sweet scent, which in some species, especially *S. omichlophila*, is moderately strong.[5] These two characteristics suggest adaptation for insect pollination. I have found hymenopterans and other insects visiting flowers of *S. peduncularis*, *S. omichlophila*, *S. brachybotrys*, and *S. chiliantha* R. E. Schultes.[6]

Fruit and seed dispersal. The fruit of *Saurauia* is a berry filled with numerous small seeds embedded in a mucilaginous pulp. The color of the fruit is green, even when mature, although sometimes there is a purple to purple-red tinge on the green, glabrous pericarp. The sepals are persistent, as are the styles. Maturity of the fruit is indicated by an abundance of mucilage, which is rather sticky, clear, sweet and edible. Dehiscence of the fruit is septicidal along the longitudinal sutures, the septa often being membranaceous; the central column and the septa remain intact after dehiscence. In *S. bullosa*, dehiscence may occur from one to three days after a ripe fruit is detached from the tree (faster when conditions are wet) with little mechanical stimulation. The dehiscence lines start at the apex of the fruit and run gradually towards the base, at the same time discharging, or more precisely, exuding the mucilage which includes the seeds. This is, I believe, the way that the seeds are dispersed naturally, aided by the rain wash. Dispersal by birds certainly is not uncommon. Birds have been seen frequently feeding on *Saurauia* fruits (common name: *moquillo* or *dulumoco*, referring to the mucilage of the fruit). However, the effectiveness of bird dispersal must be further investigated. In all probability, diaspores may not be transported great distances in *Saurauia*; survival is insured by an abundant production of the seeds.[7]

[4] Pollen of wind-pollinated plants is usually characterized by simplicity of structure, and by the small size of the grains (between 20–60 microns, cf. P. Echlin, Sci. Amer., Apr., 1968); such is the case in *Saurauia* species.

[5] *S. aromatica* R. E. Schultes and *S. narcissifragrans* R. E. Schultes were given their epithets because of the strong and heavy scent of their flowers.

[6] L. Uribe Uribe (no. *2888*) has observed numerous bees visiting the flowers of *S. Stapfiana* Busc.

[7] The seeds of *Saurauia* are usually minute, areolate, dark brown; the testa is fragile (cf. PLATE I, FIG. 21). That *Saurauia* seeds are viable for relatively long periods is evident from the following notes. *S. kegeliana* Schlecht. (1836) was "described from living plants at Halle, Germany, that grew from seeds in soil found about the roots of plants imported from Guatemala" (note by Standley & Steyermark, Fieldiana **24**(6): 431. 1949). *S. spectabilis* Hook. (Bot. Mag. **69**: *pl. 3982*. 1842) was described from a "plant raised by Mr. Knight, of the Exotic Nursery, King's Road,

Geographical distribution. The center of distribution of *Saurauia excelsa* lies in the Venezuelan Cordillera de Mérida, while that of *S. Humboldtiana* is found in the Cundinamarca region, Cordillera Oriental of the Colombian Andes. There is an overlapping of range between these two species in the Santander region. *S. ursina* is centered in Antioquia, along the Cordillera Central, and its range overlaps that of *S. Humboldtiana* and, perhaps, that of *S. excelsa* as well. *S. brachybotrys* centers in the Cauca-Valle region, between the Cordillera Central and Occidental, but its range extends north to Antioquia, and south to the Nariño-Putumayo region. The Nariño-Putumayo area is located near the Colombian-Ecuadorian frontier, where the species concentration of the genus is highest. *S. bullosa*, *S. tomentosa* and *S. omichlophila* have their centers of distribution in this region also. *S. bullosa* and *S. tomentosa* have the broadest ranges of the South American species. *S. putumayonis* occurs in the Putumayo region, along the Cordillera of Portachuelo.

The four species, *Saurauia excelsa*, *S. Humboldtiana*, *S. ursina*, and *S. brachybotrys* are not effectively isolated from one another geographically or altitudinally. Although *S. bullosa* and *S. tomentosa* overlap geographically with other species, they are effectively isolated from the others altitudinally and are themselves frequently sympatric in their distribution, geographically, ecologically, and altitudinally. *S. omichlophila* and *S. putumayonis* are effectively isolated from the others, particularly ecologically, and they are spatially allopatric.

Cytology. I have examined the meiotic chromosomes of seven of the eight species under discussion: *Saurauia bullosa*, *S. brachybotrys*, *S. Humboldtiana*, *S. tomentosa*, *S. omichlophila*, *S. putumayonis*, and *S. ursina* (Soejarto, 1969). Chromosome behavior at meiosis in these species appears to be normal, and the chromosome size and morphology are remarkably stable. The haploid chromosome number of all seven species is $n = 30$. Cytokinesis is of a simultaneous type, and the tetrad arrangement is tetrahedral. Chromosome counts were all made from pollen mother cells.

DISCUSSION

In *Saurauia*, at least among the species from South America, two kinds of flowers can be distinguished. The differences lie in the size and morphology of the styles, and in the degree of pollen fertility. Anther height and pollen size and morphology appear to be fixed. It is for this reason, perhaps, that the existence of floral dimorphism in *Saurauia* has passed unnoticed for so long. Most workers on this group considered a short-styled condition to be peculiar to a particular individual or species,

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Chelsea, England, from seeds imported from the Republic of Bolivia, in 1838." However, I have attempted several times to germinate *Saurauia* seeds for cytological studies without success.

or a sign of immaturity, and apparently did not appreciate the biological significance of their observations. The present study shows that floral dimorphism does exist in *Saurauia*, but that this type of dimorphism is *not* distyly or heterostyly in the true physiological sense of the word, since it appears (at least now) that no incompatibility system is involved. Low pollen fertility (to complete sterility) in a plant with long-styled flowers, and high pollen fertility in a plant with short-styled flowers is a mechanism that promotes outcrossing. In this respect, the flower of *Saurauia* must be described as *functionally dioecious*. The short-styled form with high pollen fertility may be considered a functionally staminate plant (the pistil being nonfunctional), while the long-styled form with low pollen fertility (to complete sterility) is a functionally carpellate plant (the stamens being nonfunctional). For those individuals, particularly populations of *S. omichlophila*, which are truly hermaphroditic (TABLE 2; hermaphrodites are characterized by a long-styled flower with pollen fertility 80% or more) within the dimorphic populations, further investigation is needed to demonstrate whether any self-compatibility between the pollen and the stigma of the same flower exists. From the pollen size and morphology, there seems to be no reason why it should not occur. If this is the case, species like *S. omichlophila* must be described as *androdioecious*.

The widespread occurrence of functional dioecy, an outbreeding sys-

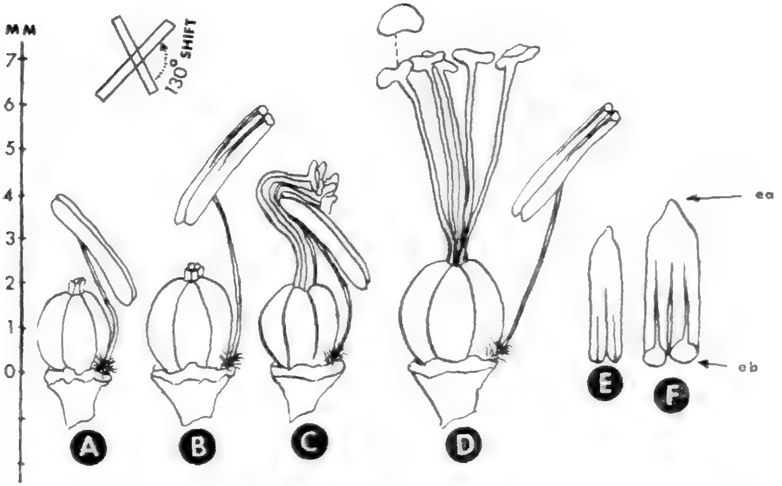

FIGURE 23A–F. Anther orientation in the flower of *Saurauia Humboldtiana* Busc. Sepals and petals removed to show details. A, short-styled form, bud stage; B, short-styled form, at anthesis; C, long-styled form, bud stage; D, long-styled form, at anthesis; E, anther, bud stage; F, anther, at anthesis. As a result of the shift of the anther position at anthesis (approx. 130°), the anthers are extrorsely oriented. ea, embryonic apex of anther; eb, embryonic base of anther.

tem, is further enforced by the peculiar anther orientation during anthesis in the American species of *Saurauia* (FIG. 23, A–F). The end of the anther (the embryonic base) is directed away from the center of the flower as it opens, and the anther rotates about 130° on the filament so that the pollen discharge is directed away from the stigmas. Pore openings and dehiscence of the anther start at the embryonic (morphological) base and "zip" ventrally about two-thirds the length of the thecae. My field observations of this dehiscence and reorientation of the anther during anthesis are confirmed by Hunter's (1966) interpretation, from histological observations of the vascular trace of the stamen (Hunter interprets the reorientation of the anther at anthesis as 180°, with which I cannot agree). Therefore, in individuals which are truly hermaphroditic, like those in *S. omichlophila*, self-pollination is averted as much as possible. Prevention of self-pollination among the hermaphrodites is indicated by the position of the stigmas which is well above the surface of the androecium. Nevertheless, the chances of self-pollination are rather good.

From an evolutionary point of view, the immediate consequence of outbreeding is its capacity for genetic recombination to produce variability for the action of selection and other external forces which direct the evolution of populations (Stebbins, 1950). The greater part of the genotypic variation within a cross-breeding population is due to segregation and recombination of genic differences which have existed in it for many generations. As a result, in a comparable environment, the outbreeders may show great, more or less continuous, morphological variation, which is an expression of genetic variability from plant to plant. Most species populations of *Saurauia*, those which are functionally dioecious, are characterized by this type of morphological and environmental continuity. Because of a low selective pressure, variability *within* a population tends to obscure any clear-cut distinction *between* populations. The situation is further confounded by a more or less free gene flow between species populations, due to an incomplete isolating mechanism: spatial, ecological, ethological or, perhaps, genetical; this last mechanism must be further investigated. The lack of a complete genetic barrier is demonstrated by the frequent occurrence of natural hybridizations where two or more species populations are in contact or where they are sympatrically distributed. I have collected several natural hybrids of *Saurauia* from southwestern Colombia, where the greatest concentration of species is located, and the hybrid status of at least four of these plants has been confirmed by meiotic irregularities of the chromosomes (Soejarto, unpubl.). Although altitudinal isolation is usually effective, nevertheless some population contact is always present. There seems to be no effective barrier against interspecific pollination in most cases, which is reflected in the relatively uniform floral morphology. Only size variation of the flower, which is conspicuous, exists within as well as between species. Correspondingly, selective pressures are relatively weak at the stage of flowering and also at the fruiting, or dispersal stage. On the chromosome level, the differences between species populations appear to be even less significant; that is, as far as

Table 2. Saurauia omichlophila R. E. Schultes

COLLECTOR	FL. BUDS OR FLS.	POLLEN FERTILITY (%)	STYLE LENGTH (mm.)	STAMEN NUMBER	FRUIT	COLLECTING DATE	ALTITUDE (m.)
Soejarto 1493	+	90	5	18	+	Aug.	2900
Core 1019	+	95	5	30	+	July	2700
Soejarto 1176	+	90	4.5	28	+	July	2500
Soejarto 1046	+	96	4	14	+	July	3200
Soejarto 977	+	—	4.5	—	+	July	3000
Soejarto 1511	–	—	4	—	+	Aug.	2800
García-Barriga 13023	+	85	4	21	–	July	2800
L. Uribe Uribe 3876	+	98	4	25	–	Sept.	3000
Soejarto 1501	+	90	0	23	–	Aug.	3000
Soejarto 1509	+	88	1.5	20	–	Aug.	3100
Schultes 3236	+	95	0	26	–	Feb.	3200
Schultes 7560	+	90	0.5	26	–	March	2900
Core 1018	+	96	0.5	37	–	July	2700
Schultes 7560A	+	88	0.5	27	–	May	2900
Soejarto 1502	+	85	0.5	29	–	Aug.	3000
Hernández 79	+	95	0	22	–	—	3000
Soejarto 1598	+	95	0	20	–	Sept.	3000
Schultes 20098	+	92	0	21	–	June	2800
Schultes 7550	+	85	0	21	–	June	3000
Schultes 7771	+	90	0	26	–	June	3000
Soejarto 914	+	0–80	0	21	–	July	3000

my present investigations on the cytology of the South American *Saurauia* show. The inevitable consequence of all this is the difficulty of drawing clear-cut boundaries between species populations, and, consequently, in the delimitation of the species within the genus. It is unfortunate that species of *Saurauia* are unfavorable subjects for garden experiments because of climatic intolerance, poor seed germination, the large size of the plants and the length of time before they reach the flowering stage. These drawbacks, however, should not discourage workers on the group from continuing their efforts. There are several other things that can and must be done; one of these is more vigorous field work and collecting of herbarium material. The more herbarium collections accumulate, the better we can evaluate and analyze the limits of variation within and between species. Considering the relatively young age of the group, Tertiary (Eocene?; cf. Langeron, 1900, Hollick, 1936), it appears to me that evolutionary differentiation is proceeding in the genus *Saurauia*.

Finally, the realization that functional dioecy is prevalent in *Saurauia* may further confirm our opinion with regard to the phylogenetic relationship of the genus with the closely allied, predominantly dioecious *Actinidia*.

SUMMARY

The reproductive system(s) of the following eight South American species have been described and discussed: ***Saurauia bullosa*, *S. brachybotrys*, *S. excelsa*, *S. Humboldtiana*, *S. tomentosa*, *S. omichlophila*, *S. putumayonis***, and ***S. ursina***. As far as the present data show, seven of the eight species appear to be functionally dioecious, and one, ***S. omichlophila***, is androdioecious. The flowers of these plants are dimorphic: a long-styled form with high pollen sterility (functionally carpellate) vs. a short-styled form with high pollen fertility (functionally staminate). Anther height is fixed, and pollen dimorphism related to style dimorphism has not been seen.

Although data have been compiled exclusively from herbarium examinations (presented here in graphic form, FIGS. 1–8), the following observations, based upon field and laboratory studies, have also been briefly described: pollen grain, androecium vs. gynoecium, pollination, fruit and seed dispersal, geographical distribution, and cytology.

The widespread occurrence of functional dioecy may be a useful guide in confirming the phylogenetic relationship between *Saurauia* and the closely allied, predominantly dioecious genus *Actinidia*. It is further suggested in the discussion, that the extensive morphological variability is the result of the outbreeding nature of the group, because the immediate consequence of outbreeding is its capacity for genetic recombination to produce variability in the action of selection and other external forces which direct the evolution of populations.

ACKNOWLEDGMENTS

I am deeply indebted to Professor Reed C. Rollins for his generous suggestions and painstaking criticism of the manuscript. Dr. Richard E. Schultes has very kindly helped me edit the English of the text, for which I wish to express my thanks. I also wish to thank Dr. Carroll E. Wood, Jr. and Dr. Beryl Vuilleumier for several discussions on heterostyly. I have received financial support from the Committee on Evolutionary Biology (NSF grants GB3167, GB7346; principal investigator, R. C. Rollins), Harvard University. Finally, I want to thank my wife, Mariela, for her constant and cheerful encouragement, and for typing the first draft of the manuscript. Any errors or misinterpretations found in this paper, however, are my sole responsibility.

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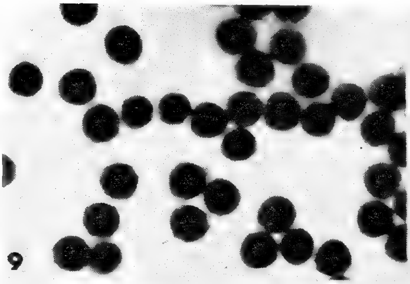
EXPLANATION OF PLATES

PLATE I

FIGURES 9–16. Pollen grains in *Saurauia*. FIGS. 9, 11, 14, 15, 16, fertile pollen; FIGS. 10, 12, 13, sterile pollen. FIGS. 9, 10, 11, 12, 13, 14, from *S. bullosa*, showing oblate spheroidal pollen grains, FIGS. 15 and 16 from *S. excelsa*, showing prolate pollen grains. All except FIG. 14 prepared from herbarium samples, stained in cotton blue; FIG. 14 prepared from anthers fixed in Carnoy's solution and stained in acetocarmine (only a generative cell clearly visible). FIGS. 9 and 10 approx. × 400, the others approx. × 1600.

PLATE II

FIGURES 17–22. FIGS. 17 and 20, long-styled flower (mature bud in FIG. 17, flower at anthesis in FIG. 20); FIGS. 18 and 19, short-styled flower (mature bud in FIG. 18, flower after anthesis in FIG. 19); all longitudinal sections. FIG. 22, upper view of the stigmas at anthesis. FIG. 21, seeds. All to the same scale as FIG. 19, and all from *S. bullosa*. FIG. 19 photographed from dried flowers (boiled and dissected), all others from material fixed in Carnoy's solution. Scale in FIG. 19 is in mm.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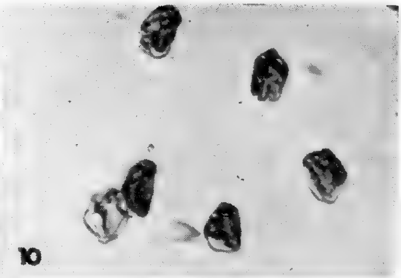
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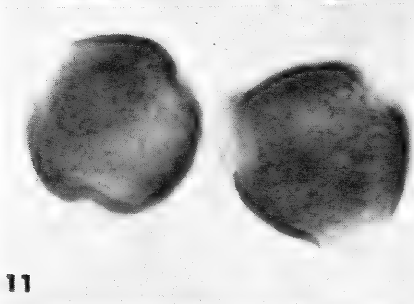
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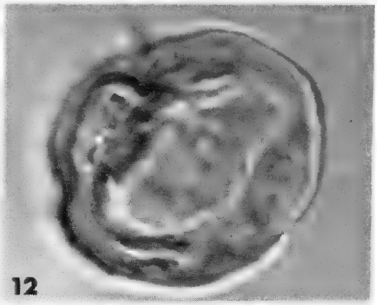
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SOEJARTO, REPRODUCTION IN SAURAUIA


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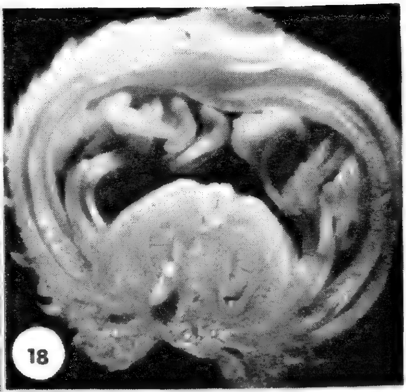
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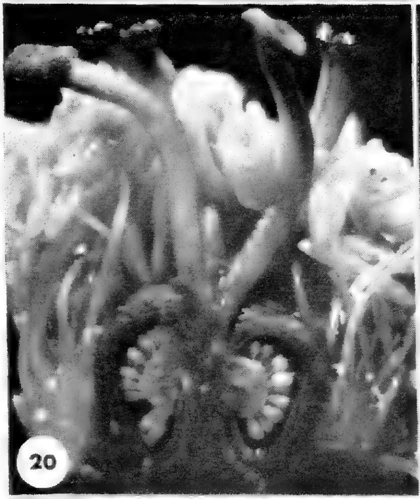
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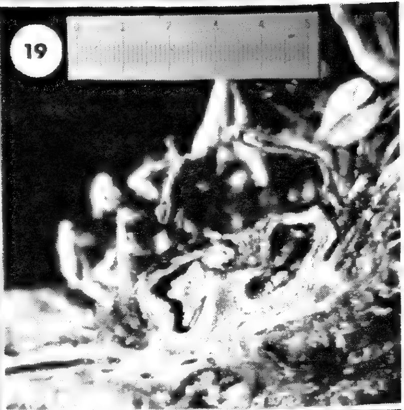
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SOEJARTO, REPRODUCTION IN SAURAUIA

THE ECOLOGY OF AN ELFIN FOREST IN PUERTO RICO, 6
AËRIAL ROOTS[1]

A. M. Gill

In temperate regions aërial roots are rare and although they may be found on a few vines they are absent from the trees and shrubs. In the moist elfin forest of Puerto Rico, however, many of the trees, shrubs, vines, and herbs form aërial roots. The tree fern *Cyathea* and the lowly *Selaginella* also form aërial roots in this environment.

Many of the aërial roots hanging freely from the plants are very characteristic of the species while some other species are difficult to distinguish by the characters of their aërial roots alone. In this study some of the distinctive characters of the roots are described and the frequency of aërial root formation on Pico del Oeste is documented.

Observations on the Distribution of Roots in toto

The roots in the study area are found in four general habitats: in the soil; immediately above the soil beneath a layer of cryptogams and/or leaf litter; appressed to the trunks and branches of the trees and shrubs; and hanging freely in the air.

All the roots in the last three habitats named may be considered "aërial." Those in the second category occur in a gaseous environment immediately below the forest floor and above the soil. A mat of roots up to five centimeters thick may be formed (Fig. 1) which appears to have arisen not merely by erosion of soil but by the growth of roots out of the soil and over its surface. On steep slopes roots of sufficient rigidity may even grow through the forest floor into the atmosphere. On gentle slopes this achievement has been attained by growth along tree trunks and fallen branches beneath a layer of cryptogams and thence out to the atmosphere.

The roots of many of the vines and of the bromeliad *Vriesea* are found closely attached to rigid organic surfaces. They are often found beneath a mantle of cryptogams but are also found where such a covering is lacking. This latter type of root may also be considered "aërial" but the affinity of the roots to their supports distinguishes them from the final group which is the main subject of this paper.

The aërial roots to be considered here are those found hanging freely in the atmosphere. They arise above ground and are not closely appressed

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[1] The first two papers in this series were published in Jour. Arnold Arb. **49**: 1968. See: R. A. Howard, The Ecology of an elfin forest in Puerto Rico, 1. Introduction and composition studies, 381–418; and H. W. Baynton, 2. The Microclimate of Pico del Oeste, 419–430.

FIG. 1. Mat of roots immediately below the litter and cryptogam layer but immediately above the soil.

to any surface. They may become anchored in the substrate and undergo considerable secondary thickening and in such cases have been termed "prop" or "stilt" roots by other authors. The aërial portions of such anchored roots may exhibit phenomena different from roots of the same species in the freely-hanging stage — those to be considered here.

AËRIAL ROOTS OF THE TREES AND SHRUBS

Many of the data pertaining to the aërial roots of the trees and shrubs of the area are shown in TABLE 1.

Origin. Aërial roots usually arise from the undersides of branches and from the main axis of the plant. They are often associated with the formation of sprouts (probably arising from dormant buds) and in such cases are found at the base of the sprout where it joins the main stem. This condition was observed in *Ocotea, Ilex, Miconia pachyphylla, Calyp-*

TABLE 1. **The aërial roots of the trees and shrubs**

	TIP PROPERTIES						AT ROOT ORIGIN		
SPECIES	Max. diam. (mm.)	Max. increment before laterals (cm.)	Max. replacement tips	Color	Rigidity and alignment	Lateral roots without injury*	Min. stem diam. (mm.)	Min. distance to leaves (cm.)	Second. thick. before ground*
Prestoea montana	17	19	4	pale orange to pale pink	stiff & brittle, simple curves	+	58	45	–
Hedyosmum arborescens	3.5	80	3	white apex, then lemon, then green behind	unbent, flexible	–	4	5	+
Ocotea spathulata	6	36	4	pink to brown	unbent, flexible	–	12	30	+
Trichilia pallida	(1.2)	9	1	creamy brown to pink	unbent, flexible	–	7.5	15	?
Ilex sintenisii	0.7	5	3	white to brown	unbent, flexible	–	13.5	110	?
Torralbasia cuneifolia	0.6	12	5	orange	unbent, flexible	–	3	30	+
Clusia grisebachiana	6	89	2	white apex, yellow and brown behind	unbent, flexible	–	13.5	50	+
Calyptranthes krugii	1.2	14	1	white to red-brown	unbent, flexible	–	2.5	8	+
Eugenia borinquensis	1.8	24	1	white to red-brown	unbent, flexible	–	110	250	+
Calycogonium squamulosum	1.5	14	3	bright pink	unbent, flexible	–	4	2	+
Mecranium amygdalinum	1.2	9	2	white to pink	unbent, flexible	–	2	2	+
Miconia foveolata				pink		–	2	3	?
Miconia pachyphylla	0.9	10	2	white to pink	unbent, flexible	–	3.5	0	+
Grammadenia sintenisii	2.0	9	2	white to light brown	unbent, flexible	–	5	16	+
Wallenia yunquensis	1.0	10	4	white to pink	unbent, flexible	+	5	1	+
Micropholis garciniaefolia	2.7	17	?	white	unbent, flexible	–	47	150	?
Symplocos micrantha	0.8	4	6	white	unbent, flex. to hanging	–	5.5	6	+

TABLE 1 — *continued*

	Tip Properties					At root origin			
Species	Max. diam. (mm.)	Max. increment before laterals (cm.)	Max. replacement tips	Color	Rigidity and alignment	Lateral roots without injury*	Min. stem diam. (mm.)	Min. distance to leaves (cm.)	Second. thick. before ground*
Haenianthus salicifolius	1.5	23	6	cream ochre to brown	unbent to hang in cluster	–	8	15	+
Tabebuia rigida	2	10	5	creamy lime to weak yellow	unbent, flexible	–	11.5	6	+
Gesneria sintenisii	0.5	4	7	white to tan	unbent, flexible	–	3	3	?
Psychotria berteriana	0.7	7	2	beetroot to pale white	unbent flexible	—	4	11	?
Lobelia portoricensis	1.5			white to pale green	unbent, flexible	–	7	0	?

* + represents presence, – represents absence.

tranthes, *Grammadenia* and *Torralbasia*. The same thing may occur below the ground with some species of trees in temperate areas. In Massachusetts it has been seen in *Fraxinus americana*: when a tree is cut down and new shoots arise at the base from beneath the soil-surface, new roots may be formed at the junction of the new shoot and the parent stem.

No root was found within the leafy zone (distal to the most proximal leaf and with or without a few leafless nodes included) of the trees and shrubs except in *Lobelia*. In TABLE 1 the minimum distance of an aërial root from the leaf zone has been noted and also the minimum stem diameter on which an aërial root has been found. Most of the species have aërial roots very close to leaf zones but not within them. *Miconia pachyphylla* was recorded with roots at the junction of the leaf zone and for most of the species aërial roots have been found within 50 centimeters of the leaf zone.

The aërial roots are usually found too far away from the leafy zone to determine if there is any association between the root origin and the nodes of the stem. With *Miconia pachyphylla* (FIG. 2) one root was found at a node and no roots were observed where a definite lack of such an association could be seen. No anatomical observation of the origin of the aërial roots was made but association with a node would suggest development of a preformed primordium giving rise to the aërial root.

Aërial roots may also arise laterally from other aërial roots, a condition discussed in a later section.

Tip properties. The maximum diameters of the root tips vary widely between species. Maximum values were taken since they are more dis-

FIG. 2. Roots of *Miconia pachyphylla* with droplets of water at the apices. (Photo. courtesy of Dr. R. A. HOWARD.)

tinctive than average values. Tip size may decrease with the order of branching, with distance from the point of origin, and in some species with the size of plant (e.g. smaller plants of the palm *Prestoea* were observed with smaller tips than those on large trees). *Prestoea* has tips up to 17 mm. in diameter (FIG. 3) while the maximum recorded for *Torralbasia* was 0.6 mm. The root tips of the other species were of diameters intermediate between these values. The significance of tip size in between-species comparisons is not known, but in the roots of the trees in central Massachusetts at least, tip size within a given root system is an important parameter, and other properties of the root are associated with it, e.g., lateral frequency, number of protoxylem poles, and other anatomical features, as well as the probability of secondary thickening.

Color variations in the tips may be distinctive. *Torralbasia* roots are often orange in color, those of *Miconia* spp. usually a bright pink, and those

FIG. 3. Aërial roots of the palm, *Prestoea montana*, showing inhibited lateral root development in the absence of injury. FIG. 4. Gelatinous material on the aërial roots of *Hedyosmum arborescens*. FIG. 5. Broom-like cluster of aërial roots of *Tabebuia rigida*, developed as a response to repeated injury. Secondary thickening is also evident near the point of attachment. FIG. 6. Distally anchored aërial roots of *Clusia grisebachiana* showing development of root tips and considerable secondary thickening.

of *Hedyosmum* most often lemon. However, the color of the roots may be considerably muted under some conditions and for many of the species darker environments may cause all color to be lost from the root tips.

Most of the newly emerged tips are straight and flexible. The palm root tips, however, may be stiff and rather brittle and they may curve down towards the soil. When the roots are longer their alignment and rigidity may change. The roots of *Clusia* become long and rubbery and the roots of *Tabebuia* and *Torralbasia* tend to hang in clusters. The roots of *Ocotea*, however, usually maintain the initial direction of growth with some bias downward.

The living roots of *Hedyosmum arborescens* are usually bathed in a gelatinous fluid.[2] This may hang down from the apex of the tip for two millimeters as part of a drop around and below the apex (FIG. 4). Shortly above the apex the material becomes much thinner and is very thin 4 or 5 centimeters from the apex. Two roots with a considerable drop on their respective apices were stripped of their coating, using two fingers to remove it. The volume from both was approximately 2 milliliters.

An experiment was initiated in an attempt to discover how quickly the material covering the root was replaced. After a week there was partial replacement of the material. After this period approximately 1 milliliter of fluid was removed from the three stripped roots. It should be noted however, that similar stripping (with care not to exert pressure) eventually resulted in root death (R. A. Howard, personal communication). In addition it may be noted that the material does not occur on dead roots nor those with brown, apparently inactive, tips.

The gelatinous substance is common on the healthy roots of *Hedyosmum* but has been found only rarely on the aërial roots of other species in this area. It has been found only twice on the aërial roots of *Calycogonium* and once on a root of *Miconia pachyphylla*. Many aërial roots of the latter two species were observed, but in only these cited cases was the gelatinous material seen. On these specimens the material was less gelatinous and more readily removed than that on roots of *Hedyosmum*. However, it was not dislodged as easily as a drop of water might be and it was jelly-like in texture.

A cut in the aërial roots of three species caused drops of milky exudate to be formed. Such material is common in the leaves and stems of the three families represented and this observation indicates that the lactiferous system does extend into the aërial roots. The plants concerned are *Clusia grisebachiana*, *Lobelia portoricensis* and *Micropholis garciniaefolia*, members of the families Guttiferae, Campanulaceae, and Sapotaceae, respectively.

Lateral root formation. Patterns of lateral root development contribute to the specific character of many of the aërial roots. The rope-like *Clusia* roots and the broom-like *Tabebuia* roots (FIG. 5) are very distinctive for this reason. In many cases the lateral root formation from the freely hanging aërial roots appears to be entirely dependent upon injury. With such a stimulus, one to seven replacement tips may arise behind the

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[2] This fluid has a high content of algae including diatoms and desmids. Some six carbon sugars were found in the material but no higher sugars (R.A.H.).

injured portion (TABLE 1). These tips may arise not only close to the injury but also several centimeters behind it (e.g. *Tabebuia* and *Torralbasia*).

With the aërial roots of the palm *Prestoea* lateral roots develop regularly without injury (FIG. 3) but have very limited growth. The laterals are short (up to 5 mm.) and pear-shaped. Their bases are narrow but their diameter increases markedly (to 2 mm.) within a short distance and then tapers to the apex. They arise in three to eight regular rows depending on parent root diameter.

Some roots may achieve great lengths before any lateral is formed. The length attained is a reflection of the growth rate and the interval between injuries, which in *Clusia* and *Hedyosmum* may amount to 2.5 to 3 meters. However, the maximum length without laterals for most of the aërial roots is usually between 4 and 40 centimeters in this area.

When a freely hanging aërial root becomes anchored in the substrate, prolific lateral root formation may occur in the subterranean portion. In addition, however, new laterals may arise on the aërial portion with no apparent stimulus from injury (FIG. 6). This contrasts with the development of lateral roots before anchorage and is evident in the aërial portions of anchored *Clusia* and *Ocotea* roots.

Growth rate. The growth rate appears to be very variable through time as single uninjured roots are found to have variations in diameter and color suggesting growth pulses. Injury, of course, prevents growth and a decrease in length may result. Injury may be environmentally induced and desiccation is a probable agent.

The growth in length of the aërial roots of ten species was measured as it occurred during a 7 to 11 day period in December, 1967. The growth rates varied from 0 to 2 millimeters per day. This may be contrasted with the rate of growth of the aërial roots of *Rhizophora mangle* (the red mangrove) in Miami, Florida, which grew up to 7 millimeters in length per day during the months of April and May, 1968 (P. B. Tomlinson and author). In the soils of New England, roots may achieve growth rates of 12 millimeters per day during summer (W. H. Lyford and author). Thus the growth rates of aërial roots in the equable climate of the elfin forest may be regarded as low.

Secondary thickening. Many of the aërial roots of trees and shrubs may commence secondary thickening well before they reach the substrate. Examples of this may be found among the roots of *Ocotea*, *Clusia*, *Miconia pachyphylla*, *Tabebuia*, *Haenianthus* and *Eugenia*. In FIGURE 5 thickening of the root of *Tabebuia* near the point of attachment to the branch may be observed readily.

The aërial roots of *Ocotea* near the base of the plant may become anchored and considerably thickened. In cross section these roots are oval with the larger axis vertical and the morphological center in the lower half. In *Clusia* however, similar roots are more nearly circular in cross section and arise from up to 3 meters above ground.

Aërial Roots of the Vines

Origin. The aërial roots of vines are often found within the leafy zone of the plant (in contrast to those of trees and shrubs). Not all roots are found within the leafy zone but this is a common occurrence. In the species under study here all the aërial roots were associated with a node in one way or another. This is not always the case with vines: in some vine species the roots are apparently formed at random along the stem as in the ornamental *Hydrangea anomala* ssp. *petiolaris* and in the native *Rhus radicans* in Massachusetts.

The associations with the node were varied. *Marcgravia sintenisii* has up to four aërial roots produced in a row parallel to the axis of the stem and running proximally from the leaf base. *Gonocalyx*, an ericaceous vine, has a similar arrangement of aërial roots but on the distal side of the leaf base. The genus *Mikania* of the family Compositae has roots formed between the leaf bases or in an axillary position. *Psychotria guadalupensis* (Rubiaceae) has aërial roots formed just distal to and between the nodes. Such specific positions of origin suggest a regular formation of root primordia in these positions as the shoot grows.

In *Marcgravia* at least, it appears that new roots may be formed on

TABLE 2. **The aërial roots of the vines**

				Tip Properties			
Species	Roots in leaf zone?	Roots assoc. with nodes?	Max. number per node	Max. diameter (mm.)	Color	Rigidity and alignment	Laterals without injury?
Rajania cordata	yes	yes	1	0.3	white	flexible, wrinkled	—
Peperomia emarginella	yes	yes	1	0.1	white	bent, flexible delicate	—
Marcgravia sintenisii	yes	yes	4	0.6 (2.0)	cream	unbent, tend to be rigid	—
Gonocalyx portoricensis	yes	yes	5	0.3	white	flexible, crinkled	+
Hornemannia racemosa	yes	yes	1	0.3	white to pale pink to brown	crinkled, flexible	+
Ipomoea repanda	yes	yes	2	0.5	white	weak flexibility, curves	—
Psychotria guadalupensis	yes	yes	4	0.5	cream to light green	flexible, crinkly	+
Mikania pachyphylla	yes	yes	3	0.5	white to pale green	flexible, crinkled	—

old parts of the vines where they may be 2 or 3 centimeters in diameter. In this case the tips produced may have different properties from those formed within the leaf zone. In TABLE 2 (summarizing the data collected for the vines) the value for tip diameter recorded on older wood is noted in parentheses. Whether these new roots develop from latent primordia formed in association with the leaves is not known.

Tip properties and lateral root formation. The tips of the aërial roots formed within or close to the leaf zone are usually very fine. Approximately 0.1 mm. to 0.6 mm. diameter is the range encountered. The larger value in this range was recorded for *Marcgravia*, which has rapidly tapering aërial roots — from 0.8 mm. to 0.4 mm. over one centimeter of length. In this species aërial roots with a length greater than a few centimeters have not been found free-hanging in or near the leafy zone.

Some of the species were observed to have lateral roots formed apparently without injury to the parent. The species in which this was observed are recorded in TABLE 2.

The aërial roots of vines appear rather fragile in comparison with those of trees and shrubs, both because of their small diameter and the fact that they are often irregularly bent.

AËRIAL ROOTS OF THE HERBS

Origin. The aërial roots of herbs may be found within the leafy zone in most species. In most cases also the roots are formed at well defined morphological positions. TABLE 3 presents a summary of the data. *Selaginella* and *Dilomilis* both form roots at the branch junctions. Most of the other species root only at the nodes but internodal roots have been observed in *Pilea yunquensis*.

Tip properties and lateral root formation. The roots of the *Selaginella* are green as are the apices of the aërial roots of *Dilomilis*. In the latter species the region of the tip behind the apex was creamy in color and green only at the apex.

A few of the species were observed to have lateral roots formed in the absence of injury and these are recorded in TABLE 3.

DISCUSSION

Frequency of formation of aërial roots in species. Some species such as *Miconia pachyphylla* are usually found with aërial roots but other species have been found to have no aërial roots. The reasons may be that too few specimens have been examined or that they do not in fact ever form them under the conditions experienced in this area. Woody plants such as *Cleyera* and *Ardisia* were not seen with aërial roots, but these species are not common on the site.

Some of the epiphytes, such as the bromeliad *Vriesea*, had readily visible roots but these were not observed hanging free of the host. Similarly no root of the vine *Peperomia hernandiifolia* was seen hanging free.

TABLE 3. **The aërial roots of the herbs**

			Tip Properties			
Species	Min. distance leaf zone (cm.)	Roots only at nodes?	Max. diameter (mm.)	Color	Rigidity and alignment	Laterals without injury
Selaginella krugii	0	branch junctions	0.4	green	flexible but wiry, unbent	–
Isachne angustifolia	0	yes	0.6	white to pale green	straight & flexible	–
Dilomilis montana	2	branch junctions	1.8	green apex, cream behind	corrugated, flexible	–
Pilea obtusata	0	yes	0.3	white to pink	curled, flexible	+
Pilea yunquensis	0	no	0.2	reddish brown	curled, flexible	+
Sauvagesia erecta	0	yes	0.2	pale cream	straight & flexible	–
Begonia decandra	1	yes	0.4	white to tan	straight & flexible	+

One large *Cecropia peltata* was examined and found to have secondarily thickened "prop" roots, but no tip was seen above ground and in this case it appeared that the roots had been exposed by erosion. Some of the grasses and carices had a preponderance of leafy tissue above ground, and very little stem tissue and no aërial root was observed. The scrambling grass *Isachne* has many stems above ground and in the most humid situations aërial roots are found. The tree fern *Cyathea* forms aërial roots in some cases but these were not studied. Other ferns were also omitted from the investigation.

The environment and aërial root formation. Two stages may be distinguished in aërial root formation. The first is the production of a primordium either in association with normal growth and development of the shoot or formed *de novo* under certain conditions and in older regions of the plant. The second stage is the growth of the primordium. At least some species appear to form primordia regularly on the shoot, among them many of the vines and herbs. *Selaginella* has roots associated with branch junctions and primordia are formed in these positions regularly during development (Webster & Steeves, 1967).

Several factors are known to influence the formation of aërial roots. In *Populus nigra* for example, root primordia are present in the aërial stem but no aërial root is formed. Under the proper conditions of moisture and darkness however, aërial roots may be forced into active growth (Shapiro, 1962). However, the "proper conditions" for the appearance of aërial roots in various species differ. The aërial roots of *Rhizophora mangle* in Florida, for example, often show great development in environments where there is always a high light intensity. In the elfin forest light intensities are low and roots often arise beneath a mass of cryptogams, but the importance of the light factor can only be surmised at present.

Mechanical tissue and/or lack of injury may be important in some species as roots are often associated with new shoots, which may cause wounding of the parent shoot as they grow and which are composed of relatively soft tissue. The humid environment may be essential to outgrowth of roots as desiccation seems to be an important cause of injury to apices.

Lateral root formation. The freely hanging aërial roots of the plants in the study area rarely produced laterals in the absence of injury. However, when these roots enter the soil they branch immediately. Thus there are two types of control to the lateral root formation, an external (environment) and an internal (through injury). In the external environment of the aërial root the high humidity appears to be incapable of inducing lateral root development in many of the species, and some other environmental factors such as light intensity and nutrient-environment may be involved.

Some plants with aërial roots fail to develop laterals in the absence of injury, although many herbs and vines do not. The major member of the latter group is the palm *Prestoea*, but its lateral roots are inhibited.

One cause of injury seems to be desiccation. The dead apices of the roots sometimes show no signs of physical injury but the rare periods of desiccation seem a likely cause of death. One case of physical injury was observed on a root of *Clusia*, which appeared to have been chewed.

Function of the aërial roots. Aërial roots may enable a plant to spread vegetatively to the surface of another plant or to the soil away from the base of the parent plant. If the roots from the shoot system reach the ground the path that nutrients have to travel will be shortened and this may be an advantage. Vegetative spread from detached portions of a tree is possible as broken branches with no connection to a parent tree or the soil have been seen with new roots and shoots. In an area where trees and shrubs may be pulled over by vines and/or the weight of epiphytes and water, or toppled on the steep slopes after a little soil erosion, the ability to form aërial roots may constitute a valuable property for survival.

The presence of copious quantities of a gelatinous material on the apices of the aërial roots of the *Hedyosmum* is remarkable. Samtsevitch (1965) has noticed relatively small gel-like caps on the roots of some plants such as *Zea mays* in soil and artificial media, and considers that they have several important functions including protection of the root apex from mechanical injury, improvement of the root penetration of soil, and promotion of root hair growth. In the area of study it seems that protection from desiccation is the most likely function of the material, as death of tips follows its removal (R. A. Howard, personal communication).

The anchored roots of *Clusia* and *Ocotea* certainly provide support to their parent trunks. In their absence however, subterranean roots may provide the plants with the same stability. Thus the adaptive value of these roots for support is questionable.

SUMMARY

In the humid conditions of the Puerto Rican elfin forest many freely hanging aërial roots are found on the trees, shrubs, vines, and herbs. Those of the trees and shrubs are not found in the leafy zone of the shoot system and lateral root development in the absence of injury is rare. In contrast the aërial roots of the vines and herbs arise in definite morphological positions within the leafy zone of the shoot system, and more commonly develop laterals in the absence of injury. Patterns of lateral root development may be distinctive, but other properties of the root tips such as color, rigidity, alignment, diameter, and the presence of secretions, may also contribute to the character of the aërial roots of the various species.

ACKNOWLEDGMENTS

This study was carried out over a period of 15 days at Pico del Oeste in the Luquillo mountains of Puerto Rico. The trip was made possible by a grant to Dr. R. A. Howard, director of the Arnold Arboretum of Harvard University, by the National Science Foundation (Grant # GB–3975). Excellent housing facilities close to the site were kindly provided by Mr. J. B. Martinson. Mrs. R. J. Wagner helped with the identification and checking of plant specimens.

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THE ECOLOGY OF AN ELFIN FOREST IN PUERTO RICO, 7. SOIL, ROOT, AND EARTHWORM RELATIONSHIPS

WALTER H. LYFORD [1]

ECOLOGICAL STUDIES of a small area of elfin woodland on the narrow ridge top of Pico del Oeste, a 1000 meter-high mountain on the extreme eastern tip of Puerto Rico where rainfall is about 453 centimeters per year (Baynton, 1968), were made over a period of two years by several investigators. The background for the overall study has been given by Howard (1968).

This report points out some soil and vegetation relationships and the possible importance that earthworms and other fauna have on soil genesis.

PROCEDURE

Soils were examined and described in three trenches, 6 to 15 meters long and about 1 meter deep, dug across the 10 to 15 meter-wide ridge of Pico del Oeste (FIG. 1) at representative sites. Soil horizons were mapped at a scale of 1:12 and a few soil samples collected for approximate deter-

FIG. 1. The broad western side of Pico del Oeste. The soil study was along the narrow spine and extended from a location near the right hand side of the photo to the summit.

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[1] Field work was carried out during March 1–13, 1967, as a part of National Science Foundation Grant GB:3975 to R. A. Howard, whom I thank for making the study possible. W. L. Theobald, W. E. Gensel and R. W. and Mrs. Wagner gave laboratory and field assistance, and A. R. Gill, a photograph, for all of which I am very grateful.

minations of ignition loss, pH, and moisture content. Weights of forest floor and the epiphyte-soil blanket on tree stems were obtained. Earthworms were collected and their influence on the soil studied.

RESULTS

Soil characteristics. On the narrow ridge of the mountain the soil, developed on residuum from fine grained volcanic rock, is wet and has a muck-like surface 25–30 centimeters thick. This mucky surface thins out and disappears as the soil becomes steep. Under the mucky surface there is a gray gleyed horizon mottled distinctly with browns, yellows, and reds. Under this, in turn, lies reddish yellow, massive, plastic, nonsticky clay, in places with a noticeable content of soft, weathered rock fragments. With greater depth the soil becomes redder and more fragments of weathered rock are present. The relationship between the horizons is shown in the scale diagram of the three trenches (Fig. 2).

Following is a detailed description of the soil. The terms are those in common use in the United States (Soil Survey Staff, 1951).

01 horizon 3–0 cm.	Forest floor: a continuous cover of recently fallen leaves and twigs with up to 25 percent of the surface covered with living green bryophytes (mostly liverworts) and algae; most leaves are fragmented

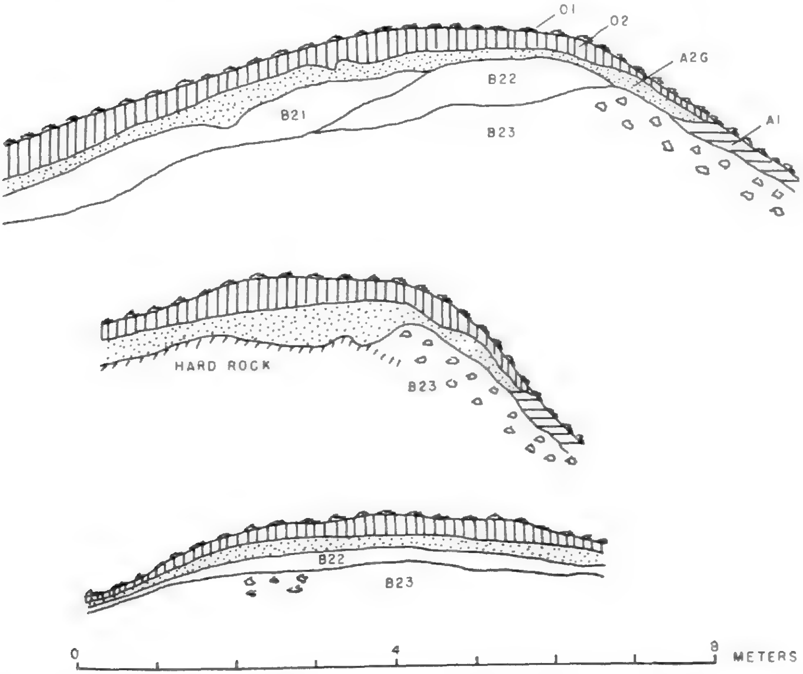

Fig. 2. Scale diagram of the soil horizons in three trenches dug across the narrow spine of the mountain.

and lie directly on the surface of the underlying soil or on roots; in most places under the leaf and twig cover there is a 2–2.5 cm. thick "root floor" consisting of clean coarse and fine roots.

O2 horizon 0–30 cm. Dark brown or very dark brown (7.5YR 3/2 or 10 YR 3/2 wet) mucklike material so well decomposed the original plants cannot be identified, about 40–60 percent organic matter as judged from ignition loss; massive in place and well permeated by fine grass-like roots and some woody roots; nonplastic, nonsticky; very large earthworms and earthworm tunnels are common.

When initially described this material was termed a peat primarily because of its brown rather than black color and also because it seemed to have less of the dark colored soluble substances that characterize many mucks. The fact that the original plants cannot be identified from the remains in the soil takes the material out of the peat class.

A1 horizon 0–30 cm. Reddish brown (5YR 4/3 wet) or dark reddish brown (5YR 4/2 with many medium, distinct mottles of dark brown (7.5YR 3/2) and olive gray (5Y 5/2), in some places with mottles of strong brown (7.5YR 5/6) and yellowish red (5YR 5/6); "silty clay loam"; massive; friable, plastic, nonsticky; many roots; distinct 1 mm. red borders around many of the dead roots; large earthworms present and many earthworm tunnels; no or few coarse fragments of strongly weathered rock.

This horizon is adjacent to the wetter A2g horizon and is at the top of the very steep slopes. As a whole this horizon has a brown color in contrast to the overall gray color of the A2g. The texture feels like a silty clay loam of the northeastern United States but the soil probably is mostly clay.

A2g horizon 30–60 cm. Dominantly olive gray (5Y 5/2 wet) with 10–20 percent dark brown (7.5YR 3/2) or reddish brown (5YR 4/3) distinct moderate size mottles; "silty clay loam"; massive; firm in place, plastic, nonsticky; many grass-like roots, many large earthworm tunnels filled with dark brown organic matter.

In places this horizon can be divided into a somewhat browner upper portion in which the colors are dark brown (7.5YR 3/2) and light olive gray (5Y 6/2) in about a 60–35 proportion with the remainder made up of red and black fine mottles. The gray mottling in this upper portion is distinct and as a whole this portion appears to be gray, but somewhat less gray than the lower part.

B21, B22 horizons 60–90 cm. Reddish yellow (7.5YR 6/8, 7/8 wet) with reddish yellow (5YR 6/8), yellowish red (5YR 5/8) and red (2.5YR 5/8) distinct mottles; "silty clay loam"; massive; firm to friable and digs out readily with a shovel, plastic, nonsticky, dense and nonporous; in places with up to 5 percent very pale brown (10YR 7/3) or nearly white fine scattered mottles; few 5–15 cm. pieces of saprolite generally with a noticeable yellow or red rind, hard but can be broken with the edge of the trowel; organic matter-filled earthworm tunnels are common but fewer than in the A2g horizon.

The B21 and B22 horizons are generally yellowish in the upper part, becoming redder with depth. Mottles are distinct and not noticeably in a reticulate (network) pattern. The B21 horizon shown in FIG. 2 has more conspicuous mottling than the B22 and was designated as a gleyed horizon (B21g) in the field. It does not, however, have enough low chroma colors to qualify as a gleyed horizon. Colors of the B2 horizon have high chromas and are "bright."

B23 horizon 90 cm. and deeper

Weak red (10YR 4/4) and strong brown (7.5YR 5/6) "silty clay loam"; massive; firm, dense, plastic, nonsticky; contains up to 60 percent angular, hard but thoroughly weathered rock fragments that break readily by a blow from the edge of a trowel.

The overall color of this horizon is reddish and this contrasts strongly with the yellowish colors of the B21 and B22 horizons.

Below the B23 horizon at depths ranging from one to several meters is red, yellowish red, and reddish yellow thoroughly weathered rock (saprolite) that retains its original stratification but is partially fragmented and the fragments can be broken readily. The bedrock probably is a fine-grained volcanic.

Analyses. The ignition loss, moisture and pH analyses of soil samples collected from the trenches are listed below. These analyses are approximate and are presented as preliminary data to provide a rough idea of the range of some of the soil characteristics.

HORIZON	Moisture to nearest 5 percent (Oven dry basis)	Ignition loss to nearest 5 percent (Oven dry basis)	pH Glass electrode 1:1 water
02 (mucky)	270	50	4.4
	320	40	4.3
	—	65	—
A1 (edge of slope)	90	20	4.7
	—	20	—
A2g (grey, gleyed)	100	25	4.5
	80	20	4.9
	—	10	—
	—	15	—
	—	10	—
B22 (yellowish)	—	15	—
	—	5	—
B23 (reddish)	60	5	4.8
	55	10	4.7
	—	5	—
	—	5	—

Although the mucky horizon (02), by feel, seems to be mostly organic matter, the ignition loss analyses indicate that about half is mineral matter. The gray, gleyed A2g horizon, on the other hand, seems by feel to be highly mineral but actually has 10 to 20 percent organic matter content.

The soil is very strongly acid throughout as would be expected for any soil developed from strongly weathered rock under extremely high rainfall.

By feel, the soil in the mineral horizons seems to be sandy, but it is probably quite high in clay-sized particles. Clay, in many soils of tropical regions, is aggregated into silt or sand-sized particles and these are not readily dispersed between the fingers by rubbing, or even by the use of dispersing agents in the laboratory. Determination of moisture characteristics, however, reveals that a high proportion of the soil is of clay size. This property is indicated in many of the soils sampled in connection with soil surveys currently being made in Puerto Rico. (Soil Survey Investigations Report No. 12, August, 1967. U.S. Dept. of Agri. Soil Conservation Service in cooperation with Puerto Rico Agri. Exp. Station.) Analysis of a soil (S58PR–11–1) collected about two miles away from the Pico del Oeste site shows that on the basis of moisture characteristics some of the "sand" and "silt" particles have clay-like properties.

The soil on Pico del Oeste seems to have the requisite properties for an oxic horizon and it qualifies for an Oxisol in the 1965 USDA Soil Classification (Soil Survey Staff, 1960, 1967). It qualifies as a Latosol in the older classification scheme.

Water in the soil. The peaty soil of the narrow ridge top is continuously wet judging from observations made during the course of the study. The path that bisects the area is always muddy and water-proof footwear is required if the feet are to be kept dry. There is a more or less continuous drip of water from the epiphyte-blanketed trees even when the sun is shining.

When the trenches were being dug water moved into the excavations primarily by seepage rather than by overland flow. This seepage water came into the trenches from all horizons suggesting that the whole soil is waterlogged and not just the upper highly organic portions. For example, when the trenches were being dug, earthworm tunnels in the B2 horizons were full of water and under a hydrostatic head, and they drained suddenly and conspicuously when exposed by the shovel.

Moisture content of the mucky horizon is high and so is that of the mineral horizons. This high content of moisture is evident if a clod of freshly collected soil is left in the sun; almost a whole day of good drying conditions is necessary before the surface of the clod dries.

A few observation wells 20 to 30 centimeters deep were made to obtain some idea about the fluctuation of the water tables in the mucky surface horizon. In these simple unlined wells, depth to the water surface varied considerably from day to day during the period March 1 to April 17, 1967, and there were only a few days when water did not stand within these shallow wells. During the period April 17 to June 15, some water generally was in the wells but the fluctuation from day to day was less.

Forest floor characteristics. A forest floor horizon, (01 horizon) about 2 to 4 centimeters thick lies on the mucky horizon (02 horizon).

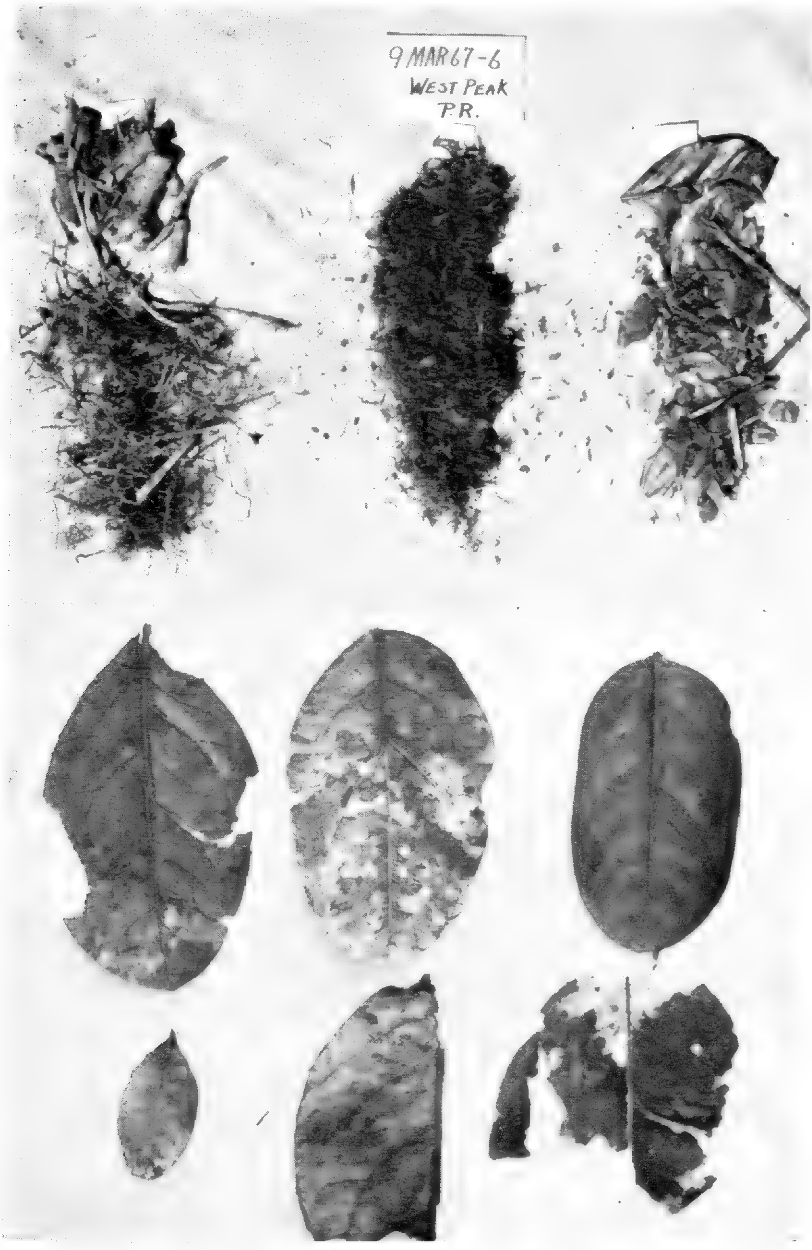

FIG. 3. Components of the forest floor from an area 30 × 30 cm. square. ABOVE: Tree leaves in various stages of disintegration are on the right, living plants (mostly liverworts) in the middle, roots on the left. BELOW: Entire and fragmented tree leaves.

This forest floor is readily separated into three components; namely, living plants growing on the fallen leaves (mostly liverworts and algae), fallen tree leaves and twigs, and roots (FIG. 3). Samples were collected from six areas 30 × 30 centimeters square and the average oven dry weight was determined for each component.

Living plants	314 g/m^2	(2800 pounds/acre)
Fallen tree leaves	78 g/m^2	(700 pounds/acre)
Roots	577 g/m^2	(5200 pounds/acre)

Bryophytes (mostly liverworts) growing on the fallen leaves occupy perhaps 10–25 percent of the area. Some are growing in place; others apparently were growing on the leaves while the leaves were still attached to the tree and continued growth after the leaves fell. In addition to the bryophytes many of the fallen leaves are about half covered by a thin layer of green algae.

Fallen leaves and twigs completely cover the surface of the soil and no bare areas can be seen. Apparently leaves of these evergreen trees fall one by one throughout the year. Most are entire when they fall but after being on the surface of the soil for a short while show some signs of disintegration: parenchyma is removed and the leaves are broken into fragments (FIG. 3). The amount of organic material (other than roots) above the mucky 02 horizon at any one time is about equivalent to the amount that falls yearly in most deciduous forests in the northeastern United States.

Clean woody roots lie in a layer between the fallen leaves and the mucky 02 horizon. This "root floor" is about 2 to 2.5 centimeters in thickness and there are many places where the roots arch away from the surface leaving open spaces beneath.

Roots in the soil. Both aërial roots and roots in the soil are common. The characteristics of aërial roots on the study area have been described by Gill (1969).

Many of the roots in the soil grow between the litter and the mucky surface and constitute the previously described "root floor." The roots in this layer are essentially free of adhering soil and are as clean as though washed with water (FIG. 4). Possibly some of these roots are clean because they have never grown in the soil beneath. Gill (1969) observed some roots growing above the soil surface; in fact, some were even exposed to the atmosphere.

Woody roots on or just under the soil surface, extend for at least 7 to 8 meters laterally and are well exposed in the path (FIG. 4). On the basis of observations made while digging the trenches it is estimated that 80–90 percent of the woody roots are either just under the fallen leaves in the "root floor" or are within the upper 2 to 10 centimeters of the surface of the soil. These woody tree roots seem to be much the same in overall growth habits as those of forest trees at the Harvard Forest in central Massachusetts (Lyford & Wilson, 1966).

FIG. 4. Woody roots in the soil. LEFT: Layer of clean roots that commonly exists just under the leaf litter. RIGHT: Woody roots in the upper portion of the soil that have become exposed in the path.

Vertically descending grass-like roots are numerous in the gray gleyed A2g horizon and give the soil material a sod-like character. Some of the dead roots in this horizon are bordered by a thin layer of red soil and these vertical "pipes" are noticeable when the soil is examined. These pipes are well known features in many wet soils.

Amount of epiphytes and soil on tree stems. A rather large mass of epiphytes and roots grows on the stems and branches of the trees. In addition there is brown soil-like material adhering to the bark and intermingled with the roots and green plants that blanket the stem. This brown mucky material is essentially identical in appearance to the brown mucky material that makes up the surface layer of the soil. To obtain some idea of the amount of this soil-like material on the trees all material around a portion (20 centimeters long) of the stem of each of six trees was removed. This was subdivided into portions comparable to those used for the forest floor, namely, living plants (mostly liverworts), roots, and soil-like material. Subdivision was made under water to enable complete separation of the soil-like material. Following are the results expressed as grams of oven dry material per square meter of stem area.

Living plants	265 g/m^2
Roots	125 g/m^2
Soil-like material	112 g/m^2

Weight of green material on the stems is 265 grams per square meter compared with 314 grams for the leaves on the forest floor. Together green material and roots on the stem total 390 grams per square meter as compared with 392 grams for the combined leaves and bryophytes on the forest floor. In other words, the amount of organic matter (other than that which makes up the soil-like material) on tree stems is not far different from that on the surface of the soil if compared area for area.

A few determinations of ignition loss were made on the soil-like material on tree stems and branches. Most of the material has a 90 to 95 percent loss on ignition so its origin probably is from the decomposition of plant material in place. The one sample with an ignition loss of 64 percent may have had a different origin.

Probably the soil-like material on stems and branches is largely the result of the decay of plant tissue in place. Some of the material however, is granular and definitely coprogenic. Fauna of various kinds are common under, and in, the plant material which clothes the stem. Millipedes, centipedes, enchytriads, beetle larvae, tiny red ants and sow bug-like insects are numerous and a black earthworm 10 to 15 centimeters long, like those in the soil, was found on one tree stem at a height of about 1 meter. This amount of faunal activity raises a question about the origin of the soil-like material. Conceivably a large part of it could originate in the soil and be carried into the trees within the bodies of fauna. In such a case, however, the casts would probably have a rather large content of mineral matter; larger than that indicated by the analyses of the

FIG. 5. Soil occurs in some trees. LEFT: Termite nest in a tree by a roadside within sight of the study area. RIGHT: Termite tunnels on a tree stem. *W. L. Theobald* is used for scale.

soil-like material observed on the study area. At lower elevations termites have large nests high in the trees (FIG. 5). They carry a good deal of material into the trees so the process leading to the presence of soil-like material in trees is not unusual.

Earthworms and their significance. Earthworms are common in the soil of the study area and were collected from each of the three trenches (FIG. 6). Two species were collected but have not yet been identified. One species is black, about 15 to 20 centimeters long and weighs about 5 grams. It seems to be most common in the upper part of the soil and, indeed, a single specimen was observed on a tree stem about 1 meter above the soil surface where it was well protected by the wet epiphyte blanket. The second species is very large and has a dark gray or dark olive color. It is up to 60 centimeters in length and 10 millimeters in diameter. Each of the earthworms weighs about 30 grams. These large earthworms are common to depths of 50 centimeters and are in all the upper horizons. Their tunnels are conspicuous when filled with dark-colored soil material and especially so in the gray gleyed A2g and the yellowish B2 horizons (FIG. 7).

Roughly 1 to 5 percent of the soil mass in the upper 50 centimeters is occupied by earthworm tunnels. Tunnels in the mineral portion of the soil are made by ingestion of soil material rather than by simple pushing aside, and some of the ingested mineral material later is expelled on the surface. Organic matter also is ingested in large amounts. Leaves on the surface of the soil serve as food and some of the disintegration of leaves

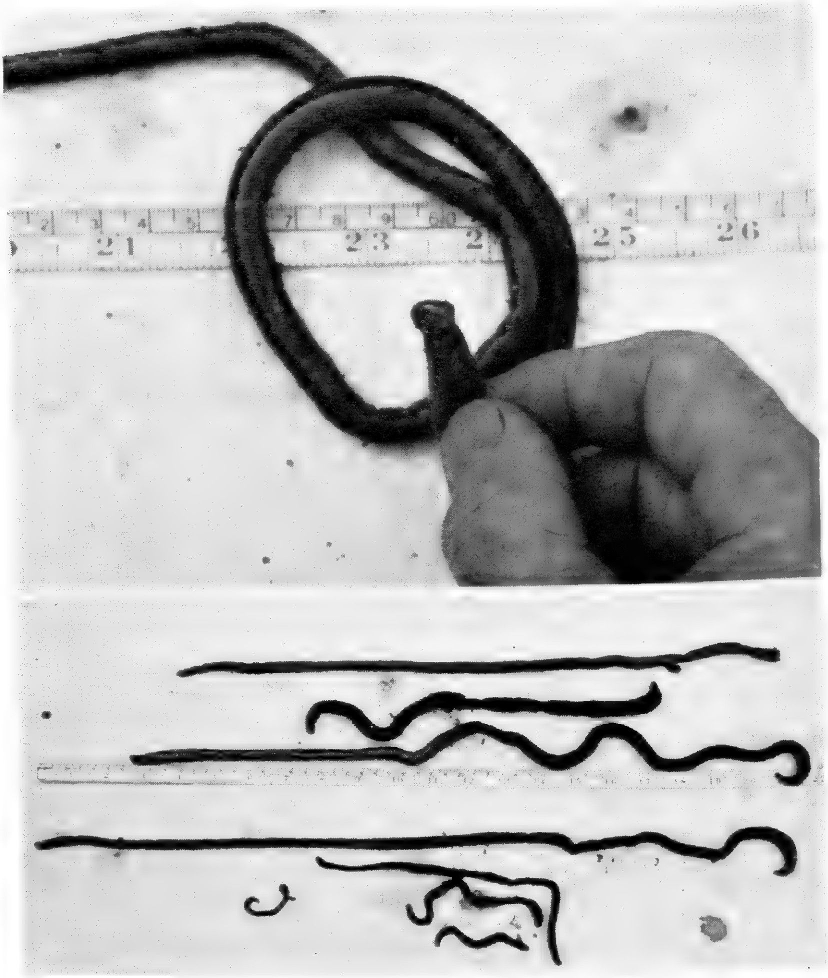

FIG. 6. Two species of earthworms from the study area. ABOVE: Close-up of one of the large olive specimens. BELOW: The four large olive earthworms shown in the upper part of the photo. are up to 60 cm. long and one cm. in diameter. The smaller black earthworms shown in the bottom part of the photo. are up to 20 cm. long.

shown in FIG. 3 is the direct result of earthworm action. Earthworms probably ingest some of the soil material near the root floor and, in fact, these roots may have their clean appearance because of the earthworms. Puddled masses of earthworm casts 5 to 10 centimeters in diameter are on roots at intervals of about 40 to 50 centimeters, showing that earthworms are active on the surface; and it is possible the open spaces beneath the root floor are the result of earthworm action.

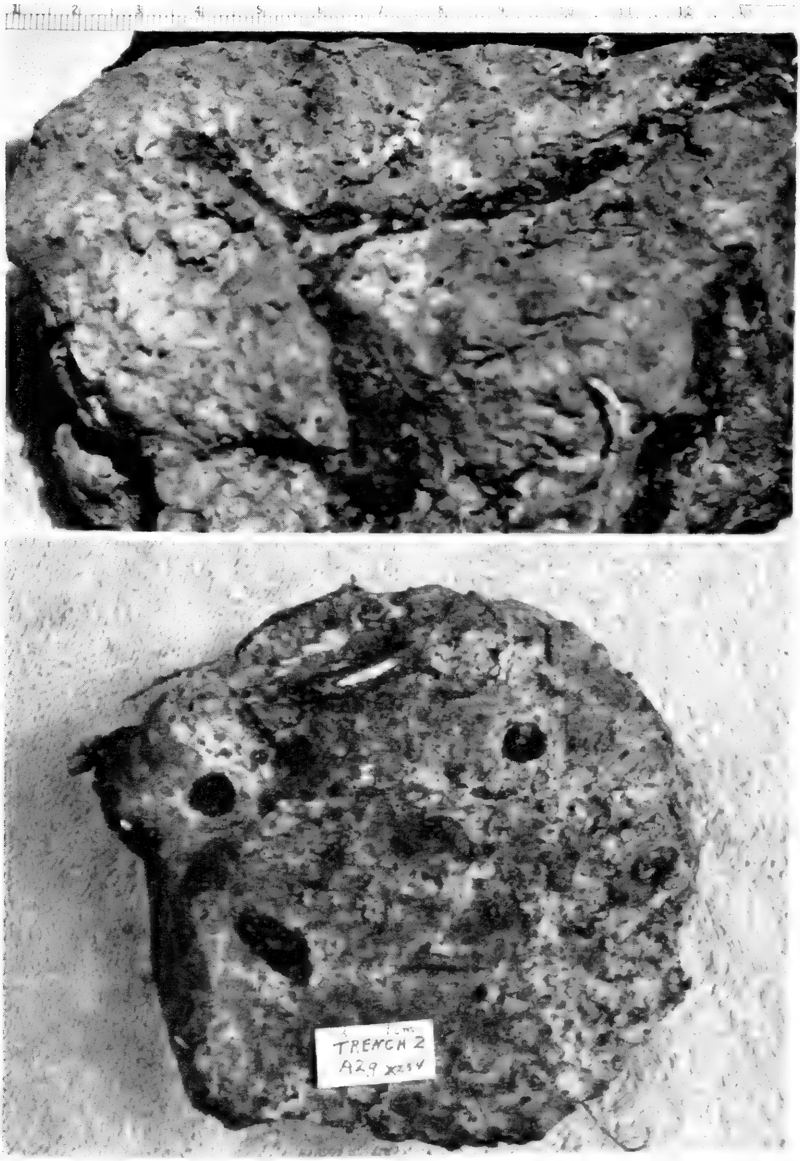

FIG. 7. Dark colored areas in the A2g clods are earthworm tunnels filled with soil of high organic matter content. Scale in the photo. above is in centimeters.

Organic matter ingestion is also evident because of the dark color and the high ignition loss of the casts in the tunnels. In the A2g horizon the ignition loss for two samples of earthworm casts from the dark-colored tunnels was 65 and 75 percent, whereas that of the soil immediately adjacent was 10 and 15 percent. A single sample of earthworm casts from a tunnel in the B22 horizon had an ignition loss of 50 percent; that of the soil immediately adjacent was 5 percent.

Thus there is considerable mixing of the organic and mineral matter of the soil within the bodies of the large earthworms, and a rather great amount of transportation from one place to another. This mixing and transportation is not rapid enough, however, to cause the soil horizons to lose their identity.

In addition to the mixing and transportation there is some segregation of the larger particles because they are too large to be ingested.

DISCUSSION

The climate and vegetation of the study area very likely is much the same now as it has been for centuries because of the particular location of the Pico del Oeste in respect to the ocean and the constantly blowing easterly trade winds. The soil, therefore, probably represents a kind that has developed and been maintained under continuously wet tropical conditions. Soil development processes may have been modified from time to time by addition of volcanic ash, but no known additions of this kind have been made recently.

Continuously wet conditions have permitted the build-up of a mucky surface because erosion on the narrow ridge is slight, and decomposition and disintegration processes are not rapid enough to cause complete mineralization of the organic matter. A considerable amount of organic matter is returned to the surface of the soil each year not only from the dead leaves of trees but also from epiphytes that grow on the leaves.

The B horizon in this soil seems to qualify as an oxic horizon. This indicates that the minerals of the original bedrock from which the present soil materials have been derived, are thoroughly weathered. The remaining materials are probably high in kaolinitic clay and the amount of iron and aluminum compounds present are considerably higher than in the unweathered bedrock. In general, this would mean a lack of available nutrients, but where the soil has a highly organic surface this is probably not the case, because organic matter has a high cation exchange capacity and holds the nutrients so they are not readily leached out.

Action of large earthworms in soil development seems to be significant. Their large tunnels allow rapid movement of water from place to place in the soil. Their movement and mixing of mineral material and organic matter by ingestion is estimated to occur actively in at least 5 percent of the soil volume. They do not seem to use the same tunnels all the time but make new ones, so much of the soil material in the upper foot or two has been passed through their bodies at one time or another.

Earthworm casts are numerous at the surface and are readily observed when the forest floor is removed. The rate of this deposition on the surface suggests that there is a minimum of a centimeter or two of soil added to the surface every 100 years. This estimation is based on similar studies with ants (Lyford, 1964). But if there is this much action there is a question how the various horizons are able to preserve their identity. Possibly, the earthworms we see now are recent colonizers or perhaps they are now experiencing an unusual population surge. The large earthworms are known to occur elsewhere in the island (Luis Maldonado, pers. comm.), but probably are confined to certain restricted habitats.

On steep slopes, the action of earthworms in returning soil to the surface is considerable. Their action was observed not only on the steep slopes of the study area but also in two other places in the Luquillo Mountain area, on steep slopes. This constant return of earthworm casts to the surface may have some rather important geomorphological implications because fresh soil material is always available on the surface for transport by running water or gravity.

Earthworms not only return soil to the surface, they also consume the leaves that fall on the surface of the soil. They do not, however, consume all the leaves but allow enough to remain to form a complete cover of the soil, thus, their activities are not completely detrimental and, perhaps they have achieved a desirable ecological balance.

Presence of a considerable amount of soil, or at least soil-like material, on the stems and branches of trees suggests that some epiphytes may have their roots in soil even though the entire plant is on a tree. "Soil" in trees raises a problem for the soil scientist because he is not in the habit of finding it here, and indeed, this makes some revision of the definition of soil in order. Yet termite mounds several meters in height are common in tropical regions. These insects not only return soil material to the surface of the soil, they raised it several meters above the original surface. It is not too much of a mental jump then to think of soils in trees, particularly when it is readily apparent that some kinds of termites, ants, and other soil-moving fauna make their nests in trees.

SUMMARY

Soil on the steep narrow ridge of Pico del Oeste is wet and the mucky surface, 25 to 30 centimeters thick, has about 50 percent organic matter. Fallen tree leaves, on which grow liverworts and algae, lie on a layer of clean roots and these in turn are on and in the soil. Tree stems and branches are blanketed with liverworts, algae, and other epiphytes, and the amount of organic matter on the stems per unit area approximates that on the surface of the soil. Soil-like material occurs on the stems and branches of trees. Some may be carried up from the soil by fauna. Large earthworms up to 60 centimeters long and 1 centimeter in diameter are common in the soil and ingest and move large amounts of it.

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THE ECOLOGY OF AN ELFIN FOREST IN PUERTO RICO, 8. STUDIES OF STEM GROWTH AND FORM AND OF LEAF STRUCTURE

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In the first paper of this study (Howard 1968), the species comprising the elfin forest on the summit of Pico del Oeste were listed in systematic order, classified by growth form, and indicated in their frequency through transect and plot studies. It was shown that 14 taxa of monocotyledons and 40 taxa of dicotyledons were the common components, and that these could be distinguished as 25 taxa of woody trees or shrubs, 19 taxa as herbs or herbaceous vines, 4 taxa as woody climbers, and 6 taxa as epiphytes.

Various suggestions to explain the reduced stature of such a forest were also listed. These suggestions involved the poor aeration of saturated soils, the reduced light reaching the forest through a heavy persistent cloud cover, the reduced transpiration suggested by the high humidity of the atmosphere and frequent and high precipitation, and the restrictive effect on growth of the high wind velocities. The frequent occurrence of trees which had blown over or had toppled due to the subsurface erosion were suggested as factors increasing the density of the woody vegetation.

The present study will consider the nature of the growth of the individual and component species as factors in the form of the forest and will document the presence or absence of characteristics of plant structure which have been observed in comparable forests elsewhere by other workers.

GROWTH AND FORM

The short stature of the elfin forest on Pico del Oeste is in part due to the nature of the growth and of the mature form of the individual species.

The growth and form of a particular plant may be the expression of a normal genetic factor exhibited at the specific, generic, or familial level as the herbaceous, climbing, woody, rhizomatous, or rosette-forming habit. Unusual or abnormal variation from the basic pattern may be an individual characteristic due to biotic factors of the environment or to muta-

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tions. We did find on rare individuals a fasciation of branches resulting from insect damage to an apical meristem. Witches' brooms or comparable fasciations due to fungi or mutations did not appear within the forest under study. A few shrubs, e.g., *Cleyera* and *Symplocos*, had scrambling branches when intermediate in height. Aberrant leaf forms were encountered and these were the result of abnormal laminal development following insect damage of primordia or very young leaves.

The genetic-based habit of the plant can often be a growth pattern associated with the production of flowers. The production of a terminal inflorescence may impede the normal vegetative extension of a stem and result in a branch dichotomy. Vegetative development may be slowed by the development of a resting or short shoot area. Die-back or self-pruning of a limited amount of shoot development occurs in some species to restrict ultimate growth. By contrast axillary or cauliflorous inflorescences can be produced below the apical meristem of the branch or in the axils of subterminal leaves and have no effect on the ultimate habit of the plant.

MONOPODIAL GROWTH

Growth can be described as continuous if a dormant terminal bud is not formed and if leaves are produced in a regular sequence throughout the year. Such a condition is often attributed to tropical forests. The terminal growth of a branch can be interrupted by a resting period, whether a bud is formed or not, and new growth can be by a flush of new leaves with the subsequent lengthening of the internodal zones. The last leaves formed in a flush of growth may be closely associated, indicating that internodal elongation was reduced. The subsequent new apical growth may also have reduced basal internodes, and in fact, the first leaves formed may be aberrant in size and shape and be termed scales or cataphylls. Internodal areas in or above the zone of scales or cataphylls may be longer than average and the flush may again terminate in an apparent rosette of leaves. Such a growth pattern is basically a monopodial production of a long shoot terminated by an area of a short shoot. *Ilex sintenisii* exhibits this growth pattern on Pico del Oeste.

SYMPODIAL GROWTH

Occasionally the long shoot is produced not from the terminus of the short shoot, but sympodially from an axillary bud of a lower leaf. When the growth of a single leader extends vertically, the lateral offset of the new shoot may be noticeable for only a short period of time. It is evident, however, that the leader was terminated by a short shoot development and although the sympodial offshoot continued growth in the same direction, a restriction was imposed in the rate of apical elongation. Such a growth pattern was found in *Torralbasia*.

Within the Pico del Oeste forest nine genera exhibited a restriction in vertical growth by the production of long shoots and short shoots and

FIGURE 1. *Wallenia yunquensis.* Plant grown from seed in greenhouses of the Arnold Arboretum. Short shoots, or terminal rosettes of leaves, and the single unit sympodial branching are all shown.

were further affected by the development of lateral branches. *Wallenia yunquensis* commonly exhibits a vertical shoot producing a single lateral flush of growth as a branch (FIG. 1). The erect main shoot of *Wallenia* may be interrupted by short shoot areas separated by areas of long shoot development. From one or more leaf axils in the short shoot zone a single fast-growing lateral branch may develop which appears naked at the base but does in fact have widely separated cataphylls of very short duration. The naked shoots are terminated with a short shoot zone possessing an aggregate of leaves. The lateral branch may also originate from the area of cataphylls. In *Wallenia* the lateral flush shoots never branched or continued growth beyond the initial flush.

An example of repeated sympodial lateral branching is readily seen in *Ocotea spathulata*. The development of flush shoots appeared to be from a short shoot zone in all cases, but there developed additional and comparable lateral shoots from the terminal short shoot zone of the lateral branch. This growth pattern results in a sympodial development of lateral branches in a flat plane. The principal branches are tiered in appearance, the tiers being separated by an unbranched, seemingly naked stem. This growth form has been described as candelabra-branching, Terminalia-branching, or as pagoda trees.

Corner (1952, p. 32) described this growth pattern for *Terminalia* as follows: "The leader-shoot rather suddenly lengthens into a long vertical finger clothed with a lax spiral of leaves . . . its growth slackens . . . and . . . another terminal rosette is produced. From the base of this rosette several twigs grow out to form the next tier of branches . . . The positions of the branches in successive tiers usually alternate so that only those of every other tier are superimposed."

Lateral branches from the terminal short shoot area may also grow vigorously, producing scales or cataphylls before developing normal leaves and, ultimately, each its own terminal shoot. Corner (1952, p. 31) described the lateral growth as follows: "Each twig which grows from the leader-shoot of the tree does so rapidly and at a wide angle from it; then, as its growth slackens, it turns up at the end and from its lower side, just at the bend, a branch arises to grow out as another twig which will follow the same course by turning up at the end and branching in its turn . . . In the first horizontal part of such a twig the internodes are lengthened; the leaves, or their scars, are widely spaced on the slender stem; and the growth has been rapid so that the new shoot has quickly been thrust beyond the parent rosette of leaves. In the second, vertical or upturned, part of the twig the internodes are very short or absent and the leaves, or their scars, are very crowded on a stout stem so that, while many more leaves are being produced than in the previous stage of the twig's development, its growth in length is much retarded: eventually the twig ceases growing, withers and falls off. When such a limb . . . is growing out from the trunk of the tree, it diverges from its neighbours and begins to branch sideways: this it does by producing every now and again not one twig but a pair of twigs, or even three, which grow out from each other at a wide angle; and thus the limb develops into a fan-shaped leafy spray."

The Terminalia-type of branching was particularly conspicuous in *Ocotea spathulata* (Lauraceae), one of the dominant trees of the elfin forest.

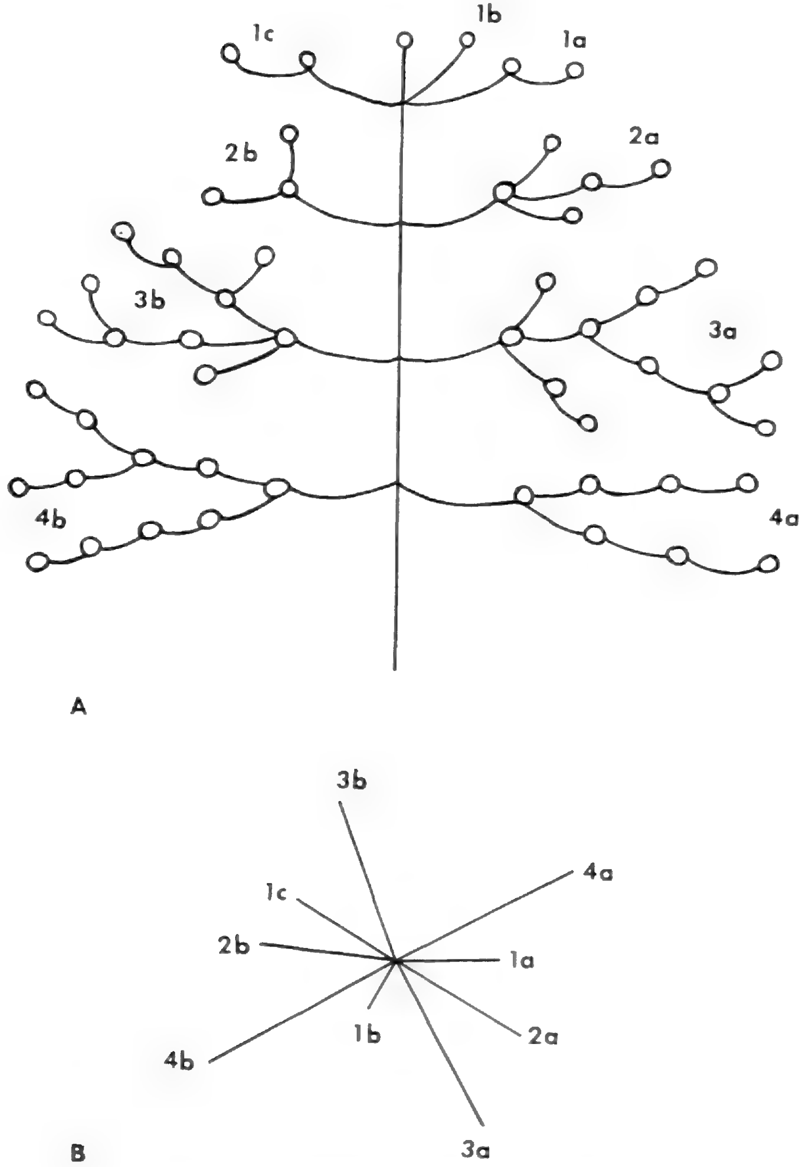

FIGURE 2. Diagram of growth pattern of *Ocotea spathulata*. A. side view showing tiers of repeated sympodial branching; B, view from above showing the relationship of the tiered branches. Drawing by *Pamela Bruns*.

FIGURE 2A shows, diagrammatically, a plant of *Ocotea* of average stature in the forest with four tiers of sympodially developed lateral branches. It is evident that the terminal growth is impeded while the lateral sympodial growth proceeds. Lateral branches at 4a or 4b show four additional flushes of growth while only 3 periods of reactivation of the terminal shoot are evident. The lateral branches, 1a and 1c, have each had one reactivation of growth while the terminal remains static. The relationship of the lateral branches is illustrated in FIGURE 2B and shows a conflict with Corner's observation that the branches of alternate vertical flushes are superimposed.

Specimens of *Ocotea* were found within the elfin forest with 27 flushes of sympodial lateral growth on the oldest branch. Only the last 13 of these sympodial flushes retained any foliage demonstrating a die-back of the upturned short shoot after a considerable period of continued lateral sympodial growth.

Terminalia-branching was also observed in *Ardisia* and *Grammadenia* (Myrsinaceae), in *Torralbasia* (Celastraceae), and in *Calycogonium* (Melastomataceae). Terminalia-branching is conspicuous in *Hedyosmum arborescens* and is due to the naked areas of elongation and the terminal production of leaf pairs or of an inflorescence. Continued growth of the sympodial branches in this species was restricted in many examples by the production of an inflorescence.

The sympodially branched lateral shoots can develop vertical extensions as well as horizontal branches. Vertically developed shoots as elongate leaders of vigorous growth have been observed on the lateral branches of specimens of *Ocotea* and *Calycogonium*, but in all cases additional sympodial branching also occurred from the same upturned short shoot and beyond it.

Attempts were made to induce either vertical elongation of the upturned shoot or the production of new or additional sympodial branching by pruning the leader shoot. During the three year time interval of the study all of the branches which had been pruned of lateral growth failed to respond by any new development from the areas of the upturned shoot. Likewise, vertical leaders when partially or completely decapitated by pruning failed to develop any sympodial lateral branches.

Although many branches were marked along the trail to record growth phenomena, we were unable to draw conclusions on the frequency with which sympodial branching occurred normally. In no case where sympodial branching was noted in early stages of development (and the branch tagged for observation) was there any further sympodial branching. We could only conclude that the sympodial branches were *not produced annually* on any branch we had marked for observation.

Gill has reported the occurrence of adventitious or aërial roots on the species within this forest. Although adventitious roots were observed on the horizontal branches of the species exhibiting sympodial lateral branching, the roots did not appear to be associated with the short shoot area or the curved portion of the lateral branch. *Ocotea,* which had the most conspicuous Terminalia-branching, rarely produced adventitious roots from the horizontal branches but did develop "prop" roots from the base of the stem.

The development of sympodial branching or of vertically continuous long shoot-short shoot growth patterns was not associated with flowering in *Ocotea*, *Grammadenia*, *Torralbasia*, *Calycogonium* or *Wallenia*. *Ardisia*, however, did develop a terminal inflorescence, and following the maturity of the fruit and the fall of the inflorescence axis, a lateral but vertical continuation of the stem developed as a sympodial flush of growth.

DICHOTOMOUS BRANCHING

The dichotomous branching of upright shoots was observed in a number of the components of the elfin forest. Dichotomous growth and branching was most conspicuous in *Calyptranthes* where it occurred, on the average, every three internodes. The new shoots developed in pairs and normally two pairs of leaves developed in each flush before elongation stopped. At the apex of each shoot there was a terminal aborted primordium. Subsequent branching occurred lateral to the terminal aborted primordia but remained consistently in one plane. *Calyptranthes* appeared to be a collection of upright fans of dichotomous branches.

The three species of *Miconia* always developed upright dichotomous shoots when growth was terminated by the production of a terminal inflorescence. Two lateral buds continued the upright vegetative growth after the inflorescence had matured fruit and had fallen. Subsequent growth consisted of but one or two pairs of leaves per flush. In mature plants flowering followed the maturation of each flush of growth on an annual basis.

In *Eugenia borinquensis* one or two pairs of leaves formed each flush of growth. Flowering occurred only on mature stems and terminated the branch or was formed in an axillary position on the old wood.

Both species of *Psychotria* produced a terminal inflorescence and there was no further vegetative growth on that shoot while the inflorescence persisted. With the maturity and desiccation of the inflorescence, however, two basal axillary buds developed in *Psychotria berteriana*, producing a dichotomous growth pattern. In *Psychotria guadalupensis*, however, only a single bud developed at the base of the inflorescence and the resulting growth was falsely monopodial.

Among the herbaceous vines *Ipomoea repanda*, with alternate leaves, produced a terminal inflorescence of many flowers which matured over an extended period of time. Axillary vegetative shoots often developed while the inflorescence was only partially mature. In *Mikania pachyphylla*, with opposite leaves, a terminal inflorescence appeared to restrict apical growth while the terminal inflorescence matured, but then a dichotomous growth pattern developed through activity of two axillary buds.

The heteroblastic growth of *Marcgravia sintenisii* also showed an association with the production of a terminal inflorescence. Subsequent growth was by the development of axillary buds below the inflorescence. In all cases observed, leaves of the initial production on this axillary shoot were of the juvenile form whether or not the branch was in contact with a trunk or branch.

Plants of *Tabebuia rigida* formed the second major component of the forest and these plants produced flowers throughout the year mostly from new growth. The terminal flush of growth consisted of an average of two pairs of leaves and several axillary and adventitious flowering branches. Most of the plants of *Tabebuia* which were observed in the canopy of the forest also showed a significant die-back of the flush growth during the winter season. Subsequent apical growth, therefore, came from adventitious buds in the axils of lower leaves or from opposite buds of such a node.

DIE-BACK

Regular die-back of terminal and, less frequently, of lateral or sympodial shoots was observed in *Ilex sintenisii, Cleyera albopunctata, Eugenia borinquensis, Hornemannia racemosa, Ardisia luquillensis, Micropholis garciniaefolia, Alloplectus ambiguus, Gesneria sintenisii* and *Lobelia portoricensis.* Although regular die-back has been described for plants of temperate areas, its occurrence as a factor in the size of a plant in tropical areas has not been recognized previously (Garrison & Wetmore 1961).

Relatively long flushes of shoot development were observed in *Gonocalyx* and *Hornemannia* consisting of 5–10 leaves or internodes per flush. The young leaves were brightly colored and soft until full extension of the shoot, or the full development of the leaf size, was completed. Both species were climbers and the soft shoot development was often injured mechanically and the entire flush of growth abscissed.

The height of the forest may be affected by the environmental factors previously suggested, but clearly the low stature of the component woody species may also be due to genetic factors expressed as long shoot-short shoot development, dichotomous branching associated with a terminal inflorescence, the abortion of the shoot tip, and the die-back of seasonal flushes of growth.

Continuous production of single leaves or leaf pairs occurred in all of the herbaceous species in the elfin forest. Continuous production of single leaves or leaf pairs appeared to occur in both juvenile and adult shoots of *Marcgravia*, in *Symplocos*, *Cleyera, Ilex*, *Gesneria*, *Clusia*, and *Micropholis*. The herbaceous vines *Rajania*, *Ipomoea* and *Mikania* also appeared to produce leaves continuously unless affected by flowering.

The rosette and epiphytic habit of the two members of the Bromeliaceae found within the elfin forest can be regarded as a family genetic character. Following flowering, however, the two species continued growth in different patterns. Rosettes of both species died following flowering, but plants of *Guzmania* produced one or, rarely, two basal vegetative rhizomes which developed laterally before terminating into a rosette or crown of leaves. This growth pattern caused the plants to form a ring around the host tree and *Guzmania* was most commonly found on the large trunks of *Prestoea montana*. *Vriesea sintenisii* by contrast, produced a single basal rhizome which tended to grow upward immediately and formed a new crown in close competition with the parent rosette. The new growth could be to the right or the left of the parent plant but always extended upward. Plants with 7 generations of rosette-rhizome vertical development were found. When *Vriesea sintenisii* occurred on a branch extending horizontally, the plants persisted for only 2 or 3 growth generations before being extended slightly off center and, seemingly top heavy, falling over to break free and drop to the ground.

BUD PROTECTION

Richards (1952, p. 77) notes that "buds of rain-forest trees and shrubs, as might be expected, are less well protected than those of trees in other climates." An examination of the terminal foliage buds or the shoot apex in resting condition revealed that the leaf primordia are better protected in the plants of the elfin forest than might be expected from Richards' statement. (PLATE I).

Protective stipules are present in *Hillia* and *Psychotria* of the Rubiaceae and in *Calyptranthes* of the Myrtaceae. In *Hillia* (PLATE Ib) the stipules form a sheath around the young leaves which is compressed at the apex. The developing young leaves force an opening in the apex of the sheath. *Psychotria* species have smaller stipules consisting of an ochrea-like base with four short free apices. The apices tend to be closely associated in very young buds but their protective function would be of short duration.

Calyptranthes possesses a peculiar type of stipule protection for which we have not found a description elsewhere (PLATE Ig). In fact Berg, in a monograph, reports the family to be estipulate, as have subsequent authors. McVaugh makes no mention of the foliage bud protection. In the original description of *Calyptranthes krugii*, Kiaerskou notes, "Quaque innovatio e duobus internodiis constat, quarum alterum breve duo cataphylla opposita cito decidua, alterum longum duo euphylla fert." In a footnote he equates "cataphylla" with "Niederblätter Germanorum." In our observations of *Calyptranthes krugii* on Pico del Oeste the vegetative shoot increase is by production of 1 or 2 pairs of leaves in a flush. The apical meristem aborts although an inflorescence of one, rarely two, flowers may be produced in one or both terminal leaf axils. Subsequently, after flowering or resting, two axillary shoots develop and in each the apex is covered with a pair of laterally folded bud scales. The young leaves increase in size uniformly and are appressed by their ventral or adaxial surfaces. As the leaves increase in size, the bud covering is forced apart or torn free at the base, and the two halves separate as conduplicate folded sheaths. The bud scales are a light yellow or cream color in contrast to the green shoots. When separate they dry white, then brown and shrivel before falling from the shoot. Although these bud scales are rarely found on herbarium sheets, they were conspicuous in the living plants of *Calyptranthes krugii* in the study area and were also found on a population of *Calyptranthes* which may represent a different species in the Cerro de Punta area. The term cataphyll although broadly inclusive for the early leaves of a plant or shoot as cotyledons, bud scales, etc. (Jackson) is scarcely descriptive of the folded protective scales of the young leaves of *Calyptranthes*.

Apical buds may be protected by leaf bases as in Clusia which has opposite leaves or by the cluster of leaves in the several genera which produce terminal or lateral long shoots where the terminal apical elongation is reduced. In *Clusia* (PLATE If) the mature leaves conceal the young buds as the leaf bases of opposite leaves of a pair are tightly appressed. In *Wallenia*, *Ocotea*, *Grammadenia*, *Torralbasia*, *Ilex* (PLATE Ic), and others, the vegetative shoot in resting condition is terminated by a dense cluster of small leaves or primordia. In subsequent development of the shoot represented by these primordia, the outer ones enlarge only slightly, frequently failing to develop a leaf blade even though the petiole may elongate. Such scales or cataphylls are found at the base of the long shoot and the internodes between them may or may not have elongated. Clearly these cataphylls have served a function of protection for the inner leaves and the apical meristem.

The buds or apical meristem of shoots of *Hedyosmum* are enclosed within the sheathing stipular base of the leaves (PLATE Ie). Bud protection here is evident in the enclosure of the primordia in the sheathing leaf base.

The apex of the stem of *Micropholis* and *Symplocos* have the young leaf primordia tightly invested in a protective covering of brown trichomes. As the leaves expand these trichomes are separated and in many cases break off. In *Tabebuia rigida* the young leaves or primordia are tightly and completely encased in a shield of brown peltate scales. Again with leaf enlargement the scales are separated and often persist in isolated positions on the mature leaves.

The species *Gesneria sintenisii* appears to have a large naked meristem where the leaf primordia are separated and evident from an early age (PLATE Id). The leaf primordia and the apex of the stem have a dense resinous covering. As the leaf starts to expand the resinous covering is cracked and usually flakes off although sections of the covering may persist even on the mature leaf blade and the petioles.

The young leaves of *Marcgravia* (PLATE Ia) and *Cleyera* are convolute in bud and appear to unroll in development. The apical meristem is enclosed within this pointed bud and the youngest leaf primordia do receive some protection.

It is clear from these examples that the young leaves are not without protection in the majority of the species that comprise the woody components of the elfin forest on Pico del Oeste.

LEAF SIZE AND MORPHOLOGY

Plants of tropical forests have been grouped on the basis of leaf size: dimensions and areas. Raunkiaer proposed a classification of life forms on leaf-size classes which has been used for comparison and description by many authors. Leaves have been termed leptophylls if their area does not exceed 0.25 $cm.^2$; nanophylls if their area is between 0.25 and 2.25 $cm.^2$; microphylls if the area is 2.25–20 $cm.^2$; mesophylls if the leaf area is 20–182 $cm.^2$; and macrophylls if the area is 182–1640 $cm.^2$ Cain *et al.*, found, in a Brazilian rain forest, that the phanerophytes are strongly mesophyllous and reported a tendency for the small leaf size classes to have a higher percentage in taller strata than in lower ones.

Brown, in his study of the mossy forest on Mount Maquiling in the Philippines, found only the leaf-size classes of microphyll and mesophyll represented in approximately the same numbers.

The elfin forest on Pico del Oeste had a single species (*Peperomia emarginella*) of a size class smaller than the nanophyll classification and the majority of plants were of the microphyll size class. The total classification in numbers of taxa and percentage of the totals is the following:

leptophylls	1	1.9%
nanophylls	6	11.5%
microphylls	30	57.6%
mesophylls	13	25.0%
macrophylls	2	3.8%

Compound leaf types were represented only by *Trichilia pallida*, a species clearly only surviving and not reproducing in the elfin forest zone. At lower elevations *Trichilia pallida* becomes a small tree while most of the plants found on Pico del Oeste were weak saplings, dependent for support on the surrounding vegetation and nearly scrambling through the elfin forest. A single plant of *Weinmannia pinnata* (Cunoniaceae) with compound leaves was found on the peak but was not encountered in the transects. Brown did not have a compound-leaved plant in the Philippine study area and Lebrun notes such plants are less than 15% in African elfin forests.

The largest leaves, macrophylls, were those of *Prestoea montana*, a palm, restricted to the leeward erosion valleys and *Anthurium dominicense*, an epiphytic member of the Araceae.

When grouped according to habit the following leaf-size classification was obtained:

LEAF SIZE	VINES-SCRAMBLERS	HERBS	EPIPHYTES	TREES & SHRUBS
leptophylls	0	1	0	0
nanophylls	1	2	2	1
microphylls	3	10	2	15
mesophylls	1	2	2	8
macrophylls	0	0	1	1

Brown added data on leaf dimensions and leaf margins to his study of the Mt. Maquiling forest in the Philippines. He found the leaves were

0–10 cm. long in 11 species or 70%, and 10–20 cm. long in 5 species or 30% of the plants. The leaves were 0–5 cm. wide in 12 species or 75%, and 5–10 cm. wide in 4 species or 25%.

In the elfin forest of Pico del Oeste the leaves were 0–10 cm. long in 7 species of monocotyledons and 31 species of dicotyledons or 70% of the total flora; and 10–20 cm. long in 7 species of monocotyledons and 9 species of dicotyledons or 30% of the total. The leaves were 0–5 cm. wide in 10 species of monocots and 33 species of dicotyledons or 79%, and 5–10 cm. wide in 4 species of monocotyledons and 7 species of dicotyledons or 21%. The leaves selected for these measurements were taken from the mature growth and were averaged for the plant. Variation in leaf size within a given plant ranged from the cataphylls and reduced leaves of initial growth of long shoots to the larger leaves of vegetative shoots, when compared with those of flowering branches. Heterophylly was found in dimorphic pairs of leaves in *Pilea krugii*, *Pilea yunquensis* (Urticaceae) and in *Alloplectus ambiguus* (Gesneriaceae). Heteroblastic growth was found only in *Marcgravia sintenisii* with appressed smaller leaves on juvenile and climbing shoots and larger leaves on the free arching branches. Heterophylly with age was observed in *Ocotea spathulata* and *Symplocos micrantha* where the leaves of seedling plants appeared to be quite different in size and shape from those of adult plants. Although *Cleyera albopunctata* appeared to have larger than average leaves on some vigorous growing branches this could not be documented with measurement of samples. However, the leaves of sterile or vegetative branches of *Clusia grisebachiana* did possess larger leaves than were found on shoots which were mature or produced inflorescences. Macrophylly on adventitious shoots was not encountered within this forest.

Much attention has been given in existing studies of tropical forests to the shape of the leaf, the nature of the margin, apex and base of the blade, and to the presence of a cuticular layer in relation to the retention of water or the presence of epiphyllous organisms.

Brown noted in his study of the mossy forest at 1000 meters in the Philippines that as the altitude increases there is a marked increase in the percentage of small leaves and a decrease in the percentage of leaves with entire margins. It has been suggested that the presence of marginal teeth aids the runoff of water from the leaf surface, and Brown found entire leaves in eleven species of Philippines plants in the study area and five species in which the margin was not entire. In Puerto Rico on Pico del Oeste 29 taxa had entire leaves while eleven taxa of dicotyledonous plants had leaf margins with coarse or blunt teeth or with marginal undulation.

The extended leaf tip, often called a drip-tip, has a popular association with wet tropical forests. The conclusion of Junger has been cited repeatedly that the function of the pointed leaf tip was to hasten the runoff of water from the leaf, and thus help prevent insects and lower plants from attacking them. Baker recorded 37 of 41 species of plants belonging to 20 families with leaves drawn out into a tip, in a forest in Ceylon, and

Richards observed, "Pointed tips to leaves are characteristic of plants of wet regions and especially of tropical rain-forests, but I doubt whether any rain forest can show the phenomenon more markedly than the Sinharaka." Richards observed that drip tips are common and better developed in the lower than in the upper strata of the forest and in juvenile than in mature leaves of tall trees. Cain *et al.* reported that 70.6% of the leaves in the Brazilian forest they studied had acuminate tips and 28% of the 150 species studied had rather abruptly long tips of the drip point type.

By contrast, Shreve found drip tips uncommon in the montane rain forest of Jamaica, and Vaughan and Wiehe reported a similar observation for upland climax forest of Mauritius.

In the Pico del Oeste forest 13 of the 14 taxa of monocotyledons had the leaves acuminate at the apex and the other taxon had leaves acute. Among the dicotyledonous plants the apex could be classified as acuminate in 15 taxa of which 6 would qualify as drip tips; 14 taxa had the leaves acute at the apex and 11 had the leaves obtuse, blunt, or emarginate.

Although previous authors have not considered the leaf base, it seems that if leaf shape is important for drainage in one direction, it is equally so in the other. Only 5 of the 14 taxa of monocotyledons have petioles and of those, *Prestoea montana*, the mountain palm, has lacerate or compound leaves; *Rajania cordata* and *Anthurium dominicense* have the basal lobes extended and *Renealmia antillarum* and *Brachionidium parvum* have the leaf base obtuse. Of the dicotyledonous plants 24 taxa had the leaf base blunt, acuminate, or decurrent on the petiole while 16 are best described as cordate to peltate at the base.

All of the leaves which were cordate, hastate, or peltate at the base had an acuminate apex or a drip tip. All leaves which were blunt at the apex or rounded or emarginate had acute or decurrent leaf bases except for *Micropholis garciniaefolia* and *Eugenia borinquensis*. In these two taxa the attitude of the leaves to the stem tended to be either upright or drooping and in this manner adapted to the runoff of water. Excepting *Eugenia*, those leaves with short petioles or with petiole:blade ratios 1:10 or larger, all had tapering blade bases with the leaves mostly arranged upward in attitude. *Cleyera albopunctata* has short petioles but the leaves have a noticeable curvature. *Marcgravia sintenisii*, again with a short petiole, also has a slight curvature and a drip tip.

The frequency of taxa having leaves of strongly curved form suggests a selective value can be attached to this growth form. The blades may be noticeably curved longitudinally as well as laterally or in but one plane. This curved form is particularly evident in taxa of *Calycogonium*, *Cleyera*, *Gesneria*, *Gonocalyx*, *Hornemannia*, *Ilex*, *Miconia pycnoneura*, *Symplocos*, *Tabebuia*, and *Torralbasia*, that is in 10 of the 40 taxa of dicotyledons or 25% of the flora.

A heavy upper cuticle was found in 22 taxa or 55% of the dicotyledonous plants. *Ardisia*, *Cleyera*, *Clusia*, *Calyptranthes*, *Calycogonium*, *Eugenia*, *Gonocaylx*, *Haenianthus*, *Hillia*, *Hornemannia*, *Ilex*, *Marcgravia*, *Miconia foveolata, Miconia pachyphylla, Miconia pycnoneura, Micropholis, Ocotea, Psychotria guadalupensis, Symplocos, Trichilia, Torralbasia, Tabebuia,* and *Wallenia,* that is, all woody taxa except *Mecranium amygdalinum, Grammadenia sintenisii, Hedyosmum arborescens* and *Psychotria berteriana* possess a heavy upper cuticular layer.

Junger found that leaves with drip tips were less frequently overgrown with algae, fungi, lichens and bryophytes than those without. He believed that the presence of these epiphyllae interfered with assimilation to such an extent as to be a serious handicap to the plant. *Micropholis garciniaefolia* and *Eugenia borinquensis,* which stand out as the only taxa of the 40 dicotyledons or 29 woody plants in which the leaves were rounded or cordate at the base and rounded at the apex and appear to lack any special adaptation for getting rid of surface water, seemed to support the larger populations of epiphyllous plants. The abundance of epiphyllous leafy Hepaticae on different species will be considered later in this paper in relation to the metabolism of the forest.

In a superficial classification of the texture of leaves within the forest components, the leaves would be considered as membranaceous in all of the monocotyledons except *Anthurium,* which had leathery leaves. Among the dicotyledonous plants 13 taxa would have the leaves classified as membranaceous, 8 taxa would be described as fleshy or succulent, and 21 taxa as having the leaves leathery or coriaceous. The high percentage of water in the tissues or the relatively small amount of material forming dried weight will be considered later and is indicated in TABLE 1, column 8.

The heavy texture of the leaves, the thickness of the blade, and the amount of succulence all support previous suggestions that the flora of the mountain summit shows many xeromorphic characteristics. Bews regards the rain forest type of leaf as xeromorphic and associates its characters with the low specific conductivity of the wood for water. Shreve remarks that the prolonged occurrence of rain, fog, and high humidity at relatively low temperatures places the vegetation of a montane rain forest under conditions which are so unfavorable as to be comparable with the conditions of many extremely arid regions. Xeromorphy is usually interpreted from such anatomical characteristics as cuticle, hypodermis, thin palisade layers, pubescence or idioblasts.

Wylie (1954) noted that a xerophytic flora may have a high proportion of representatives with leaves having a hypodermis. In his studies of plants of North Island in New Zealand, Wylie, even though avoiding "extreme xeromorphs and succulents," concluded that the species studied revealed a high average thickness of leaves, extensive spongy mesophyll and palisade parenchyma areas, great cuticular depth, and "the proportion having a hypodermis were greater than for any group previously studied." Wylie (1946) compared his studies of the New Zealand plants with previous ones of his own, based on plants of Florida and of other temperate areas.

Wylie reported that the leaves of the New Zealand species studied, ranged in blade thickness from 731 μ for *Pseudopanax* to 172 μ for *Olearia,* and the 38 species averaged 406 μ. This was much greater than the corresponding thickness of 216 μ for 121 Florida dicotyledons and 80 μ for 80 species of northern dicotyledonous trees. Philpott reported a mean blade thickness of 234 μ for 24 species of *Ficus* growing in Florida and Cooper found a mean laminar thickness of 336 μ for 19 species of woody dicotyledonous plants in the climax chaparral in western California.

Within the Pico del Oeste forest the woody plants by comparison had leaves ranging in thickness from 787 μ in *Clusia grisebachiana* to 146 μ in *Psychotria berteriana* and averaged 379.6 μ in thickness. The herbaceous flora had leaves ranging in thickness from 625 μ in *Peperomia hernandiifolia* to 141 μ in *Sauvagesia erecta*, and all herbs had leaves averaging 281.6 μ in thickness (Table 2, column 1).

Wylie reported that a hypodermis was found in 24 or 63% of the 38 species examined in the New Zealand study area. Eighteen species had a hypodermis on both the upper and lower surface, 5 species had only an upper hypodermis, and one species is described as having only a hypodermis on the lower side.

In the Pico del Oeste elfin woodland 19 of 40 taxa or 47% have a hypodermis. Two taxa, *Begonia decandra* and *Hillia parasitica* had both an upper and a lower hypodermis. No plant was observed with only a lower hypodermis. Seventeen taxa had an upper hypodermis alone. Twenty-one taxa did not possess a hypodermis (Table 2, columns 2, 3).

The presence of a hypodermis is often regarded as a xeromorphic character, although a multiple hypodermis is also an anatomical characteristic of taxonomic value. Carlquist noted that "continued periclinal division of the epidermis is of taxonomic importance in certain families such as the Piperaceae." Within the plants of Pico del Oeste, multiple hypodermal layers were found in taxa of *Peperomia* (Piperaceae), *Hedyosmum*, (Chloranthaceae), *Ocotea* (Lauraceae), *Clusia* (Guttiferae), *Calycogonium* (Melastomataceae), and *Hornemannia* (Ericaceae).

A ratio was determined between the thickness of the upper epidermis and that of the upper hypodermis in this mossy forest. Ratios varied from 1:1 in most plants with a hypodermis, to 1:15 in *Psychotria guadalupensis* and averaged 1:4.1. Although Wylie did not use such a figure calculation, the figures in *table 2* of his paper (1954) suggest a ratio range in the New Zealand plants from 11:1 to 1:21.3 but an average of 1:3.8, or less than that found in the Puerto Rican vegetation.

Stålfelt considers the mechanical strengthening of leaves through the development of sclerenchyma as particularly common among xerophytes as a means of reducing the injurious effect of wilting. Branched idioblasts were found in but four taxa within the mossy elfin forest (Table 2, column 8 and Plate IIa).

Watson concluded that the formation of palisade tissues in leaves might be a morphological response to light. He suggested that the cigar-shaped palisade cells are formed in increasing number with increasing light intensity during leaf development. We examined the leaves on Pico del Oeste to see if palisade mesophyll development was reduced with the reduced light intensities we have reported there (Baynton 1968, 1969). Two taxa, *Lobelia portoricensis* and *Mikania pachyphylla*, seemed to be without a definite palisade layer in the leaves examined (PLATE IId). Further, 19 of the remaining 38 taxa possessed a palisade mesophyll of but a single cell in thickness. The remaining 19 taxa had a palisade mesophyll in part exceeding a single cell layer to 3 to 4 cells in thickness (TABLE 2, column 9). In taxa which could be measured, the palisade layer exceeded the spongy layer in thickness in only 4 taxa, while the ratio of palisade to spongy, in 34 taxa, ranged from 1:1 to 1:7.4 and averaged 1:2.4 (TABLE 2, column 10). Referring to Wylie's study of New Zealand plants, of the 38 taxa he examined 7 had a thicker palisade layer than spongy layer and the comparable ratios determined from the figures he gave show a range from 1:1 to 1:3.3 with an average of 1:1.5.

On the basis of limited comparative data it appears that the leaves of the plants growing in the elfin forest on the summit of Pico del Oeste are thicker than usual and approach leaves of admittedly xeromorphic type. The frequency of a hypodermal layer or multiple hypodermal layers is high. The ratio of thickness of palisade and spongy mesophyll layers suggests that the plants surviving on Pico del Oeste have adjusted to the low light values through a reduction in the palisade mesophyll zone and an increase in the amount of spongy mesophyll.

LEAF DEVELOPMENT

Richards has reviewed the earlier literature which claimed that a few species in Buitenzorg were ever-growing and showed no foliar periodicity whatever. On further study it was shown that one plant at least was in continuous leaf production when young, but when older leaf production was distinctly periodic. Richards (1964, p. 193) concluded that "it is certainly true that most rain-forest trees produce new leaves, not continuously, but in periodic flushes, so that a single shoot bears several 'generations' of leaves at the same time."

Our observations on the development of stems were in relation to the production of leaves (TABLE 3). Initially we observed that certain plants did grow in obvious flushes where the young leaves were brightly colored or soft in texture in comparison with the mature leaves. We recognized 20 taxa which grew in flushes, 8 of which had conspicuous terminal long shoot-short shoot growth patterns. Twelve taxa were considered to be in continuous production of leaves but this varied from branch to branch on a given plant. A large specimen of *Clusia grisebachiana*, for example, failed to produce a single new leaf during the period of this study. A marked plant of *Trichilia pallida* did not add a single leaf, or lose any, for a period of three years after the plant was tagged for observation. *Ilex sintenisii* which appeared to have young green leaves all of the time proved to have only some of the individual shoots on the plant in a stage of growth or expansion at any given time. A shoot of *Ilex* tagged for observation was shown to produce a flush of leaves and then remain in a mature but quiescent stage before renewing its growth. Some of the shoots renewed growth with no change in the size of the leaves while others had an initial renewal of growth in the production of leaves, or a single leaf of smaller size or reduced to cataphyll proportions. When the internodes along a stem were measured carefully there was evidence that growth of the internodes had been reduced in some areas giving further evidence to a periodicity of growth.

Clearly, it is difficult to determine that a given shoot has not added a leaf, but the majority of plants observed in the elfin forest did exhibit some degree of periodicity of growth and leaf production during the period of study.

The suggestion has been made that leaves develop quickly in tropical forests. Studies of leaf expansion within a temperate area at the Arnold Arboretum in Boston have indicated that leaf expansion takes place within a 10-day to three-week period in most native and cultivated species. Although many species studied within the elfin forest did complete the expansion of leaves within that period, there were notable exceptions. Tagged shoots where fairly large leaves were counted and observed at regular intervals showed the following times for development from a noticeable leaf primordium to full expansion.

Symplocos micrantha	5 weeks
Clusia grisebachiana	7 weeks
Hedyosmum arborescens	6–8 weeks
Calycogonium squamulosum	8 weeks
Gesneria sintenisii	10 weeks
Miconia pycnoneura	14 weeks

NUMBER AND PERSISTENCE OF LEAVES PER PLANT

Regular observations of the elfin forest components impressed upon us the fact that some plants had many leaves and that others, equally characteristically, had few leaves. Although the leaves may have been produced in flushes of growth or seemingly continuously, there was a leaf fall that in most plants seemed to equal leaf production. We selected 24 plants of comparable size and age of *Miconia pachyphylla, Wallenia yunquensis* and *Dilomilis montana*, counted the leaves, and found less than 5% variation in the number of leaves on a given plant of the species. Branches of *Miconia foveolata* or *Psychotria berteriana* characteristically had but 3 pairs of leaves at the end of a shoot. When new growth occurred the new shoot had a comparable number of leaves and the leaves of the former growth generation abscissed. The largest number of leaves on a mature plant was found on *Micropholis garciniaefolia* with 10,487, while *Brachionidium parvum* characteristically had but 4 leaves per plant.

The following table indicates the plants with the greatest number of leaves in comparison with the total photosynthetic area represented on the plant, and the rank of the plant in frequency counts for transects reported in the first paper of this series. Leaf numbers and total photosynthetic area for all species is given in TABLE 1. The leaf count was obtained as a by-product of gathering foliage material for a chemical survey of the plants within the elfin forest.

TOTAL NUMBER OF LEAVES		TOTAL PHOTOSYNTHETIC AREA		FREQUENCY *
Micropholis	10,487	*Prestoea*	289,460 cm.^{2}	*Pilea krugii*
Ilex	8,684	*Micropholis*	96,480	*Wallenia*
Calyptranthes	4,539	*Tabebuia*	60,040	*Calycogonium*
Tabebuia	2,680	*Hedyosmum*	44,908	*Vriesea*
Hedyosmum	2,339	*Eugenia*	23,000	*Ocotea*
Calycogonium	1,345	*Lobelia*	20,300	*Calyptranthes*
Ardisia	1,857	*Calyptranthes*	18,609	*Pilea obtusata*
Gonocalyx	1,345	*Psychotria berteriana*	18,093	*Dilomilis montana*
Haenianthus	1,294	*Haenianthus*	17,339	*Miconia pachyphylla*
Marcgravia (adult)	1,280	*Ardisia*	17,458	*Tabebuia rigida*
Cleyera	678	*Ilex*	15,631	*Eugenia borinquensis*

* Frequency = descending order of frequency in transects.

Holttum noted that in the uniform climate of Singapore, trees of a number of deciduous species change leaves annually, many in February, others in August, apparently because of leaf senescence.

Within the elfin forest of Pico del Oeste the greatest noticeable leaf fall in the dominant plants of the forest occurred in February for *Eugenia*, *Ocotea*, and *Tabebuia* and was conspicuous in March for *Lobelia*. In each of these plants the leaf fall preceded the development of new year's growth, and the plants presented a barren appearance for a short period in contrast to their normal condition. Other species developed new growth before the erratic abscission of the older leaves.

Richards notes the many widely different types of behavior among tropical trees in regard to leaf fall and leaf persistence. According to Warming and Graebner the average length of leaf life of tropical species is about 13–14 months. We made an attempt to mark branches and to record the number of leaves, the nature of the new growth, and the length of time individual leaves persisted (TABLE 3). In general, the results were unsatisfactory. Often the tagged branch failed to develop any new leaves during the period of observation, while an adjacent branch of the same plant for which data had not been recorded produced a flush of leaves, or flowered, or died. It is not possible to report with accuracy that the growth flush in a long shoot-short shoot growth pattern represented an annual increment of growth as may be done in temperate areas with deciduous or bud-forming plants. We did observe that some leaves remained on the plant during two full years of observation. Branches of *Ilex sintenisii* which appeared to have two flushes of leaves per year retained some leaves through 20 internodes, which represented 7 flushes as determined by areas of short internodes and by cataphylls. *Torralbasia cuneifolia*, which also grows in flushes with the production of many cataphylls, also retained leaves for 20 nodes representing 7 flushes in this plant. Only one or two of the larger leaves persisted while cataphylls and smaller leaves abscissed. *Gonocalyx* produced 3 to 4 leaves per flush and retained 20 leaves in 5 recognizable flushes with all leaves persisting. *Tabebuia* tended to retain only 1 pair of leaves of each flush of 2 pairs and the oldest persisting leaves were 10 internodes below the apex, suggesting that some leaves have persisted for five years.

In general, younger plants in the undergrowth tended to hold more leaves per shoot for a longer period of time than did the plants with shoots exposed in the canopy.

FACTORS OF PRODUCTIVITY OF THE LEAVES

Although it has been suggested that the persistent cloud cover, high humidity saturated soil, and the growth form of individual plants all influence growth rate or development of the forest, we found additional factors worthy of mention.

The very slow growth of some component trees within the elfin forest has been recorded by Wadsworth and Bonnet in their comparative study of the tabonuco (*Dacryoides excelsa*) rain forest and the colorado (*Cyrilla*) forest in Puerto Rico. Although *Cyrilla racemiflora* was not encountered in the elfin forest of Pico del Oeste, four other taxa of the colorado forest were. No distinctive growth rings have been seen in the woody trunks of the Pico del Oeste plants. Wadsworth and Bonnet grouped the trees in diameter-size classes and estimated the age of the trees by summing the period required for a plant to pass from one diameter class to another. They concluded that a 4″ trunk of *Ocotea spathulata* was 200 years old; one of *Micropholis garciniaefolia*, 170 years old; and one of *Calycogonium squamulosum*, 80 years old. The annual growth rate for saw timber and polewood species in the Luquillo Mountains was 0.07 inches for *Tabebuia rigida*, 0.05 inches for *Micropholis garciniaefolia*, and 0.04 inches for *Calycogonium squamulosum* and *Ocotea spathulata*. They concluded that the soil is the common factor most important in the forests they studied. The saturated, poorly aerated organic soil inhibited root penetration and the absorption of water and resulted in the very slow growth.

The cloud and fog cover, the high humidity and abundant rain documented by the studies of Baynton suggest that photosynthetic activity in the elfln forest is low. We were unable to test the amount of photosynthesis carried on by the component species. Tests of evaporation with potometers and of transpiration with cut branches within the forest were complete failures. Gates, however, demonstrated by infra-red temperature measurements that transpiration did occur during brief periods of sunshine and clear sky. As there were longer periods, even days of full sunshine on the peak, the plants grew even though the growth rate was slow.

A survey was made of the stomatal types, size, and distribution to determine any specializations that might occur within the elfin forest components (TABLES 3, 4). Sinnott suggested that xerophytes tend to have a high stomatal frequency but cites no reference. Regrettably, we have failed to find any comparative data for other forest zones.

Although stomatal apparatus types are commonly associated at the family level, there are variations and exceptions as reported throughout the work of Metcalfe and Chalk. We found the anomocytic type of stomatal apparatus (PLATE IIIa) to be most common as represented in 16 taxa of dicotyledons and 4 taxa of monocotyledons. The paracytic type (PLATE IVa) was present in 13 taxa of dicotyledons and 3 monocotyledons. Anisocytic type (PLATE IIIc) was present in 9 taxa of dicotyledons. The gramineous type (PLATE IVd) was present in all 6 taxa of Cyperaceae and Gramineae. A didymocytic stomatal apparatus (PLATE IIIb) was represented in 1 taxon of monocotyledons and 1 of dicotyledons (TABLE 3, column 9; TABLE 4, column 3).

Stomatal openings of varying sizes were found in *Justicia martinsoniana* where large numbers of the stomatal apparatus appeared to abort before the final cell division which, we suspect, would have formed the guard cells. The openings, therefore, were of varying sizes. *Pilea krugii* (PLATE Va) also had stomatal apparatus of varying size with very small guard cells approximately 0.002 mm. long appearing over the veins, while mesophyll tissue was surmounted by guard cells averaging 0.023 mm. in length. *Marcgravia sintenisii* with heteroblastic growth showed the same number of stomata per square mm. for juvenile and adult foliage, but the guard cells were 0.037 mm. long on the juvenile leaves and only 0.028 mm. long on the adult leaves. The stomatal apparatus, however, appeared to be broader in the adult leaves.

Stomata occurred in definite patterns in many of the monocotyledons, as expected, but they were found in groups of 2 to 3 or 3 to 7 in *Grammadenia* (PLATE Vb) and in groups of 6 in *Gesneria sintenisii* and with 2 to 3 very closely associated, almost united, in *Sauvagesia*.

On leaves of *Pilea yunquensis* stomata were found only on the upper surface of the leaf. Metcalfe and Chalk refer to work of Mohler, who found stomata on the lower surface in the species of *Pilea* he examined except for *Pilea spruceana*, where they were on the upper surface. Stomata tended to be oriented around the long hairs on *Cleyera*.

Accessory or subsidiary cells to the guard cells were usually clearly defined and commonly contrasted with those of the epidermis. Unusually shaped subsidiary cells appeared in *Alloplectus* (PLATE IIIc) and in *Justicia martinsoniana* and in *Renealmia antillarum* (PLATE IIId).

The subsidiary cells had a characteristic homogeneous yellow-brown pigmentation in *Clusia* in contrast to the adjacent epidermal cells. In *Tabebuia rigida* the subsidiary cells were generally clear in contrast to the mottled appearance of the epidermal cells. The walls of the subsidiary cells of *Micropholis* were straight in conspicuous contrast with the sinuous walls of the other epidermal cells.

No conspicuous elevation of stomatal apparatus was discerned in the components of the elfin forest. *Torralbasia* was the only taxon with the guard cells noticeably sunken and overlain by 6 epidermal cells (PLATE IVc).

The length of the guard cells was measured and those found in 14 taxa of monocotyledons averaged 0.035 mm. in length while in 39 taxa of dicotyledons the guard cells averaged 0.028 mm. in length. Within the monocotyledons the largest guard cells were in *Eleocharis*, measuring 0.048 mm. long, while *Isachne* had the smallest, 0.023 mm. long. Within the dicotyledons the longest guard cells were found in *Hedyosmum arborescens* and *Peperomia emarginella*, each 0.048 mm. long, while the smallest were those of *Miconia pycnoneura*, 0.010 mm. in length.

In considering the length of the guard cells in relation to the habit of the plant we found the following lengths:

8 taxa of herbaceous plants	average 0.031
2 taxa of woody epiphytes	average 0.030
24 taxa of trees or shrubs	average 0.028
5 taxa of woody climbers	average 0.027

The number of stomatal openings ranged from 18 per square mm. in *Guzmania berteroniana* to 230 per square mm. in *Isachne angustifolia*. Within the dicotyledons *Peperomia emarginella* had 22 stomata per square mm. while *Miconia pycnoneura* had 2230. While *Guzmania* had only 18 stomata per square mm., there were 96 stellate hair clusters in the same area.

Vriesea sintenisii, another bromeliad, was examined in several sections of the leaf. The upper portion of a mature leaf showed 11.4 stomatal apparatus per square mm. with 41.4 stellate hair-glands in the same area; the middle portion of the leaf had 28 stomata per $mm.^2$ and 19 stellate glands, while a basal portion above the water level showed 49.4 stomata per $mm.^2$ and 19 glands in the same area.

It has been suggested that metabolic activity of individual plants or leaves might be impaired by the presence of epiphyllous algae and leafy hepatics. The young leaves of most species within the forest are a bright green color when they first develop. In other species the young leaves were colored when young or expanding and developed a green color when near maturity. Young leaves of *Rajania* and *Ipomoea*, herbaceous vines, were bronze in color when young. Young leaves of the woody climbers *Gonocalyx* and *Hornemannia* were pink to red or orange-red in color. *Cleyera* and *Symplocos* also produced young leaves bronze in color, while *Calycogonium* had the young leaves reddish. The herbaceous *Peperomia hernandiifolia* had reddish young leaves. *Miconia pachyphylla* was unique in losing the green pigments and having the leaves turn a bright red or orange immediately before falling.

Upon reaching mature size, the leaves of most species in the Pico del Oeste elfin woodland acquired a covering of epiphyllous non-vascular plants. Spores, gemmae, gemmalings and sporelings, or fragments of liverworts are wind-borne and settle on the new leaves of most species. They appeared most quickly on species with depressed midrib or veins such as *Marcgravia, Ilex, Symplocos, Gonocalyx* or *Tabebuia*, and were rarely seen on the pubescent leaves of *Miconia foveolata* or the rugose leaves of *Miconia pycnoneura*. Dr. Margaret Fulford, in work to be reported later, examined a collection of leaves from plants within the forest and in 94 collection numbers found approximately 680 specimens belong to 40 genera and more than 75 species. There appeared to be an average of eight species per sample with a maximum of 18 species. Preliminary data showed the following epiphyllous species distribution on representative leaves:

Anthurium dominicense	4	*Miconia pachyphylla*	5
Ardisia luquillensis	3	*Miconia pycnoneura*	8
Calyptranthes krugii	8	*Ocotea spathulata*	6
Eugenia borinquensis	2	*Peperomia emarginella*	1
Gonocalyx portoricensis	2	*Symplocos micrantha*	1
Grammadenia sintenisii	7	*Trichilia pallida*	6
Ilex sintenisii	12	*Wallenia yunquensis*	11
Micropholis garciniaefolia	8		

The number of epiphyllous taxa on any given leaf is not indicative of the leaf size or the percentage of the surface covered. The speed with which epiphyllae grew and covered the surface of the host was startling. Leaves of *Eugenia borinquensis* were completely and densely covered with liverworts in less than five months after leaf expansion. The amount of light reaching the photosynthetic area of the leaf is certainly reduced by the abundant epiphyllous growth. Epiphyllous growth occurred on leaves exposed at the summit of the canopy although the number of seemingly dead or desiccated plants was high. The leaves of the lower and inner branches of the forest components were more densely covered. Epiphyllae were less common on leaves of the truly herbaceous species.

LEAF DAMAGE

An additional factor in reducing the potential metabolic production of the plants in the elfin forest is evident in the amount of damage to the foliage of individual species. This has generally been attributed to wind. Damage done by animals as found in the Pico del Oeste forest has not been recorded.

The sheared effect and directional growth of woody plants along sea coasts have been attributed to wind and to salt spray. Beard and Gleason and Cook have suggested the same factors are important in the shaping of the mountain-top forests in the West Indies. The effects of wind were observed in the canopy of Pico del Oeste. Within a few feet of the roof of our observation tower a slender stem of *Eugenia borinquensis* had worn a circular opening in the canopy of surrounding species. Branches of *Tabebuia rigida* were worn smooth through the cambium to the xylem by friction against each other due to movement in the wind. The leaves of *Prestoea montana* were broken and lacerated when they exceeded the shelter of the lee forests. The soft leaves of *Psychotria berteriana* were severely lacerated on a few plants growing in open areas. The soft flush growth of *Hornemannia*, *Gonocalyx* and *Marcgravia* was broken and leaves torn when the leading branches were whipped about in gusting winds.

Microscope slides which were exposed to collect wind-blown particles also revealed crystals of salt. We failed to find any quantities of salt crystals on leaves or any indications of leaf damage due to salt spray from ocean storms. Apparently the large amounts of rain water or precipitation from the clouds washed the leaves free of salt.

The succulent young leaves were severely damaged by the populations of insects which existed on Pico del Oeste. In column 6 of TABLE 1 is recorded the percentage of leaves of each species that was affected by animal damage.

The program of collecting foliage material for drying and future chemical tests permitted an assessment of damage to leaves on representative plants. Among the monocotyledons, animal damage was relatively light and only plants of *Rajania cordata* and *Brachionidium parvum* appeared to be severely affected. Many dicotyledonous species, however, were eaten with great regularity. In one plant of *Clusia grisebachiana* selected for study 98% of all leaves had been partially eaten and the reduction in leaf surface was 24%. These figures were computed by an actual count of the leaves which had been eaten by insects, and the degree of surface loss computed by reconstructing the outline where possible, and measuring the area lost by planimeter. Eighty percent of all leaves on representative plants of *Haenianthus salicifolius*, *Wallenia yunquensis*, *Eugenia borinquensis* and *Miconia foveolata* were similarly eaten. *Miconia* showed a reduction in leaf surface of 35% and *Eugenia borinquensis* exhibited loss of 25%. The following table shows the plants most susceptible to insect damage.

	PERCENT DAMAGED	PERCENT REDUCTION IN SURFACE AREA	pH	PERCENT WATER
Clusia grisebachiana	98	24	3.9–4.3	66
Haenianthus salicifolia	86	19	5.1–5.2	62
Wallenia yunquensis	84	16	3.5–4.2	75
Eugenia borinquensis	81	25	4.8	30
Miconia foveolata	81	35	3.9–4.0	71
Miconia pachyphylla	79	21	3.7–4.3	60
Grammadenia sintenisii	77	—	4.1–4.5	84
Hornemannia racemosa	73	—	3.9–5.3	67
Rajania cordata	70	—	4.9	—
Peperomia hernandiifolia	70	—	4.6–5.1	—

The nature of the leaf damage varied. In most cases the insect began on the margin and ate for varying distances towards the midrib. In other cases the apex of the leaf was chosen as the point of initial attack. *Miconia pachyphylla* and *Miconia foveolata*, with the characteristic reticulate network of veins of the family, were characterized by holes in the leaves. No evidence was found of insect or animal attacks on the petioles or pulvini. Insect attacks seemed to be present at all months of the year. Damage to unexpanded primordia was rarely seen. Young leaves of a flush might be consumed completely as quickly as they began to expand in *Calyptranthes* and *Eugenia*. Other leaves were attacked only as the lamina developed. The majority of the damaged leaves persisted on the plant following the insect attack. The leaves subsequently developed callous tissue or what appeared to be cork in many instances along the margin of laminar tissues that had been eaten.

Regrettably, we have been unable, up to this stage, to obtain scientific names or determinations for the insects seen or collected during this study. The following tabulation suggests that the food habits of the insects were often specific:

Gray caterpillar which stings: *Cleyera*, *Grammadenia*, *Miconia pycnoneura.*
Gray caterpillar with tufts of orange hairs and longer white hairs: *Ilex*, *Clusia.*
Slender green walking stick: *Eugenia*, *Marcgravia.*
Tan-colored stouter walking stick: *Miconia pycnoneura.*
Large spiny walking stick: *Ardisia*, *Calycogonium*, *Micropholis*, *Wallenia.*
A weevil: *Calycogonium.*
Spittle bugs: *Eugenia.*
Green grasshopper with white lines: *Tabebuia.*
Black grasshopper: *Tabebuia.*
Leaf hopper: *Cyathea.*
Leaf miners: *Hornemannia.*
A slug (*Gaeotis nigrolineata* Shuttleworth): *Lobelia.*
A snail (*Luquillia luquillensis* Shuttleworth): *Lobelia.*
Gall-producing insects: *Ocotea.*

No domatia were encountered in leaves of species within the elfin forest, although domatia were found in other species of plants in forests of lower elevations.

The nature of the attraction in the leaves of the component species to the insects cannot be determined. It was evident that the leaves varied in their texture, the amount and the color of the liquid within the tissues, their aromatic constituents and the pH of the cell contents. *Clusia* (Guttiferae), *Micropholis* (Sapotaceae), and *Lobelia* (Campanulaceae) possessed a latex, as is characteristic for the families involved. Ninety-eight percent of the leaves of *Clusia,* 33% of the leaves of *Micropholis* and 11% of the leaves of *Lobelia* were damaged by insects or snails. *Ipomoea repanda* also has cells containing a yellow material, although this did not flow when the leaf tissue was broken, and 61% of the leaves of this plant were damaged by insects. *Hedyosmum arborescens*, *Calycogonium squamulosum*, *Miconia foveolata*, and *Symplocos micrantha* could be classified as "bleeders," for the leaves, petioles or stems exuded a clear liquid when cut or broken. The percentage of leaves damaged by insects in these taxa were: *Hedyosmum*, 61%; *Calycogonium*, 21%; *Miconia foveolata*, 81%; *and Symplocos*, 14%. Aromatic principles were present in the leaves or bark of some species and can be described as follows: *Calycogonium* — cider odor; *Ilex* — odor of hay; *Mecranium* — sweet; *Miconia foveolata* — rank; *Miconia pachyphylla* — sweet; *Miconia pycnoneura* — sweet; *Symplocos* — rank and acidic; *Tabebuia* — medicinal; and *Wallenia* — odor of spinach. The nature of insect damage in these taxa is reported in TABLE 1, column 6.

In the preparation of several pounds of dried material of leaves or branches for shipping and subsequent chemical analysis, it was evident that the species of the elfin forest contained different amounts of liquid and solid materials. Large quantities of certain plants would produce only a few pounds of dry weight material while other species clearly had less liquid to evaporate. Standard weight samples of leaves were obtained and dried in an oven to obtain the percentage of water in the leaves of each species. For mature leaves the percentage of water ranged from 93% in *Psychotria guadalupensis* and *Begonia decandra* to 44% for *Calyptranthes krugii.* Only 1% of the leaves of *Psychotria guadalupensis* were damaged by insects, 26% of the leaves of *Begonia* and 41% of the leaves of *Calyptranthes.* In the list of 10 most severely damaged species previously given, the percentage of water in leaf tissue varied from 60% to 84% of the taxa for which we have data. Clearly some factor other than the amount of liquid in the plant tissue was responsible for the insect damage.

The abundance of liquid in some leaves led us to a simple measurement of the pH of the plant liquid which could be extracted (TABLE 1, column 7). Further details on these tests will be given in a later paper. For each species, leaves of a size normally eaten by insects were crushed between clean microscope slides and several drops of liquid were tested immediately with a Beckman pH meter. The acidity varied from 2.4 in *Begonia decandra* to 6.5 in *Justicia martinsoniana.* The values of the plant sap in the 10 most commonly eaten species ranged from 3.5 in *Wallenia yunquensis* to 5.3 in *Hornemannia racemosa* but averaged 4.4.

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Table 1

COLUMN 1 — Total number of leaves per plant. COLUMN 2 — Total photosynthetic area in $cm.^2$ COLUMN 3 — average blade area in $cm.^2$ COLUMN 4 — Ratio, blade length:width. COLUMN 5 — Ratio, blade length:petiole length. COLUMN 6 — Percent of leaves attacked by animals. COLUMN 7 — pH of leaf sap. COLUMN 8 — Percent of water in leaf tissue.

COLUMN NUMBER	1	2	3	4	5	6	7	8
GRAMINEAE								
Arthrostylidium sarmentosum	168	523	1.2	7.6:1	sessile	—	—	—
Ichnanthus pallens	12	97	8.1	3.5:1	sessile	0	—	—
Isachne angustifolium	18	144	8.0	10:1	sessile	0	—	—
CYPERACEAE								
Carex polystachya	27	2240	11.9	38:1	sessile	0	—	—
Eleocharis yunquensis	54	609	—	terete	sessile	0	—	—
Scleria secans	14	3101	62.0	70:1	sessile	0	—	—
PALMAE								
Prestoea montana	10	289,460	28,946.0	—	—	0	5.1–6.2	—
ARACEAE								
Anthurium dominicense	10	918	91.8	6.8:1	1:1	0	5.0–5.8	—
BROMELIACEAE								
Guzmania berteroniana	20	4,392	225.0	—	sessile	0	4.0	—
Vriesea sintenisii	19	1,581	80.0	3.7:1	sessile	0	5.1	83
DIOSCOREACEAE								
Rajania cordata	20	370	18.0	2.5:1	1:1	70	4.9	—
ZINGIBERACEAE								
Renealmia antillarum	8	736	92.0	3.1:1	constr.	0	4.8–5.3	—

COLUMN NUMBER	1	2	3	4	5	6	7	8
ORCHIDACEAE								
Brachionidium parvum	4	7.5	1.8	2.1:1	2:1	25	—	—
Dilomilis montana	17	140	8.0	4.1:1	decur.	0	—	—
PIPERACEAE								
Peperomia emarginella	62	12	0.19	1:1	1:1	0	5.0–5.5	—
Peperomia hernandiifolia	10	146	14.6	1.7:1	1:1	70	4.6–5.6	—
CHLORANTHACEAE								
Hedyosmum arborescens	2,339	44,908	19.1	2.3:1	7.5:1	61	4.5–5.6	83
MORACEAE								
Cecropia peltata	6	7,497	1,249.5	1.1:1	1.6:1	0	5.1	—
URTICACEAE								
Pilea krugii (larger lf.)	16	137	8.5	2.8:1	10:1	12	5.1–6.0	—
Pilea yunquensis (larger lf.)	11	100	9.0	1.6:1	2.2:1	14	5.5–6.4	—
LAURACEAE								
Ocotea spathulata	433	10,452	24.1	1.7:1	27:1	25	4.8–5.1	59
MELIACEAE								
Trichilia pallida	10	1,618	16.1	2.6:1	22:1	16	5.2–5.6	—
AQUIFOLIACEAE								
Ilex sintenisii	8,684	15,631	1.7	1.4:1	5.3:1	10	5.1–5.3	63
CELASTRACEAE								
Torralbasia cuneifolia	229	1,762	7.7	2:1	18:1	7	4.7–5.0	63
OCHNACEAE								
Sauvagesia erecta	205	153.9	0.75	2.8:1	9:1	0	4.9–5.6	—

MARCGRAVIACEAE								
Marcgravia sintenisii								
juvenile leaf	—	—	1.0	1.3:1	sessile	34	—	—
adult leaf	1,280	13,824	10.8	2.5:1	26:1	47	4.6–5.4	72
THEACEAE								
Cleyera albopunctata	678	7,661	11.2	2.0:1	14:1	20	3.8–4.2	56
GUTTIFERAE								
Clusia grisebachiana	243	1,956	8.0	1.5:1	32:1	98	3.9–4.3	66
BEGONIACEAE								
Begonia decandra	63	1,109	17.6	2.9:1	6.5:1	26	2.4–2.9	93
MYRTACEAE								
Calyptranthes krugii	4,539	18,609	4.0	1.2:1	15:1	41	4.0–5.1	44
Eugenia borinquensis	573	23,493	41.0	1.0:1	41:1	81	4.8	51
MELASTOMATACEAE								
Calycogonium squamulosum	1,345	14,660	10.9	2.3:1	6:1	21	3.3–3.7	92
Mecranium amygdalinum	519	8,615	16.6	2.0:1	6.8:1	42	3.2–3.8	77
Miconia foveolata	131	4,661	35.5	1.9:1	3.4:1	81	3.9–4.0	69
Miconia pachyphylla	296	6,089	20.5	2.6:1	4.4:1	79	3.7–4.3	60
Miconia pycnoneura	84	1,637	19.4	2.2:1	5.0:1	26	3.3–3.8	—
ERICACEAE								
Gonocalyx portoricensis	1,315	2,235	1.7	1.2:1	6.0:1	10	3.3–4.0	79
Hornemannia racemosa	1,315	2,235	22.2	1.7:1	21.0:1	73	3.9–5.3	55
MYRSINACEAE								
Ardisia luquillensis	1,857	17,458	9.4	2.2:1	11.0:1	50	4.3–4.4	68
Grammadenia sintenisii	579	7,411	12.8	2.4:1	12.0:1	73	4.1–4.5	84
Wallenia yunquensis	18	300	16.6	3.3:1	28.0:1	84	3.5–4.2	74

COLUMN NUMBER	1	2	3	4	5	6	7	8
SAPOTACEAE								
Micropholis garciniaefolia	10,487	96,480	9.1	1.6:1	8.0:1	33	4.1–4.8	52
SYMPLOCACEAE								
Symplocos micrantha	32	268	8.3	2.5:1	20.0:1	14	4.0–4.8	60
OLEACEAE								
Haenianthus salicifolius	1,294	17,339	13.4	2.7:1	8.0:1	86	5.1–5.2	62
CONVOLVULACEAE								
Ipomoea repanda	18	205	11.3	2.5:1	5.0:1	61	4.5–6.2	—
BIGNONIACEAE								
Tabebuia rigida	2,680	60,040	22.4	1.9:1	8.3:1	60	5.0–5.5	72
GESNERIACEAE								
Alloplectus ambiguus	16	168	10.5	2.2:1	9.5:1	43	4.6–5.5	—
Gesneria sintenisii	256	9,022	35.2	2.3:1	8.9:1	67	5.3–5.7	84
ACANTHACEAE								
Justicia martinsoniana	9	47	5.2	2.5:1	11.4:1	0	4.1–6.5	—
RUBIACEAE								
Hillia parasitica	48	564	11.7	2.7:1	5.6:1	29	4.7–4.9	83
Psychotria berteriana	305	18,093	59.3	2.0:1	4.5:1	62	5.0–5.7	85
Psychotria guadalupensis	213	410	1.9	2.0:1	1.4:1	1	4.9–5.0	93
CAMPANULACEAE								
Lobelia portoricensis	416	20,300	48.7	3.4:1	4.5:1	11	4.7–5.0	79
COMPOSITAE								
Mikania pachyphylla	46	274	5.9	1.4:1	4.5:1	10	5.1–6.0	—

Table 2

Column 1 — Leaf thickness in μ. Column 2 — Upper hypodermis (present x, absent 0). Column 3 — Lower hypodermis. Column 4 — Ratio, upper epidermis:upper hypodermis. Column 5 — Upper cuticle. Column 6 — Lower cuticle. Column 7 — Crystals (ra = raphides, rh = rhombic, d = druses, f = furuncle. Column 8 — idioblasts or sclereids present. Column 9 — Multiple palisade layer. Column 10 — Ratio of palisade layer to spongy mesophyll. Isodiam. = isodiametric cells only.

COLUMN NUMBER	1	2	3	4	5	6	7	8	9	10
PIPERACEAE										
Peperomia emarginella	275	x	0	1:10	0	0	d,ra	0	0	1:4.7
Peperomia hernandiifolia	625	x	0	1:3.0	0	0	d	0	0	isodiam.
CHLORANTHACEAE										
Hedyosmum arborescens	311	x,2x	0	1:1.3	0	0	0	0	0	1:2
MORACEAE										
Cecropia peltata	91	0	0	—	0	0	d	0	0	1:0.39
URTICACEAE										
Pilea krugii	146	0	0	—	0	0	f	0	0	1:1
Pilea yunquensis	146	0	0	—	0	0	f	0	0	1:1
LAURACEAE										
Ocotea spathulata	475	2x	0	1:1.2	x	x	0	0	x	1:1.5
MELIACEAE										
Trichilia pallida	209	0	0	—	x	x	rh	0	0	1:2.3
AQUIFOLIACEAE										
Ilex sintenisii	421	0	0	—	x	x	d	0	x	1:1.8
CELASTRACEAE										
Torralbasia cuneifolia	458	0	0	—	x	x	d	0	x	1:4.5
OCHNACEAE										
Sauvagesia erecta	141	x	0	1:1.5	0	0	d	0	0	1:1

COLUMN NUMBER	1	2	3	4	5	6	7	8	9	10
MARCGRAVIACEAE										
Marcgravia sintenisii	512	0	0	—	x	0	ra	0	x	1:2.13
THEACEAE										
Cleyera albopunctata	512	0	0	—	x	x	0	x	x	1:1.4
GUTTIFERAE										
Clusia grisebachiana	787	4–5x	0	1:10.5	x	x	d	0	x	1:2.0
BEGONIACEAE										
Begonia decandra	311	x	x	1:4.7	0	0	0	0	0	1:3.0
MYRTACEAE										
Calyptranthes krugii	549	0	0	—	x	x	rh	x	x	1:5.5
Eugenia borinquensis	512	0	0	—	x	x	d	0	x	1:2.8
MELASTOMATACEAE										
Calycogonium squamulosum	292	2x	0	1:2	x	0	rh	0	x	1:2.4
Mecranium amygdalinum	180	x	0	1:1.3	0	0	d	0	x	1:0.4
Miconia foveolata	180	x	0	1:1	x	0	d	x	x	1:0.8
Miconia pachyphylla	258	x	0	1:2	x	0	d	0	x	1:1
Miconia pycnoneura	209	x	0	1:1	x	0	d	0	x	1:1.2
ERICACEAE										
Gonocalyx portoricensis	625	x	0	1:1	x	x	rh	0	0	1:3.2
Hornemannia racemosa	384	2x	0	1:1	x	0	rh	0	x	1:3.5
MYRSINACEAE										
Ardisia luquillensis	274	0	0	—	x	0	d	0	0	1:4.0
Grammadenia sintenisii	329	0	0	—	0	0	d	0	0	1:2.2

Wallenia yunquensis	384	0	0	—	x	x	rh	0	x	1:1.5
SAPOTACEAE										
Micropholis garciniaefolia	512	x	0	1:1	x	x	0	0	x	1:1.6
SYMPLOCACEAE										
Symplocos micrantha	293	0	0	—	x	x	d	0	x	1:1.7
OLEACEAE										
Haenianthus salicifolius	457	0	0	—	x	0	0	x	x	1:1.6
Ipomoea repanda	329	0	0	—						
CONVOLVULACEAE					x	x	d	0	0	1:3.8
BIGNONIACEAE										
Tabebuia rigida	625	x	0	1:1.2	x	x	0	0	x	1:2.56
GESNERIACEAE										
Alloplectus ambiguus	256	0	0	—	0	0	0	0	0	1:2.5
Gesneria sintenisii	450	x	0	1:3	x	0	0	0	0	1:2.5
ACANTHACEAE										
Justicia martinsoniana	257	0	0	—	0	0	f	0	0	1:3.5
RUBIACEAE										
Hillia parasitica	403	x	x	1:2.7	x	x	ra	0	0	1:2.87
Psychotria berteriana	146	0	0	—	x	0	ra	0	0	1:0.7
Psychotria guadalupensis	823	x	0	1:15.2	x	x	ra	0	0	1:2.5
CAMPANULACEAE										
Lobelia portoricensis	147	0	0	—	x	0	0	0	0	isodiam.
COMPOSITAE										
Mikania pachyphylla	300	0	0	—	x	0	0	0	0	isodiam.

Table 3

COLUMN 1 — Habit of plant: H = Herb; S = Shrub; T = Tree; WC = Woody climber; HC = Herbaceous climber; E = Epiphyte. COLUMN 2 — Position of inflorescence: T = Terminal; A = Alternate; C = Cauliflorous. COLUMN 3 — Type of growth or branching: M = Monopodial; S = Sympodial; A = Alternate; D = Dichotomous. COLUMN 4 — Branches abort or show die-back. COLUMN 5 — Type of leaf production: C = appearing continuously on plant; numbers refer to leaves or pairs of leaves produced in a flush. COLUMN 6 — Number of leaves present. Hyphenated numbers refer to clear examples of number of leaves and number of flushes represented. COLUMN 7 — Length of guard cells in mm. COLUMN 8 — Number of stomata per sq. mm. COLUMN 9 — Type of stomatal apparatus.

COLUMN NUMBER	1	2	3	4	5	6	7	8	9
PIPERACEAE									
Peperomia emarginella	H	T	M	—	C	–	.046	22	Anomocytic
Peperomia hernandiifolia	H	T	M	—	C	7	.032	65	Anisocytic
CHLORANTHACEAE									
Hedyosmum arborescens	S	T	S	—	3 pr	–	.046	75	Anomocytic
MORACEAE									
Cecropia peltata	T	A	A	—	C	–	.018	500	Anomocytic
URTICACEAE									
Pilea krugii	H	A	M	—	C	–	.023	65	Anisocytic
Pilea yunquensis	H	A	M	—	C	–	.023	110	Anomocytic
LAURACEAE									
Ocotea spathulata	T	A	S	—	1–3(7)	14–ss	.032	306	Paracytic
MELIACEAE									
Trichilia pallida	S	A—C	M	—	1	6–	.032	205	Anomocytic
AQUIFOLIACEAE									
Ilex sintenisii	S	A	A	DB	3–4	20–7	.023	140	Anomocytic
CELASTRACEAE									
Torralbasia cuneifolia	S	A	S	DB	C	20–7	.032	130	Anomocytic

OCHNACEAE									
Sauvagesia erecta	H	A	A	—	C	31–	.032	187	Paracytic
MARCGRAVIACEAE									
Marcgravia sintenisii	C	T	M	—	C	40–	.028	90	Anomocytic
THEACEAE									
Cleyera albopunctata	T	A	A	DB	C	3–	.037	280	Anomocytic
GUTTIFERAE									
Clusia grisebachiana	T	T	D	—	2 pr	4–2	.036	177	Paracytic
BEGONIACEAE									
Begonia decandra	H	T	A	—	C	–	.035	270	Paracytic
MYRTACEAE									
Calyptranthes krugii	S	A	D	—	1–2 pr	–	.030	310	Paracytic
Eugenia borinquensis	T	A,C	D	DB	1–3 pr	15–20	.023	884	Anisocytic
MELASTOMATACEAE									
Calycogonium squamulosum	S	A	D	—	C	–3	.016	550	Anisocytic
Mecranium amygdalinum	S	A,C	A	—	—	6–	.018	680	Anomocytic
Miconia foveolata	S	T	D	—	3–5 pr	5–	.016	1180	Anomocytic
Miconia pachyphylla	S	T	D	—	C	5–	.035	130	Anomocytic
Miconia pycnoneura	S	T	D	—	C	9–	.010	2230	Anomocytic
ERICACEAE									
Gonocalyx portoricensis	C	A,C	A	—	3–4	20–4	.020	411	Paracytic
Hornemannia racemosa	C	A	A	DB	C	9–	.021	340	Paracytic
MYRSINACEAE									
Ardisia luquillensis	T	T	S	DB	5	–4	.025	230	Anisocytic
Grammadenia sintenisii	S	A	S	—	C	–	.025	159	Anisocytic
Wallenia yunquensis	S	A	S	—	—	5–	.030	177	Paracytic

COLUMN NUMBER	1	2	3	4	5	6	7	8	9
SAPOTACEAE									
Micropholis garciniaefolia	T	A	A	DB	2–6	20–4	.027	230	Anomocytic
SYMPLOCACEAE									
Symplocos micrantha	S	A	A	—	2–6	–	.030	230	Paracytic
OLEACEAE									
Haenianthus salicifolius	T	T	D,S	—	C	–	.025	327	Anomocytic
CONVOLVULACEAE									
Ipomoea repanda	WC	A	A,T	DB	C	9–	.032	110	Paracytic
BIGNONIACEAE									
Tabebuia rigida	T	T	D	DB	1–2 pr	10–4	.023	230	Anomocytic
GESNERIACEAE									
Alloplectus ambiguus	H	A	M	DB	C	22–	.032	56	Anisocytic
Gesneria sintenisii	S	A	M	DB	C	20–	.035	168	Anisocytic
ACANTHACEAE									
Justicia martinsoniana	H	T	D	—	—	–	.025	170	Paracytic
RUBIACEAE									
Hillia parasitica	S,E	T	D	—	—	–	.037	100	Paracytic
Psychotria berteriana	S	T	D	—	2 pr	3–	.029	210	Paracytic
Psychotria guadalupensis	S,E	T	½D	—	C	8–	.025	110	Paracytic
CAMPANULACEAE									
Lobelia portoricensis	S,H	T	A	DB	—	37–	.040	190	Anomocytic
COMPOSITAE									
Mikania pachyphylla	C	A,T	M	—	—	–	.035	196	Anomocytic

Table 4

TAXON	STOMATAL SIZE IN MM.	STOMATA NUMBER MM ^{2}	TYPE OF STOMATAL APPARATUS
GRAMINEAE			
Arthrostylidium sarmentosum	0.027	205	Gramineous
Ichnanthus pallens	0.043	140	Gramineous
Isachne angustifolium	0.023	230	Gramineous
CYPERACEAE			
Carex polystachya	0.041	102	Gramineous
Eleocharis yunquensis	0.048	120	Gramineous
Scleria secans	0.030	110	Gramineous
PALMAE			
Prestoea montana	0.025	140	Paracytic
ARACEAE			
Anthurium dominicense	0.046	56	Paracytic
BROMELIACEAE			
Guzmania berteroniana	0.044	18	Didymocytic
Vriesea sintenisii	0.039	28	Didymocytic
DIOSCOREACEAE			
Rajania cordata	0.035	120	Anomocytic
ZINGIBERACEAE			
Renealmia antillarum	0.027	140	Paracytic
ORCHIDACEAE			
Brachionidium parvum	0.039	37.5	Didymocytic
Dilomilis montana	0.032	120	Anomocytic

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EXPLANATION OF PLATES

PLATE I

a. Terminal bud of an adult branch of *Marcgravia sintenisii*. b. Stem of *Hillia parasitica* showing the flattened stipular sheath. c. Stem apex of *Ilex sintenisii* showing the rosette of small leaves and cataphylls. d. Shoot apex of *Gesneria sintenisii* showing the individual leaf primordia; each primordium is encased in a resinous covering. e. Section through the apex of *Hedyosmum arborescens* revealing the stem apex and young leaves encased in the sheathing bases of petioles. f. *Clusia grisebachiana*, in which the leaves of the apical pair are tightly appressed and enclose and protect the terminal bud. g. Three views of the stem apex and terminal leaf pair of *Calyptranthes krugii*, left figure shows the mature leaves; central figure shows the plicate stipule pair separated at the base; right figure shows the plicate stipule pair separated at the apex.

PLATE II

a. Cross section of a leaf of *Haenianthus salicifolius* showing the multiple layers of palisade parenchyma and two branched idioblasts. b. View of the upper epidermis of *Pilea krugii* showing two furuncles. c. Cross section of a leaf of *Peperomia hernandiifolia* showing the irregular epidermis, the multiple hypodermis, a layer of parenchyma containing druses and the undifferentiated mesophyll containing chloroplastids. d. Cross section of a leaf of *Mikania pachyphylla* showing the undifferentiated mesophyll.

PLATE III

Epidermal cells and stomatal apparatus of: a, *Miconia pachyphylla*; b, *Brachionidium parvum*; c, *Alloplectus ambiguus*; d, *Renealmia antillarum*.

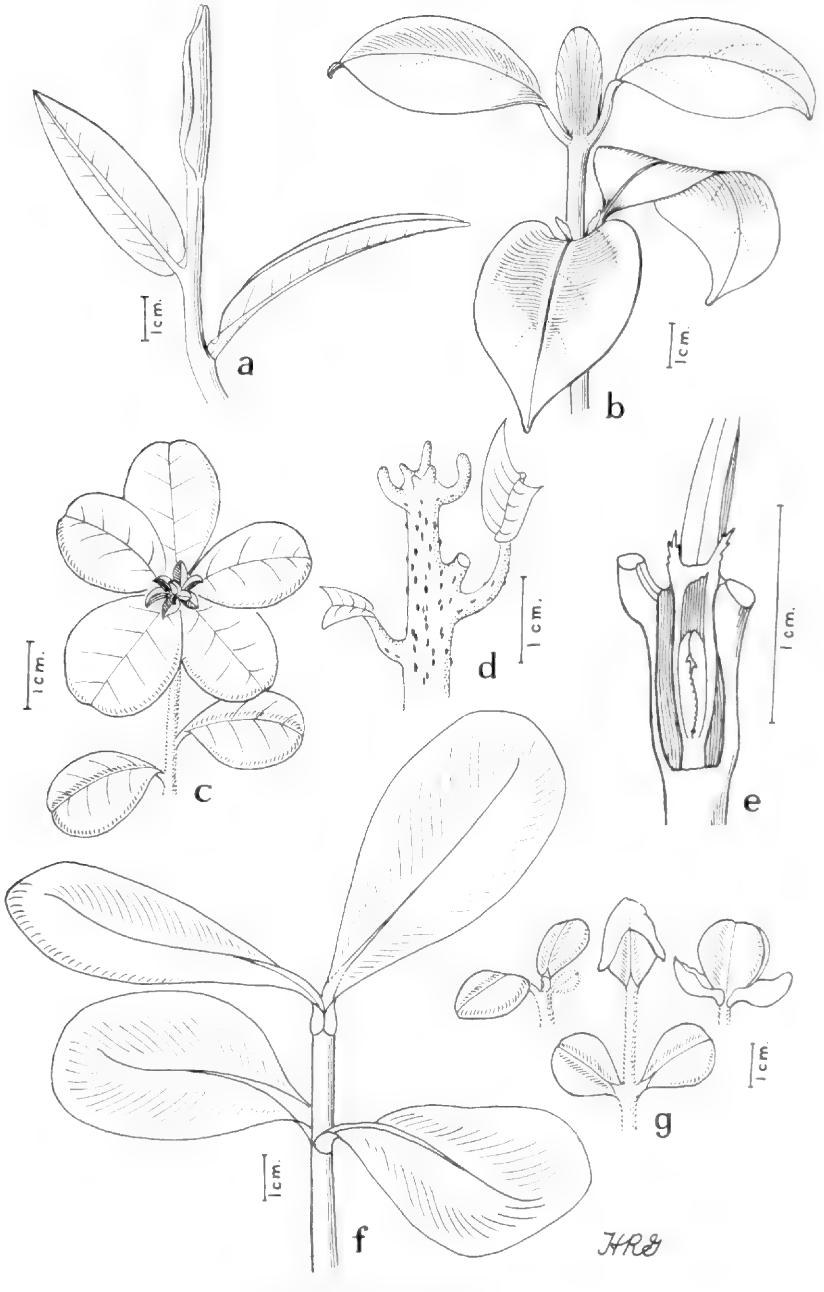
PLATE IV

Epidermal cells and stomatal apparatus of: a, *Anthurium dominicense;* b, *Hillia parasitica*; c, *Torralbasia cuneifolia*; d, *Scleria secans*; e, *Haenianthus salicifolius* var. *obovatus*; f, *Gonocalyx portoricensis.*

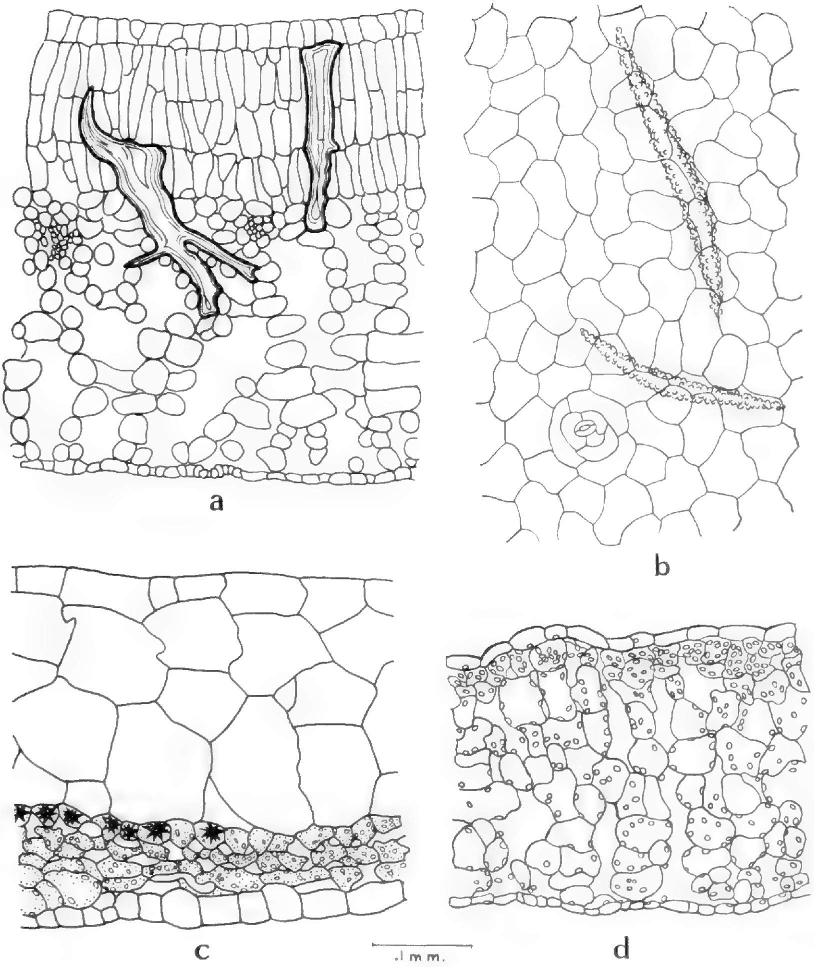
PLATE V

a. Lower epidermal surface of *Pilea krugii* showing the cluster of small stomata over a vascular bundle, a multicellular gland, and two of the larger stomatal apparatus. b. The lower epidermal surface of a leaf of *Grammadenia sintenisii* showing the stomatal apparatus grouped in clusters of three.

PLATE I



HOWARD, ELFIN FOREST, 8



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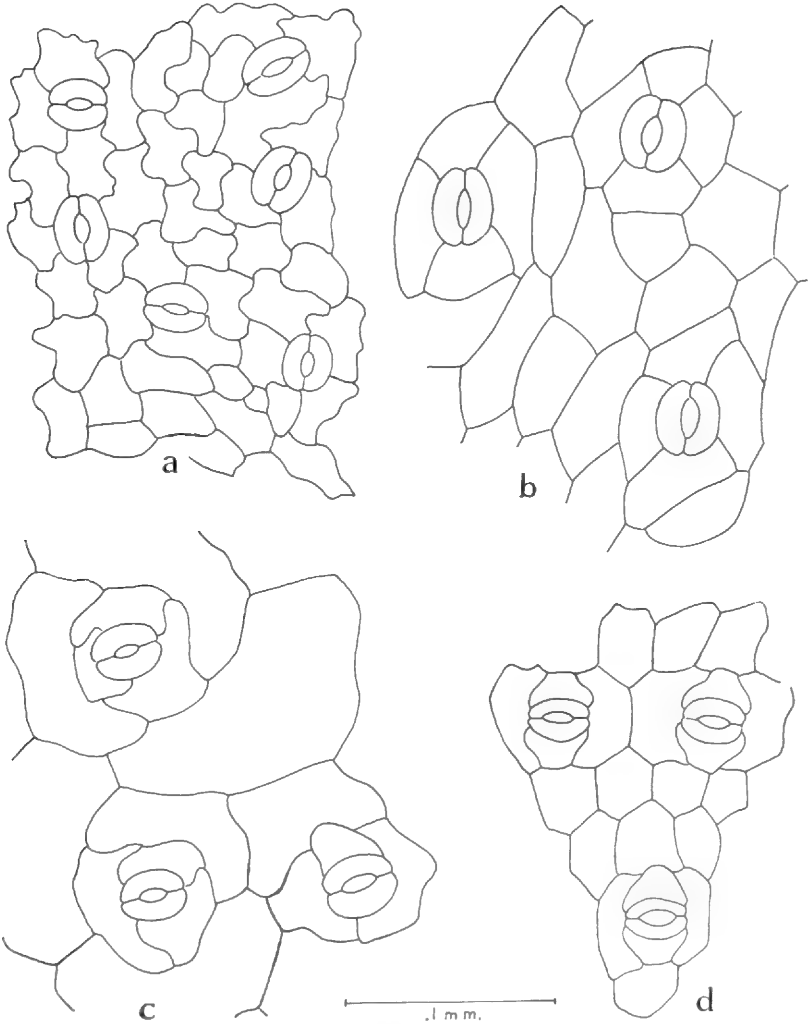

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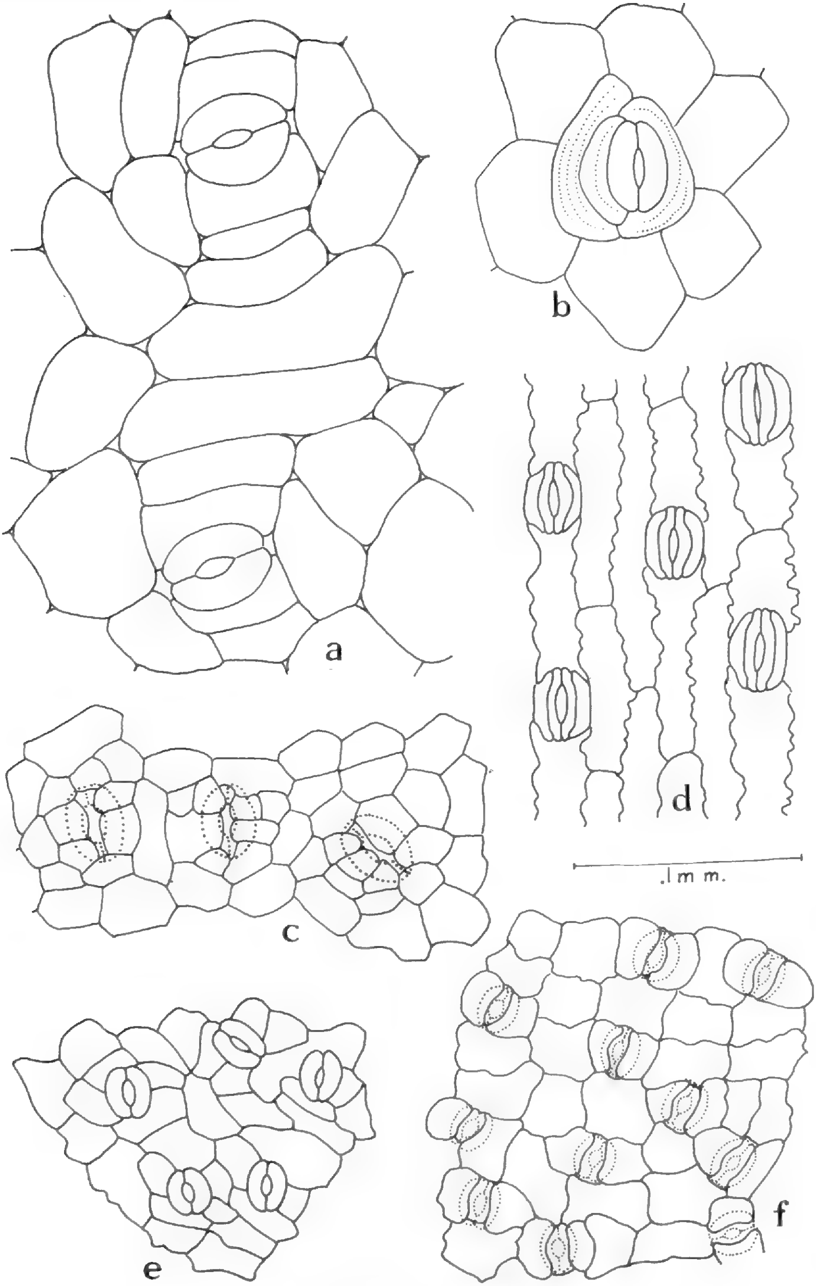

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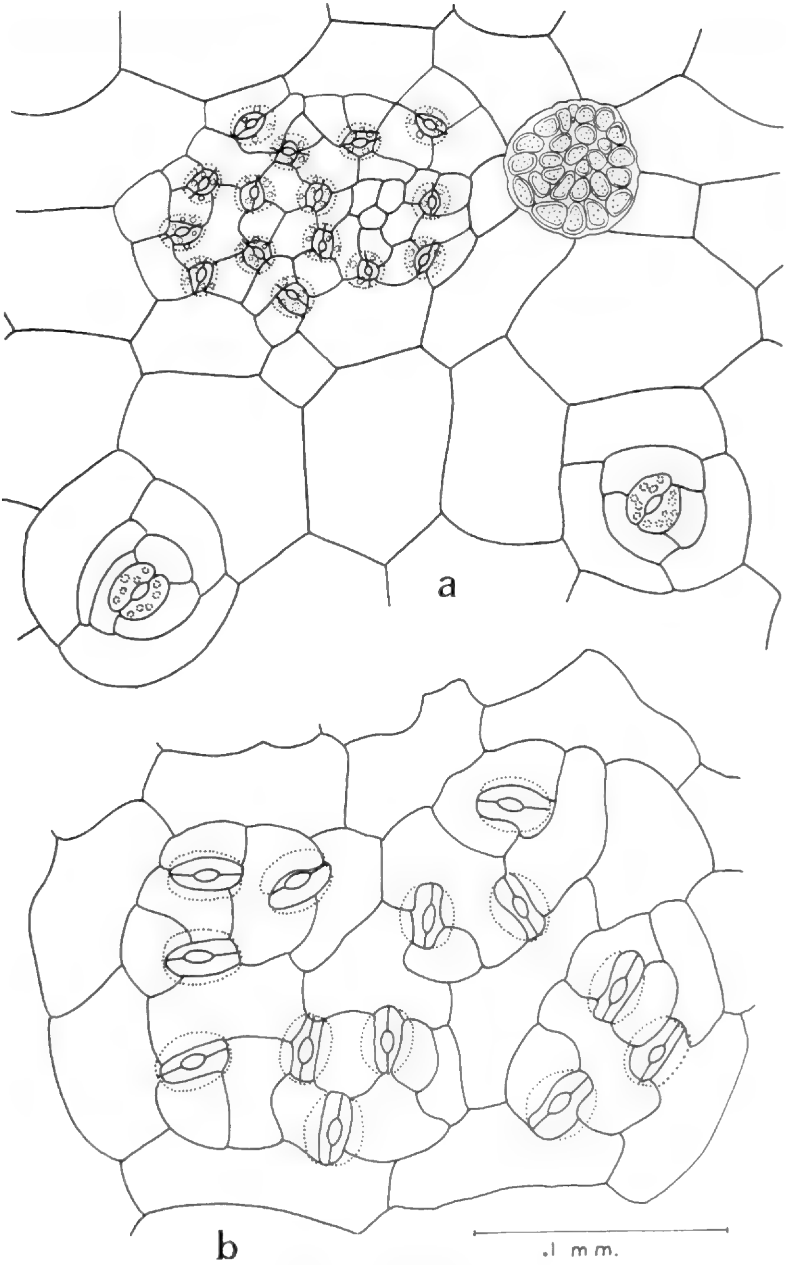

HOWARD, ELFIN FOREST, 8

LECTOTYPIFICATION OF CACALIA L. (COMPOSITAE-SENECIONEAE) [1]

BERYL S. VUILLEUMIER AND C. E. WOOD, JR.

THE INTERNATIONAL CODE of Botanical Nomenclature (1966) provides, by means of nomenclatural types, stability in the application of names at, or below, the rank of family. The use of a name is determined by the nomenclatural type of that name, and changes may result when, or if, the choice of a type is shown to be incorrect. To avoid disadvantageous changes in the application of names provision is also made in the Code to preserve current usage and to avoid the confusion which could result from varying opinions concerning the choice of a lectotype. The senecionid genus *Cacalia,* as circumscribed by Linnaeus (1753, 1754) was quite heterogeneous, and the process of choosing a lectotype has been both complicated and subject to individual interpretation. Three different species have been proposed as lectotype, and even now there are conflicting opinions (Cuatrecasas, 1960, and Pippen, 1968, *vs.* Pojarkova, 1961, and Vuilleumier, 1969). It seems expedient to review the typification of this genus once more. *Cacalia* as typified here (by *C. hastata* L., a choice made by Kitamura, 1942) provides an example in which the choice of a lectotype in accordance with the guides outlined in the Code also complies with the recommendation (7B) that a lectotype be so chosen as to preserve current usage.

In the first edition of *Species Plantarum* (2: 834–836. 1753), Linnaeus described and named ten species of *Cacalia* which he divided into two groups: "Frutescentes," consisting of four shrubby species, and "Herbaceae," with six herbaceous species. In 1754, Miller (Gard. Dict. Abr. ed. 4. 2: ord. alph.) split *Cacalia*, placing the four shrubby species in *Kleinia* Mill. *Cacalia* was thus restricted to the herbaceous species, and it is from the six original species of this group that all choices of lectotype have been made. To our knowledge, no one has suggested that *Cacalia* be typified by one of the species removed to *Kleinia*.

There has been, however, considerable disagreement as to which of the six herbaceous species should be designated as lectotype. Rydberg (1924) concluded that *Cacalia alpina* should be the type species; Cuatrecasas (1955, 1960) and Pippen (1968) have concurred in this choice.

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[1] One of an informal series of peripheral papers arising from research toward a *Generic Flora of the Southeastern United States* being carried on through the generous help of the National Science Foundation (Grant GB–6459X, C. E. Wood, Jr., principal investigator).

We acknowledge with thanks the assistance of Dr. Bernice G. Schubert and Dr. Elizabeth Shaw and we are indebted to Andrey I. Baranov for his translation of a portion of A. Pojarkova's treatment of *Cacalia* in Flora URSS.

Hitchcock and Green (1927) chose another type, *C. atriplicifolia*, which Pojarkova (1960) also adopted. Kitamura (1942), however, made a third choice, *C. hastata*, and Pojarkova (1961), changing her opinion, agreed with him. Quite independently, Shinners (1950) came to the conclusion that either *C. suaveolens* or *C. hastata* should be the lectotype species. After a careful review of the arguments and of the nomenclatural and taxonomic history of *Cacalia* in conjunction with the application of the Rules and Recommendations of the Code, we are convinced that *C. hastata* should be the lectotype species.

Since the nomenclature of species of vascular plants begins in 1753 and that of genera in 1754, in most instances the application of a name prior to 1753 should be given little weight relative to a post-1753 application, especially since Linnaeus not infrequently reapplied older names in a completely different sense. However, one of the principal arguments advanced, first by Rydberg, and then by Cuatrecasas and Pippen for the selection of *Cacalia alpina* as the type species of *Cacalia* is an historic one. Rydberg wrote (*loc. cit.*, p. 370), "Of the species of the second [herbaceous] group only the last two, *Cacalia atriplicifolia* and *C. alpina*, had been known as *Cacalia* before Linnaeus' time.[2] The name *Cacalia*, applied to the last one, dates back to Vaillant and L'Obel. *C. alpina* L. or *Adenostylis alpinus* is therefore the historical type of *Cacalia*." Cuatrecasas (1960, p. 182) reiterated, "There is no doubt that the name *Cacalia* was first applied to *C. alpina* and that Linné had this species in mind when he established the genus in his Genera Plantarum. Therefore, *Cacalia alpina* is the type of *Cacalia*." Pippen added (1968, p. 377), "It seems clear that *C. alpina* L. is the most logical lectotype of *Cacalia*. This species, named *C. alpina* by Linnaeus (1753), embodied the Linnaean and pre-Linnaean concept of *Cacalia* in that essentially all of the species of *Cacalia* described by pre-Linnaean botanists (L'Obel, 1581; Clusius, 1601; Bauhin, 1623; Morison, 1699; Tournefort, 1700) actually represented the same species."

The adoption of this historical argument would restrict the name *Cacalia* to a genus consisting of four or five species of Europe which has been known since 1816 as *Adenostyles* Cassini. Contrary to all three authors, however, the use of arguments concerning the application of names before the starting point for botanical nomenclature can result only in further confusion, as is shown below.

In the first edition of *Genera Plantarum* (1737, p. 252), *Cacalia* in the sense of Tournefort (that is, *C. alpina* L.) is found in the synonymy of *Tussilago*: "TUSSILAGO*. *Tournef.* 276. *Vaill.* A. G. 1720. f. 46. Cacalia

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[2] In the next paragraph Rydberg added, ". . . only Linnaeus himself had used *Cacalia* for *C. suaveolens* in his Hortus Upsaliensis." Rydberg probably was misled by Linnaeus's reference to *Hortus Upsaliensis* immediately following the diagnostic phrase name (specific name) of *Cacalia suaveolens* in *Species Plantarum* (1753, p. 835). In *Hortus Upsaliensis* (1748, p. 254), Linnaeus treated this as a species of *Kleinia* ("Kleinia caule herbaceo," etc.); the diagnosis is the same in *Species Plantarum,* except that *Cacalia* has been substituted for *Kleinia*. We have not found any mention of *Cacalia* in *Hortus Upsaliensis*.

Tournef. 258. Petasites *Tournef. 258. Vaill.* A. G. 1719." Following the description the observation is added: "Cacalia *T. caule ramoso est, & corollulis hermaphroditis quadrifidis, sine radio ligulato.*" On the same page is found *Kleinia*: "KLEINIA. Cacalianthemum *Dill.* elth. 54. 55. An Tithymaloides ? *Klein.* monagr." The corolla is described as with the limb "quinquefido, erecto," and the stigmas as "duo, oblonga, revoluta." In the second edition (1742, p. 401), the synonymy of *Tussilago* is amplified by the addition of "*Vaill.* A. G. *1719.*" to the reference to *Cacalia*, and to that of *Kleinia* (p. 394) is added "Porophyllum *Vaill.* A. G. 1719. t. 20. f. 39." which Linnaeus had maintained as distinct in the *Hortus Cliffortianus* (1738, p. 494). Neither description was changed in any way in this edition. The synonymy and descriptions of *Tussilago* and *Kleinia* in the editions of 1743 and 1752 are identical with those of the second, but these editions were not prepared by Linnaeus.

In the fifth and crucial edition (1754, p. 362), Linnaeus treated *Cacalia* of Vaillant and Tournefort as congeneric with *Kleinia* and combined the two under the name *Cacalia*: "CACALIA.* *Vaill.* A. G. 1719. *Tournef.* 258. Kleinia *edit. prior.* Cacalianthemum *Dill. elth.* 54. 55. An Tithymaloides ? *Klein. monagr.* Porophyllum *Vaill. A. G.* 1719. *t.* 20. *f.* 39." Most interestingly, the generic description is identical with that of *Kleinia* of the first four editions of *Genera Plantarum*! There is no mention of the tetramerous corolla of *Cacalia alpina* which had appeared in earlier editions under *Tussilago*.

Rydberg argued (*loc. cit.*) that "Linnaeus' description of the genus [*Cacalia*] points to this species [*C. alpina*] especially the description of the style tips: 'Stigmata duo, oblonga, revoluta.' This is characteristic of *Adenostylis alpinus* which on account of its oblong style branches had been placed in the tribe EUPATORIEAE, but which Dr. B. L. Robinson rightly restored to the SENECIONEAE. *C. atriplicifolia* as well as *C. suaveolens* has a true *Senecioid* style, with truncate style-branches." Cuatrecasas further argued, "Among all the species of *Cacalia* in Linné's Species Plantarum, *Cacalia alpina* is the only one with elongate, curled stigmas and 4-merous corollas." Cuatrecasas is correct, but Linnaeus's description (1754) of the corollas of *Cacalia* as five-fid and the stigmas as "duo, oblonga, revoluta" does not apply to *C. alpina* but to the species which he had formerly placed in *Kleinia*, a name which he abandoned in favor of *Cacalia* in 1753. Moreover, the description of the corolla and stigmas is precisely the same as in *Senecio* (Gen. Pl. ed. 5. 373).

A note under *Cacalia alpina* in *Species Plantarum* (1753, p. 836) reads: "*Hanc speciem genere cum antecedentibus convenire docuit autopsia, hinc genere conjugenda*: Cacalia *cum* Kleiniis." In the second edition (1763, p. 1171) this note is clearer and is amplified: "*Hanc speciem genere cum antecedentibus convenire docuit autopsia, hinc genere conjugendae* Cacaliae *cum* Kleiniis. *Calyx hujus speciei flosculis 3 s. 4 tantum.*" We translate this to read: "My observation has shown this species to agree generically with the preceding ones; hence the Cacalias are to be joined in a genus with the Kleinias. The involucre of this species with only 3 or 4 florets." From this comment and the placement of the species last in the genus it appears that Linnaeus regarded *C. alpina* as somewhat aberrant in, but belonging to, the genus which he had formerly called *Kleinia*. The use of the plural of *Cacalia* also suggests that he had in mind more than one species.

Linnaeus did not change the description of *Cacalia* in the sixth edition of the *Genera*, but the authors of the seventh and eighth editions noted the departures of *C. alpina* from the others of the genus. Reichard (Gen. Pl. ed. 7. 411. 1778) observed, "C. *alpina foliolis calycis conglutinatis corollulisque quadrifidis differt*." Schreber (Gen. Pl. ed. 8. 545. 1791) included in the description of the corolla "*limbo* quadri-f. quinquefido, erecto," and Haenke in his edition (Gen. Pl. ed. 8. 709. 1791) had precisely the same description and observation as Reichard. Cuatrecasas (1960, p. 182) attributes a comment to Schreber (1791, p. 545) which we have been unable to locate in the copy available to us: " 'Cacalia differt a Senecione flosculis quadrifariam scissis.' "

To return to 1753, *Cacalia* as set forth by Linnaeus in the works which are the starting points for botanical nomenclature has a protologue which is that of *Kleinia* of the first four editions of the *Genera Plantarum*, with the exception of the pre-Linnaean Vaillant and Tournefort references to *Cacalia*, both of which apply to *C. alpina*. *Cacalia alpina* does not agree with the generic description in either corolla or stigmas, but a number of the other species do, among them species currently assigned to *Cacalia* and those removed by Miller to *Kleinia*. It appears that this is but another example of Linnaeus's changing the name of a genus (*Kleinia*) to one which he liked better (*Cacalia*), even though the species which had borne that name historically was somewhat aberrant within an already heterogeneous genus. In the interests of nomenclatural stability, it seems to us most unwise and unwarranted to do anything but to begin the nomenclatural and taxonomic history of *Cacalia* at 1753 and to proceed from that year in the choice of a type species. The species chosen should be in agreement with the protologue and must be one of the ten described in *Species Plantarum* in 1753, taking into consideration those which have been removed to other genera. In reaching the conclusion that *Cacalia hastata* must be the lectotype species, our reasoning follows essentially the same arguments as those succinctly presented by Shinners (1950).

All of the ten original species have been transferred to one or more other genera at one time or another. The chronological sequence of the more important of these transfers follows:

C. papillaris, *C. anteuphorbium*, *C. kleinia*, and *C. ficoides*: Segregated as the genus *Kleinia* by P. Miller (Gard. Dict. Abr. ed. 4. **2**: ord. alph. 1754), although the combinations under that genus were not made until much later by Haworth (1812) and De Candolle (1838).

C. alpina: Transferred to *Tussilago* L. by Scopoli (Fl. Carniol. ed. 2. **2**: 156. 1772) as *T. Cacalia* Scop. (not *T. alpina* L.). Placed in a new genus, *Adenostyles*, by Cassini (Dict. Sci. Nat. Paris **1**(Suppl.): 59. 1816).

C. Porophyllum: Removed by Cassini (Dict. Sci. Nat. Paris **43**: 56. 1826) to *Porophyllum* Guett. as *P. ellipticum* Cass.

C. suaveolens: Placed in *Senecio* L. by Elliott (Sketch Bot. S. Carol. & Ga. **2**: 328. 1823); later placed in *Synosma* Raf. ex Britton & Brown (Illus. Fl. No. U.S. Canada **3**: 474. 1898).

C. sonchifolia: Tentatively removed to *Crassocephalum* Moench (= *Gynura* Cass., nom. cons.) by Lessing (Synop. Comp. 395. 1832). Later placed in *Emilia* Cass. by De Candolle as *E. sonchifolia* (L.) DC. ex Wight (Contr. Bot. India 24. 1834).

C. hastata L.: Tentatively referred to *Ligularia* L. by Lessing (Synop. Comp. 390. 1832), but the combination under *Ligularia* not made. Later transferred to *Senecio* as *S. sagittatus* by Schultz Bipontinus who united *Cacalia* with that genus (Flora **28**: 498. 1845).

C. atriplicifolia L.: Transferred to *Mesadenia* Raf. (nom. superfluum = *Arnoglossum* Raf.) by Rafinesque (New Fl. N. Am. **4**: 79. 1838). Treated as a *Senecio* by Hooker, who combined *Cacalia* with *Senecio* (Fl. Bor.-Am. **1**: 332. 1834).

By the beginning of 1838 only *Cacalia hastata* and *C. atriplicifolia* of the original species had not been transferred formally to other genera. Early in 1838 appeared Volume six of A. P. de Candolle's *Prodromus*, which included a revision crucial in the typification of *Cacalia*. De Candolle divided *Cacalia* into four sections, retaining only three of Linnaeus's original species: *C. hastata* and *C. suaveolens*, which he placed in section *Eucacalia* DC., and *C. atriplicifolia*, which was a member of section *Conophora* DC. Thus, he effectively limited the choice of lectotype to either *C. hastata* L. or *C. suaveolens* L. Since *C. suaveolens* had been transferred to *Senecio* by Elliott (1823), who left *C. atriplicifolia* in *Cacalia*, *C. hastata* becomes the lectotype species. This species is quite in accord with the original description of the genus (Linnaeus, Gen. Pl. ed. 5. 362. 1754), and we can see no reason for choosing another species.

The selection of *Cacalia hastata* as lectotype for *Cacalia* L., primarily on the basis of the removal of the other species to different genera, is in accordance with both the Guide for the Determination of Types set forth in the International Code and the recommendation (7B) that the lectotype should be so selected as to preserve current usage. As so typified, *Cacalia* is a genus of North America and Asia (including easternmost Europe). The question of whether a number of genera should be segregated from *Cacalia* as now circumscribed taxonomically is not yet settled, but no matter what the outcome of future investigations, *Cacalia* as typified by *C. hastata*, will be stable and a minimum of new combinations will have to be made.

We regard the species of *Cacalia* in eastern North America as belonging to two sections: CACALIA, represented in North America by *C. suaveolens* L. and in Asia by *C. hastata* L. and a number of allied species; and CONOPHORA DC., restricted to eastern North America. (Cf. Vuilleumier, 1969.) The pertinent synonymy of these sections is shown below:

Cacalia L. Sp. Pl. **2**: 834 1753; Gen. Pl. ed. 5. 362. 1754.

Sect. **Cacalia**.

Cacalia sect. *Eucacalia* DC. Prodr. **6:** 327. 1838. LECTOTYPE SPECIES: *C. hastata* L.

Synosma Raf. ex Britton & Brown, Illus. Fl. No. U.S. Canada **3:** 474. 1898. TYPE SPECIES: *S. suaveolens* (L.) Raf. ex Britton & Brown (*C. suaveolens* L.).

Hasteola Raf. ex Pojarkova, Not. Syst. Leningrad **20:** 380. 1960, nom. superfluum. TYPE SPECIES: *H. suaveolens* (L.) Pojark. (*C. suaveolens* L.). [Not validly published by Rafinesque, New Fl. N. Am. **4:** 79. 1838; as validated by Pojarkova includes the type species of *Cacalia*.]

Sect. **Conophora** DC. Prodr. **6:** 329. 1838. LECTOTYPE SPECIES: *C. atriplicifolia* L.

Arnoglossum Raf. Fl. Ludovic. 64. 1817. TYPE SPECIES: *A. plantagineum* Raf. = *C. plantaginea* (Raf.) Shinners (*C. tuberosa* Nutt.).

Mesadenia Raf. New Fl. N. Am. **4:** 78. 1838, nom. superfluum. LECTOTYPE SPECIES: *M. atriplicifolia* (L.) Raf. (*C. atriplicifolia* L.). [Includes the type species of *Arnoglossum* Raf.]

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A REVISION OF THE MALESIAN AND PACIFIC RAINFOREST CONIFERS, I. PODOCARPACEAE, IN PART

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THE RAINFOREST FLORA of a considerably submerged land area extending from southeast Asia through Indonesia and New Guinea to the Tonga Islands includes an important conifer element for much of which systematic examination is essentially lacking. It will be the purpose of this study to present in three parts a critical account of the genera of Coniferales that occur primarily in this area, that is to say, all of the tropical rainforest conifers beyond the mainland of Asia except two species of *Pinus* whose ranges extend into Indonesia and the Philippines, plus such species in southeast Asia as belong to the island rainforest groups.

Conifers are, in general, strongly divided into northern hemisphere and southern hemisphere elements (Li, 1953). The characteristically southern hemisphere families are Podocarpaceae and Araucariaceae, both of which reach their greatest luxuriance in the area under consideration. In addition, several genera of Cupressaceae occur in the southern hemisphere as does one genus of Taxodiaceae, but of these only *Libocedrus* is truly a part of the rainforest and included here. Taxaceae, formerly considered in the Coniferales, is not important, posing no taxonomic problems here, and will be omitted also. The rainforest conifers to be studied involve twelve genera and well over one hundred species. New Caledonia alone, centrally located with respect to the floristic region but recently remarkably isolated, has preserved some forty species, all endemic, while the extensive forests of New Guinea have yielded nearly as many again. Indonesia in general has a conifer flora of equal richness to New Guinea, sharing many species, while the rainforests of Queensland, Fiji, and lesser areas have fewer elements many of which are endemic.

More than a third of the species being described, both new and previously recognized, were studied in their natural state during two extensive field trips to the Pacific in 1957 and in 1964–65. In addition, the directors and personnel of many herbaria contributed greatly to the completeness of the study by their sympathetic help, and I should like to extend my deep gratitude to them. The following key identifies the herbaria whose specimens were consulted:

A	Arnold Arboretum of Harvard University, Cambridge
BM	British Museum (Natural History), London
BRI	Botanic Museum and Herbarium, Brisbane
FI	Herbarium Universitatis Florentinae
GH	Gray Herbarium of Harvard University, Cambridge
ILL	University of Illinois Herbarium, Urbana

K	Royal Botanic Gardens, Kew
L	Rijksherbarium, Leiden
LAE	Department of Forests, Division of Botany, Lae
NA	U.S. National Arboretum, Washington
NSW	National Herbarium of New South Wales, Sydney
NY	New York Botanical Garden, New York
P	Muséum National d'Histoire Naturelle, Paris
RSA	Rancho Santa Ana Botanic Garden, Claremont
SBT	Hortus Botanicus Bergianus, Stockholm
US	U.S. National Museum (Department of Botany), Smithsonian Institution, Washington, D.C.
Z	Botanic Garden and Institute of Systematic Botany of the University, Zürich

In addition, I should like to thank M. Corbasson, Director, Bureau des Eaux et Forêts, Nouméa, New Caledonia, H. S. McKee, of the same address, M. Schmid, Centre O. R. S. T. O. M., Nouméa, Lucien Lavoix of Nouméa, and J. W. Parham, Department of Agriculture, Suva, Fiji, for their help both in the field and in obtaining additional important specimens.

The following comments apply to the citation of specimens:

1. Each specimen is accompanied by a symbol denoting its development and sex. These include "j" for juvenile, "s" adult but sterile, "♀" female structures present, and "♂" male structures present. When more than one stage is included on the same sheet, more than one symbol will be used. Where appropriate and available, elevation figures will be included ("m." for meters or "ft." for feet).

2. Where collections are numbered in series (sometimes without a collector's name) the standard abbreviation will be used. These include:

ANU	Herbarium Australiense, C.S.I.R.O.
BRUN	Brunei, Forest Department
BSIP	British Solomon Islands Protectorate
BW	Boswezan, Forestry Division, Netherlands New Guinea
NGF	New Guinea Forest Department
NIFS	Netherlands Indies Forest Service: bb: series bossen buitengewesten — islands outside Java
SAN	North Borneo Forest Department, Sandakan
SFN	Singapore Field Number

Podocarpaceae is a well differentiated family that is distinguished by such characters as one wingless seed per fertile scale, two sporangia per microsporophyll, and two cotyledons, each of which has two vascular bundles apparently representing a fusion of two units (de Laubenfels, 1962). In addition, the group generally has such unique embryonic characters as a binucleate condition of the first embryonic cells (Buchholz, 1941). The seeds in many genera are produced on structures so modified from the cone morphology that one can not easily refer to them as cones, although true seed cones and intermediate structures are found in the family. Pollen cones are always truly cone-like and for all but two genera are developed strictly on separate plants from the seed structures. Nine of the twelve genera being recognized here occur in the tropics and four of these are endemic to the tropics. All but a few species of the family grow in very moist areas, some, particularly in Tasmania, being found beyond the tree line as small or prostrate shrubs. Most, however, are large forest trees, many with broad leaves quite unlike the usual conception of conifers.

Within Podocarpaceae there has been great variation in the size and complexity of the recognized genera. The genus *Podocarpus* as generally treated involves up to eight sections and well over one hundred species, the differences between some of these sections being every bit as great as those which separate most other genera. It is being proposed here to divide *Podocarpus* into five separate genera in order to produce a more balanced treatment of the family. In addition, one new genus is separated from *Dacrydium* because of the different form of the fertile shoots and the strikingly different foliage morphology. The result is a total of twelve genera in the family, of which nine are to be considered in this study, six in part I and three in part II.

KEY TO THE GENERA OF PODOCARPACEAE

1. Seed cone compact, seeds not subterminal.
    2. Ovules inverted.
        3. Cones produced on ordinary foliage branches; adult leaves in the form of scales.
            4. Seed partly covered by an epimatium; leaves opposite, decussate. . . . . (*Microcachrys*, not tropical).
            4. Seed completely enveloped in the fertile scale or epimatium; leaves spirally arranged. . . . . (some species of *Dacrydium*, not tropical).
        3. Fertile shoot specialized; adult leaves linear, flat, constricted at the base. . . . . (*Saxegothaea*, not tropical).
    2. Ovules erect.
        5. Fertile scale lacking; adult leaves developed. . . . . (*Microstrobus*, not tropical).
        5. Fertile scale an epimatium; adult leaves suppressed in favor of phylloclads. . . . . *Phyllocladus*.
1. Seeds one or a few, subterminal or dispersed near the end of a fertile branch.
    6. Seed free, projecting above an epimatium (fertile scale).
        7. Seed structures terminal on ordinary foliage branches; leaves crowded, awl-like, linear, or scale-like. . . . . *Dacrydium* (most species).
        7. Seed structures lateral on specialized shoots; leaves bilaterally flattened and distichous. . . . . *Falcatifolium*.
    6. Seed covered by or fused with the scale.
        8. Fertile bract forming a terminal crest over seed complex; leaves awl-like. . . . . *Dacrycarpus*.
        8. Fertile bract separate from the seed complex; leaves flat.
            9. Seed complex becoming erect; leaves bilaterally flattened. . . . . *Acmopyle*.

9. Seed complex remaining inverted, leaves bifacially flattened.
    10. Fertile shoot terminal on ordinary foliage branches; leaves scale-like; parasitic shrub. [*Podocarpus* sect. *Microcarpus*].[1]
    10. Specialized fertile shoot, usually axillary; leaves broad and flat, usually distichous; not parasitic.
        11. Fertile shoot scaly; leaves never with both hypoderm and accessory transfusion tissue.
            12. Seed with a beak; leaves with hypoderm, usually amphistomatic and decussate, oval or lanceolate. .... *Decussocarpus.*
            12. Seed without a beak; leaves without hypoderm, spirally placed and hypostomatic, linear. .... *Prumnopitys.*
        11. Fertile shoot divided into a naked peduncle and a specialized fleshy receptacle; leaves with both hypoderm and accessory transfusion tissue. .... *Podocarpus.*

Phyllocladus L. C. & A. Rich. ex Mirbel, Mém. Mus. Hist. Nat. Paris **13**: 48. 1825, nom. cons. Type species: *Phyllocladus billardieri* Rich. ex Mirbel [*Phyllocladus aspleniifolius* (Labill.) Hooker].

Podocarpus Labill. Nov. Holl. Pl. Sp. **2**: 71. *t. 221.* 1806. Type species: *Podocarpus aspleniifolius* Labill. [*Phyllocladus aspleniifolius* (Labill.) Hooker].
Brownetera L. C. Rich. Ann. Mus. Paris **16**: 299. 1810. *Nomen nudum* based on *Podocarpus aspleniifolius.*
Thalamia Sprengel, Anleitung zur Kenntniss der Gewächse. ed. 2. **2**: 218. 1817, based on *Podocarpus aspleniifolius.*

Small to large trees; bark dark brown or blackish and smooth, reddish and fibrous within, shed in large thin flakes; abundantly branched, branches often in whorls; juvenile leaves linear or slightly broader near the apex, acute or rounded but with a small spine-like point, 1 mm. or more wide and about 1 cm. long, changing rapidly on small plants to flattened leaf-branch complexes or phylloclads with scale-leaves on non-foliage branches; leaves represented by small spurs on the margins of the phylloclads, strongly keeled on the dorsal side, triangular in cross section and on older plants scarcely or not distinguishable; phylloclads extremely variable in shape, broad, dorsiventrally slightly differentiated in some cases, reaching several cm. in length or aggregated along branches in complexes to more than 20 cm. long or transitional as a large deeply lobed phylloclad; monoecious, but individual trees may be unisexual; pollen cones in clusters but the central axis of the cluster in most cases continuing growth, nearly sessile or stalked; seed cone consisting of several or numerous scales some of which are sterile, single ovules erect in the axil of a scale; seed cones terminal or marginal on fully grown or reduced phylloclads or clustered as are the pollen cones, becoming swollen, fleshy or leathery; erect seeds as many as 20 per cone but usually only 2 or 3, with a filmy aril (symmetrical but rough edged epimatium) growing as

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[1] To be taken up as a genus elsewhere.

a cup around the lower half, protruding beyond the scale when ripe, oval, wider than thick, with the micropyle as a crooked tip, about 3 mm. long.

The genus consists of five closely related species in mild to cool and very moist climates, three in New Zealand, one in Tasmania, and one in mountain areas from the Philippines to New Guinea. *Phyllocladus* is sharply distinguished from related taxa by the distinctive phylloclads which give it the popular name of "celery-topped pine." The bark contains abundant tannin and the wood is of good quality but, because all of the forest species grow as scattered individuals, its commercial value is limited. One species in New Zealand and part of the population in Tasmania grow as bushy pioneer plants around mountain meadows. The one tropical example of this genus is the only podocarp species growing in the tropics whose seeds are produced in a recognizable cone. This certainly suggests that the family Podocarpaceae, so abundantly developed within the tropics, had its origins in cooler climate areas.

1. **Phyllocladus hypophyllus** Hooker f. Icon. Pl. *t. 889*. 1852. Type: *Low s.n.*, Mt. Kinabalu.

Phyllocladus hypophyllus var. *protracta* Warb. Monsunia **1**: 194. 1900. Syntypes: *Warburg 14722*, S. Mindanao, mountain forest of Dagatpan and *18272*, Batjan (not seen).

Phyllocladus protractus (Warb.) Pilger, Pflanzenreich IV. **5** (Heft 18): 99. 1903.

Phyllocladus major Pilger, Bot. Jahrb. **54**: 211. 1916. Type: *Ledermann 9872*, Lordberg, NE. New Guinea.

Common small tree on ridges or becoming quite large in the forest, 30 m. or more high; bark hard, rough with large lenticels, dark brown, breaking off in large scales; inner bark straw color; branches more or less whorled around the main stem and densely ramified; foliar buds on young plants with long thin and somewhat spreading bracts, these becoming tighter and more globular on older plants; phylloclads sometimes glaucous, particularly underneath, variable in shape, deeply lobed on young specimens but becoming less lobed in maturity, margins nearly entire to wavy with individual lobes ca. 5 mm. wide and 2 mm. long, oval to triangular, 3 or 4 cm. long and 2 cm. wide, single or aggregated alternately along lateral branches of limited growth; pollen cones clustered around a shoot that continues growth, peduncle 5–25 mm. long; mature pollen cones to 15 mm. long, 3 mm. in diam.; seed cones clustered on stalks about 1 cm. long or terminal on a slightly modified phylloclad or any possible intermediate condition, small, with 1–3 or more fertile scales, first red when mature, then brown and leathery.

DISTRIBUTION. Luzon and Borneo to New Guinea, scattered and often common in moist forests and on ridges generally, from 1,500 to 3,200 meters, and occasionally from 900 to 4,000 meters. MAP 1.

Sarawak. Mt. Poi, upper cave, *Clemens 20026* j (NY). Mt. Laiun, *Richards*

2421 s 1,100 m. (K). Mt. Mulu (Baram), *Winkler 512* j 1,200 m. (L), *Shockton 2699* s 6–7,000 ft. (K), *Anderson 4544* ♀ 7,000 ft. (K, L), *Hotta 14743* ♀ 1,600–2,200 m. (L). Mt. Temedu, Hose Mts., *Ashton S19025* s (K). Mt. Dulit, *Richards 1058* j 1,000–1,230 m. (A, BM, K, L, US), *1628* j 1,230 m. (K), *2476* s 800 m. (A, BM, K, L). Marigan Range, Lawas, *Brunig S9984* ♀ 1,000 m. (L). Without loc. *Beccari 2391* s (K), *3220* ♀ (K). **Brunei.** Mt. Ulak, *Ashton BRUN 1033* s 4,300 ft. (K, L). **North Borneo.** Jesselton, Kumu Rengis, *Wyatt-Smith* [?] *71650* ♀ 80 ft. [sic] (K, L, US). Penampang, *Leaño-Castro 5992* s 6,000 ft. (K, L), *Clemente 6217* s 5,000 ft. (K). Ranau, *Meijer SAN 21968* ♀ 5–6,000 ft. (K), *Mikil 56277* s 7,000 ft. (K), *Burgess SAN 25167* s 4,500 ft. (K). Mt. Kinabalu, *Low s.n.* ♀ 8,000 ft. (K-holotype), *s.n.* ♂ 10,000 ft. (K), *Gibbs 4088* j 7,000 ft. (BM, K), *4152* ♀, j 6,000 ft. (BM, K), *4238* s (BM), *4273* ♀ 9–12,000 ft. (BM, K), *Clemens 10556* ♂ (A), *10565* ♀ (A, GH, K), *10654* ♀ (A), *10957* s (BM), *27930* ♀ 6,000–13,500 ft. (A, BM, K, L, NY), *29328* ♀ 10,000 ft. (A, BM, ILL, K, L, NY), *29743* ♀ 8–9,000 ft. (BM, K, NY), *30029* ♀ 7,000 ft. (A), *30030* ♀ 10,500 ft. (K, NY), *31838* ♂ 7,000 ft. (A, L), *31927* ♂ 8–9,000 ft. (NY), *32459* s (BM, L), *50626* s (BM), *50784* ♀ 7–9,000 ft. (A, BM, L), *50797* ♀ 10,000 ft. (BM, L), *51220* s (BM), *Haviland 1092* ♀, ♂ 11,000 ft. (A, BM, K, L), *Sinclair & Kadim 9053* s 6,950 ft. (L), *Chew & Corner RSNB 710* ♀ 7,500 ft. (K, NY), *RSNB 4172* ♀ 5,000 ft. (K), *RSNB 4824* ♀ 6,000 ft. (K), *Smythies S10622* ♀ 9,000 ft. (K, L), *Wyatt-Smith 80370* s (K), *80371* ♀ (K, L), *Anderson S27089* ♂ 11,800 ft. (K), *S27090* ♀ 11,300 ft. (K, L), *Meijer SAN 22114* s 4,000 ft. (K), *SAN 29271* ♂ 9,700 ft. (K, L). *Nicholson SAN 17823* ♀, ♂ 8,800 ft. (K, L), *Fuchs & Colenette 21430* ♀ 3,375 m. (K), *Carr SFN 27617* s 11,500 ft. (BM). Trusmadi Kudat, *Mikil SAN 31784* ♂ (L). Sobong Peak, *Lobb* (1857) s 4,000 ft. (BM, K). **Borneo.** W. Region, Bengkajang, Banan, *NIFS bb9671* j 1,400 m. (L), *bb24777* j 1,200 m. (A, L). B. Raja, *Winkler 1036* s 1,600 m. (L). Ulu Kelan, *Molengraaf B3477* s (L). Top of Semedum, *Hallier 697* ♀ (A, K, L, NY). Mt. Palimasan, W. Kutei (Belajan R.), *Kostermans 12894* s 700 m. (BM, K). Mt. Niapa on Kelai R., *Kostermans 21482* ♂ 1,000 m. (K, L). **Philippines.** LUZON: Mt. Panai (Benguet), *Gillis 27257* s (A, K, L, US), *Merrill 4753* j (K, L, NY, US), *Quisumbing & Sulit 82404* s 7,700 ft. (NY). Mt. Siñgakalsa (Benguet), *Sulit 7669* ♂ 2,500 m. (A, L). Benguet, *Alvarez 18364* s (BM). Lepanto Dist., *Curran 10957* ♂ (K, L, NY, US). Mt. Data, *Steiner 2150* j 2,200 m. (L). Mt. Pukis (Bontoc), *Ramos & Edaño 37757* ♂ (A, US). Mt. Tabuan-Buan (Cagayan), *Ramos 77401* ♀ 5,800 ft. (K, NY). Center, *Loher 4851* s (K), *5203* ♀ (A, K, NY, US). MINDORO: Mt. Halcon, *Merrill 5788* s (K, NY, US). Mt. Dulangan, *Whitehead* (1896) s 5,000 ft. (BM). MINDANAO: Mt. Katanglad (Bukidnon), *Sulit 10052* ♀ 2,200 m. (A, L), *10124* ♂ 2,300 m. (A). Mt. Candoon (Bukidnon), *Ramos & Edaño 38738* ♀ (A, US). Kaatoan Chinchona (Bukidnon), *Britton 439* ♀ 1,380 m. (L). Mt. Apo (Davao), *Elmer 11463* s (A, BM, FI, K, L, NY, US, Z), *Clemens 15675* j (A, NY), *Mearns & Hutchinson 4679* s (L). Mt. KcKinley, *Kanehira 2676* j (NY). **Celebes.** Mt. Wuka Tampai, Palu (Menado), *NIFS bb15154* ♀ 2,500 m. (L). Parigi Lombok (Menado), *NIFS bb15026* s 1,100 m. (L). Sawito (Enrekang), *NIFS bb20782* s 1,750 m. (L). Mt. Tahole, Labu (Malili), *Burki bb24089* ♀ 1,500 m. (L). Porehu (Malili), *NIFS bb19564* ♀ 1,500 m. (A). Makale-Toloko (Manggala), *NIFS bb20270* s 1,200 m. (A, L). **Moluccas.** Batjan, *de Haan bb23236* s 2,199 m. (L). Obi, *de Haan bb23812* s 700 m. (L). Buru, *NIFS bb21509* s 800 m. (L), *Binnendyk s.n.* j (K, L). Middle Ceram, G. Sofia, *Stresemann 133* s 2,200 m. (L). **New Guinea.** VOGELKOP: Mt. Nettoti, *van Royen 3873* s 1,960 m. (L), *van Royen & Sleumer 7403* s 1,750 m. (K, L), *Versteegh BW 10407* s 1,700 m.

(L). Neentjapaki Mts., Kebar Valley, *Kalkman BW 6373* s 1,090 m. (L). Adjar, Kebar Valley, *Koster BW 6887* ♀ 1,110 m. (L). Tobie Mts., Kebar Valley, *Schram BW 7972* s 720 m. (L). Anggi Lakes, *Gibbs 5992* ♀ 7–9,000 ft. (BM, K), *Versteegh BW 248* s 2,000 m. (A, K, L), *BW 253* ♀ 2,100 m. (A, K, L), *BW 281* s (A, L), *Kanehira & Hatusima 13704* s (A), *14096* s (A), *Stefels BW 2008* j 1,875 m. (L), *BW 2010* s 1,860 m. (L), *BW 2031* s 2,200 m. (L). Koebri Ridge, *Gibbs 5657* s 8,500–9,000 ft. (BM, K). Ransiki, Sioriep, *Mangold BW 2262* s 1,200 m. (K, L). Mt. Mundi (Ransiki), *Mangold BW 2254* s 1,900 m. (L). WESTERN HALF: Mt. Genofa (E. of Arguni Bay), *Salverda bb22564* s 750 m. (L), *Versteegh BW 7596* ♀ 1,000 m. (L). Wissel Lakes, *Eyma 4954* ♂ 1,750 m. (A, K, L), *5228* ♂ (A, K, L), *5371* ♀ (A, K, L), *Versteegh BW 3009* ♀ 1,750 m. (A, L), *Johannes BW 3262* s 1,750 m. (L), *Vink & Schram BW 8764* ♀ 1,500 m. (L), *BW 8945* s 1,850 m. (L). Nassau Mts., *Docters v. Leeuwen 10906* s 2,600 m. (A, K, L). Mt. Doorman (Mamberamo R. Region), *Lam 1628* ♀ 3,250 m. (L), *1647* ♀ 3,500 m. (L), *1742* ♀ 3,250 m. (L), *1984* s 2,560 m. (L). Lake Habbema, *Brass 9058* ♂ 3,225 m. (A, BM, K, L), *9090* ♀ (A, BM, K, L), *10528* ♀ 2,800 m. (A, BM, K, L), *Brass & Meyer-Drees 10432* ♀ 3,225 m. (A, L), *Brass & Versteegh 10446* ♀ 2,840 m. (A, BM, L), *10446A* ♂ 3,200 m. (A, BM, L). Barnhard Camp, *Brass & Versteegh 11931* ♀ 1,850 m. (A, BM, K, L), *12523* s 1,100 m. (A, BM, L), *12523A* ♀ 1,150 m. (A, K, L), *13520* ♀ 900 m. (A, BM, L), *13520A* ♀ (A, L), *Brass 12191* ♀ 2,100 m. (A, L). Cycloop Mts., *van Royen 3721* s 1,560 m. (L), *van Royen & Sleumer s.n.* s 1,700 m. (L). Mt. Antares, Star Mts., *Kalkman 4439* ♀ 2,360 m. (BM, L), *4539* ♀ 3,300 m. (L). TERR. NEW GUINEA: Lordberg (Sepik Region), *Ledermann 9872* ♂ 1,000 m. (K, L-isotypes of *Phyllocladus major*). Wabag-Maramuni Road, *Saunders 1025* s 10,000 ft. (L). Wankl (Mt. Hagen), *Hoogland & Pullen 5871* s 7,600 ft. (A, BM, K, US). Mt. Wichmann, *Pulle 982* s 2,500 m. (K, L), *1018* s (K, L), *1042* ♂ 3,100 m. (A, K, L). Upper Minj Valley, *Pullen 273A* j 9,000 ft. (A, L). Al River Mts. (Nondugl), *Womersley NGF 5351* ♀ 7,000 ft. (A, BM, K, L). Mt. Kabanunt, Sirimbki, *Walker ANU 859* ♀ 9–9,500 ft. (A, K, L), *859A* j 9,500 ft. (A, K, L). Chimbu, *Cavanaugh NGF 3333* ♀ (K). Waimambuno (Chimbu), *Saunders 824* s 9,000 ft. (A, BM, K, L, US). Mt. Wilhelm, *Stauffer 5651* s 2,600 m. (K, L, Z). Lake Inim, *Flenley ANU 2177* s 8,300 ft. (K, L). Ogeramnang, *Clemens 4942* s 6–7,000 ft. (A, Z), *5117A* ♀ 6,000 ft. (A). Samanzing, *Clemens 9384* ♂ 7–8,000 ft. (A), *9549* ♂ 8–9,000 ft. (A). Mt. Enggom, Sarawaket Range, *van Royen NGF 16182* ♂ 11,000 ft. (K, L). Mannasat, Cromwell Mts., *Hoogland 9482* ♀ 7,600 ft. (K). Bolan, *Lauterbach 303* s 2,400–3,000 m. (BM). Mt. Kaindi (Bulolo), *Brass 29692* ♀ 2,150 m. (A, K, L, NY, US), *Millar & Womersley NGF 12255* s 7,000 ft. (A, K), *McVeagh NGF 7580* ♀ 3,000 ft. (A, BM, K, L), *de Laubenfels P481* ♂ 6,500 ft. (A, K, L, RSA, SBT), *P481A* j (A), *Toropai NGF 17153* ♀ 6,900 ft. (K, L), *Havel & Kairo NGF 17341* ♀ 7,000 ft. (K). Wau-Salamaua Road, *Millar NGF 22785* ♀ 6,400 ft. (K). Mt. Amungwiwa, S. of Wau, *Womersley NGF 17946* s 11,400 ft. (L). Wagau, Buang Region, *Womersley NGF 17902* s 4,500 ft. (K, L). PAPUA: Mt. Giluwe, *Schodde 2014* ♀ 8,800 ft. (K, L). Mt. Tafa (Cent. Div.), *Brass 4035* s (A, NY). Murray Pass, Wharton Range, *Brass 4578* s 2,840 m. (A, BM, NY), *4584* ♀ (A, K, L, NY, US). Mt. Obree, Owen Stanley Range, *Lane-Poole* (1923) s 7–9,000 ft. (A, K). Mt. Dayman, Maneau Range, *Brass 22453* ♀ 2,230 m. (A). Mt. Maneao, *Crutwell 519* s 7,500 ft. (K). Mt. Mon [Mau?], *Crutwell 896* j 6,800 ft. (K). Mt. Vinevo, Goodenough, *Crutwell 1423* s 7,000 ft. (K).

ILLUSTRATION. HOOKER, f. Icon. Pl. *t. 889.* 1852.

MAPS showing distribution of: 1, *Phyllocladus hypophyllus* Hooker f.; 2, *Dacrydium elatum* (Roxburgh) Wallich (dots west of line), *D. novo-guineense* Gibbs (dots east of line), *D. nausoriensis* de Laubenfels, known only from the Fiji Islands; 3, *D. pectinatum* de Laubenfels (dots west of line), *D. nidulum* de Laubenfels (dots east of line), *D. balansae* Brongniart & Gris, known throughout New Caledonia, and *D. cupressinum* Solander ex Lambert, known from New Zealand.

In addition to its completely disjunct distribution, *Phyllocladus hypophyllus* can be differentiated from all other species of the genus by its distinctly larger phylloclads. In other species the larger structures are deeply lobed and transitional to branch systems, those without deep lobes are less than 20 mm. wide or 25 mm. long. *Phyllocladus hypophyllus* is unique also in frequently having the seed cones terminal rather than lateral on the phylloclads, and in having peduncles on both pollen and seed cones up to twice the length observed in other species. The two species with intermediate sized phylloclads approaching the lower limit of those of *P. hypophyllus* are *P. glaucus* and *P. aspleniifolius*, both of which share the glaucous habit with *P. hypophyllus*. The former has seed cones with numerous fertile scales and the latter has particularly small and nearly sessile pollen cones. The species *P. major* and *P. protractus* have been differentiated from *P. hypophyllus* on the basis of the shape of the cladodes, the position of the seed cone, and by their glaucous aspect. These differences, however, are found within local populations related to age of the tree or even on different parts of the same specimen.

Dacrydium Solander ex Lambert, Descr. Genus Pinus **1**: Appendix 93. 1807. Type species: *Dacrydium cupressinum* Solander ex Lambert.

Lepidothamnus Phil. Linnaea **30**: 730. 1860. Type species: *Lepidothamnus fonkii* Phil. [*Dacrydium fonkii* (Phil.) Benth.].

Shrubs and trees varying considerably in stature; juvenile leaves awl-shaped (falcate needles), longer than the adult, or in some species bifacially flattened and linear; adult leaves quite variable among the species from scale leaves to leaves resembling the juvenile needles and with either gradual or abrupt transitions uniting the different forms during their ontogeny; dioecious (or rarely monoecious in some New Zealand species); pollen cones cylindrical, terminal, or lateral and sessile, or both; seed cones much reduced, with bracts hardly modified from foliage leaves, often becoming fleshy when ripe, terminal, often on a short lateral branch; ovules inverted on bracts in a nearly terminal position and partly covered by an epimatium; seeds usually becoming erect, projecting well beyond the apex of the modified cone, occasionally occurring in pairs or three together, sometimes surrounded by the leaf-like extremities of the cone bracts, oval with the micropyle forming a small tip, usually somewhat flattened, on some species remaining inverted and covered by the fertile scale.

The genus *Dacrydium* occurs in a wide range of temperature and soil conditions but rarely in anything less than a very moist climate. It is readily divisible into two subgroups based on the internal morphology of the wood, leaves, and pollen (Tengnér, 1965). In one of the groups, called by Florin (1931) Group C, the adult leaves are more or less overlapping, broad, bluntly keeled scales (in one species, a prostrate alpine shrub, plants with juvenile type short flat leaves sometimes are fertile). The other group, called Group B, lacks scale leaves in all but two species where the scale is narrowly and sharply keeled and strongly appressed.

The seeds in this group always become more or less erect, while in Group C some species have inverted mature seeds covered by the fertile scale. Group C is entirely extra-tropical and will not be treated here. Group B is primarily tropical, the two groups overlapping in New Zealand where most of the Group C species are found. In Group B the juvenile leaves are scarcely distinguishable between the various species, being lanceolate, slender, and bifacially flattened on the seedling but soon becoming strongly keeled and awl-shaped. For the most part, the seeds are also very similar throughout, so that the species are distinguished primarily by the form of the seed and pollen cones, and by the adult leaf form. Four common leaf types occur, one with fairly short needles (2–5 mm.) changing gradually from the juvenile form (*cupressinum, balansae, nidulum, pectinatum*), a longer type with more flexible needles (*beccarii*), a type with narrow, flat, and lanceolate leaves (*xanthandrum*), and one with scale leaves changing abruptly from the juvenile needles (*elatum, novo-guineense*). In addition, there are a number of local species, usually with distinctly bifacially flattened leaves and, in most cases, rather rare. Most of the species are too small in growth form or are too rare to be useful, but a few, as *D. cupressinum*, are valuable lumber trees.

KEY TO THE SPECIES OF DACRYDIUM

1. Trees or prostrate shrubs with adult leaves broad, imbricate, bluntly keeled scales (Group C).
1. Trees or bushes with adult leaves narrow, appressed, sharply keeled scales or longer spreading leaves (Group B).
    2. Abrupt change between juvenile and adult leaves, which are minute (not more than 1.5 mm. long).
        3. Bracts in the fertile area similar to scale-like foliage leaves. . . . . 2. *D. elatum*.
        3. Bracts in the fertile area distinctly longer than the foliage leaves or scales.
            4. Seeds and pollen cones not small; foliage leaves scale-like. . . . . 3. *D. novo-guineense*.
            4. Seeds and pollen cones small; foliage leaves spreading. . . . . 4. *D. nausoriense*.
    2. Gradual change from juvenile to adult leaves, which are at least 2 mm. long.
        5. Bracts in the fertile area not surpassing the epimatium and not longer that the foliage leaves.
            6. Microsporophylls narrowly lanceolate; leaves thick (0.6 mm.) straight. . . . . (*D. cupressinum*).
            6. Microsporophylls long triangular; leaves less than 0.4 mm. thick, curved upwards at the tip.
                7. Slender, linear leaves with the tip turned upwards. . . . . 5a. *D. pectinatum* var. *pectinatum*.
                7. Thick, sharply tapering and spreading leaves. . . . . 5b. *D. pectinatum* var. *robustum*.
        5. Bracts in the fertile area distinctly longer than the epimatium and, where the foliage leaves are not long, distinctly elongated by contrast.

8. Bracts in the fertile area distinctly longer than the foliage leaves of the subtending branch; microsporophyll triangular.
    9. Bracts, in the fertile area, and foliage leaves strongly keeled, triangular or quadrangular in cross section.
        10. Developing seed extending well beyond the elongated bracts of the fertile area; foliage leaves not more than 0.8 mm. wide.
            11. Leaves approximately as thick as wide, tip more or less blunt and not incurved. .... 6a. *D. nidulum* var. *nidulum.*
            11. Leaves noticeably wider than thick, tip distinctly armed with a slight prickle, generally incurved and crowded. .... 6b. *D. nidulum* var. *araucarioides.*
        10. Developing seed completely surrounded by elongated bracts, the tip protruding slightly on maturity; foliage leaves robust, more than 1.0 mm. wide.
            12. Pollen cones 2.0 mm. in diameter; leaves curved upwards but not inwards, markedly tapering, quadrangular in cross section. .... 7. *D. balansae.*
            12. Pollen cones 2.5–3.0 mm. in diameter; leaves strongly incurved, linear, axial surface concave towards the apex. .... 8. *D. araucarioides.*
    9. Bracts in the fertile area and foliage leaves distinctly flat, more than twice as wide as thick.
        13. Seed and pollen cone small; leaves lanceolate, 3–4.5 mm. long. .... 9. *D. lycopodioides.*
        13. Seed and pollen cone not small; leaves linear, 4–7 mm. long. .... 10. *D. spathoides.*
8. Bracts in the fertile area no longer than the foliage leaves of the subtending branch; microsporophylls elongated, lanceolate.
    14. Fertile bract not surpassing the mature seed, leaves 5–10 mm. long.
        15. Pollen cone 20–25 mm. long by 5–7 mm. in diameter; leaves less than 0.8 mm. wide.
            16. Seed cone terminal on ordinary foliage branches; mature seed surrounded by bracts. 11. *D. magnum.*
            16. Seed cone terminal on shoots with reduced leaves; seed well exposed when mature.
                17. Leaves quadrangular or triangular in cross section, imbricate.
                    18. Leaves uniform, more than 5 mm. long, at least ten times as long as wide.
                        19. Leaves spreading outward. .... 12a. *D. beccarii* var. *beccarii.*
                        19. Leaves incurved and compact. .... 12c. *D. beccarii* var. *rudens.*
                    18. Leaves variable, sometimes less than 5 mm. long, less than eight times as long as wide. .... 12b. *D. beccarii* var. *subelatum.*
                17. Leaves twice as wide as thick, spreading at nearly right angles to the stem. .... 13. *D. xanthandrum.*

15. Pollen cone 20–25 mm. long by 5–7 mm. in diameter; leaves at least 1.0 mm. wide. .... 14. *D. gibbsiae.*
14. Fertile bract much longer than the seed, leaves 12–20 mm. long.
    20. Leaves quadrangular in cross section, linear. .... 15. *D. guillauminii.*
    20. Leaves flat, lanceolate. .... 16. *D. comosum.*

2. **Dacrydium elatum** (Roxburgh) Wallich, London Jour. Bot. 2: 144. 1843.[2]

Juniperus elata Roxburgh, Fl. Indica **3:** 838. 1832. Lectotype: *Wallich 6045*, Malay, Penang.

Dacrydium junghuhnii Miquel, Pl. Junghuhn. **1:** 4. 1851. Type: *Junghuhn s.n.*, Sumatra.

Dacrydium pierrei Hickel, Bull. Soc. Dendr. France **76:** 74. 1930. Lectotype: *Pierre 1396*, Cochin China, Phu Quoc Island.[3]

Tree to 40 m., much branched with masses of erect twigs forming a dome-like crown; bark furrowed and flaky, reddish-brown, inner bark pink; juvenile leaves acicular, to at least 12 mm. long, gradually becoming shorter and more robust before changing abruptly on young trees, about 6–8 mm. long, sharply keeled on four sides and nearly straight, spreading, acute; mature foliage branches cord-like, 1–2 mm. in diam., covered with imbricate scales which are acute and sharply keeled, 1–1.5 mm. long by 0.4–0.6 mm. wide, occasionally passing through a semi-adult or transitional stage of short spreading leaves about 1.5 mm. long; branches with juvenile leaves occasionally fertile; pollen cones terminal, usually on short lateral branches, thus sometimes almost lateral, cylindrical, 4–5 mm. long and 1.2 mm. wide; microsporophylls triangular, acute; seed cone terminal, generally on short lateral branches, bracts of the cone becoming slightly enlarged, red and fleshy when mature; the solitary naked seed becomes almost erect, tapering to a blunt apex, reaching 4–4.5 mm. in length.

DISTRIBUTION. In humid mountain forests from north central Thailand and Tonkin to central Sumatra and Sarawak, from 500 to 1,700 meters in elevation or even down to sea level where suitable conditions exist. MAP 2.

Thailand. NORTH CENTRAL: Loei, Phu Krading, Tham Nam, *Royal Forest Dept. 3631* j, 1,045 m. (US), *Kerr 8727* j (K), *8727A* ♀ (K), *8727B* ♂ (K), *Larsen 2263* j 1,300 m. (A). Without loc., *Smitinand 19058* j 1,200 m. (K). CENTRAL: Nakhaun Nayok, *Phengkhlai 691* ♂, j (K, L). **Cambodia.** Plateau overlooking Gulf of Siam, *Showe* (1927) s, j 3,000 ft. (BM). North of Kampot, *Poilane 14707* ♀ (NY). Near Komplon (Phnom Penh), *Bejoud 717* ♀ (ILL). Without loc., *Pierre 19074* s (K). **Tonkin.** Than Moi, *Balansa 596* ♂, j (ILL, K). **Annam.** Summit Mt. Bani, near Da Nang, *Clemens 4280* j (K, NY, US). Bana, near Tourane, *Poilane 1539* s, j 1,200 m. (NY-syntype of *D. pierrei*), *7095* ♀ (A-

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[2] Species are numbered consecutively through the whole paper.

[3] Hickel did not specify a type, but listed many specimens of which *Balansa 576* is the first. The one specimen collected by Pierre is here chosen as the lectotype because of the specific epithet.

syntype of *D. pierrei*). Kontum Prov., *Poilane 33351* s 1,200 m. (ILL). Nhatrang, *Poilane 25* j (A-syntype of *D. pierrei*), *3455* ♀ (A-syntype of *D. pierrei*), *3782* ♀ (A, K-syntypes of *D. pierrei*), *4411* ♀ (A-syntype of *D. pierrei*). **Cochin China.** Phu Quoc Island, Gulf of Siam, *Pierre 1396* ♂, j (A, K, NY-isotypes of *D. pierrei*), *Harmand* (*Godefroy*) *901* ♂ (A-syntype of *D. pierrei*). Without loc., *Poilane 32825* ♂ (ILL), *Godefroy-Lebeuf s.n.* ♂ (K). **Malaya.** Thailand border (Botong), G. Ina, *Kerr 7554* s, j (K). Penang, *Wallich 6045* s (BM-lectotype of *Juniperus elata*; K-isotype), *Sinclair 39094* s, j (K, L), *Walker 70* j (K), *Maingay 2262* s (K), *2753* s (K), *Curtis 2880* s, j (K). Perak, *Ernst 1213* s, j (Z). G. Butu, *Wray 1028* j (K), *3899* s, j (K). Pahang, G. Tahan, *Haniff & Nur s.n.* ♂ (K), *SFN 7959* s, j 5,500 ft. (A, K), *Wray & Robinson 5354* s 3,300 ft. (K), *5380* j (K). Pahang, G. Lesong, *Wakau 4155* j (K). Jahore, Mt. Ophir, *Maingay 1503* ♀ (FI, GH, K, L), *Moxon s.n.* s (L). **Sumatra.** Between Tapanuli and Silindong, *Junghuhn s.n.* j 2,000 ft. (L-holotype of *D. junghuhnii*). Pajakumbuh, W. Taram, *Meijer 6938* ♂, j 500–1,000 m. (K, L), *7040* ♀ (L). Poya Kombo, *Teysmann 21647* ♂ (K), *s.n.* s (K). Without loc., *Praetorius s.n.* j (L). **Sarawak.** Merurong Plateau (Bintulu), *Brunig S9991* s 750 m. (L). Mt. Dulit, *Richards 1962* s 1,250 m. (BRI, K, L, US). Between Biak R. and Sut, *Pickles 2991* ♂ 2,360 ft. (L, US). Lawas, *Brunig S10673* ♂, j 900 m. (L). **Borneo.** Without loc., *De Vriese s.n.* j (L).

ILLUSTRATIONS. RIDLEY, H. N. Fl. Malay Peninsula *t. 227.* 1925. CORNER, E. J. H. Gard. Bull. Straits Settlements **10:** *t. 5.* 1939.

Dacrydium elatum differs from *D. novo-guineense* in the form of the female cone, in the form of the juvenile leaves, size of the pollen cone, size of the mature tree, and in its occurrence generally at lower elevation. Specimens of *D. pectinatum* have been much confused with *D. elatum* because the *pectinatum* foliage is similar to the juvenile foliage of *D. elatum* but, the leaves of *D. pectinatum* are, in fact, shorter and distinctly curved. The known range of these two species overlaps only in Sarawak. The name *elatum* has further been applied to almost any uncertain *Dacrydium* specimen from Borneo to the Fiji Islands. Hickel described *D. pierrei*, contrasting it with *D. beccarii*, which he mistook for *D. elatum*.

3. **Dacrydium novo-guineense** Gibbs, Contrib. Phytogeography and Flora of the Arfak Mountains 78. 1917. Lectotype: *Gibbs 5648*, New Guinea, Arfak Mountains.

Tree to about 10 m. with branches rigidly ascending into a rounded crown; juvenile leaves acicular, spreading and incurved, lanceolate, acute, keeled on the back, to 7 mm. long by 0.7 mm. wide but variable in size, changing abruptly to the adult form, occasionally passing through a semiadult or transitional stage of short spreading leaves about 1.0–1.5 mm. long; mature foliage in imbricate scales, acute and sharply keeled, 1.0–1.5 mm. long by 0.4–0.6 mm. wide; foliage branches 1.0–2.0 mm. in diameter, penultimate branches becoming larger; pollen cones terminal, usually on short erect lateral branches, cylindrical, 8 mm. long, microsporophylls triangular; seed cones terminal on short curved lateral branches, bracts long and spreading, reaching 3 mm. at the cone apex, the whole cone becoming red and fleshy when mature, the single apical seed becoming almost erect and extending well beyond the cone bracts, 5 mm. long, edges slightly keeled, tapering to a small blunt apex.

Distribution. In open to mossy forests, often on ridge tops from 1,300 to 2,750 meters in elevation, occasionally lower. Locally common but apparently localized; from Obi and the mountains of western New Guinea at least as far as the Western Highlands of the Territory of New Guinea. The collections from the Celebes are tentatively included here until it can be determined whether these represent *Dacrydium elatum* or *D. novo-guineense*. Map 2.

Celebes. Manado, Poso, *Eyma 1623* s 1,700–1,800 m. (L), *3642* ♂ (L). Masamba, Kuniapu, *NIFS bb24964* s 1,500 m. (L). Masamba, Omboan, *NIFS bb26288* j 1,800 m. (L). Enrekang, *NIFS bb20786* j 1,900 m. (L). **Moluccas.** NW. Buru, *Stresemann 395* s, j 1,800–2,000 m. (L). Buru, *Martin s.n.* j (L). Obi, *de Haan bb23813* s 700 m. (L), *bb23814* s, j (L). **New Guinea.** Vogelkop: Tamrau Mts., *Van Royen & Sleumer 7219* s, j 2,000 m. (L). Kebar Valley, *Van Royen 3857* s, j 1,980 m. (L). W. of Mt. Nettoti, *Van Royen & Sleumer 7948* ♀ 2,100 m. (K, L, LAE), *7948B* j (L). Arfak Mts., *Gibbs 5648* ♀ 9,000 ft. (BM-lectotype; K-isotype), *5508* s, j 7,000 ft. (BM, K-syntypes), *Kanehira & Hatusima 13518* s 2,000 m. (A), *Gjellerup 1032* s, j 1,800 m. (L). Anggi Lakes, *Versteegh 256* ♀ 2,100 m. (L), *262* ♀ (L), *269* ♂ (L), *Stefels BW 2015* j 1,860 m. (L), *BW 2033* s, j 2,100 m. (L). Western Half: Wissel Lakes, *Eyma 4422* s, j 1,750 m. (A, K, L), *4519* ♀ 1,760 m. (A, K, L), *Vink & Schram BW 8746* s 1,820 m. (L). Hellwig Mts., *Pulle 663* ♀ 1,300 m. (L), *966* s 2,600 m. (K, L). Barnhard Camp, *Brass & Versteegh 11967* ♂ 1,520 m. (A, BRI, K, L), *12507* j 2,100 m. (A, BRI, L). Territory of New Guinea: Western Highlands, Mt. Hagen, *Cavenaugh NGF 3337* s, j (A, BRI, L). Tagen R., Jimmi Valley, *Womersley & Millar NGF 7680* ♀ 4,300 ft. (A, BRI). Minj-Jimmi Divide, *Robbins 598* ♂, j 6,500 ft. (A, BRI, K, L, US). Nondugl, *Womersley NGF 4420* ♀, j (A, BRI, K, L). Papua: Sibium Range, *Pullen 5930A* j (L).

Illustration. Gibbs, L. S. Contrib. Phytogeography and Flora of the Arfak Mountains, *t. 3.* 1917.

Being one of the scale-leaved species of *Dacrydium*, *D. novo-guineense* cannot be distinguished in the sterile form from *D. elatum* from which it differs in the elongated bracts of the seed cone and to a lesser extent in the form of the juvenile leaves and the size of the pollen cone. Juvenile specimens can often be separated from *D. beccarii*, with whose range it overlaps, by their coarser and less dense growth. From *D. nidulum* the juvenile leaves differ in their variable size including, for the most part, greater length. The rapid change from juvenile to adult form is so striking and comes when the tree is yet quite small so that collectors generally include mature leaf forms when dealing with *D. novo-guineense*. The rigid ascending branches are another distinctive character.

4. **Dacrydium nausoriensis** de Laubenfels, sp. nov.

Arbor ad 25 m. alta, ramosissima. Folia plantarum iuvenilis acicularia, ad 9 mm. longa, ad formam adultam abrupte convertentes; folia plantarum

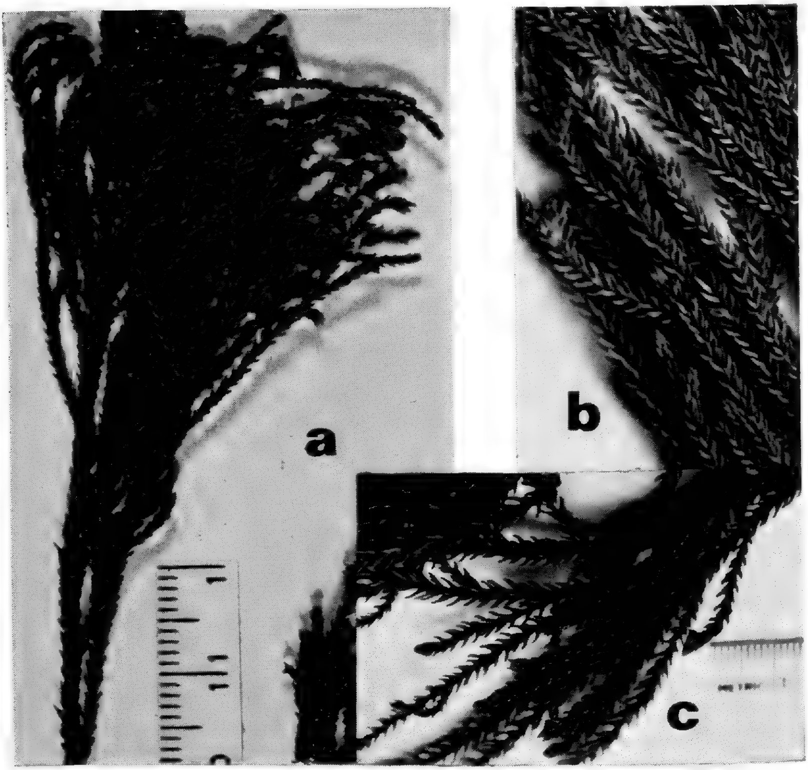

FIGURE 1. a, *Dacrydium nausoriensis* de Laubenfels, portion of the holotype, *de Laubenfels P302* (A), enlarged; b, *D. pectinatum* de Laubenfels var. *pectinatum*, portion of the isotype, *Nicholson SAN 17292* (L), enlarged; c, *D. pectinatum*, var. *robustum* de Laubenfels, portion of the holotype, *Meijer SAN 37908* (L), enlarged; b and c are at same magnification.

adultarum parva, patula, acuta, dorsaliter carinata, densa, 1 mm. longa, 0.4 mm. lata. Strobili masculi cylindracei, terminales vel laterales, saepe utroque, parvi (?), ad 2.5 mm. longi. Strobili feminei ad apicem ramulorum saepe brevi; folia ad basem seminis longiora, ad 2 mm. longa; semen protrudendum, 3.5–4 mm. longum. Holotypus: *de Laubenfels P302* (A), Fiji, Nausori Highlands. FIG. 1a.

DISTRIBUTION. In slightly open forest on the leeward sides of the large islands of Fiji and apparently of limited extent.

Fiji. VITI LEVU: Nausori Highlands, *de Laubenfels P302* ♀ 1,900 ft. (A-holotype; K, RSA, SBT-isotypes), *P303* j (A, RSA, SBT), *P304* ♂ (A, RSA, SBT), *Damanu NH19* ♀ (K), *NH23* ♀ (K), *Johns 2* ♀ (K), *Kuruvoli 13326* ♀ (K). VANUA LEVU: Lambassa, Sarava, *Damanu L14* s (K), *Anon. FD832* ♀ 400 ft. (K).

The species of *Dacrydium* with sharp scale-leaves, changing abruptly from juvenile to adult form (*D. elatum* and *D. novo-guineense*) stand apart from the other species, with *D. nausoriensis* representing a somewhat transitional position. The abrupt change from fine juvenile needles to the more robust and very short adult leaves is in accord with the scale-leaved species, while the still spreading orientation is the common condition for other species. Occasional specimens of *D. elatum* and of *D. novo-guineense* have transitional leaves abruptly marked off from the juvenile leaves and closely resembling the adult leaves of *D. nausoriensis*. The bark of this new species is virtually the same as in all other species of the group, with large thick flakes, fibrous and brown within but with a tough smooth surface generally well supplied with lenticels and weathering gray. The seeds are also of the usual type showing a slight marginal keel and becoming a rich brown color. The pollen cones seen may not be fully grown.

5. **Dacrydium pectinatum** de Laubenfels, sp. nov.

Arbor ad 40 m. alta, ramosissima; cortex canus vel rufulus; folia brevia, oblique adscendentia, patentia pectinatum, apice paulo incurva, dorsus carinata, 2–5 mm. longa, 0.4–0.8 mm. lata (iuvenilis ad 20 mm. longa). Strobili masculi cylindracei, terminales, 9–12 mm. longi, 2 mm. lati. Strobili feminei ad apicem ramulorum, saepe ramulorum brevium; folia ad basis parviora; folia strobilorum sub semine maturo parva, crescentes carnosa rubra; 1–2 folia ultima fertilia. Semen 4.5 mm. longum, non tegens foliis strobilorum. Holotypus: *Nicholson SAN 17292* (A), North Borneo, Sandakan. FIGS. 1b and 2.

The short bracts in the fertile area not even surpassing the epimatium and not longer than the foliage leaves, distinguish this new species from all but two others, one of which, *Dacrydium elatum* has distinctly smaller pollen cones and scale-like foliage leaves abruptly marked off from the juvenile leaves, while the second, *D. cupressinum*, has very elongated microsporophylls and thick straight stubby foliage leaves. The short spreading needles distinguish sterile specimens of *D. pectinatum* from other species with which its range overlaps. Two varieties have been recognized because of rather marked differences in leaf form.

5a. Var. **pectinatum.**

Folia gracilia, linearia, acicularia, 2–5 mm. longa, 0.4–0.6 mm. lata.

DISTRIBUTION. From Hainan through the Philippines to Billiton Island, at low elevations up to 1,500 meters but mostly below 600 meters. Several specimens are reported from sandy soils. MAP 3.

Hainan. Yaichow, *Liang 62041* s (NY), *62619* j (NY), *62670* ♀ (NY, US), *63214* s top of mt. (A, NY, US). Hung Mo Mt., *Tsang & Fung LU18100* ♀ (A, NY), *LU18152* ♀ (A, NY), *McClure 18303* j 1,000–1,500 m. (NY). Po-ting, *How 72869* ♀ (A). Five Finger Mt., *Chun 1367* j (A), *2089* s (A). Dai Land, Dung Ka, *Chun & Tso 4380* 2,400 ft. (A, NY). Chim Fung Mt., *Lau 5283* ♂ (A).

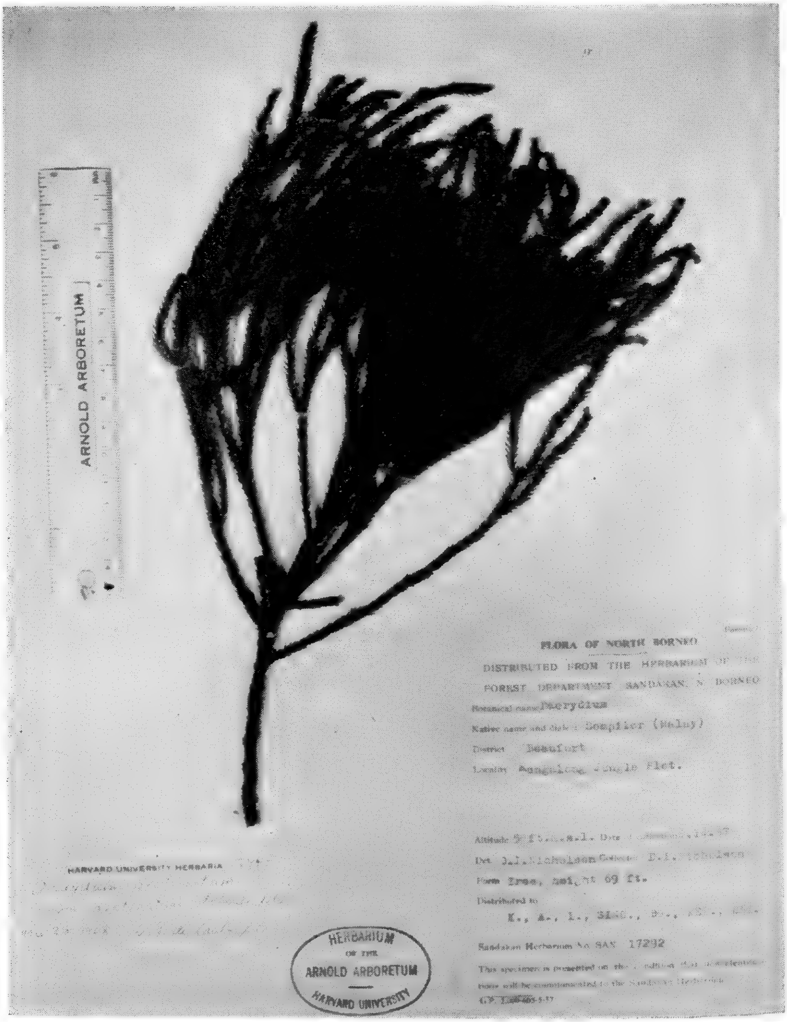

FIGURE 2. *Dacrydium pectinatum* de Laubenfels var. *pectinatum*, photograph of the holotype, *Nicholson SAN 17292* (A).

Without loc., *How & Chun 70144* ♀ 2,000 ft. (A, NY, US), *Liang 63693* ♂ (NY, US), *65094* ♂ (A, NY), *Wang 33651* s (A, NY), *36532* ♂ (A, NY), *Tang 457* ♀ (A), *Hance 22162* j (BM). Billiton. *NIFS bb32284* ♀ (A, L), *Rossum 122* ♀ (L), *784* ♀ (L). **Sarawak.** Bako National Park (20 miles NE. of Kuching), *Purseglove P5066* j 400 ft. (K, L), *P5553* ♂ 350 ft. (K, L, NY), *Brunig S12073* ♂ 120 m. (L), *S12074* s 130 m. (L), *Sinclair & Kadim 10318* s (A, K, L), *Sing JC/59* s 300 ft. (K), *Rashid S9546* s 400 ft. (L), *Nicholson 1319* s 200–300 ft. (US). Limbang, *Brunig S1101* ♀ 1,400 ft. (K, L). Kuching, *Beccari 643* j (FI, K), *644* ♀ (A, F, K). Mt. Mattang, *Beccari 2626* ♀ (FI, K), *3119* ♂ (FI). **Brunei.** *Ashton*

BRUN 5024 s (K, L). **North Borneo.** Ranau, *Meijer SAN 20951* j 3–4,000 ft. (L). *SAN 20952* s 4,000 ft. (L), *SAN 20970* s 4,200 ft. (K, L). Sipitang, *Cuadra A3291* s (A, BRI, K, L), *Erdtman SAN 22643* s (K), *Meijer SAN 21854* j (L). Beaufort Dist., Sandakan, *Nicholson SAN 17292* ♀ 5 ft. (A-holotype; BRI, L-isotypes). Beaufort, *Cuadra A1329* s (K), *Singh SAN 24336* s (K). Mt. Melian near Kiabau Labuk (Sandakan), *Meijer 51586* j 2,500 ft. (L). Bulungan, *Kostermans 9274* s (BRI, L). Without loc., *Cuadra A1348* s 400 ft. (K), *Melegrito 1575* ♀ (K), *Camber 4009* ♂ 1,500 ft. (K), *4010* ♀ (K), *4011* j (K). **Borneo.** Singkawang, *NIFS bb3903* ♂ 5 m. (L), *Sulaiman 2* s (K, L). Masaran, *NIFS bb19869* ♂ 40 m. (L), *bb19870* j (L). Karimata Arch., *Teysmann 11599* s (L), *Mondi 182* s (K, L). Sampit, *Buwalda 57* (*bb32434*) ♂ 3 m. (L), *NIFS bb33046* ♂ 9 m. (L). Upper Mahakam, Taliba, *NIFS bb26589* s 600 m. (A, L). Muartewe, middle Barito R., *NIFS bb27736* s (L), *bb28751* s (A, L), *bb28752* j (A, L), *bb28753* j (A, L), *bb28754* ♀ (A, L). Kenpai, *Hallier 1422* j (L, NY), *2164* j (L, NY), *Teysmann 8617* j (L). G. Klam, *Hallier 2360* ♂ (K, L, NY), *2374* s (L, NY). Samarinda, *Posthumus 2175* j (K, L). W. Kutei, *Endert 1604* j 20 m. (L). W. Kutei, Mt. Palimasan, *Kostermans 12782* j (L). Karran, *Müller s.n.* s, j (L). Without loc. *Korthals 1863* s (K), *Beccari s.n.* s (L). **Philippines.** Palawan, Mt. Gantung, *Edaño 77619* s (NY). Mindoro, *Merritt 8527* j (US), *8528* j (NY, US). MINDANAO: *Ramos & Pascasio 34497* j (A); Mt. Malindang, *Morao 6010* ♀ 1,200–1,400 m. (A); Monica (Zamboanga), *Pascua 15692* j 1,000 m. (L).

ILLUSTRATIONS. BLUME, C. L. Rumphia 3: *t. 172B, fig. 1, t. 172C, fig. 2.* 1849, as *Dacrydium elatum.*

The slender leaves of this variety, with more or less parallel margins, distinguish it from variety *robustum* which, in addition, grows in wet places. Variety *pectinatum* has foliage which is essentially identical to that of *D. nidulum* var. *nidulum*, although the majority of the specimens have leaves less than 3 mm. long, whereas *D. nidulum* only occasionally has such short leaves. The form of the seed-bearing structure is the important specific distinction. The bark is brown with loose scaly flakes. The four species, *D. cupressinum*, *D. balansae*, *D. nidulum*, and *D. pectinatum* must be considered a series of closely related species that are separated geographically.

5b. Var. **robustum** de Laubenfels, var. nov.

Folia robusta, apicem versus angusta, cuneata, 2–3 mm. longa, 0.6–0.8 mm. lata, basis 0.6–1.0 mm. crassa. Holotypus: *Meijer SAN 37908* (L), North Borneo, Mt. Silam. FIG. 1c.

DISTRIBUTION. The island of Borneo in mossy forest and in peat swamps, from low elevation to 850 meters.

Sarawak. Kuching, *Omar SFN 376* s (LAE). Lawas, Keyangeran, *Tagei 1795* ♂ 12 ft. (K, L). Without loc., *Spurway 376* s (K). **Brunei.** W. Kayangeran F. R., *Brunig 1006* ♂ (K, L). **North Borneo.** Weston, *Mikil SAN 31985* j (K, L). Mt. Silam, Lahad Datu, *Meijer SAN 37908* ♀ 2,500 ft. (K-isotype; L-holotype), *Wood SAN 4172* ♂, j 2,500 ft. (BRI, K, L). Sipitang, *Charington SAN 22299* ♀ 10–25 ft. (L).

The short, spreading, and sharply tapering leaves of this variety give it a distinctive appearance that sets it apart from related taxa. There is often a whitish deposit on the branches. The bark is reddish gray, fissured, and scaly.

6. **Dacrydium nidulum** de Laubenfels, sp. nov.

Arbor ad 30 m. alta, ramosissima; folia brevia, linearia, oblique adscendentia, dorsaliter carinata, 2–5 mm. longa, 0.4–0.8 mm. lata. Strobili masculi cylindracei, terminales, 9–12 mm. longi, 2 mm. lati. Strobili feminei ad apicem ramulorum, saepe ramulorum brevium; folia ramuliorum fertilium parviora sed folia ad apicem longiora semen cingendum niduliformum; apex seminis maturis protrudendus; 1–2 folia ultima fertilia. Semen 3.5–4 mm. longum. Holotypus: *Vink BW 15271* (L), New Guinea, Vogelkop. FIG. 3a.

The widespread specimens of this new species have usually been carelessly labelled *Dacrydium elatum* which, in the mature form, is quite distinct, although (as is also true of *D. novo-guineense*) the juvenile leaves of *D. elatum* are similar in shape, and range in size from equal to longer. *D. nidulum* differs from most species in the bracts of the fertile structure which, as they grow on the end of a fertile shoot, whose leaves are often shorter than the usual foliage leaves, are considerably elongated, clasping the growing seed in a protective nest. As the seed grows and becomes almost erect, it protrudes well beyond the tips of its cluster of bracts. Other species with similarly elongated bracts in the fertile area include *D. lycopodioides* and *D. nausoriensis*, whose bracts are distinctly flattened and whose pollen cones are distinctly smaller, *D. spathoides* also with flattened bracts and with flat linear leaves, and *D. novo-guineense* with scale-like foliage leaves.

A wide variety of forest conditions is tolerated by *D. nidulum* from peaty swamps and wet primary forest to light secondary forest, but always in very moist climatic conditions or with a high ground water-table. The feathery seedling leaves gradually shorten and change in form to the adult type. The brown bark exfoliates in thin sheets or rough plates. As might be expected over so large a range, there is some variation in form, particularly in the size of the leaf. Two varieties have been recognized on the basis of contrasting leaf forms and a slight difference in the microsporophylls.

6a. Var. **nidulum.**

Folia non conferta, patula, acicularia; apice paulo incurva, obtusa. Squama strobilorum masculorum triangularia, imbricata, apice elongata.

DISTRIBUTION. From Celebes to Fiji, and particularly in the western part of New Guinea from near sea level to 1,800 meters (most collections are below 1,000 meters), and in wet rainforest areas. MAP 3.

Celebes. Masamba, *Steup bb23045* j 1,700 m. (K, L). Lasurume R. (SE.), *El-*

bert 3126 j 250–755 m. (L). Sawankudu R. (SE.), *Elbert 3726* j 150–497 m. (A). Lampia (Malili), *NIFS bb19709* s (A, L). Taparan-masapi (Malili), *NIFS bb20535* s 434 m. (A, L). **Moluccas.** Halmahera, *NIFS bb24934* ♀ 450 m. (A, BRI, L), *Nedi 301* j 600 m. (L). **New Guinea.** VOGELKOP: Segior (L. Ajamaru), *Vink BW 15271* ♀ 220 m. (L-holotype; K, LAE, Z-isotypes). Tehach (L. Ajamaru), *Versteegh BW 7378* ♀ 250–300 m. (L). Ajamaru, *Versteegh BW 4985* s 275 m. (L), *Vink BW 15249* s 240 m. (L, Z). Tobi Mts. (Kebar Valley), *Versteegh & Kalkman BW 5594* ♀ 900 m. (L, LAE), *Sijde BW 5596* s 900 m. (L). Kebar Valley, *Koster BW 6885* ♀ 1,100 m. (L). JAPEN IS.: Aisau, *Iwanggin BW 9225* ♂ 210 m. (K, L, LAE). Mariattu, *NIFS bb30321* j 800 m. (A, L), *bb30475* s 500 m. (A, L). Without loc., *NIFS bb14390* j 150 m. (L). N.W. NEW GUINEA: Rouffaer R., *Leeuwen 10280* s 250 m. (A, K, L). Sidoarsi Mts., *Schram BW 9271* s 660 m. (L). Bodem R., *Lans BW 2373* j 99 m. (L, LAE). Dalman, 45 km. inland from Nabire, *Kanehira & Hatusima 12324* s 400 m. (A). CYCLOOP MTS.: *Versteegh BW 4754* ♀ 120 m. (L, LAE), *Van Royen & Sleumer 6246* ♂ 750 m. (K, L, LAE, Z), *Koster BW 235* s 80 m. (L), *BW 239* s 80 m. (A, K, L), *BW 1182* ♀ 50 m. (A, K, L), *Brass 8806* s 20–100 m. (A, BRI, L). CENTRAL NEW GUINEA: Weta-batie, *Mangold BW 667* s 205 m. (L). Upper Digul, *NIFS bb14519* ♂ 15 m. (K, L). Digul R., *Versteegh BW 4891* ♀ cultivated by natives (L, LAE). TERR. NEW GUINEA: Sattleburg, *Clemens 7954* ♀ (A), *7954A* j (A), *7907B* j (A). WESTERN DIVISION, PAPUA: Oriomo R., *Brass 5875* ♂ 10–20 m. (A, K, L, NY, US), *5876* ♀ (A, K, L, NA, NY, US), *5876A* j (A, L, NY, US), *Hart 5021* s (A, BRI, K, L, US), *White & Gray NGF 10407* ♂, j 70 ft. (BRI). EAST PAPUA: Betw. coast and Owen Stanley Mt., *Burke 377* ♂ (K). N. of Mapo (Milne Bay), *Smith NGF 1352* s 2,700 ft. (BRI, L, LAE). Normanby I., *Brass 25573* ♂ (A, K, L, US), *25482* j (A, L). **Fiji.** VITI LEVU: Reservoir Road, *de Laubenfels P312* j (A, K, RSA, SBT), *P312a* j (A, K, RSA, SBT), *P313* j (A, K, RSA, SBT), *P315* ♂ 300 ft. (A, RSA, SBT), *Tothill 854* s (K). Naitasiri, *Gillespie 2142* j 150 m. (K, NY, US). Namboutini, *Anon. FD834* s (K), *de Laubenfels P308* s 1,000 ft. (A, RSA, SBT), *P307* j (A, RSA, SBT). Mt. Korumbamba, *Meebold 16529* j summit (K). Near Burreata, *Milne 55* ♂ (K). Mawata, *Kuruvoli & Parham 13433* s (K). Nandarivatu, *A. C. Smith 6244* s 1,250 m. (A, BRI, ILL, K, US). Mt. Nomama–Mt. Tomanivi, *A. C. Smith 5734* j 1,050 m. (ILL.). Without loc., *Storck 906* ♀ (A, K), *Seemann 573* j (K), *Horne 613* ♀ (K). VANUA LEVU: Drekati, *Mead 2003* j (K), *2004* s (K), *2005* s (K). Nanduri, *Tothill 553* s (K). Thakaundrove, Mt. Kasi, *A. C. Smith 1773* ♂ 300–400 m. (A, K, NY, US), *Tuidrokadroka s.n.* ♀ 300–430 m. (A). Without loc., *Stauffer & Kuruvoli 5841* ♀ (Z), *5842* j (Z). KADAVU IS.: *Damanu KU19* ♀ (K), *53* ♀ (K).

The variety *nidulum* differs from the variety *araucarioides* in its more dispersed leaves with blunter and less incurved tips. Not more than the upper third of the leaf is incurved and the leaves are not distinctly wider than thick. Transitional specimens can be found, particularly with the penultimate branches more araucarioid. The ripe cone is said to be brown. The brown bark peels in thin flakes and has lenticels.

6b. Var. **araucarioides** de Laubenfels, var. nov.

Folia conferta, valde incurva, imbricata, acuta, latiora quam crassa. Squama strobilorum masculorum triangularia, apice non elongata. Holotypus: *Versteegh BW 3041* (A), New Guinea, Wissel Lake. FIG. 3b.

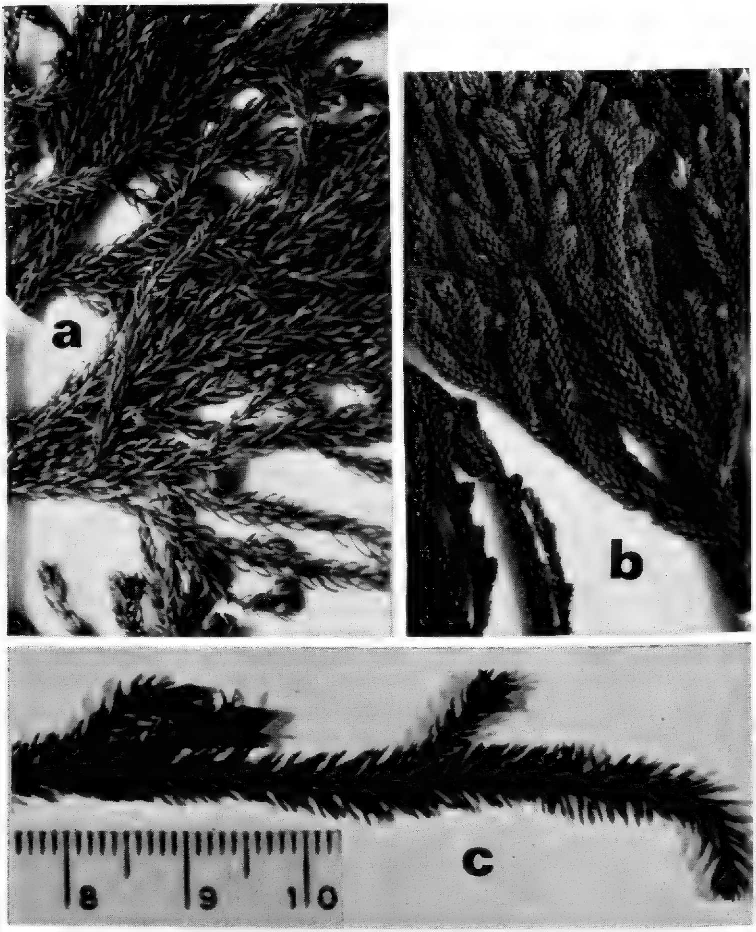

FIGURE 3. a, *Dacrydium nidulum* de Laubenfels var. *nidulum*, portion of the holotype, *Vink BW 15271* (L); b, *D. nidulum* var. *araucarioides* de Laubenfels, portion of the isotype, *Versteegh BW 3041* (L), a and b natural size; c, *D. spathoides* de Laubenfels, portion of the holotype, *Brass 12659* (A), enlarged.

DISTRIBUTION. At intermediate elevations along the main mountain chain of New Guinea, 1,750–2,770 (rarely down to 750) meters, mostly in peat and swamp forest.

New Guinea. WISSEL L.: *Versteegh BW 3041* ♀ (A-holotype; K, L-isotypes), *Eyma 4790* ♀, ♂ (A, K, L), *5103* ♂ 1,750 m. (A, K, L). Near Kebo, *Vink & Schram BW 8620* s 1,755 m. (L), *BW 8796* s 1,800 m. (L, LAE), *BW 8914* ♀ 1,750 m. (L, LAE). WESTERN MTS.: Mt. Genofa, *Salverda bb22571* j 1,000 m. (L), *bb22576* s 750 m. (L). CENTRAL MTS.: Endarotali, *Rappard BW 697* ♀ 1,750 m. (L). Mt. Hellwig, *Pulle 801* ♂ 1,450 m. (L). TERR. NEW GUINEA:

Kandep Valley, *Robbins 3266* ♂ 7,500 ft. (L, LAE), *Flenley ANU 2828* ♀, j (L). Upper Kaugel Valley, *Bowers 188* j (LAE). PAPUA: S. Highlands, 8 miles E. of Mendi, *Pullen 2674* s 5,700 ft. (L, LAE), *2680* j (LAE).

The crowded and incurved leaves of *Dacrydium nidulum* var. *araucarioides*, which expose only their rounded dorsal surface, are reminiscent of *D. araucarioides* and of the leaves of various *Araucaria* species. The pollen cones available have sporophylls which are less elongated and less imbricate than is true of related taxa. The gray-brown bark is flaky. The ripe cone is red.

7. **Dacrydium balansae** Brongn. & Gris, Bull. Soc. Bot. France **16**: 328. 1869. Type: *Balansa 1380*, New Caledonia, Bourail.

A tree 4 to 12 m. high, sometimes taller; bark in thick brown plates, fibrous within but the surface with a tough smooth cuticle and numerous small lenticels, weathering gray; branching into many small spreading shoots; juvenile leaves fine needles up to 13 mm. long, gradually changing to the adult form; mature foliage leaves thick, strongly tapering from a decurrent base 1–2 mm. wide, spreading and slightly incurved at the blunt tip, strongly keeled, particularly on the dorsal side, margins sharp, 3–4.5 mm. long, on branches bearing fertile structures somewhat smaller, often slightly glaucous; pollen cones cylindrical 8–15 mm. long, 2 mm. in diam., terminal, often on short branches, or lateral, or both together; microsporophyll triangular, acute but not elongated; seed cones terminal on long or short branches with somewhat reduced leaves for as much as 2 cm. below the cone; often with a twist below the fertile area; seed cone scales elongated, 3.5–4 mm. long, not more than 1 mm. wide, not tapering, one or rarely two of the uppermost fertile; ovule at first inverted and buried among the cone scales but gradually becoming nearly erect; mature seed spreading the cone scales apart but more or less surrounded and emerging slightly if at all, oval-elongated, wider than thick, tapering to a blunt tip with marked lateral keels, up to 5 mm. long, 3.5 mm. wide.

DISTRIBUTION. Throughout New Caledonia in drier forests, generally over serpentine at low elevation (up to 900 meters), and occasionally in more moist forest.

New Caledonia. Valley of Amona near Wagap, *Vieillard 3262* ♂ (GH, K, NY, P, Z). Mt. Koniambo-Koné, *Däniker 909* s 400–600 m. (P, Z). Mt. Paéoua, *McKee 17028* s 600–900 m. (P). Mt. Boulinda above Oua Nepoua, *McKee 17194* s 800 m. (P). Above Houailou, Me Maoya, *McKee 9891* s 800–900 m. (P). Below Téné near Bourail, *Balansa 1380* ♀ (P-holotype; BM, K-isotypes). Kuana R. E. of Table Unio, *Buchholz 1601* j (ILL, P). Bogota Penn., *Brousmiche s.n.* s (P). Col de Perchicara (Thio-Canala), *Veillon 145* s 200 m. (P). Col de Nakety (Thio), *Guillaumin, Chevalier & Hürlimann 1445* s 150 m. (P, Z). Dothio Kieho Valley, *McKee 16510* j 100 m. (P). Ouroné (mouth of Dothio), *Balansa 3484* ♀ (BM, NY, P). Lower valley of Thio, *McKee 15433* ♂ 10–100 m. (P), *McMillan 5158* ♂ (A, K, P). Slopes of Mt. Douetampo (Thio), *Corbasson 13914* s 800 m. (P). N'Goye R., *Veillon 511* s 10 m. (P). Mt. Vulcain (upper

Tontouta), *Buchholz 1574* ♀ (ILL, K, P), *de Laubenfels P412* ♀ 560–900 m. (A, K, RSA, SBT), *P412A* j (A, RSA, SBT), *P413* ♂ (A, RSA, SBT), *Aymard 16346* ♀ 600 m. (P), *Virot 400* s 300 m. (A, P), *Baumann-Bodenheim 8053* s (P, Z), *8168* s (P, Z), *8268* s (P, Z), *8808* s (P). Valley of Kalauéhola (Tontouta), *Däniker 587a* s (Z), *Hürlimann 1679* s 150 m. (P, Z). Ni, *Hürlimann 1708* s 850 m. (P, Z). Slopes of Mt. Mou, *White 2001* s (K, P). E. slopes of Erembéré, *Virot 37* j 600 m. (A, P). Trail to Mt. Dzumac (N. of Couvelée R.), *Franc 2492* ♀ (K, NY, P, US, Z), *2493* ♂ (K, NY, P, US, Z), *2494* s (A, K, Z), *Le Rat 2864* ♀ (P), *2866* s (K), *Virot 187* ♂ (A, NY, P, US), *de Laubenfels P155* ♀ 600 m. (SBT), *Bernier 302* j (P), *303* ♂ (P), *Hürlimann 1088* s (P), *McKee 2521* ♂ (A, P), *2522* j (A). Banks of Couvelée R., *Balansa 1380A* ♂ (NY, P). Banks of Dumbéa R., *Pancher s.n.* s (P), *Vieillard 1278* s (P). Forest of Mois de Mai (upper Yaté), *Buchholz 1381* j (ILL, K, P), *Baumann-Bodenheim 14987* j (P, Z), *14993* s (P, Z), *14997* j (P, Z), *Bernier 309* ♂ (P). R. Bleue (Walker Forest), *Bernier 304* j (P), *305* ♂ (P), *306* j (P), *307* j (P), *308* s (P), *de Laubenfels P393* ♂ 160 m. (A, K, RSA, SBT), *McKee 12906* ♂ (P), *Aubréville & Heine 184* ♂ (P), *Hürlimann & Lucien 3486* s 200 m. (Z). Pirogues R., *White 2238* s (K, P). South, *Raoul s.n.* s (ILL, P). Without loc. *Franc 1964* s (A, BM, NY, P, US, Z).

ILLUSTRATIONS. PILGER, R. Pflanzenreich IV. **5** (Heft 18): *fig. 5D.* 1903; Nat. Pflanzenfam. ed. 2. **13**: *fig. 118D.* 1926; SARLIN, P. Bois et Forêts de la Nouvelle-Calédonie, *t. 20.* 1954.

The elongated bracts surrounding the mature seed distinguish this species from all other except *Dacrydium araucarioides* which has larger pollen cones and differently formed foliage leaves. Sterile specimens have more robust leaves than those of other species where a similar leaf shape is found. When growing in wet forests, particularly the collections from R. Bleue, the trees can grow to more than 20 m. and the leaf form is more incurved and acute in the manner of *D. nidulum* var. *araucarioides.* No seed structures have been collected for this variant and its status remains uncertain.

8. **Dacrydium araucarioides** Brongn. & Gris, Ann. Sci. Nat. Paris V. **6**: 244. 1866. Lectotype: *Vieillard 1277*, New Caledonia, Canala.

Dacrydium arthrotaxoides Carrière, Traité Conif. ed. 2. 697. 1867. Type: *Vieillard 1277.*

Podocarpus araucarioides (Brongn. & Gris) Sebert & Pancher, Not. Bois N. Caléd. 171. 1874.

Small tree 3–6 m. high; bark in thick rough flakes, dark brown and slightly fibrous within, more or less smooth on the surface at first with occasional lenticels, weathering gray; branches spreading and becoming erect candelabra-like, rather open; juvenile leaves acicular, dense, curved, up to 12 mm. long; transitional leaves shorter and thicker, closely resembling the mature leaves of *D. balansae*, but somewhat longer, 5–7 mm. long; mature foliage leaves developing gradually from the transitional stage, spreading but distinctly incurved with the blunt tip sharply curved and directed towards the branch axis, imbricate, only the angularly keeled upper middle dorsal part of the leaf exposed, aggregating to form a smooth thick branch 4–6 mm. in diam., strongly keeled on the axial side toward the leaf base, becoming concave toward the leaf tip, 3–5 mm. long, 1–1.4 mm. wide; pollen cones terminal, often on short lateral branches, or lateral just below a terminal cone, cylindrical, 9–18 mm. long, 2.5–3 mm. in diam.; microsporophylls long triangular, acute with an incurved tip; seed cone terminal on short to long branches whose leaves are about 3 mm. long and strongly curved, cone bracts noticeably longer and straighter, at the cone apex about 5 mm. long, the tip slightly hooked, the whole cone becoming red and fleshy when mature; 1–3 seeds surrounded by the bracts, becoming erect and almost as long as the enclosing bracts, oval but tapering to a blunt apex and wider than thick, 4.5 mm. long.

DISTRIBUTION. Common and locally dominant throughout the serpentine scrub of the southern half of New Caledonia at low elevation and up to at least 1,000 meters.

New Caledonia. S. of Poro, *McKee 14886* s 600 m. (P). Mts. above Canala, *Vieillard 1277* ♀, ♂ (P-lectotype of *Dacrydium araucarioides* and holotype of *D. arthrotaxoides*; A, BM, GH, K, NY, Z-isotypes). Bogota Peninsula, *Sarasin 294* ♀, ♂ 500 m. (Z). Messioncoué near Port Bouquet, *Balansa 2507* ♀ (K, P), *2508* s (P). Mts. above N'Goye, *Schlechter 15175* s (K, P, Z), *15176* ♀ 1,000 m. (A, BM, K, P, Z). Ridge N. of Mt. Tonta, *McKee 17247* s 950–1,150 m. (P). Mt. Humboldt, *Däniker 2914* s (Z). Mt. Dzumac, *Le Rat 633* s (K, P), *Franc 764A* s (P), *766* (Z), *Alleizette 119* ♂ (P). Upper Ouinné, *Bernier 320* s, j (P). Plateau leading to Mt. des Sources, 700–800 m. *Virot 152* s (A, P), *s.n.* s (A, P), *Bernier 4* s (P), *5* ♂ (P), *6* ♀ (P), *Buchholz 1059* ♂ (ILL, P), *1060* ♀ (ILL), *1194* j (ILL, K, P), *1215* ♀ (ILL, P), *de Laubenfels P373* ♀ (RSA), *P374* ♂ (A, SBT), *McKee 2202* ♀ (A, P, US), *5669* ♂ (P), *Hürlimann 211* s (P, Z). Upper R. Bleue, *Baumann-Bodenheim 8575* ♀ (P, Z), *8576* ♂ (P, Z). Mois de Mai (R. Blanche), *McMillan 5128* ♂ 600 ft. (A, K, P), *Hürlimann 1561* s (P), *Baumann-Bodenheim 15002* j (P, Z). Mt. Ouenarou, *Baumann-Bodenheim & Guillaumin 11818* s (P, Z). Mt. Dore, *Pancher s.n.* s (P-syntype of *D. araucarioides*), *Baumann-Bodenheim & Guillaumin 11407* ♀ (P, Z), *11430* j (P, Z). Mt. Niocol, *Pancher 380* ♀, ♂ (K, P). Pirogues R., *White 2122* s (A, K, P). Bois du Sud, *Bernier 317* ♀, ♂ (P), *Baumann-Bodenheim & Guillaumin 11028* ♂ (P, Z), *12497* j (P, Z). Marais Kiki, *McKee 1124* s 150 m. (A), *Baumann-Bodenheim 6232* s (P, Z), *6256* ♂ (P, Z), *6338* ♂, j (P, Z), *6363* ♂ (P, Z), *13322* s (P, Z). Yaté R., *Däniker 205 pt.* ♀, j (Z), *Hürlimann 681* s (P, Z), *1561* ♂ (Z), *Baumann-Bodenheim 6071* s (P), *Baumann-Bodenheim & Guillaumin 6514* s (P, Z), *6729* ♀ (P, Z), *6752* ♂ (P, Z), *Thorne 28568* ♂ (P), *Baas-Becking & Stratin 6071* ♂ (Z). Upper Vallé du Pin, *Baumann-Bodenheim & Guillaumin 11941* j (P, Z). Creek Pernod, *Hürlimann 3144* ♂ 170 m. (Z), *3145* ♀ (Z). Plaine des Lacs (Madelaine R.), *Compton 320* ♀, ♂ j (BM), *Le Rat 2631* ♂ (A, P), *Franc s.n.* s (A, K), *Foster s.n.* s (P), *Bernier 316* j (P), *318* ♀, ♂ (P), *319* j (P), *Buchholz 1428* ♀ (ILL, K, P), *1466* ♀ (ILL, K, P), *Denizot s.n.* s (P), *de Laubenfels P114* ♀, ♂ j (SBT), *P342* ♂ (A, RSA), *McKee 16324* j (P), *Guillaumin 8370* s (P, Z), *Aubréville & Heine 171* ♂ (P), *133* ♀ (P), *Däniker 205* p.p. s (Z); *2781* s, j (Z), *Baas-Becking 6071* ♀ (Z), *Blanchon 737* ♀ (P), *Stauffer & Blanchon 5812* ♀ (P, Z), *Bernardi 9368* ♂ (P). Upper Pirogues R., *Baumann-Bodenheim & Guillaumin 11598* s (P, Z). Prony, *Balansa 187* ♀, ♂ (K, P), *Franc 764* ♀, ♂ (A, BM, K, NY, P, US, Z), *Bernier 801* ♀ (P), *Cribbs 1581* s (P). Pic Foi, *Brousmiche 502* s summit (P). South, *Raoul s.n.* ♂ (P). Without loc., *Deplanche 171* ♀ (P), *Le Rat 1085* s (P), *Veitch s.n.* ♀ (K), *Franc s.n.* (A), *Petit 177* ♂ (P), *Baudouin 620* s (P), *Hürlimann 409* ♂ (P).

ILLUSTRATIONS. BRONGNIART & GRIS, Nouv. Arch. Mus. Hist. Nat. Paris **4**: *t. 2.* 1868. PILGER, R. Pflanzenreich IV. **5** (Heft 18): *fig. 49, F.* 1903; Nat. Pflanzenfam. ed. 2. **13**: *fig. 118, F.* 1926; SARLIN, P. Bois et Forêts de la Nouvelle-Calédonie, *t. 17.* 1954.

This species is one of the several specialized plants with bizarre form flourishing in the serpentine scrub or maquis in the southern part of New Caledonia under moderate to heavy rainfall. It has enough in common with *Dacrydium balansae* to suggest that it is derived from that species. The robust form parallels that of *D. gibbsiae*, another endemic on serpentine.

9. **Dacrydium lycopodioides** Brongn. & Gris, Bull. Soc. Bot. France **16**: 329. 1869. Type: *Pancher* in 1869, New Caledonia, Mt. Mou.

Tree to 25 m. or more, profusely branched; bark in brown flakes, fibrous and lighter within, surface more or less smooth and covered by numerous small lenticels; juvenile leaves acicular, very fine, up to 10 mm. long, changing gradually to the adult form; mature foliage leaves flat, lanceolate, slightly keeled on the dorsal surface, with a distinct rib on the axial surface, pungent, spreading and curved so that the tips are parallel with the branch, 3–4.5 mm. long, 0.7–0.8 mm. wide; pollen cones terminal and often also lateral directly at the base of a terminal cone, cylindrical, 4–7 mm. long, 1.2 mm. in diameter; microsporophylls triangular, somewhat elongated, acute, overlapping; seed cone terminal, often on a short branch, leaves just below the fertile structure smaller than ordinary foliage leaves, sometimes only 1 mm. long, bracts of the cone larger towards the apex, up to 2.5 mm. long and partly covering the epimatium, normally only one fertile bract; seed becoming partly erect and completely exposed, rich shining chocolate brown, oval but tapering to a blunt tip, wider than thick, 3–3.5 mm. long.

DISTRIBUTION. In moist forests within a restricted part of southern New Caledonia, from about 900 to 1,400 meters elevation.

New Caledonia. Mount Mou, 1,140 m. *Pancher* (1869) ♀ (P-holotype), *Vieillard (Pancher) 3265*[4] ♀ (BM, K), *Vieillard 3265* j (GH, K, P), *Pancher* (1870) ♀ (K, P), *Hennecart s.n.* ♂ (P), *547* ♀, ♂ (P), *Balansa 2863* ♀, j (BM, K, NY, P), *Virot 9* j (A, P), *40* j (A, P), *de Laubenfels P134* ♀, ♂ (SBT), *P348* ♀ (A, RSA, SBT), *P350* j (A, RSA, SBT), *P351* j (A, RSA, SBT), *Bernier 291* j (P), *Chevalier s.n.* j (ILL), *Buchholz 1083* j (ILL, P), *Däniker 2827* ♀, j (Z), *Hürlimann 1581* j (P), *McKee 2269* j (P), *3514* j (A, P), *3515* j (A, P), *Thorne 28734* j (P), *Baumann-Bodenheim 15611* j (P, Z), *15612* s (P, Z), *Cale & Naturel 1581* j (Z).

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[4] This collection is probably the same as the type. Vieillard's material is mingled with that of Pancher, sometimes with both names, sometimes with the number, and sometimes without.

Ridge above Ouinné R., *de Laubenfels P448* ♀ 1,000 m. (A, K, RSA, SBT), *P449* ♂ (A, RSA, SBT), *P450* j (A, K, RSA, SBT), *Bernier 289* j (P), *290* s (P), *Bernardi 1248* s 800–1,000 m. (P). Mt. Humboldt, *Baumann-Bodenheim 15355* j 1,400 m. (P, Z), *15405* s (P, Z). Without loc., *Mueller 94* j (P), *Baudouin 553* j (P).

ILLUSTRATION. SARLIN, P. Bois et Forêts de la Nouvelle-Calédonie, *t. 18.* 1954.

The small seeds and pollen cones and the short flat acute leaves set *Dacrydium lycopodioides* apart from all other species of the genus but its morphology is not far removed from many of them. It is a rather delicate looking tree with feathery light green foliage which is actually quite tough. Within its limited range it is strictly a canopy tree of mountain forests and does not penetrate the mossy forests along the exposed ridges.

10. **Dacrydium spathoides** de Laubenfels, sp. nov.

Arbor ad 34 m. alta; cortex bracteatus, niger; folia recta, marginalibus parallelis, apice subacuta, plana forma spatharum, dorso carinata, patula, 4–7 mm. longa, 1–1.2 mm. lata. Strobili masculi cylindracei, laterales, aliquot folia minora ad basem, 10 mm. longi, 2.5 mm. crassi; antherae triangulares. Strobili feminei ad apicem ramulorum saepe cum foliis brevibus 2 mm. longis; folia ad basem seminis longiora, 3 mm. longa; semen protrudendum, 4 mm. longum. Holotypus: *Brass 12659* (A), New Guinea, Barnhard Camp. FIG. 3C.

DISTRIBUTION. In mossy mountain forests from 1,050 to 2,200 meters elevation, on the islands of Borneo and New Guinea.

Sarawak. Mt. Dulit, *Mjoberg 23* ♂ 1,200–1,500 m. (A, K, NY), *Richards 1997* s 1,300 m. (A, K, L). Meruong Plateau, *Brunig S8722* ♀ 3,400 ft. (K, L), *S9992* ♀ 1,050 m. (L). **New Guinea.** Idenberg R., 18 miles SW. of Barnhard Camp, *Brass 12659* ♀ 2,150 m. (A-holotype; BRI, K, L-isotypes), *12660* j (A, BRI, L), *Brass & Versteegh 11996* 2,200 m. (A, BRI, L).

The very flat bracts in the fertile region, longer than the somewhat reduced leaves of the subtending branch, and covering about half of the mature seed, distinguish *Dacrydium spathoides* from all other species except perhaps *D. lycopodioides*, which has distinctly smaller seeds and pollen cones, and much smaller lanceolate rather than linear leaves. These foliage leaves are unusual within Podocarpaceae in their resemblance to juvenile leaves of Cupressaceae, particularly *Juniperus*, differing, however, in their spiral placement. The specimens from Borneo have longer (10–15 mm.) leaves and on *Richards 1997*, which may be slightly juvenile, they spread at right angles to the branch rather than at an angle of about 45°, as in other specimens. The Borneo material may possibly represent a separate taxonomic entity.

11. **Dacrydium magnum** de Laubenfels, sp. nov.

Arbor ad 30 m. alta; ramosissima; rami dense foliati, 6–7 mm. diametro; folia acicularia, acuta, falcata, dorsaliter carinata, 4–6 mm. longa, 0.3–

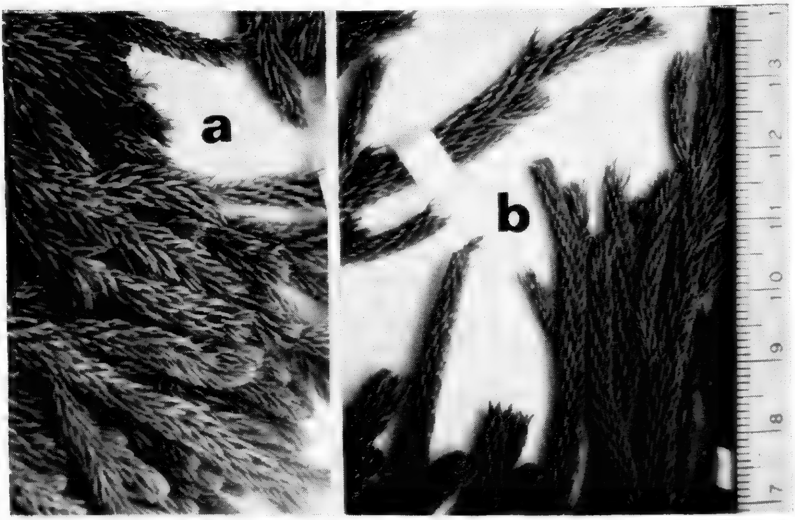


FIGURE 4. a, *Dacrydium magnum* de Laubenfels, portion of the holotype, *de Haan bb23806* (L), enlarged; b, *D. beccarii* Parlatore var. *rudens* de Laubenfels, portion of the holotype, *Brass 27821* (A), enlarged; a and b are at same magnification.

0.4 mm. lata. Strobili feminei ad apicem ramulorum, saepe ramulorum brevium folia diminuta, folia strobili semen solitarium cingendum. Semen 5 mm. longum. Holotypus: *de Haan bb23806* (L), Moluccas, Obi. FIG. 4a.

DISTRIBUTION. The island of Obi in the Moluccas in primary forest and locally common.

Moluccas. Obi, *de Haan bb23806* ♀ 500–600 m. (L-holotype), *bb23807* j (L).

This isolated collection from a poorly studied region is distinct from all other *Dacrydium* species in having the seed surrounded by slender bracts no longer than the foliage leaves, protruding only slightly when mature. It differs from *D. beccarii* and *D. xanthandrum*, whose seeds are well exposed when mature but are produced on branches with distinctly reduced leaves, whereas the fertile branch of *D. magnum* has unreduced leaves. The leaves are also more spreading and rigid than those of *D. beccarii* but not at all flattened as in *D. xanthandrum*. This new species differs from *D. gibbsiae* by the slender bracts in the fertile area, that are less than half as wide and not flattened. Juvenile leaves are at least 17 mm. long. The mature foliage leaves are slightly incurved so that their tips are not exposed.

12. **Dacrydium beccarii** Parlatore in DC. Prodr. **16** (2): 494. 1868. Lectotype: *Beccari 2385*, Sarawak, Mt. Poe.

Bush 3–4 m. high to tree, rarely up to 35 m.; bark smooth, thin, gray, and fissured, sometimes scaly, brownish within; profusely branched forming an umbrella-shaped crown with the twigs stiffly erect; juvenile leaves very slender, up to 20 mm. long, changing gradually to the adult form; mature foliage leaves needle-like, strongly keeled on the dorsal side, spreading but curved axially, acute, crowded; pollen cones ovoid, at least 10 mm. long and 3 mm. in diam., subtended by a few reduced needle-leaves, lateral as short side branches, or terminal; microsporophyll lanceolate, acute, more than twice as long as wide; seed cones placed in the same manner as the pollen cones and formed of spreading reduced needle-leaves, becoming reddish when ripe; seed solitary or a pair in a nearly terminal position, becoming nearly erect, oval-elongated, wider than thick, 4 mm. long, well exposed when ripe.

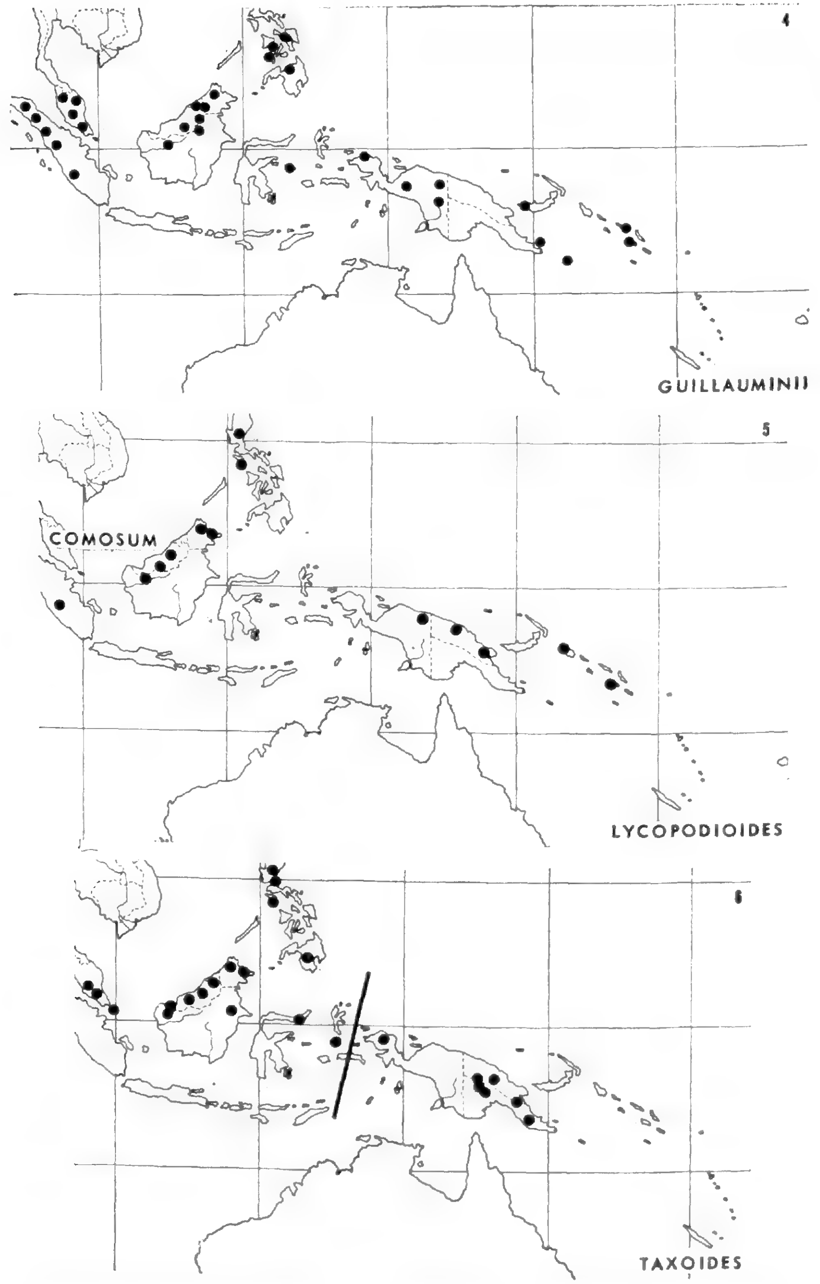
The reduced needles of the fertile shoots and the not elongated cone bracts distinguish this species from all others except *Dacrydium xanthandrum* whose foliage leaves have a different form. Sterile specimens are characterized by their fine slender crowded needles without incurved tips, strongly resembling the juvenile leaves of many other species but generally more crowded and shorter. Three varieties have been recognized based on contrasts in leaf form.

12a. Var. **beccarii.**

Leaves dense, crowded, 5–8 mm. long or longer, 0.4–0.8 mm. wide.

DISTRIBUTION. In scrub formations on exposed ridge tops and in high mossy forests, from Malaya to the Solomons generally in somewhat isolated localities, from 1,000 to over 2,000 meters, or rarely as low as 500 meters. MAP 4.

Malaya. Kedah Peak, *Kochumen 79133* ♂ 3,800 ft. (K, L), *Robinson & Kloss 6053* j (K). G. Luas (Perak), *Yapp 493* j 5,200 ft. (K). Perak, *Scortechini s.n.* ♀ (A, K). G. Benom (Pahang), *Mus* (1925) ♂ 5,000 ft. (K). Mt. Ophir (Jahore), *Griffith 5003* ♀ (GH, K), *s.n.* ♂ (L), *Kerr 3155* ♀ 1,300 m. (K), *Maingay 2750* ♀ (K). Without loc. *Holttum 20711* s 6,000 ft. (BRI). **Sumatra.** Atjeh, Gajoland, *Van Steenis 8357* ♂ 2,600 m. (L). Atjeh, Tamyang, *NIFS bb10748* ♂ 950 m. (L). Karoland (E. Coast), *NIFS bb7707* j 1,400 m. (L). Siborong (Tapanuli), *NIFS bb3829* s 1,900 m. (L). Silindung (Tapanuli), *NIFS bb5671* s 1,300 m. (L). Lubuksikaping, *NIFS bb6737* j (L). Betw. Djambu Dolok and Baturangin, *Surbeck 107* ♀ (A, L). **Sarawak.** Mt. Poe (G. Rumput), *Beccari 2384* s 5,000 ft. (FI), *2385* ♀ (FI-lectotype; K-isotype), *Clemens 20385* s, j 6,000 ft. (A, K, NY), *Anderson 190* ♀ 2,000 m. (K), *Hewitt* (1900) s (K). Merurong Plateau, *Brunig S9990* s 2,300 ft. (L). Mt. Dulit, *Richards 1059* j 1,230 m. (A, K, L), *1808* ♀ 1,100 m. (A), *1996* s 900–1,000 m. (A, K, L). Mt. Penrissen, *Mjoberg 221* j 4,400 ft. (A, NY). **North Borneo.** Mt. Kinabalu, *Smythies S10607* s 6,000 ft. (K, L). Ranau, *Mujin 33774* ♀ 5,300 ft. (K, L). Kota Belud, *Meijer SAN 21086* ♂ 5,000 ft. (K), *SAN 21100* s (K, L). Without loc., *Comber 101* ♀ 5–6,500 ft. (K). **Borneo.** West, Bengkajang, G. Bawang, *NIFS bb24779* s 1,442 m. (A, L). G. Damus, *Hallier 510* s (L). Ulu Kelan, *Molengraaff B3475* j 1,000 m. (L, NY), *3476* j (L). Amai Ambit, *Hallier B3431* s (L, NY). Mt. Bongo,



MAPS showing distribution of: 4, *Dacrydium beccarii* Parlatore (dots), *D. guillauminii* Buchholz, known only from New Caledonia; 5, *D. xanthandrum*

Haviland 2070 s (K). **Philippines.** LEYTE: Biliran, *Sulit 21694* s 1,350 m. (L). NEGROS: Dumaguete, Or, *Herre 1150* s 4–6,000 ft. (A, NY). Mt. Canlaon, *Edaño 21936* j 1,860 m. (L). Mt. Marapara, *Curran & Foxworthy 13612* s (L, NY, US). Mt. Silay, *Everett 4227* j (NY, US). Without loc., *Britton 343* s 1,700 m. (L). MINDANAO: Mt. Malingdang, *Mearns & Hutchinson 4547* s (K, L, NY, US), *4731* s (NY, US). **Moluccas.** Taliabu, *Hulstijn 126* ♀ (L). **New Guinea.** Vogelkop, Upper Aifat Valley, *Moll BW 12853* s 870 m. (L); Tamrau Ra., *Van Royen & Schram 7791* s 920 m. (K, L, LAE). Cycloop Mts., *Gjellerup 572* s 600–1,500 m. (A, K, L). Hellwig Mts., *Lorents 1698* s 2,100 m. (K, L). Wissel L., Maiare, *Eyma s.n.* s (L). Normanby I., *Brass 25660* ♀ mt. crest (A, K, L, LAE, US). **New Britain.** Mt. Tangis, *Frodin NGF 26902* s 3,500–5,000 ft. (L). **Solomon Is.** Santa Ysabel, *Baea BSIP 2475* ♀ well above 3,000 ft. (ridge top) (K, L, LAE), *Brass 3264* ♂, j 1,100 m. (A, BRI, L). Guadalcanal, Mt. Popomansiu, *Braithwaite 4810* ♀ (K), *Hill 9004* j 7,000 ft. (K).

ILLUSTRATION. CORNER, E. J. H. Gard. Bull. Straits Settlements **10**: *t. 6.* 1939.

The branches of this variety have a definite bushy aspect because of the fine dense growth of needles. Several specimens with leaves more robust than normal for the species have been included here, although their status is a little uncertain. These include *Van Steenis 8357, Brass 3264,* and *Brass 25660.*

12b. Var. **subelatum** Corner, Gard. Bull. Straits Settlements **10**: 243. 1939. Type: *Corner SFN 33224,* Malaya, Pine Tree Hill.

Adult leaves noticeably less bushy than in the typical variety, variable in length, 3–6 mm. long; up to three seeds in a fertile structure.

DISTRIBUTION. Mixed with var. *beccarii* in the mossy forests and exposed ridges of Malaya, from 1,200 to 2,300 meters.

Malaya. G. Bubu (Perak), *Wray 3875* ♀ 5,000 ft. (A, K). G. Tahan (Pahang), *Haniff & Nur SFN 7994* ♂ 5,500–7,000 ft. (K). G. Tapis (Pahang), *Symington & Kiah s.n.* ♀ 4,600 ft. (K). Fraser Hill (Pahang), *Cubitt 6519* s (K). Pine Tree Hill (Pahang), *Corner SFN 33224* s 4,200 ft. (K-isotype). G. Padang (Trengganu), *Moysey SFN 31072* s 4,000 ft. (K), *SFN 31841* s 3,800 ft. (K).

ILLUSTRATIONS. CORNER, E. J. H. Gard. Bull. Straits Settlements **10**: *t. 7 & 8.* 1939.

Only the shorter needles distinguish this variety from variety *beccarii*, and intermediates between them can be found.

12c. Var. **rudens** de Laubenfels, var. nov.

Folia patula incurvata conferta in forma *rudenti.* Holotypus: *Brass 27821* (A), Sudest Island. FIG. 4b.

Pilger (dots), *D. comosum* Corner, known only from the Malay peninsula, *D. lycopodioides* Brongniart & Gris, known only from New Caledonia; 6, *Falcatifolium falciforme* (Parlatore) de Laubenfels (dots west of line), *F. papuanum* de Laubenfels (dots east of line), *F. taxoides* (Brongniart & Gris) de Laubenfels, known only from New Caledonia.

Distribution. New Guinea to Sudest I., from 300 to 3,000 meters in elevation.

New Guinea. Western Half: Mt. Goliath, *de Kock 42* s 3,000 m. (L). Without loc., *Brandenhorst 132* s (L), *133* s (L), *van Römer 1233* s (L). Sudest (Tagula) I., *Brass 27821* ♀ 500–600 m. (A-holotype; K, L, US-isotypes), *28187* ♀ 300 m. (A, K, L, US), *28188* j (A, L, US).

This variety with incurved leaves forming a compact and smooth rope-like branch system contrasts strongly with the two varieties which have spreading leaves and a ragged appearance. Otherwise var. *rudens* does not differ significantly from the remaining varieties of this species.

13. **Dacrydium xanthandrum** Pilger, Bot. Jahrb. **69**: 252. 1938. Lectotype: *Clemens 4504*, New Guinea, Morobe District.

Tree to 30 m. high, sometimes stunted on ridges; densely branched; bark chocolate brown or reddish, peeling in thick flakes, bearing lenticels; leaves spreading obliquely, slightly incurved, linear-lanceolate, generally wider than thick, keeled on the back, acute, 6–10 mm. long, or longer on vigorous branches and when juvenile, 0.6–0.8 mm. wide, not crowded; pollen cones lateral or terminal and subtended by several reduced leaves, oval to cylindrical, 5–13 mm. long; microsporophylls narrowly triangular to lanceolate, acute, 2–2.5 mm. long; seed cones terminal, often on very short branches, fertile bracts in the form of reduced leaves; seeds rich tan, 2-angled, 5 mm. long, more or less protruding when mature. Fig. 5.

Distribution. The island of Borneo and the Philippines to the Solomons, in the mountains from 1,000 to 2,400 meters, rarely down to 500 meters above sea level. Map 5.

Sumatra. Road from coast to Tapanuli (Toba L.), *Bangham 1070* ♀ 4,100–4,500 ft. (A, K, NY). **Sarawak.** Mt. Luiga, *Beccari 3948* ♂ (FI). Baram, *Anderson 4545* ♀ 4,800–7,000 ft. (K, L). G. Mulu, *Hotta 14597* ♂ 1,200–1,600 m. (L). **North Borneo.** Kinabalu, *Nicholson SAN 17827* ♀ 8,800 ft. (BRI, K, L), *Clemens 32502* s 6,000 ft. (A, K, L, NY), *34341* ♀ 5–6,000 ft. (A, K, L, NY). Ranau, *Nicholson SAN 39768* ♀ 8,000 ft. (K), *Meijer SAN 29153* s 7,000 ft. (K, L). Tambunan, *Mikil SAN 32086* ♂ montane (K, L). Penampang, *Clemente 5980* s 5,000 ft. (K, L), *Leaño-Castro 5985* s (K, L). Mt. Alab, *Keith 5965* j 6,000 ft. (K, L). **W. Borneo.** B. Raja, *Winkler 1037* ♂ 1,600 m. (L). **Philippines.** Mt. Umingan (Nueva Ecija), Luzon, *Ramos & Edaño 26510* ♀ (A, K, US). Mt. Halcon, Mindoro, *Rabor 20485* ♂, j 1,600 m. (L), *Edaño 3265* s 780 m. (A), *Merrill 5714* s (US), *5789* j (NY, US). Calapan, Mindoro, *Vidal 3910* ♀ (A, K). **New Guinea.** Cycloop Mts., *Karstel BW 5440* s 510 m. (L, LAE). Sepik region, *Ledermann 9395* s (L). Chimbu, *Cavenaugh NGF 3334* j (A). Morobe District, Ogeramnang, *Clemens 4504* ♂ (A-lectotype; Z-isotype), *5390* ♀ 5,900 ft. (A-syntype), *6398* ♀ 5,850 ft. (A-syntype), *6408* s 5,850 ft. (A), *6488* s 4,500 ft. (A). **Bougainville Is.** *Kajewski 1694* ♂ 950 m. (A, BRI), *1709* ♀ 1,000 m. (A, BRI, L). **Solomon Is.** Guadalcanal, *Walker BSIP 247* ♀ 1,500 ft. (A, BRI, K, L), *Kajewski 2652* s 1,200 m. (A, BRI, L).

The range of this species overlaps that of *Dacrydium beccarii* with which it is often confused, both being found for example, at Ranau and

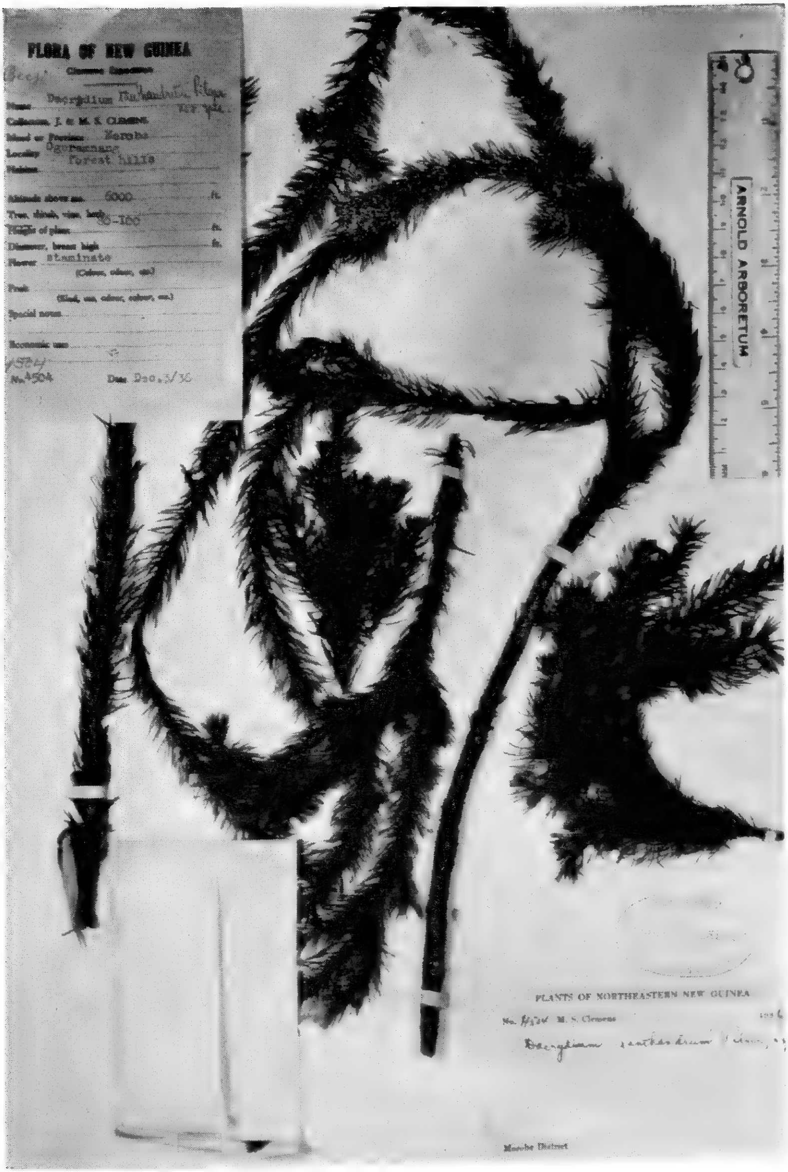


Figure 5. *Dacrydium xanthandrum* Pilger, photograph of the lectotype, *Clemens 4504* (A).

on Mt. Kinabalu. *D. xanthandrum* differs in the noticeably flattened leaves which are widely spreading and distinctly less dense. It also grows with *D. gibbsiae* and its leaves strongly resemble the transitional leaves of that species, but, not only are the adult leaves of *D. gibbsiae* much more robust, the pollen cone is much larger, and the fertile shoots have unreduced leaves. The specimen from Sumatra cited here has much more robust leaves similar to nearly mature leaves of *D. gibbsiae* and may, with more material, be found to represent a distinct taxonomic unit.

14. **Dacrydium gibbsiae** Stapf, Jour. Linn. Soc. Bot. **42**: 192. *t. 4.* 1914. Type: *Gibbs 4162*, North Borneo, Mt. Kinabalu.

Dacrydium beccarii var. *kinabaluense* Corner, Gard. Bull. Straits Settlements **10**: 244. 1939. Type: *Carr SFN 26437*, North Borneo, Mt. Kinabalu (not seen; photo included in description).

Much branched tree to at least 12 m. high; juvenile leaves acicular, 12–20 mm. long, spreading but slightly incurved; mature foliage leaves becoming wider and thicker but distinctly flattened, incurved and imbricate (an angular keel on the dorsal side), acute, aggregated into rope-like shoots about 8 mm. in diameter, individual leaves 5–7 mm. long, 1.0–1.3 mm. wide, rigid; pollen cones terminal or lateral, cylindrical, 20–25 mm. long by 5–7 mm. in diameter; microsporophyll lanceolate, 5 mm. long; seed cone terminal, often on a very short lateral branch, formed of largely unmodified leaf-like structures and with one or two fertile apical leaves, becoming reddish when mature; seeds becoming almost erect, surrounded by but spreading apart the subtending leaves, oval and tapering slightly towards the apex, 4.5 mm. long.

DISTRIBUTION. On the slopes of Mt. Kinabalu, in serpentine soils where it is common from 1,500 to 3,300 meters.

North Borneo. Mt. Kinabalu, *Gibbs 4162* ♀ over 6,000 ft. (BM-holotype; K-isotype), *4050* j (BM), *Clemens 10685* ♀ (A, GH, K), *10879* j (A), *11091* ♂ (A), *28542* s 11,000 ft. (K), *30922* j 4–5,000 ft. (A, L, NY), *33037* ♀, j 5,000 ft. (A, L, NY), *40151* ♀ 6,500 ft. (A, NY), *Griswold 67* j (A), *Haviland 1183* s 6,600 ft. (K), *Chew & Corner 4303* j (K), *4361* j 7,000 ft. (K), *8024* ♀ (K), *Nicholson SAN 17826* ♀ 9,000 ft. (BRI, L), *Meijer SAN 21097* s 5,500 ft. (K), *SAN 21098* j, 5,000 ft. (K), *SAN 23500* s 6,000 ft. (K), *Colenette 543* s 8,000 ft. (K). Pinosok Plateau, *Colenette 542* ♀ 5,100 ft. (K).

ILLUSTRATION. CORNER, E. J. H. Gard. Bull. Straits Settlements **10**: *t. 9.* 1939, as *Dacrydium beccarii* var. *kinabaluense*.

This is one of the many distinctive endemics of Mt. Kinabalu and, like many, is characteristically robust in form. The pollen cone is unique. With the discovery of fertile *Dacrydium xanthandrum* specimens well up on Mt. Kinabalu, many of the "juvenile" specimens may actually be that species.

15. **Dacrydium guillauminii** Buchholz, Bull. Mus. Hist. Nat. Paris II. **21**: 282. 1949. Type: *Buchholz 1728*,[5] New Caledonia, Rivière des Lacs.

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[5] In the description of this species the collection number given is *1278*, clearly a typographical error.

Erect bush 1–2 m. high; bark with small dark rough flakes, fibrous brown within, surface more or less smooth at first and covered with numerous small lenticels, developing many small cracks with age; profusely branched; leaves becoming denser and less spreading with age but not at all reduced in size, acute, needle-like or slightly compressed, bushy imbricate, 13–17 mm. long, 1.0 mm. wide; pollen cones terminal and lateral, the lateral ones at the base of a terminal cone and smaller, 8–14 mm. long, tapering from the base; microsporophylls with a long lanceolate tip from 5 mm. at the base of the pollen cone to not more than 2 mm. long near the apex; seed cones terminal, sometimes on very short lateral branches; bracts of the seed cone unmodified or slightly reduced leaves; seeds up to five in a cone, subterminal, oval, wider than thick, laterally keeled, the tip rounded with the micropyle projecting, 4.5 mm. long.

Distribution. Probably the most restricted species of the genus, found only for a few kilometers along the Madelaine River (Rivière des Lacs) and on the margins of Lac en Huit, from which that river flows, and only at the very edge of the water.

New Caledonia. Rivière des Lacs, *Buchholz 1728* ♂ (ILL-holotype; K, P-isotypes), *de Laubenfels P341* ♀ (A, RSA), *P341A* ♂ (A, RSA), *Bernier 323* j (P), *s.n.* ♂ (P), *Sarlin 242* s (P), *Däniker 205* p.p. (Z), *Baumann-Bodenheim & Guillaumin 11798* s (P, Z), *Hürlimann 3471* s 146 m. (Z), *Bernardi 9360* s (P, Z), *Blanchon 1162* s (P). Lac en Huit, *de Laubenfels P116A* ♂ (SBT), *P116B* ♀ (K, SBT), *McKee 3385* ♂ (A, K, P, US).

Illustration. Sarlin, P. Bois et Forêts de la Nouvelle-Calédonie, *t. 21.* 1954.

This distinctive bush, a component of the serpentine maquis, bears strong resemblances to *Dacrydium beccarii* and probably represents an endemic pedomorphic variant of that species.

16. **Dacrydium comosum** Corner, Gard. Bull. Straits Settlements 10: 244. 1939. Type: *Corner 33222*, Malaya, Pine Tree Hill.

Tree 4–12 m. high; profusely branched with an umbrella-shaped crown; bark in small flakes; foliage branches bushy, densely leafy; leaves spreading at an angle and then incurved near the base, lanceolate-pungent, distinctly flattened, 12–20 m. long and 0.7–1.3 mm. wide; juvenile leaves up to 33 mm. long; pollen cones unknown; seed cone on a short lateral branch, often with two seeds; seeds 4–5 mm. long.

Distribution. Mossy forest on exposed ridges, from 1,200 to 2,000 meters elevation in parts of Malaya, common locally but of restricted range.

Malaya. Pahang. Pine Tree Hill, *Corner SFN 33222* s 1,500 m. (K-isotype), *Burkill & Holttum 8536* s (A, K), *Melville & Landon 4814* s (K). G. Tahan, *Haniff & Nur SFN 8307* s 1,500–2,000 m. (A, K).

ILLUSTRATION. CORNER, E. J. H. Gard. Bull. Straits Settlements **10:** *t. 10.* 1939.

Like *Dacrydium guillauminii*, *D. comosum* is apparently a pedomorphic variant of some other species, perhaps *D. xanthandrum*. The distinctly flattened and much longer leaves set it apart from *D. beccarii* which grows in the same area. The relationships between the flattened but falcate-leaved *Dacrydium* species (*xanthandrum*, *comosum*, *gibbsiae*, *spathoides*, and *lycopodioides*) are unclear. They may be a group with a common origin or each may have developed separately from other stock. It is worth noting that, where known, their juvenile leaves at intermediate stages have an unflattened form. Thus the flattening, for some at least, does not represent a continuation of the seedling flattened-leaf condition. This is in distinct contrast to the flat and not falcately incurved leaves in other genera of the family.

Falcatifolium de Laubenfels, gen. nov. Type species: *Falcatifolium falciforme* (Parlatore) de Laubenfels.

Frutex vel arbor; folia patentia, falcata, bilateraliter complanata. Ad basem ramorum foliosorum et ramulorum fertilium squamae numerosae, tenues carinatae. Strobili masculi axillares vel terminales in ramulis brevissimis. Strobili feminei in ramulis brevissimis, axillares; squamula ultima sola ovulifera; ovulum unicam inversum, epimatio involutum; semen tandem suberectum, epimatio cristato basi breviter involucrato, crista lateraliter prominens; strobili maturi carnosi.

This new genus was previously included as a part of *Dacrydium*, identified as group A by Florin (1931, pp. 256–259) because of its differences from other members of that genus. Tengnér (1965) also discussed the distinctions between Florin's group A and the rest of *Dacrydium*. Several basic differences justify the separation of *Falcatifolium* as a new genus. The fertile structures in *Falcatifolium* are produced on specialized axillary shoots whereas in *Dacrydium* they grow terminally on ordinary foliage branches. The epimatium of the new genus has a pronounced hump which projects laterally from the mature cone, in contrast with the smaller epimatium of *Dacrydium* which becomes a cup-like fringe at the base of the mature seed, not projecting at all. Very striking in *Falcatifolium* are the bilaterally flattened leaves which spread out distichously, contrasting not only with the fertile shoots and basal scales of new growth, but also with the bifacially flattened juvenile leaves which give way rapidly to the adult form at about the second year of growth. In *Dacrydium* bilaterally flattened leaves do not occur. The name *Falcatifolium* reflects the basal falcate curvature of the leaves away from the branch. Tengnér (1965) further reports a lack of vascular fibers and pollen differences which separate this new genus from *Dacrydium*. Four species can be differentiated, primarily on the basis of leaf form, distributed from Malaya to New Caledonia in moist mountain forests, where they occur as undershrubs or small understory trees.

KEY TO THE SPECIES OF FALCATIFOLIUM

1\. Leaves broad and flat.
  2\. Leaves blunt to acute, normally more than 20 mm. long and 3 mm. wide.
    3\. Pollen cone 20–30 mm. long by 2–3 mm. in diam.; upper edge of the leaf normally curved upwards, leaf variable in size and generally more than 25 mm. long. .... 17. *F. falciforme.*
    3\. Pollen cone 15–25 mm. long by 1.5–2.0 mm. in diam.; upper edge of leaf rarely even slightly curved upwards, leaf rarely as much as 25 mm. long. .... 18. *F. taxoides.*
  2\. Leaves apiculate, 12–17 mm. long by 2–3.5 mm. wide. .. 19. *F. papuanum.*
1\. Leaves narrow, keeled. .... 20. *F. angustum.*

17. **Falcatifolium falciforme** (Parlatore) de Laubenfels, comb. nov.

Podocarpus falciformis Parlatore in DC. Prodr. **16**(2): 685. 1868. Lectotype: *Beccari 2437*, Sarawak, Mt. Poe.
Nageia falciformis (Parl.) Kuntze, Rev. Gen. Pl. 800. 1891.
Dacrydium falciforme (Parl.) Pilger, Pflanzenreich IV. **5** (Heft 18): 45. 1903.

Tree 3–10 (rarely to 25) m. tall; bark more or less smooth, rich purple-brown, inner bark dark reddish; leaves variable in size, on mature fruiting trees from 20 to 65 mm. long and 5–7 mm. wide, smoothly curved outward from near the base to the widest part (about one third of the length from the base), then tapering and curving more or less gradually towards the acute tip, smaller leaves which may be almost straight and probably not fully developed, sporadically occurring along with normal leaves, narrowed at the base to a short, angled petiole and then decurrent; pollen cone axial or terminal on a short, 2–3 mm., scaly stalk, cylindrical, 20–30 mm. long and 2–3 mm. in diam.; microsporophyll small, triangular-acute; seed cone on a short scaly shoot up to 5 mm. long, the cone made up of about a dozen larger, acuminate scales, the apical one fertile, the whole cone becoming fleshy on maturity; seed with a humped epimatium at the base, oval, flattened and narrowed to a blunt apical ridge, 6 mm. long, 5 mm. wide, and 4 mm. thick.

DISTRIBUTION. Mostly an understory tree in open rainforests from 600 to 1,650 meters in elevation, from Malaya and Luzon to Obi in the Moluccas. MAP 6.

Malaya. Mengkuang, *Wyatt-Smith 93115* ♂ 5,000 ft. (K, L, US). Batu Gajah, Perak, *Ridley 5695* ♂ (K). G. Tahan, *Haniff & Nur SFN 7851* ♂ (K), *Ridley 16026* ♂ (K), *16178* s (K). Pine Tree Hill, Penang, *Poore 6228* s 4,300 ft. (K). Fraser Hill, *Nur 10507* s 4,000 ft. (A). **Lingga Archipelago.** *Teysmann 169* ♀ (L), *Hullett 5695* ♂ (A, BM). **Sarawak.** Santubong top, *Beccari 2126* ♂ (F), *Haviland* (1890) ♂ 2,800 ft. (K). Mt. Dulit, *Richards 1834* ♂ 900 m. (A, BM, K, L), *1836* j (BM, K). Mt. Poe, *Beccari 2437* ♀ (FI-lectotype; A, K-isotypes), *Clemens 20238* s 6,000 ft. (NY), *20263* s 5,000 ft. (A, NY). Mt. Mattang, *Beccari 1331* s (FI), *1697* s (FI), *2941* ♀ (FI), *Koley 11669* s (K). Trusan, *Brunig S8743* s (K, L). Meruong Plateau, *Brunig S9994* s 800 m. (L). Without loc. *Anderson 8365* ♂ 2,000 ft. (K, L), *Gibbs 4400* s 3,000 ft. (BM, K). **Brunei.** *Ash-*

ton BRUN 1031 s 4,300 ft. (K, L), *1066* s 4,750 ft. (K, L). **North Borneo.** Kinabalu, *Clemens 10962* s (A, K), *27851* j 7,000 ft. (BM, K, NY), *33078* ♂ 5,000 ft. (A, K, L, NY), *s.n.* s 4–5,000 ft. (A, L, NY), *Gibbs 4067* s (K), *Chew & Corner 1863* ♂ 5,500 ft. (K), *4847* s 5,000 ft. (K). Lahad Datu Dist. (Mt. Silam), *Wood SAN A4179* s 2,500 ft. (A, BRI, L), *Meijer & Anak SAN 37497* ♂ 2,000 ft. (K, L), *SAN 22705* s (K). Penampang, *Clemente 5995* s (K), *Leaño-Castro 5986* s (K). Ranau, *Meijer SAN 20953* s (K), *Anon. SAN 20279* j 4,000–4,500 ft. (L). **Borneo.** Bengkajang, *NIFS bb9664* s 1,400 m. (L), *bb24778* s 1,200 m. (A, L), *bb25157* s 1,100 m. (L). G. Damus, *Hallier 506* s (L). Mt. Palimasan, *Kostermans 12779* s 500 m. (L). Lianggagang, *Hallier 2688* s (L). **Philippines.** MINDANAO: Davao, *De La Cruz 27746* j (US). MINDORO: Mt. Halcon, *Merritt 4425* ♀ (F, US), *Merrill 5744* s (K, L, NY, US), *Rabor 20482* s 1,600 m. (L). Without loc. *Whitehead* (1896) s, j (BM). LUZON: Mt. Umingan, Nueva Ecija, *Ramos & Edaño 26394* ♂ (A, NY, US). Mt. Camatis, Tayabas, *Edaño 4508* ♀ (A). **Celebes.** Manado, *Eyma 3671* j (L), *NIFS bb17544* s 1,400 m. (A, L), *bb21294* ♀ 1,200 m. (L), *bb24778* s (A). **Obi.** *de Haan bb23815* j 700 m. (L).

ILLUSTRATIONS. PILGER, R. Pflanzenreich IV. **5** (Heft 18): *fig. 4 D-G.* 1903; Nat. Pflanzenfam. ed. **13**: *fig. 227 D-G.* 1926; GIBBS, L. S. Jour. Linn. Soc. Bot. **42**: *t. 8.* 1914, all as *Dacrydium falciforme.*

Shape of pollen cone and mature leaf size and shape distinguish *Falcatifolium falciforme* from other species in the genus. In contrast, *F. taxoides* has a more slender pollen cone and mature foliage leaves with only sporadically the slightest upward curve of the upper leaf margin, while in *F. falciforme* such a curve is normally pronounced and only sporadically absent. The mature leaf size of *F. papuanum* is completely below the great size range of *F. falciforme,* differing also in a straight profile and apiculate tip. The larger, probably deep-shade-grown leaves of *F. falciforme* with the sweeping curve of their upper part are attractive and quite unique, paralleled only in *F. angustum* whose leaves are quite narrow.

18. **Falcatifolium taxoides** (Brongn. & Gris) de Laubenfels, comb. nov.

Dacrydium taxoides Brongn. & Gris, Ann. Sci. Nat. Paris V. **6**: 245. 1866. Lectotype: *Vieillard 1259* p.p. New Caledonia, Balade.

Podocarpus taxodioides Carrière, Traité Conif. **2**: 657. 1867. Type: *Vieillard 1259* p.p. New Caledonia, Wagap.

Podocarpus taxodioides var. *gracilis* Carrière, *ibid.* 658. Type: *Vieillard 1259* p.p. New Caledonia, Balade.

Nageia taxoides (Brongn. & Gris) Kuntze, Rev. Gen. Pl. 800. 1891; as *N. taxodes.*

Bush or small tree from 2 to perhaps 15 m. high, bark thin, more or less smooth, scattered with lenticels, light reddish brown and fibrous within, occasionally breaking off a flake; loosely branched; juvenile leaves bifacially flattened, long ovate, almost linear, tapering to a sharp tip, keeled on the lower surface, 15–20 mm. long and 1.5 mm. wide; mature foliage leaves somewhat variable, smoothly curved outward at the base and expanding to the greatest width at about one third their length, then tapering slightly toward the rounded or acute apex, sometimes almost linear, the tip usually straight and pointing directly outward or occasionally bent slightly towards the branch apex without a corresponding bend in the upper leaf edge (or rarely a slight curve), more or less narrowed at the base to a petiole and then decurrent; pollen cone axillary or terminal, often with several on a short axillary branch with minute scales, cylindrical, 15–25 mm. long and 1.5–2.0 mm. in diam.; microsporophyll with a minute acuminate tip; seed cone on a slender scaly branch up to 6 mm. long, the cone with about a dozen larger elongated scales up to 2 mm. long, the apical one fertile, the whole cone becoming fleshy on maturity; seed with a humped epimatium at the base, oval, strongly keeled on the sides with an elongated blunt tip, 7 mm. long, 4 mm. wide, and 3 mm. thick.

DISTRIBUTION. In moist rainforests (but not mossy forests) as an understory shrub or small tree throughout New Caledonia wherever these conditions occur, which is most commonly in the 800 to 1,200 meter range but occasionally reaching almost to sea level and to at least 1,400 meters.

New Caledonia. Balade, *Vieillard 1259* p.p. s (P-lectotype of *Dacrydium taxoides* and holotype of *Podocarpus taxodioides* var. *gracilis*). Ignambi, *Compton 1571* ♀ 3,500 ft. (BM). Upper Diahot, *Hürlimann 1887* ♂ (P, Z). Mt. Colnett, *Hürlimann 1965* ♂ (P, Z). Tao, *Baumann-Bodenheim 15881* s (P, Z). Wagap, *Vieillard 1259* p.p. s (P-holotype of *Podocarpus taxodioides*; A, BM, GH, ILL, K, NY, Z-isotypes). Mt. Paéoua, *McKee 17038* ♀ 900–1,100 m. (P), *17061* s (P). Mt. Boulinda, *McKee 17359* ♂ 1,150–1,300 m. (P). Haute Boulari, *Virot s.n.* s (A, P). Mt. Do, *McKee 15968* ♀ 900–1,000 m. (P). Mt. Humboldt, Baumann-Bodenheim *15372* s 1,400 m. (P, Z). Mt. Mou, *Virot 39* s (P), *469* s (A, P), *Franc 610* ♂ (A, P), *2090* s (A, NY), *2091* s (A, NY), *Pitard 2090* s (A), *Buchholz 1084* ♂ (ILL, K, P), *1447* ♂ (ILL), *1585* s (ILL, K, P), *1586* ♂ (ILL, K, P), *1786* s (ILL, K, P), *1787* s (ILL, K), *de Laubenfels P131* ♂ (SBT), *P352* ♀ 1,140 m. (A, RSA), *P353* ♂ (A, RSA), *P354* ♂ (A, RSA, SBT), *McKee 3541* ♂ (A, P), *Thorne 28705* s (P), *Baumann-Bodenheim 5654A* s (P, Z), *15680* ♂ (P, Z), *Baumann-Bodenheim & Guillaumin 11259* s (P, Z), *11262* s (P, Z), *11286* s (P, Z), *11287* s (P, Z), *11292* s (P, Z), *11296* s (P, Z), *Blanchon 340* s (P). Mt. Dzumac, *Barets 7* s (P), *Blanchon 1247* s 700–900 m. (P). Dumbea, Sunshine Mine, *Hürlimann 1587* s 650 m. (P, Z), *1609* s (P, Z). Mt. Koghis (Mone, Bebo), *Pancher 379* ♂ (BM, K, NY, P), *Thoret s.n.* ♂ (K), *Balansa 185* ♂ (K, P), *Stauffer 5729* s (P, Z), *Baumann-Bodenheim 14848* s 750 m. (Z), *14856* s (Z), *14912* s 900 m. (Z). Mt. des Sources, *Denizot s.n.* ♂ (P), *Bernier 293* ♀ (P), *295* s (P), *296* ♂ (P), *297* s, j (P), *Buchholz 1198* s (ILL, K), *1203* s 800 m. (K, P), *1204* ♂ 800 m. (ILL, K, P), *1205* j 950 m. (ILL, K, P), *1218* ♀, j 750 m. (ILL, K, P), *Hürlimann 265* s 900 m. (P, Z), *920* s (P, Z), *de Laubenfels P366* ♀ (RSA, SBT), *Thorne 28644* s (P), *Blanchon 566* s 300 m. (P). Upper R. Bleue, *Bernier 301* s (P), *Baumann-Bodenheim 15021* ♀ (P, Z), *de Laubenfels P400* ♂ 800 m. (RSA, SBT), *Aubréville & Heine 187* s, j (P), *Bernardi 9404* s (P, Z). Upper Mois de Mai, *Buchholz 1390* s (ILL, P). NE. of Lac Naoué, *Hürlimann 3180* s 500 m. (Z). Bois du Sud, *Baumann-Bodenheim 12492* s (P, Z), *14996* ♀ (P, Z). Upper Kuébini, *Hürlimann 3542* ♀ 265 m. (Z), *3543* s (Z). Without loc., *Balansa 184* ♂ (P), *Deplanche 169* s (P), *Mueller s.n.* s (P), *Sarlin 229* s (P), *Baudouin 387* s (P).

ILLUSTRATIONS. BRONGNIART & GRIS, Nouv. Arch. Mus. Hist. Nat. Paris **4**: *t. 3.* 1868, as *Dacrydium taxoides*; PILGER, R. Pflanzenreich IV. **5** (Heft 18): *fig. 4 H–L.* 1903, as *Dacrydium falciforme*; Nat. Pflanzenfam. ed. 2. **13**: *fig. 227 H–L.* 1926, as *Dacrydium taxoides*; SARLIN, P. Bois et Forêts de la Nouvelle-Calédonie, *t. 19.* 1954, as *Dacrydium taxoides.*

From *Falcatifolium falciforme* this species differs in its smaller leaves and pollen cones and in the straight rather than upwardly curved leaf tips. From *F. papuanum* it differs in lacking a pungent leaf tip and having distinctly larger leaves. These two species and *F. taxoides* are clearly quite closely related, being geographic segregates. *F. taxoides* is sometimes the host to another conifer as a root parasite (de Laubenfels 1959).

19. **Falcatifolium papuanum** de Laubenfels, sp. nov.

Arbusculus vel arbor ad 22 m. altus; folia patentia, ad apex apiculata, linearia vel ovato-linearia, 12–17 mm. longa, 2–3.5 mm. lata. Strobili masculi ignoti; strobili feminei cum ramulis brevissimis, squamis lanceolatis, 1.0–1.5 mm. longis, bracteis strobilorum ca. 2 mm. longis; semen lateraliter et terminaliter carinatum, 6 mm. longum, 4.5 mm. latum, 3.5 mm. crassum. Holotypus: *de Laubenfels P483* (A), New Guinea, Morobe District. FIG. 6a, b.

DISTRIBUTION. In moist rainforests as an understory plant in the eastern part of the island of New Guinea (possibly in the Vogelkop), from 2,000 to 2,400 meters in elevation. MAP 6.

New Guinea. VOGELKOP: Mt. Nettoti, *Van Royen & Sleumer 8203a* j 1,920 m. (L). TERR. NEW GUINEA: Al R. Mts., *Womersley NGF 5354* s 7,000 ft. (A, BRI, K, L). Mt. Hagan Sta., *Hoogland & Pullen 5891* ♀, j 7,600 ft. (A, BRI, L). Mt. Kum, *Womersley NGF 9419* s 7,000 ft. (BRI, K, L). Nondugl, *Womersley NGF 4483* s 7,000 ft. (A, K, L). Morobe Dist., Edie Creek (Mt. Kaindi), *de Laubenfels P483* ♀ 6,500 ft. (A-holotype; K, RSA, SBT-isotypes), *Brass 29127* s, 7,200 ft. (L), *Womersley NGF 11038* s 6,700 ft. (BRI, K, L), *NGF 13922* ♀ 7,200 ft. (K, L). PAPUA: Mt. Tafa, Cent. Div., *Brass 5107* s 8,000 ft. (BRI, NY). Ridge betw. Adai and Turui Rivers, *Lane-Poole 397* s (A, K).

The apiculate and somewhat small leaves, whose mature size is completely below the considerable range of both *Falcatifolium falciforme* and *F. taxoides*, distinguish this new species. The leaf profile is straight as in *F. taxoides*, but without the rounded tip of that species. The juvenile leaves reach 22 mm. in length and 4 mm. in width. The bark, gray to dark brown, and flaky with large lenticels, and a red-brown inner bark, is not unusual. A remarkable specimen from the Vogelkop, an entire small plant of *Falcatifolium*, has distinctly smaller leaves, 6–10 by 2 mm. (FIG. 6b). Inasmuch as juvenile leaves are usually distinctly larger than those of the adult, it may be that this isolated specimen represents a distinct entity.

20. **Falcatifolium angustum** de Laubenfels, sp. nov.

FIGURE 6. a, *Falcatifolium papuanum* de Laubenfels, portion of the holotype, *de Laubenfels P483* (A), slightly enlarged; b [inset], *the same*, fragment of *Van Royen & Sleumer 8203a* from the Vogelkop, New Guinea (L), enlarged.

Arbor ad 20 m. alta; folia plantarum iuvenilis acicularia, crassiora quam lata, lanceolata, falcata, patentia, e basi curvata extrinsecus, ad apici curvata sursum, ca. 7 cm. longa, basem versum 1.2 mm. crassa; folia plantarum adultarum minus curvata vel quasi recta, pungentia, carinata

FIGURE 7. a, *Falcatifolium angustum* de Laubenfels, portion of the holotype, *Brunig S8866* (L); b, *Dacrycarpus expansus* de Laubenfels, portion of the holotype, *Hoogland & Schodde 7463* (L); a and b, approximately natural size.

a latere, 18–35 mm. longa, 1–2.5 mm. crassa; strobili masculi terminales vel laterales, immaturi ovati, 8 mm. longi, 2 mm. diametro; strobili feminei ignoti. Holotypus: *Brunig S8866* (L), Sarawak, Bintulu. FIG. 7a.

DISTRIBUTION. At low elevation along the coast of Sarawak.

Sarawak. Bintulu, *Brunig S8860* ♂ 300 ft. (L), *S8866* ♂ 400 ft. (L-holotype), *S963* j 500 ft. (K, L). Kuching, *Anderson 12448* s 800 ft. (K).

This distinct new species with its narrow but nevertheless bilaterally flattened leaves is intermediate between the other species of *Falcatifolium* and *Dacrydium*, and seems to represent an early stage of the development of the genus. In the transition between seedling leaves and normal foliage leaves of *F. taxoides* are found leaves of identical morphology to the adult leaves here. The bark is purplish-brown, irregularly flaky to scaly, weathering gray.

[*To be continued*]

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A REVISION OF THE MALESIAN AND PACIFIC RAINFOREST CONIFERS, I. PODOCARPACEAE, IN PART *

DAVID J. DE LAUBENFELS

Dacrycarpus (Endlicher) de Laubenfels, stat. nov.

Podocarpus sect. *Dacrycarpus* Endlicher, Syn. Conif. 221. 1847. Type species: *Podocarpus imbricatus* Blume [*Dacrycarpus imbricatus* (Blume) de Laubenfels].

Podocarpus sect. *Dacrydioideae* Bennett ex Horsfield, Pl. jav. rar. 41. 1838. Type species: *Podocarpus dacrydioides* Rich. [*Dacrycarpus dacrydioides* (Rich.) de Laubenfels].

Folia parva vel squamata. Strobili feminei terminales; receptaculum verruculosum, tandem carnosum; unus vel duo bracteae terminalae fertiles, cum ovulo connatum in forma crista superans; ovulum inversum epimatium contingens.

The distinguishing character of *Dacrycarpus* is the union of the bract with the seed and seed scale on one side, forming a projecting crest particularly noticeable on immature fruit. As in most of the family, the seed is inverse and *Dacrycarpus* resembles *Podocarpus*, of which it has long been treated as a section, because of the union of the fertile scale with the seed and its distinct receptacle. In addition to the fusion of the fertile bract with the corresponding scale and seed, however, is the fact that the cone is produced terminally on leafy branches and not on specialized shoots or peduncles. The leaves of *Dacrycarpus* also differ markedly from *Podocarpus* and resemble those of *Dacrydium*, being sometimes difficult to distinguish in the sterile form. There are, in addition, New Zealand species of *Dacrydium* in which the seed is covered by the scale and remains inverted. A fleshy development upon maturity of the structure below the seed is normal in *Dacrydium*. In short, *Dacrycarpus* is as closely related to *Dacrydium* as to *Podocarpus* while the union of the bract with the seed sets it sharply apart from either of them. The wartyness of the receptacle is unusual, a character shared only with *Acmopyle*. In the juvenile form *Dacrycarpus* is interesting in that

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* Continued from volume 50, p. 314

the leaves are distinctly bilaterally flattened, often spread out distichously, yet this character is usually lost in the mature form. Elsewhere among the conifers only in *Falcatifolium* and *Acmopyle* are bilaterally flattened leaves found but without change in the adult form. Where the foliage leaves are bilaterally flattened or acicular, sterile specimens of *Dacrycarpus* can be identified by the sharply dimorphic leaves because the penultimate branches always have bifacially flattened leaves or scales.

Dacrycarpus is composed of nine species ranging from Burma to New Zealand. Some of the species are geographically isolated and the one species in New Zealand (*D. dacrydioides*) is not tropical in habitat. The various species are distinguished primarily by the shape of the involucral leaves subtending the receptacle and the shape of the foliage leaves. Most discussion of specific differences in the morphology of the seed-complex simply involves degrees of maturity. Among the various species there are several wide ranging groups. A more or less scale-leaved type involves *D. dacrydioides* and *D. imbricatus* and is the most important for lumber and afforestation. Longer acicular leaves and a relation to moist habitats characterize *D. steupii* and *D. vieillardii*. Long involucral leaves and a mid-mountain distribution are characteristic of *D. cumingii* and *D. cinctus*. The remainder of the species are mostly localized and are found at high elevations.

KEY TO THE SPECIES OF DACRYCARPUS

1. Involucral leaves spreading and not enclosing the seed and receptacle at all; mature leaves not distinctly flattened.
    2. Leaves short to scale-like (less than 2 mm.).
        3. Pollen cones terminal, linear; involucral leaves very short, not longer than the foliage leaves. . . . . (*D. dacrydioides*).
        3. Pollen cones lateral, ovoid; involucral leaves about as long as the receptacle and longer than the foliage leaves.
            4. Leaves slender (0.4–0.6 mm. wide).
                5. Leaves imbricate. . . . . 21a. *D. imbricatus* var. *imbricatus*.
                5. Leaves spreading. . . . . 21b. *D. imbricatus* var. *patulus*.
            4. Leaves robust (0.6–1.0 mm. wide).
                6. Leaves spreading. . . . . 21c. *D. imbricatus* var. *robustus*.
                6. Leaves imbricate. . . . . 21d. *D. imbricatus* var. *curvulus*.
    2. Leaves elongate (at least 2 mm.).
        7. Involucral leaves less than 2 mm. (shorter than the foliage leaves); foliage leaves strongly variable and more or less imbricate. . . . . 22. *D. vieillardii*.
        7. Involucral leaves more than 3 mm. (longer than the foliage leaves); foliage leaves more constant and strongly spreading. . . . . 23. *D. steupii*.
1. Involucral leaves clasping the seed and receptacle; mature foliage leaves flattened.
    8. Leaves bilaterally flattened.
        9. Involucral leaves long (7–10 mm.), surpassing the mature seed; foliage leaves slender. . . . . 24. *D. cumingii*.

9. Involucral leaves short (5–7 mm.), not covering mature seed; foliage leaves robust. .... 25. *D. kinabaluensis.*
8. Leaves bifacially flattened.
    10. Involucral leaves long (5–6 mm.); foliage leaves long and narrow (2–5 mm. by 0.4–0.6 mm.). .... 26. *D. cinctus.*
    10. Involucral leaves less than 5 mm. long; foliage leaves short and wide (2–4 mm. by 0.6–1.0 mm.).
        11. Pollen cone lateral; seed not large (5–6 mm. long); foliage leaves spreading. .... 27. *D. expansus.*
        11. Pollen cone terminal; seed large (7–8 mm. long); foliage leaves imbricate. .... 28. *D. compactus.*

21. **Dacrycarpus imbricatus** (Blume) de Laubenfels, comb. nov.

Podocarpus imbricata Blume, Enum. Pl. Javae **1:** 89. 1827. Lectotype: *Blume s.n.*, W. Java.

Podocarpus cupressina R. Br. ex Mirb. Mém. Mus. Hist. Nat. Paris **13:** 75. 1825 (*nomen*); R. Br. ex Horsfield, Pl. Jav. Rar. **1:** 35. *t. 10.* 1838. Type: *Horsfield s.n.*, Java.

Podocarpus horsfieldii Wallich, Cat. No. *6049.* 1832. *Nomen nudum.*

Nageia cupressina (R. Br.) Muell. Phyt. New Hebr. 20. 1874.

Tree up to at least 30 m. tall; bark dark brown or blackish on the surface, weathering gray, inside a rich red-brown and granular (slightly fibrous), breaking off in small thick scales with a rough surface; juvenile leaves bilaterally flattened and distichous, nearly linear, curving outward from the base and upward at the tip, narrowing rapidly to a fine mucro, 10–17 mm. long and 1.2–2.2 mm. wide, shorter toward the branch tip and base, the first leaves at the branch base short and acicular, the whole foliage branch of limited growth; leaves on seedlings and on penultimate branches quite distinct, bifacially flattened, lanceolate, mucronate, imbricate, decurrent, 2–4 mm. long and 0.7–1.0 mm. wide; terminal shoots on young plants sometimes very long, whip-like, up to 20 cm.; on older plants more compact, the foliage leaves becoming progressively smaller, fertile specimens sometimes having distichous and bilaterally flattened leaves 3–5 mm. long and 0.6–0.8 mm. wide; foliage leaves in older trees eventually becoming short and needle-like or more or less scale-like, about 1–1.8 mm. long, strongly keeled and acute but neither flattened nor distichous; pollen cones lateral or rarely terminal, subtended by a few scale leaves on a branchlet 1–3 mm. long, oval but elongating with the shedding of pollen, to 6–12 mm. long and 2–2.5 mm. in diam. (about 5 mm. long before elongating); microsporophyll triangular, acute to apiculate; seed cone terminal, often on a short lateral branch bearing scales which become elongated just below the receptacle, forming an involucre, the involucral leaves spreading and generally less than 4 mm. long, acicular and sharply pointed; seed cone a short, warty, glaucous receptacle 3–4 mm. long, formed of enlarged bract bases, the tips of one or two bracts (resembling the involucral leaves) projecting from the receptacle, one or two terminal bracts fertile, the whole receptacle becoming red upon maturity; mature seed globose, slightly ribbed on the back with a blunt crest, 4–6 mm. in diam., 5–6 mm. long.

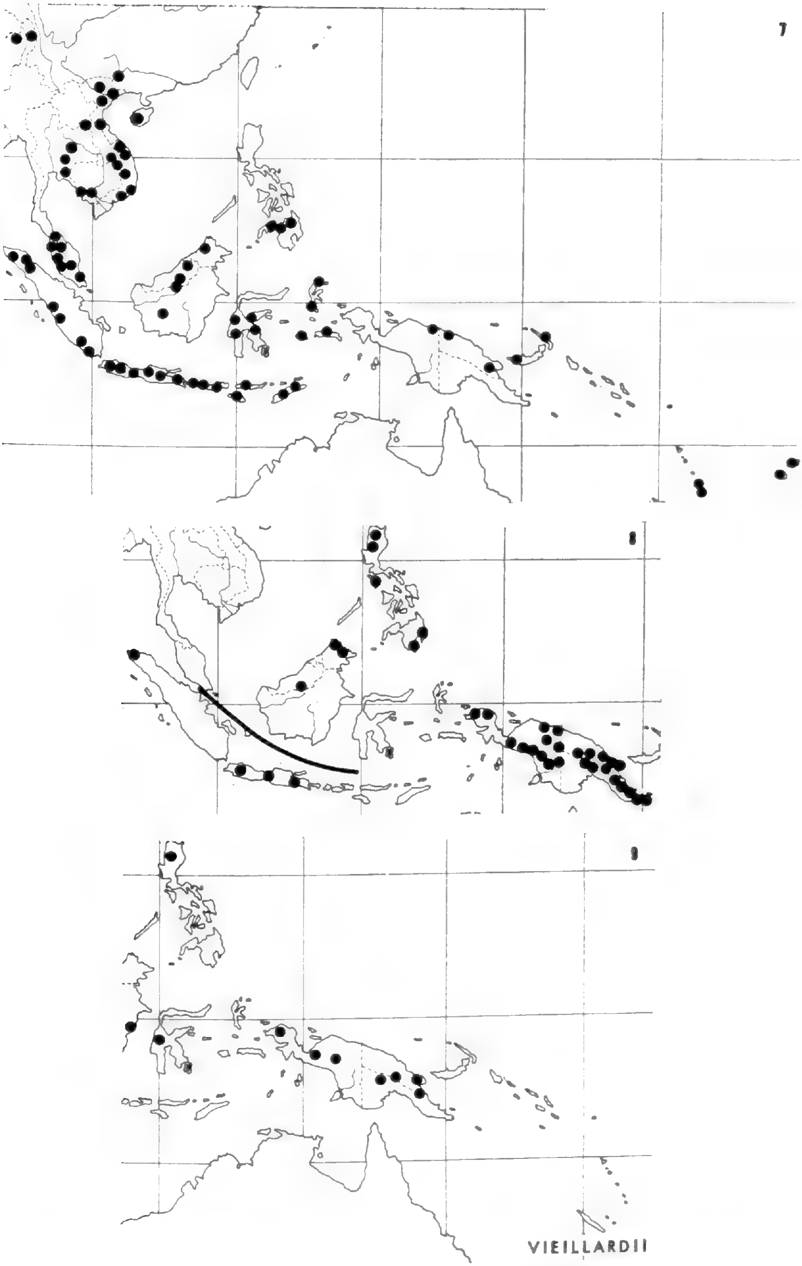
The short acicular or scale leaves and the lateral more or less oval pollen cone distinguish this widespread species from other members of the genus. Longer leaves occur on fertile specimens but, if present, are less than 5 mm. long and very robust (var. *robustus*) or are distichous. *Dacrycarpus imbricatus* can be subdivided into four varieties on the basis of mature foliage leaf form (FIG. 8). The reproductive structures and immature leaves of the varieties are indistinguishable. When identifying these varieties, care must be taken to compare the leaves of only the ultimate foliage branchlets and not the distinct penultimate scale-covered branches (the penultimate branches of all varieties resemble the foliage branches of var. *imbricatus*).

21a. Var. **imbricatus.**

Mature foliage leaves strongly appressed, slender, about 1.5 mm. long and 0.6 mm. wide, the whole foliage branch 0.75–1.25 mm. in diam.; involucral leaves 2–4 mm. long. FIG. 8a.

DISTRIBUTION. Scattered and common in rainforests from low elevation up to about 3,000 meters, but particularly from 700 to 2,400 meters (agriculture has commonly destroyed the forests at low elevation); in Java and the Lesser Sunda Islands, and occasionally in Celebes and Borneo. MAP 7.

Java. G. Salak, *Koorders 24182* j (L), *Lobb s.n.* s (K). Tjibodas (Preanger), 1,400–1,500 m. *Koorders 1270* s (L), *1273* s (L), *15534* j (L), *25922* ♀ (L), *Koorders & Huven s.n.* s (L), *Burlage s.n.* j 600 m. (L), *Raap 713* ♀ 1,400 m. (L), *768* ♀ (L). G. Gedeh, *De Vriese s.n.* ♀ (L), *Van Steenis 17544* ♀ (L), *Verheul* (1957) ♂ (L), *Kuntze 4702* s 2,000 m. (NY). Dorowati, *Kuntze 5865* s (NY). G. Pangranggo, *Schiffner 1475* ♂ 1,900 m. (L), *Palmer & Bryant 988* j 2,900 m. (US), *Winkler 1866* j 2,400 m. (K). Gegerbintang (Preanger), *Den Berger 549* ♀ 1,100 m. (L). Mt. Tankuban Prau, *Anderson 67* s (K). Upper Lembang, *Junghuhn s.n.* ♀ (L). Bandang, *Junghuhn s.n.* s (L). Takokok (Preanger), 1,150 m. *Koorders 15535* ♀ (A, L), *27704* s (L). G. Besser, *Winckel s.n.* j 1,100 m. (L). Pangentjongan (Preanger), *Koorders 1275* j (L), *14141* ♀ (L). Preanger, *Warburg 11119* j (NY), *Koorders 12608* ♀ (A), *39364* ♂ (A) *39366* ♀ (A). Tjibeber, *Backhuizen 1811* s, j 1,000 m. (L), *1936* j 1,300 m. (L). G. Slamet (Pehalongen), *Brascamp 18* j 1,800 m. (L). G. Malabar, *Reinwardt s.n.* (L). G. Ungaran (Semarang), 1,000–1,350 m. *Koorders 1283* s (L), *1284* j (L), *1285* j (L), *27705* ♀ (K, L). G. Kukusan (Lawu), *Elbert 52* j 1,500–1,700 m. (L). Ngebel (Madiun), 1,450 m. *Koorders 1278* s (L), *1279* j (L), *1280* ♀ (L), *1281* s, j (L), *1282* j (L), *29188* j (L), *29189* ♀ (A), *38626* j (L), *38652* j (L). G. Ardjuno (Pasuruan), *Koorders 38187* ♀ 2,100–2,400 m. (L). Ngadasari, *Koorders 37922* s (L), *37923* j (K, L). Ngadiwono, *La Rinere s.n.* s 1,600 m. (L). Idjen Plateau (Besuki), 1,700 m. *Koorders 1290* j (L), *1296* ♀ (L), *1297* j (L). G. Kendeng, *Koorders 28507* ♀ (A). G. Tapandajan, *Coert 637* j 1,750 m. (L). G. Tenga (Parverua), *Dugeh 1382* j 1,600 m. (L). Parverua, *Oillerings 175* s (L). G. Guntar, *Anderson 429* j 4–6,000 ft. (K). E. Java, *Coert 1437* s



MAPS showing distribution of: 7, *Dacrycarpus imbricatus* (Blume) de Laubenfels, var. *imbricatus* and var. *patulus* de Laubenfels; 8, *D. imbricatus* var. *robustus* de Laubenfels (dots north of line), and var. *curvulus* (Miquel) de Laubenfels (dots south of line); 9, *D. steupii* (Wasscher) de Laubenfels (dots), *D. vieillardii* known only from New Caledonia.

(L), *Went s.n.* j (L). Without loc. *Blume 492* ♀ (L), *s.n.* ♀ (L-lectotype of *Podocarpus imbricata*), *Junghuhn s.n.* j (L), *Horsfield s.n.* ♀ (K-holotype of *Podocarpus cupressina*; GH-isotype), *108* s (K), *1166* ♀ (K), *Korthals s.n.* j (L), *van Hasselt s.n.* s, j (L), *Simmoro s.n.* s 3–4,000 ft. (L), *Coert 1209* s (L), *Zollinger 2262* ♀, j (A, Z), *De Vriese s.n.* ♀ (K), *Miquel s.n.* s (K). **Lesser Sunda Is.** BALI: Mt. Batukan, *Kostermans, Kuswata, Sugeng & Supadmo KK & SS 138* ♀ 1,300 m. (A, K, L), *Sarip 371* j 1,930 m. (L). Buleleng, *NIFS bb17269* ♂ 1,300 m. (A, L). LOMBOK: Mt. Rindjani, *Elbert 2266* j 700–1,700 m. (A, L). Lenek (mid.), *NIFS bb15504* ♀ 700 m. (K, L). Plambi (SW.), *Elbert 2428* j 200–400 m. (L). SUMBAWA: Batu-Lanteh Mts. (N.), *Elbert 4191* j 1,500–1,700 m. (A, L, US). FLORES: *Rensch 1307* j (K). G. Kasterso, *Posthumus 3235* j 1,800 m. (L). SUMBA: Lairondja (E.), *Ibut 547* j (L), *NIFS bb9003* j 1,000 m. (K, L). TIMOR: Nenas (mid.), *NIFS bb11803* ♀ 1,600 m. (L). Mt. Perdido (cent. Port.), *Van Steenis 18267* ♂ 1,600–1,750 m. (L). Without loc., *Forbes 3855* ♂ (A, L). **Sarawak.** Kuching, *Clemens s.n.* j (NY). Mt. Dulit, *Richards 1768* j 1,300 m. (K, L). Kapit, Upper Rejang R., *Clemens 21066* j (NY). **Brunei.** B. Ulak, *Ashton BRUN 1032* j 4,300 ft. (K, L). B. Pagon, *Ashton BRUN 1065* ♂ 4,750 ft. (K, L). **North Borneo.** Ranau, *Sadau 42890* ♀ 4,920 ft. (K, L), *Sario SAN 32246* ♂ (K), *Lajangah SAN 33085* j (K). Tambunan, *Mikil SAN 32070* j (K). **Borneo.** Sakumbang, *Korthals s.n.* s, j (L). B. Raja, *Winkler 1035* j 1,700 m. (L). **Celebes.** G. Bantaeng, *Bünnemeyer 11903* s 2,300 m. (K, L), *12019* ♀ 2,060 m. (A, L), *NIFS bb5460* ♀ 2,000 m. (L), *Everett 42* j 7–10,000 ft. (K). Roto (Masamba), *NIFS bb24957* j (L). G. Kambuno (Masamba), *Eyma 1369* j (L). Enrekang (Rantelmo), *NIFS bb29195* j 1,600 m. (A, L). Upper Binuang, *NIFS bb20202* j (A, K, L, NY). Mt. Mambuliling, *DeFroidville 173* j (L). Betw. Angin-Angin and Pintealon (Enrekang), *Eyma 570* j 1,550–2,600 m. (A, K, L).

ILLUSTRATIONS. BENNETT, J. J., Pl. Jav. Rar., *t. 10.* 1838, as *Podocarpus cupressina*; BLUME, K. L., Rumphia **3**: *t. 172 & t. 172B.* 1849, as *Podocarpus cupressina*; PILGER, R., Pflanzenreich IV. **5** (Heft 18): *fig. 7E.* 1903; Nat. Pflanzenfam. ed. *2.* **13**: *t. 124E.* 1926, as *Podocarpus imbricatus*; KOORDERS, S. H., & TH. VALETON, Atlas der Baumarten von Java **3**: *t. 585 & 586.* 1915, as *Podocarpus imbricata*; WASSCHER, J., Blumea **4**: *t. 4, fig. 2.* 1941, as *Podocarpus imbricata.*

The variety *imbricatus* is well known in Java and the Lesser Sunda Islands and is widely cultivated. Because there have been only scattered collections elsewhere, the possibility of artificial introduction must be considered. Juvenile plants can not be identified to variety in this species so they have been assigned to whatever mature form is known in the vicinity. Some rather large juvenile leaves appear in the collections from the Lesser Sunda Islands.

21b. Var. **patulus** de Laubenfels, var. nov.

> *Podocarpus kawaii* Hayata, Bull. Econ. Indochine **20**: 439. 1917. Type: *Hayata* in 1917, Tonkin.

Folia patula, acicularia, falcata, basi carinata, acuta, 0.8–1.5 mm. longa, 0.4–0.6 mm. lata; ramuli foliis inclusis 1–2 mm. diametro; folia involu-

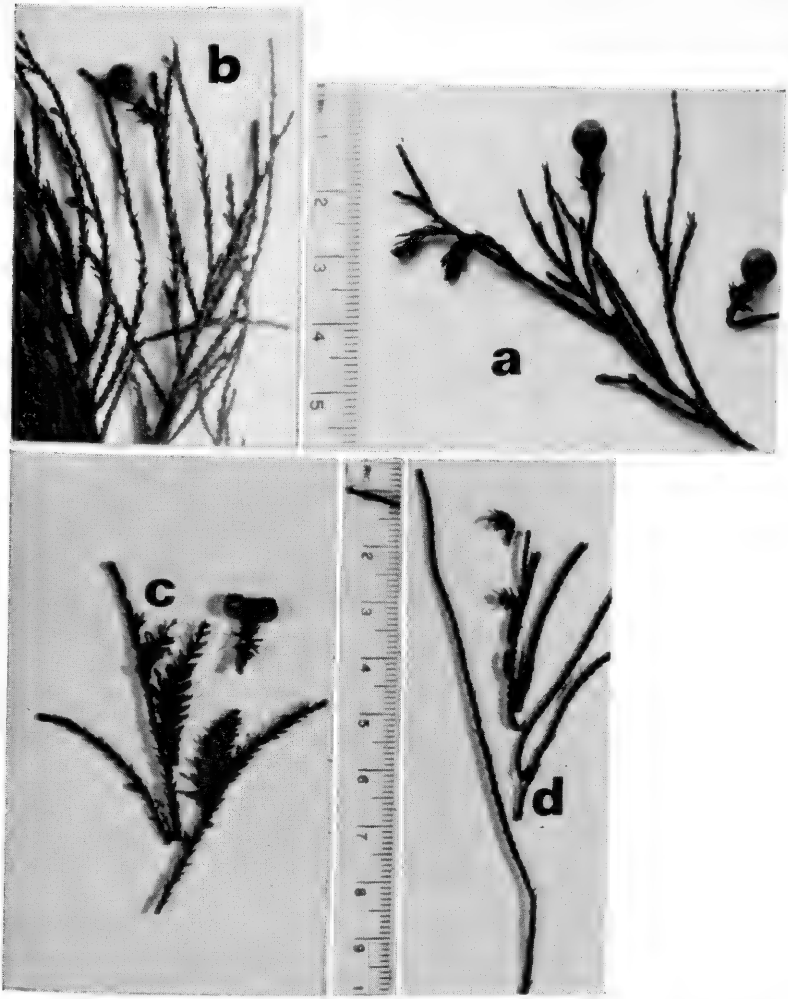


FIGURE 8. a, *Dacrycarpus imbricatus* (Blume) de Laubenfels var. *imbricatus*, fragments showing mature foliage form; b, var. *patulus* de Laubenfels, portion of holotype *de Laubenfels P328* (A); a and b, × 0.9; c, var. *robustus* de Laubenfels, fragments showing mature foliage form; d, var. *curvulus* (Miquel) de Laubenfels, fragments, showing mature foliage form, c and d, × 0.8.

cralia 1–3 mm. longa. Holotypus: *de Laubenfels P328* (A), Fiji Nandarivatu. FIG. 8b.

DISTRIBUTION. Scattered and common in rainforests from low elevation up to 2,500 meters, particularly from 700 to 1,700 meters and lower where moist forests occur; from Upper Burma to Fiji, particularly from South China to Sumatra, otherwise apparently in a more or less discontinuous distribution overlapping with other varieties of the species and in isolated populations east of New Guinea. MAP 7.

Burma. Hukong Valley, *Hole 21* s (K). Serpentine Mines (S. of Hukong Valley), *Griffith 5007* j 1,600–2,600 ft. (GH, K). Tampyu (Kachin), *Thompson* (1896) ♂ (K). Northern Triangle, Arahku, *Kingdon-Ward 20626* j (A, BM), *21295* j (A, BM), *21393* s 4–5,000 ft. (A, BM), *21626* j (A, BM). **Thailand.** Nakhan Rachasima, *Phengkhlai 568* j (K). Pulom Lo, Dan Sai, *Kerr 5788* ♀ 1,000 m. (BM, K). Kao Kuap, *Kerr 17715* s 500 m. (BM, K). Kao Soi Dao, Trang, *Kerr 19435* j 500 m. (K). Botong, Pattani, *Kerr 7648* ♂ 600 m. (K). **Laos.** Betw. Dasia and Cateng, Taravane Prov., *Poilane 16092* ♀ (A). Tram-la, Tranninh Prov., *Poilane 2147* j (A, K, L). Boloven near Attopeu, *Poilane 15922* ♀ (NY). Without loc., *Alleizette* (1932) s (L). **Cambodia.** Kuang Repoe, Opong Prov., *Pierre 5528* p.p. s (in mts.) (A, K). Sckrâl Mts., Samrongtong Prov., *Pierre 5528* p.p. j (A, K, NY). Phnom Penh Forest, *Bejaud 718* ♂ (ILL). Elephant Ra., *Poilane 320* ♀ (A), *23118* ♀ (BM). **Tonkin.** Hayata (1917) j (A-isotype of *Podocarpus kawaii*). **Annam.** QUANG TRI PROV.: Dent de Tigre, *Poilane 10293* ♀ (A, K, L). Bach Ma (N. of Da Nang) *Poilane 29960* ♀ (ILL). Dong-tri Massif, *Poilane 10995* j (A, L). Dong-co-pah Massif, *Poilane 11110* ♀ (A, L, NY). Without loc. *Poilane 13644* ♀ (A, K). SOUTH: Near Dakto, *Poilane 35595* j (ILL). Dalat (Lang Bian Massif), *Evrard 1779* ♀ (A, NY), *238* j (A, NY), *Chevalier 30027* j 1,400 m. (A), *Poilane 4038* j (A). Nonh-hoa (near Nhatrang), *Poilane 6509* ♀ (A, NY). Nhatrang, *Poilane 3387* j (A, K), *9103* j 500–1,500 m. (ILL). Chapu, *Petelot s.n.* ♀ 1,500 m. (NY). Without loc. *Delacour & Low* (1927) ♀ (BM), *Kloss s.n.* s 5,200 ft. (BM), *Vim s.n.* ♀ 1,500 m. (US). **China.** Kwangtung-Tonkin border, *Tsang 27332* j (A, K). Chen Pien Dist, Kwangsi, *Ko 55900* j (A). Tsin Hung Shan, N. Him Yen, *Ching 7034* j 4,000 ft. (A, NY, US). Kwangsi, *Wang 39608* ♀ (A). **Hainan.** Fan Ya (5 Finger Mt.), *Chun & Tso 44250* s 4,000 ft. (A, L, NY), *McClure 8705* ♀ 700–1,000 m. (A, BM). Seven Finger Mts., *Liang 61783* j (A, NY). Dung Ka, *Chun & Tso 43955* ♀, j 2,400 ft. (A, NY). Kan-en Dist., *Lau 3556* j (A). Without loc. *McClure 18304* j 1,000–1,500 m. (NY), *18279* ♀ (NY), *How 72870* ♀ (BM), *Chun 1390* ♀ (A), *Liang 65187* j (A, NY), *65257* j near summit (A, NY, US), *Tang 438* j (A), *Wang 35591* ♀ (NY, US). **Malaya.** Kedah Peak, *Low 28* j (K), *Kochumen 70988* j 3,200 ft. (K, L). Penang, *Curtis s.n.* j (US). Gov't Hill, Penang, *Maingay 2239* s (K). G. Batu Pateh, Perak, *Wray 1198* ♂ (K). G. Benom, Pahang, *Whitmore 3268* ♀ (K); Sungai Telom, *Strugnell 23931* j 2,800 ft. (A); Kluang Terbang, *Barnes 10907* ♀ (K). Selanger, Pahang Track, *Ridley 8636* s 1,500 ft. (A). Fraser Hill, *Deris 22563* ♀ (K). Batang Padang, Selangor, *Murdoch 11964* j (K). B. Etam, Selangor, *Kekall 19814* s (K). Malacca, Mt. Tapah, *Werner* (1912) j (Z). **Sumatra.** G Pagarang, Gajo Luas, *Atmodjo 82* j (L). Dairi Lands, *Dames 57* j 1,550 m. (K, L). Pantjurbatu (NW. of L. Toba), *Lörzing 7117* s 1,400 *m.* (L). NW. side of Toba L., *Bangham 1074* j 4,100–4,500 ft. (A, K, NY), *1127* ♀ (A, K, NY). East Coast, path Talven na Uli to Tomuan Dolok, *Boeea 10697* ♀ (A, K, L). Siosar, *Lörzing 8627* j 1,575 m. (L). Mt. Sibajak, *Lörzing 13509* ♀ 1,000–1,600 m. (L). Karoland, Sigurunggurung, *NIFS bb5443* ♀ 1,500 m. (L). Karoland, Tongkoh, *NIFS bb28147* s (A, K, L). Karoland, *NIFS bb2768* ♀ 1,400 m. (L), *bb7708* ♀ (L). Simelungun, *Yates 2148* j (L, NY), *Esche bb35321* s 1,200 m. (L), *Lörzing 11508* j 400 m. (L); Marehat Huta, *NIFS bb4866* j 700 m. (L). Berastagi, *Yates 1987* j (L). Mt. Singalan, Upper Padang, *Beccari 49* j 2,000 m. (FI, K, L), *Schiffner 1473* j 1,700 m. (L), *1474* s 2,500 m. (L), *Ernst 851* j (Z). Solok, *NIFS bb4130* j 1,000 m. (L). Kerintji Indrapura, *NIFS bb18752* j 1,200 m. (A, L). Siolok Daras (G. Kerintji), *Robinson & Kloss s.n.* s 3,000 ft. (K). G. Tudjuh (G. Kerintji), *Meijer 6584* ♂ 1,500–1,700 m. (L), *7267* j 1,500–2,000 m. (L), *Jacobs 4483* j 2,000–2,200 m. (K, L). Taram, R. Tjampo, *Meijer 6780* j 500–1,000 m. (L). Bengkulen, Redjang, Paja Magelang, *Renwarin bb2436* ♂ (L). Kriu, Waimengaku, *NIFS bb8737* j 950 m. (L). Bengkulen, G. Pesagi, *Rappard P19* j 1,700 m. (A, L). G. Pesagi, Liwa, *De Voogd 119* s 1,800 m. (L), *134* j 1,700 m. (L). Lae Pondom, *Surbeck 532* j 1,600–1,800 m. (L). Leaukavear, *Balten Pooll s.n.* s 1,630 m. (L). Palembang, Seminung, *Rappard S28* s 1,800 m. (A). **Philippines.** MINDANAO: Mt. Katanglad, Bukidnon Prov., *Sulit 9896* ♀ 1,800 m. (A, L). Lanao Prov., *Alvarez 25176* j (A, US). Mt. Malindang, Mizamis Prov., *Mearns & Hutchinson 4666* ♂ (K, L, NY, US). Mt. Batangan, *Warburg 14721* j (NY). **Celebes.** Pamula dama, B. Koroueë (Masamba), *NIFS bb24951* ♀ 2,000 m. (A, L). Ululu (Masamba), *NIFS bb24956* s 1,700 m. (A, L). Palu, Wuka Tampai Mt. (Masamba), *NIFS bb15155* s 2,500 m. (L). Porehu (Malili), *NIFS bb19559* ♂ 1,200 m. (A, L). **Moluccas.** Buru, Fakal, *Toxopeus 485* j 1,100 m. (L). Morotai, *Kostermans 1215* j 1,000 m. (A). Middle Ceram, *Stresemann 158* j 1,000 m. (L), *354* ♂ 1,450 m. (L), *363* j 1,100 m. (L). **New Guinea.** Cycloop Mts., *Karstel BW 5441* ♂ 510 m. (L). Terr. New Guinea, E. Highlands, Osaka, *Womersley NGF 24928* ♀ 4,000 ft. (LAE). **New Britain.** Mt. Tangis, *Frodin NGF 26889* j 3,000–4,500 ft. (L). **New Hebrides.** Erromanga, *Corbasson 18123* j 200 m. (P). Aneityum, *Kajewski 849* ♀ 500 ft. (A, NY, US, Z). **Fiji.** Nandarivatu, *Gibbs 775A & B* s (BM), *Smith 4901* j 800–900 m. (L, US), *6245* ♀ 850–970 m. (A, L, US), *Degener 14315* ♀ (NY, US). *Gillespie 4263* j 900 m. (NY), *Lam 6876* ♂ 850 m. (L), *Vaughn 3258* s (BM), *de Laubenfels P328* ♀ 2,000 ft. (A-holotype of *Dacrycarpus imbricatus* var. *patulus*; K, RSA, SBT-isotypes), *P331* j (A, RSA). Nausori Highlands, *de Laubenfels P306* j 1,900 ft. (A, RSA). Namboutini, *de Laubenfels P310* j 1,000 ft. (A, RSA).

From its distribution, one might guess that *Dacrycarpus imbricatus* variety *patulus* is the primitive representative of the species which has been largely displaced over much of its range by other varieties, but survives alone both on the western and the eastern parts of the range. Specimens from Fiji, when compared with specimens from Sumatra and southeast Asia, can not be distinguished. In the Philippines, Celebes, and New Guinea where overlap with other varieties occurs, specimens are difficult to identify because juvenile and transitional stages are indistinguishable and all too often are all that is collected. In the Philippines forms transitional to var. *robustus* apparently occur, while in Borneo and Celebes the very few mature specimens seem transitional between var. *imbricatus* and var. *patulus*. Several specimens from lower elevations in New Guinea do not have a robust form and have been referred to the var. *patulus*.

21c. Var. **robustus** de Laubenfels, var. nov.

Podocarpus papuanus Ridley, Trans. Linn. Soc. London. II. **9**: 158. 1916. Syntypes: *Kloss* in 1913, New Guinea, Mt. Carstensz and *Giulianetti & English* in 1897,[6] Wharton Range.

Podocarpus leptophylla Wasscher, Blumea **4**: 414. 1941. Type: *De Kock 39*, New Guinea, Mt. Goliath (not seen).

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[6] Ridley refers only to Giulianetti.

Folia brevia, patula, acuta, ad apicem incurvata, fortiter carinata, robusta, 1.2–1.8 mm. longa, 0.6–0.8 mm. lata, ramuli foliis inclusis 1.5–2.5 mm. diametro; folia involucralia 2–3 mm. longa. Holotypus: *Brass 30568* (A), New Guinea, Mt. Wilhelm. FIG. 8c.

DISTRIBUTION. Scattered and common in moist rainforests from near sea level to 3,300 meters, but mostly 1,000 to 2,700 meters from North Borneo and the Philippines to the eastern end of New Guinea. MAP 8.

Sarawak. Mt. Poe, *Beccari 2431* j 3,000 m. (FI), *Clemens 20134* j summit (A, NY). Mt. Mah, *Beccari 2812* ♀ (FI, K). **North Borneo.** Penampang, *Clemente 5981* j 5,000 ft. (A, K, L), *6216* s (K), *Leaño-Castro 5988* j (K, L), *5991* j 3,500 ft. (K, L). Tenompok Pass (Kinabalu), *Smythies S10601* ♀ 4,500 ft. (K, L), *Clemens 28631* ♂ 5,000 ft. (A, ILL, K, L, NY), *29779* j (A, K, L, NY), *Melegrito A471* j 4,700 ft. (K, L). Pentaran Basin (Kinabalu), *Clemens 33618* ♀ 8,000 ft. (A, K, L, NY). Masilan R. (Kinabalu), *Clemens 51635* ♀ 8,000 ft. (A, K, L). Mt. Gedeh (Kinabalu), *Clemens 30371* j 6–9,000 ft. (NY). Kinabalu, *Colenette 579* s 8,000 ft. (K), *Clemens 28954* j 8,000 ft. (BM, K), *Chew & Corner RSNB 4084* j (K). Tiong Pass, *Keith 5930* ♂ 5,500 ft. (K, L), *5967* j 5,300 ft. (K, L). **Philippines.** LUZON: Mt. Santo Thomas (Benguet), *Elmer 6550* ♀ (K, NY, US), *6551* ♀ (K, NY, US), *Williams 1298* ♀ (GH, K, NY, US), *1299* ♀ (NY). Panai (Benguet), *Mearns 4405* ♀ 7,000 ft. (L, US), *Santos 31817* ♀ (A, US), *Gillis 27255* ♀ (A, US), *Sulit 7586* ♂ (BRI). Mt. Osdung (Benguet), *Quisumbing & Sulit 82481* j (NY). Benguet Dist., *Leaño 20673* s (US), *20674* j (US). Lepanto Dist., *Curran 10960* s (US), *Darling 14498* j (L), *Vidal 1818* s (K). Mt. Data (Lepanto), *Alcasid 1847* ♂ (L), *1897* j (L), *Merrill 4503* j (K, NY, US), *4546* j (K, L), *Stern 2242* j 7,050 ft. (ILL), *Stern & Rojo 2289* j 7–8,000 ft. (ILL), *2292* j (ILL). S. of Bontoc, *Walker 7526* j 6,000 ft. (US). Mt. Banahao, *Barthe* (1857) s (A). MINDORO: *Merrit 8529* j (K, NY, US). MINDANAO: Mt. McKinley (Davao), *Kanehira 2652* j (NY), *2726* s (NY). Tupi, Mt. Matutum (Cotabato), *Sumajit* (1966) ♀ 293 ft. (L). **New Guinea.** VOGELKOP: Nettoti Ra., *Versteegh BW 10411* ♂ 1,700 m. (L), *Van Royen & Sleumer 7948A* j 2,100 m. (L). Kebar Valley, *Van Royen 3895* j 1,750 m. (L). Anggi Lakes, *Gibbs 5540* ♀ 7–9,000 ft. (K), *Versteegh BW 250* ♀ 2,000 m. (A, L), *Kostermanns 2197* s 2,000 m. (L), *Stefels BW 2014* j 1,860 m. (L), *BW 2006* j 1,875 m. (L). Arfak Mts., Hatam, *Beccari* (1875) s 5–7,000 ft. (FI). G. Saru, Gmbai, *Stefels BW 2038* s 1,980 m. (L). Sioriep, Ransiki Dist., *Mangold BW 2263* ♂ 1,200 m. (K, L). Arfak Mts., *Kanehira & Hatusima 13933* ♀ (A), *13446* s (A), *Versteegh BW 12610* s 1,750 m. (L). WESTERN HALF: Motito (Wissel L.), *Vink & Schram BW 8731* j 1,800 m. (L). Enarotali (Wissel L.), *Rappard BW 698* j 1,750 m. (A, K, L). Mt. Carstensz, *Kloss* (1913) ♂ (K-syntype of *Podocarpus papuanus*; BM-isotype). Doorman Top, *Lam 2153* j 2,550 m. (L). L. Habbema (Bele R.), *Brass & Versteegh 11148* ♀ 2,350 m. (A, L), *Brass 11347* s 2,300 m. (A, L). Barnhard Camp, *Brass & Versteegh 11980* j 1,480 m. (A, L), *12522* ♀ 1,140 m. (L), *Brass 12990* s 1,200 m. (A, K, L), *13044* ♀ 1,000 m. (A, K, L), *13084* ♂ 900 m. (A, L), *13146* ♀ 950 m. (A, K, L). Mt. Antares (Star Mts.), *Kalkman 4465* ♂ 2,360 m. (L). Sidoarsi Mts., *Iwanggin BW 9059* s 660 m. (L). Hellwig Mts., *Lorentz 1699* s 2,100 m. (K, L). Cycloop Mts., *Versteegh & Koster BW 14* s 750 m. (A, K, L). TERR. NEW GUINEA: 12 miles N. of Wabag, *Womersley NGF 11260* ♀ 7,000 ft. (K, L), *11067* j 7–8,000 ft. (L, NSW). Wabag, *Saunders 1048* j 7,100 ft. (L, LAE). Tambul (Mt. Hagen), *Womersley NGF 14253* j 8,000 ft. (L). Mt. Kum (Mt. Hagen), *Womersley NGF 9430* s 7,000 ft. (A, L, NSW). Wankl (Mt. Hagen), *Hoogland & Pullen 5868* s, j 2,300 m. (A, K, L, US). Mt. Hagen, *Cavanaugh NGF 3322* j (A, K). L. Inim, *Flenley ANU 2176* s 8,300 ft. (K, L). Al R. Mts. (Nondugl), *Womersley NGF 5338* j 7,000 ft. (A, K, L, NSW), *NGF 5353* j (A, K, L). Waimambuno (Chimbu), *Saunders, 823* j 9,000 ft. (A, L). Mt. Wilhelm, *Brass 30568* ♀ 2,650 m. (A-holotype of *Dacrycarpus imbricatus* var. *robustus*; K, L, NY, US-isotypes), *30570* j (K, L, NY, US). Chimbu, *Cavanaugh NGF 3332* j (A, K, L), *Stauffer 5652* j 2,600 m. (K, L, Z). Fatima R., Marafunga-Chimbu Div. (Goroka), *Womersley NGF 24563* s 7,700 ft. (K, L). Marafunga, Upper Asaro Valley (Goroka), *Womersley & Sleumer NGF 14013* ♀ 8,200 ft. (K, L), *Anden JARA 7* s 8,300 ft. (K). Danlo (Goroka), *Saunders 861* j 8,500 ft. (L), *865* (L). Above Goroka, *Womersley & Floyd NGF 6138* ♂ 8,300 ft. (A, K, L). Purosa (Okapa), *Brass 31660* j 1,950 m. (A, L, NY, US), *31852* ♂ (A, K, L, NY, US). Wagau, *Sayers NGF 21613* j 4,500 ft. (L). Samanzing, *Clemens 3323* ♀ 4,600 ft. (A, Z), *5473* j (A), *8848* j (A). Sarawaket, *Clemens 5586* ♀ 7,000 ft. (A). Mt. Rawlinson, *Hoogland & Craven 9553* ♀ 6,000 ft. (K), *9354* j (K), *9355* j (K). Wau, *Womersley & Millar NGF 8324* s 5,500 ft. (A, L, NSW), Mt. Kaindi (Edie Creek), *McVeagh NGF 7581* ♂ 5,850 ft. (A, K, L, NSW), *Womersley & de Laubenfels NGF 19460 (P485)* ♀ 7,500 ft. (A, K, L, RSA, SBT), *de Laubenfels P482* j 6,500 ft. (A, K, RSA, SBT), *Brass 29577* s 2,060 m. (L, US), *29598* s 2,250 m. (A, L, NY, US). *29599* s (A, L, NY, US), *Havel & Nauari NGF 17134* s 7,300 ft. (K, L). Morobe Dist., *Anon. NGF 3128* j (L). PAPUA: Anga Valley near Ebenda (S. Highlands), *Schodde 1561* s 6,500 ft. (K, L). Alola, *Carr 14194* ♀ 6,000 ft. (A, L, NY). Boridi, *Carr 13264* j 4,700 ft. (A, NY). Mt. Mau, *Crutwell 897* j (K). Murray Pass, *Brass 4768* j 2,840 m. (NY). Mt. Scratchley, *Giulianetti* (1896) s 12,200 ft. (K). Wharton Ra., *Giulianetti & English* (1897) ♀ 11,000 ft. (K-syntype of *Podocarpus papuanus*). Mt. Tafa, *Brass 4962* s 2,400 m. (A, NY), *5115* j (NY). Owen Stanley Ra., *Lane-Poole 264* j 5,000 ft. (A). Sibium Ra., *Pullen 5914* j 2,650 ft. (A, L), *5930* ♂ 3,520 ft. (A, K, L). Mt. Dayman (Milne Bay), *Brass 22582* ♀ 2,000 m. (A, K, L), *23393* ♂ 1,700 m. (A, K, L, US).

ILLUSTRATIONS. GIBBS, L. S., Contrib. Phytogeography and Flora of the Arfak Mountains, *t. 4.* 1917, as *Podocarpus papuanus*; WASSCHER, J., Blumea **4**: *t. 4, fig. 3.* 1941, as *Podocarpus papuana.*

There has been a great deal of difficulty in separating this variety, when treated as a species (*Podocarpus papuanus*), from the type (*Podocarpus imbricatus*) (Gibbs, 1917; Wasscher, 1941). When specimens of fully mature forms are placed side by side they are definitely distinct, but the various juvenile and transitional forms so often met with can not be distinguished and have been greatly confused in the herbaria. Inasmuch as the reproductive structures are essentially identical, it seems best to maintain it in varietal status. Certainly where var. *robustus* occurs, other varieties are usually rare or absent. A few mature specimens in the Philippines are more or less intermediate between varieties *robustus* and *patulus*, including *Leaño 20673* and (see var. *patulus*) *Mearns & Hutchinson 4666*. Perhaps these two varieties tend to merge in the Philippines. Certainly typical var. *robustus* specimens have come from Borneo. Variety *robustus* differs most from the typical variety, *imbricatus*. From var. *curvulus* it differs in the same way that var. *patulus* differs from var. *imbricatus*. From var. *patulus* it differs in the same way (except for habit) that var. *curvulus* differs from var. *imbricatus*. The status of *Podocarpus leptophylla* is uncertain as I have not seen the type. From its description it appears to belong to this species but perhaps not to this variety.

21d. Var. **curvulus** (Miquel) de Laubenfels, comb. nov.

Podocarpus cupressina var. *curvula* Miquel, Pl. Junghuhn. **1:** 4. 1851. Lectotype: *Junghuhn s.n.*, Java, Mt. Prahu.
Podocarpus imbricata var. *curvula* (Miquel) Wasscher, Blumea **4:** 398. 1941.

Mature foliage leaves strongly adpressed, robust, ca. 1.2–2.0 mm. long and 0.8–1.0 mm. wide, the whole foliage branch 1–1.25 mm. in diam. and drooping; involucral leaves 2.5–4.5 mm. long, more or less clasping the receptacle. FIG. 8d.

DISTRIBUTION. Generally on mountain ridges, often in solid stands and sometimes dwarfed or procumbent, from 1,350 to 3,300 meters in elevation but mostly above 2,000 meters, from Sumatra and Java. MAP 8.

Sumatra. Atjeh, Gajoland, *Van Steenis 8423* ♀ 2,100–2,250 m. (A, K, L) and ♂ (K, L, NSW). **Java.** Mt. Gedeh (Pengalengan), *Junghuhn s.n.* ♂ 4–7,000 ft. (L-syntype). Dieng Mts., Mt. Prahu, *Junghuhn s.n.* ♂ 5–7,000 ft. (L-lectotype). Kedec, Wonosobo, *Zwart 6517* ♀ (L). Without loc., *Junghuhn s.n.* ♀ (L), ♂ (NY), *4* j (L), *Blume s.n.* ♀ (L).

ILLUSTRATION. WASSCHER, J., Blumea **4:** *t. 4, fig. 2β*. 1941, as *Podocarpus imbricata* var. *curvula*.

The most striking character of var. *curvulus* is its weeping habit, but herbarium specimens can be readily distinguished by their robust branches with adpressed scale leaves.

22. **Dacrycarpus vieillardii** (Parlatore) de Laubenfels, comb. nov.

Podocarpus taxodioides var. *tenuifolia* Carrière, Traité Conif. **2:** 658. 1867. Type: *Vieillard 1260*, New Caledonia, Paita (juvenile form).
Dacrydium elatum Wallich var. *compactum* Carrière, *ibid.* 693. Type: *Vieillard 1262*, New Caledonia, Paita.
Dacrydium elatum Wallich var. *tenuifolium* Carrière, *ibid.* Type: uncertain.[7]
Podocarpus vieillardii Parlatore in DC. Prodr. **16**(2): 521. 1868. Type: *Vieillard 1262.*
Podocarpus tenuifolia (Carrière) Parlatore, *ibid.* (based on *Dacrydium elatum* var. *tenuifolium*) Type: *Vieillard 1260.*
Nageia vieillardii (Parlatore) Kuntze, Rev. Gen. Pl. 800. 1891.
Nageia tenuifolia (Carrière) Kuntze, *ibid.*

Tree to ca. 25 m., often much less; bark hard, slightly rough with scattered low lenticels, breaking off in small thick flakes or short strips, dark but weathering gray, brown and slightly fibrous or granular within; juve-

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[7] Apparently Carrière meant to replace this by his *Podocarpus taxodioides* var. *tenuifolia* (with the same type specimen) but failed to delete it from the manuscript.

nile leaves bilaterally flattened and distichous, up to 10 mm. long and 1.0 mm. broad, spreading and acute with a minute spine turned upward more or less parallel to the branch, smaller towards the base and apex of a branch, gradually reduced in size, thickened and losing the distichous habit; adult leaves acicular, sometimes not bilaterally flattened, straight, spreading at an angle of about 30°, acute, with a minute spine turned upward, not distichous, from 2 to at least 4 mm. long in the middle, but beginning as scales at the base of a branch growth unit, ca. 0.4–0.6 mm. wide, 0.4–0.8 mm. thick, sometimes continuing growth into additional growth units; non-foliage leaves of main shoots scale-like, appressed, bifacially flattened, at least 2 mm. long; pollen cones lateral and subtended by a short stalk with a few small scales or rarely terminal on a short branch, linear, 7–12 mm. long and 1 mm. in diam.; microsporophyll triangular and acute; seed cone on a lateral or terminal scaly shoot 6–8 mm. long, the scales 0.6–0.8 mm. long and appressed, the cone subtended by 6–10 spreading involucral leaves 1–2 mm. long, robust, keeled, acute, the cone itself formed of a small warty receptacle 2–3 mm. long with one projecting sterile bract and one or occasionally two apical ovules; seed oval or globular, generally with a blunt double crest and somewhat elongated at the base, 4 mm. in diam., 5.5–6 mm. long.

Distribution. Throughout New Caledonia, particularly in areas of serpentine rock, along river banks and in moist draws generally where flooding is common, from sea level to 800 meters.

New Caledonia. Mt. Paéoua, *McKee 17029* s 600–900 m. (P). Mt. Boulinda, *McKee 17199* j 750–850 m. (P), *17176* j (P), *Stauffer, Blanchon & Boulet 5778* ♀ (P, Z), *Veillon 142* j 750 m. (P). Baraua R., *McMillan 5173* ♂ (A, K, P), *McKee 2547* s (P), *MacDaniels 2290* s (P), *Guillaumin 13345* s (P, Z). Ouen Koura Valley (Upper Dothio), *McKee 13671* s 300–400 m. (P). W. of Messioncoué near Port Bouquet, *Balansa 2502* s (P). Combui R., *Compton 2227* ♀, j (BM). Kalouehola (Tontouta), *Däniker 587* s (Z). Upper Ouinné R., *Bernier 259* s 600–800 m. (P), *Baumann-Bodenheim & Guillaumin 12834* s 800 m. (P, Z). Canloëthe Mts., *Caldwell s.n.* j (K). Paita, *Vieillard 1262* ♂ (P-holotype of *Podocarpus vieillardii* and of *Dacrydium elatum* var. *compactum*), *1260* j (P-holotype of *Podocarpus tenuifolia* and of *Podocarpus taxodioides* var. *tenuifolia*; BM, K-isotypes). Couvelée R., *Balansa 1382* ♂ (K, NY, P), *Franc 2418* ♀ (A, K, NY, P, Z), *2419* ♂ (A, K, NY, P, Z). Dumbea R., *Balansa 181* ♀ (K, P), *Pancher s.n.* ♀ (BM, P), *White 2112* ♀ (A), *2285* s, j (A, K, P), *Franc 35* j (K, P), *Bernier 69* s (P), *205* j (P), *253* j (P), *257* ♂ (P), *Buchholz 1140* s (ILL, K, P), *1146* ♂ (ILL, K, P), *Hürlimann 1040* s (P, Z), *McKee 2353* ♂ (P), *2567* ♂ (P), *3353* ♂ (K, P). Mt. Koghis, *Brousmiche* (1882) ♀ (P), *Le Rat 2372* j (A). Mine Werguin (base of Pic du Rocher), *Virot 206* ♂ 200 m. (A, ILL, NY, P). Unia, *Vieillard 1261* j (P). R. Bleue, *Foster 202* j (P), *Sarlin 244* j (P), *Hürlimann 1533* s (P, Z), *de Laubenfels P389* ♀ 165 m. (A, K, RSA), *P389a* j (A, RSA), *P444* ♂ 160 m. (A, RSA), *Baumann-Bodenheim 15040* s (P, Z), *15041* s (P, Z), *Aubréville & Heine 182* s (P). R. Blanche (Upper Yaté), *Bernier 206* s (P), *Anon. 241* s (P), *Buchholz 1349* ♀ (ILL, K, P), *1425* ♀ (ILL, K, P), *1464* s (ILL, K), *1465* s (ILL, K, P), *1553* ♀ (ILL, P), *1708* ♀ (ILL, K, P), *de Laubenfels P111* s (SBT), *Baumann-Bodenheim & Guillaumin 10843* ♀ (P, Z). Mare Kiki, *Hürlimann 3109* j (Z), *3158* ♂ (Z), *3159* j (Z). Canyon of Yaté R., *Bernier 254* j (P), *255* s, j (P), *256* j (P), *258* ♀, j (P). Plaine des Lacs, *McKee 1142* ♀ (A). Prony, *Le Rat 222* j (P), *1719* s (P). Southwest, *Moore 4* ♂ (K). Without loc. *Balansa s.n.* ♀ (BM, K), *Pancher 4* s (P), *Mueller 68* s (P), *Sarlin 237* s (P), *341* s (P), *Baudouin 335* j (P).

ILLUSTRATIONS. PILGER, R., Pflanzenreich IV. **5** (Heft 18): *fig. 7F.* 1903; Nat. Pflanzenfam. ed. 2. **13**: *fig. 124F.* 1926; SARLIN, P., Bois et Forêts de la Nouvelle-Calédonie, *t. 25.* 1954, all as *Podocarpus vieillardii.*

The elongated pollen cones distinguish *Dacrycarpus vieillardii* from other species except *D. dacrydioides* (the pollen cones of *D. steupii* are not known). The leaves of *D. dacrydioides* are far shorter than those of *D. vieillardii* and the pollen cone is normally terminal rather than lateral. The leaves of *D. steupii* are shorter and more spreading while the involucral leaves are longer than the foliage leaves, opposite to the condition in *D. vieillardii.* The species with leaves resembling those of *D. vieillardii* have much longer involucral leaves and sharply spreading and not imbricate foliage leaves. The low elevation river-bank habitat is also a unique character.

23. **Dacrycarpus steupii** (Wasscher) de Laubenfels, comb. nov.

Podocarpus steupii Wasscher, Blumea **4**: 405. 1941. Type: *NIFS bb22857,* Celebes, Rantelmo (not seen).

Tree to 36 m. but usually much less; bark brown or gray, inner bark pink, peeling in thin strips; juvenile leaves bilaterally flattened and distichous, up to 8 mm. long and 0.9 mm. thick, becoming shorter and not distichous, transitional leaves (sometimes fertile) variable in length, the longest in the middle of a shoot, 3–4 mm. long, acicular, tip pungent but turned upward parallel to the branch, becoming more constant in size at 2 or 2.5 mm. in length as a mature form, strongly keeled on the sides and back and spreading at an angle of 60° or more from the stem; leaves on non-foliage branches lanceolate, bifacially flattened, almost appressed, 2–3 mm. long; pollen cones unknown; seed cone on a short leafy lateral shoot 3–5 mm. or more long, the involucral leaves at the base of the cone elongated and becoming widely spreading as the seed develops, 3–5 mm. long, the cone made up of a small warty receptacle 2–3 mm. long with a sterile bract protruding on one side, one or two terminal bracts fertile; seed globular with a small crest, 5–6 mm. long and 4.5–5 mm. in diameter.

DISTRIBUTION. Locally common but widely dispersed on high wet peaks or in bogs from 1,000 to 3,420 meters in elevation, mostly 1,600 to 3,000 meters, from Borneo to eastern New Guinea. MAP 9.

Borneo. Peak of Balikpapan, *Kostermans 7350* ♀ 1,000 m. (A, K, L). **Philippines.** Luzon, Benguet, *Curran 10829* s (L). **Celebes.** ENREKANG: near Pintealon, spur of Pokapindjang, *Eyma 572* ♀ 2,350 m. (A, BRI, K, L). Tinabang, W. side of Rante Mario, *Eyma 675* ♀ 3,000 m. (A, BRI, K, L, LAE), *778* j (K, L),

Manado: Palu, E. of Linden Sea, *Blumbergen 3976* s 2,250 m. (A, L), *3977* j (L). **New Guinea.** VOGELKOP: Aifat Valley, *Moll BW 12820* s 860 m. (L), *12840* ♀ 920 m. (L), *12876* s 1,050 m. (L). WESTERN HALF: Wissel L., *Eyma 5101* s 1,750 m. (A, K, L). Kadaitadie, E. of Motito, Wissel L., *Vink & Schram BW 8667* s 1,900 m. (L, LAE). Baliem R., *Brass & Versteegh 11187* ♀ 1,600 m. (A, K, L, LAE). TERR. NEW GUINEA: Wabag near L. Inim, *Flenley ANU 2175* s (K, L), *2769* ♀ 8,300 ft. (K, L). Aiyura, *Womersley NGF 4428* ♀ 6,000 ft. (A, BRI, K, L, LAE). Sattleberg, Sambanga, *Clemens 7258* s 5,000 ft. (A), *7562A* s (A), *7902B* ♀ 6,000 ft. (A). Mt. Amungwiwa, S. of Wau, *Womersley NGF 17939* s 11,400 ft. (L). PAPUA: Ialibu, L. Buneh (S. Highlands), *Pullen 2716* ♀ 6,950 ft. (BM, L, LAE), *2716A* j (L). Uriko, road from Woitape to Kosipi (Cent. Div.), *Van Royen NGF 20289* ♀ 6,500 ft. (K, L).

ILLUSTRATION. WASSCHER, J., Blumea **4**: *t. 4, fig. 4.* 1941, as *Podocarpus steupii.*

The preference for wet conditions which appears to characterize this species probably explains why it is only occasionally found over its broad range. Many specimens have been filed with other species. Sterile specimens are distinguished by the short spreading acicular leaves becoming nearly uniform in size on mature specimens. The leaves are generally shorter and less (or not at all) bilaterally flattened than for comparable stages of *Dacrycarpus cumingii.* On the other hand the leaves of *D. compacta* are short and uniform but differ in being distinctly bifacially flattened, fairly broad, and nearly appressed. The seed cones in each case give positive identification. The one specimen from the Philippines is somewhat uncertain because it is sterile and more or less juvenile.

24. **Dacrycarpus cumingii** (Parlatore) de Laubenfels, comb. nov.

Podocarpus cumingii Parlatore in DC. Prodr. **16**(2): 521. 1868. Lectotype: *Cuming 803,* Luzon, Mt. Banahao.

Nageia cumingii (Parlatore) Kuntze, Rev. Gen. Pl. 800. 1891.

Podocarpus imbricatus Blume var. *cumingii* (Parlatore) Pilger, Pflanzenreich IV. **5** (Heft 18): 56. 1903.

Tree to at least 20 m.; juvenile leaves bilaterally flattened and distichous, up to 12 mm. long and 1.2 mm. thick, the tip curved and parallel with the branch, soon losing the distichous habit and becoming coarser; mature foliage leaves bilaterally flattened, spreading, somewhat falcate, acute with a fine spine curved upward, strongly variable in length, the longest in the middle of a branch unit, 6 mm. long and 0.6 mm. thick; leaves on non-foliage branches bifacially flattened, lanceolate, nearly appressed, 2–4 mm. long and 0.6 mm. wide; pollen cones lateral on short shoots 2–5 mm. long, oval, 8–10 mm. long and 2–3 mm. in diam., microsporophylls lanceolate; seed cone on a short, usually lateral shoot 6–10 mm. long or more, leaves elongated greatly at the base of the cone so that the curving involucral leaves surround even the mature seed, the longest at least 10 mm. long and 0.5 mm. thick, the cone formed of a small warty receptacle 2–3 mm. long with one or rarely two apical fertile bracts; the mature seed with a distinct asymmetrical crest, 4.5–5 mm. in diam. and 5–6 mm. long.

DISTRIBUTION. In mountain forests up to 3,000 meters in the Philippines, Borneo, and (according to Wasscher, 1941) in Sumatra. MAP 10.

Sarawak. Mt. Penrissen, S. of Kuching, *Jacobs 5017* ♀ 1,400 m. (K, L, US). **Philippines.** LUZON: Mt. Polis (Mountain Prov.), *Steiner 2207* s 2,040 ft. (L). Mt. Pulog (Benguet), *Curran, Merritt & Zschokke 18049* ♀ (L), *Ramos & Edaño 45005* s (A), *Steiner 2032* j 2,400 m. (L). Mt. Banahao (Tayabas), *Cuming 803* ♀ (A-lectotype; F, K, L-isotypes), *Foxworthy 2387* ♂ (L). *Loher 7137* ♀ (K, US), *7138* ♂ 2,250 m. (K), *Curran & Merritt 7886* ♀ (NY, US), *Ramos 19557* s (US), *Klemme 66* ♂, j (A), *874* ♀ (NY, US), *Whitford 951* ♀ (K, NY, US), *Holman 4* ♀ (A), *Vidal 623* ♀ (A, K, L), *Barthe* (1857) ♀ (A-syntype), *Ocampo 27926* s (A), *Robinson 5656* ♀ (BRI), *Sulit 30051* s (BRI). Lucban (Tayabas), *Elmer 7465* ♀ (A, K, L, Z). Mt. Mahaihai (Luconia), *Wilkes s.n.* s (GH). Central Luzon, *Loher 4852* ♀ (A, K, US). Without loc. *Loher 2138* s, j (US). MINDORO: Mt. Halcon, *Merrill 5563* s (NY). PANAY: Mt. Midiaas (Antique), *Yoder* (1905) ♀ (L). NEGROS: Canlaon Volcano along lake (E. Negros), *Edaño 21935* j 1,860 m. (L), *21944* j (L). MINDANAO: Mt. Apo (Davao), *Elmer 11684* ♀ (A, K, L, NY, US, Z). Mt. McKinley (Davao), *Edaño 993* s (A).

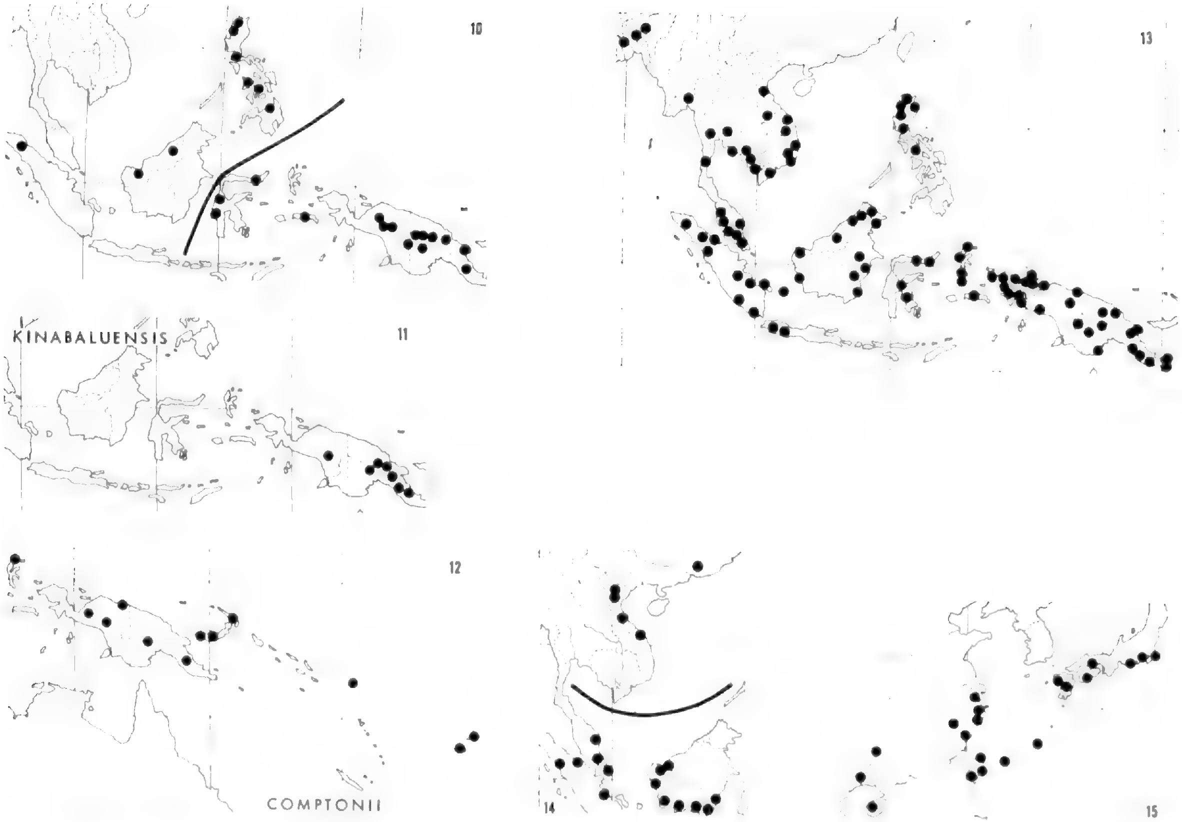
ILLUSTRATION. WASSCHER, J., Blumea **4**: *t. 4, fig. 5.* 1941, as *Podocarpus cumingii.*

The long involucral leaves are the most distinguishing character of this species, being approached only by *Dacrycarpus cinctus* which has very different leaves. The bilaterally flattened mature foliage leaves are the same as *D. kinabaluensis* but not as robust. Juvenile leaves of *D. steupii* resemble mature leaves of *D. cumingii.*

25. **Dacrycarpus kinabaluensis** (Wasscher) de Laubenfels, stat. nov.

Podocarpus imbricatus Blume var. *kinabaluensis* Wasscher, Blumea **4**: 400. 1941. Type: *Clemens 27854*, North Borneo, Mt. Kinabalu.

Small tree or shrub down to 2 m. high; juvenile leaves bilaterally flattened and distichous at first, at least 10 mm. long and 1.2 mm. thick, falcate with a long upturned acuminate apex; mature foliage leaves bilaterally flattened, robust (stiff), falcate, spreading at about a 30° angle, strongly curved upwards at the apex and pungent, the spine not projecting, markedly variable in length, becoming reduced on older plants so that the longer spreading leaves may be as short as 2 mm., 0.5 mm. thick, and nearly quadrangular in cross section; leaves on non-foliage branches bifacially flattened, lanceolate and pungent, curved upwards, 1–2 mm. long and 0.5–1.0 mm. wide, the size varying with the robustness of the branch but not within a given branch; pollen cones lateral on a short branchlet about 3 mm. long, globular, 8 mm. long and 3 mm. in diam.; seed cone on short lateral or terminal shoots 5–15 mm. long and bearing, as is usual for the genus, the non-foliage type leaves; at the base of the cone the leaves elongated to the size of foliage leaves



MAPS showing distribution of: 10, *Dacrycarpus cumingii* (Parlatore) de Laubenfels (dots west of line), and *D. cinctus* (Pilger) de Laubenfels (east of line); 11, *D. compactus* (Wasscher) de Laubenfels (dots), *D. kinabaluensis* (Wasscher) de Laubenfels, known only from N. Borneo; 12, *Decussocarpus vitiensis* (Seemann) de Laubenfels (dots), *D. comptonii* (Buchholz) de Laubenfels, known only from New Caledonia; 13, *D. wallichianus* (Presl) de Laubenfels; 14, *D. fleuryi* (Hickel) de Laubenfels (dots north of line), *D. motleyi* (Parlatore) de Laubenfels (dots south of line); 15, *D. nagi* (Thunberg) de Laubenfels.

and nearly surrounding the young ovule but not reaching beyond the middle of the ripe seed, up to 7 mm. long and 1.0 mm. thick, the cone made up of a small warty receptacle 2–4 mm. long with one or two sterile protruding bracts and an apical fertile bract; the mature seed with a distinct asymmetrical crest, 5–5.5 mm. in diameter and 7 mm. long.

DISTRIBUTION. In mountain dwarf forests sometimes forming almost pure stands on Mt. Kinabalu from 2,750 to 4,000 meters at the timberline.

North Borneo. Mt. Kinabalu, Paka Cave area, *Clemens 10636* ♀ (A, GH, K), *10662* ♀ (A), *10686* s (A), *27092* s 13,000 ft. (A, K, L, NY), *27854* ♀ (A, K, L-isotypes), *28910* ♀ 11,000 ft. (A, K, L, NY), *Wood & Wyatt-Smith SAN A4493* s 10,500 ft. (A, BRI), *Meijer SAN 21988* ♀ 9,500–11,000 ft. (K), *SAN 29265* ♂ 10,000 ft. (K). Mt. Kinabalu, Marai Parai, *Clemens 32316* ♀ 10–11,000 ft. (A, K, L, NY), *32317* ♀ 11,000 ft. (A, L, NY), *32318* j 11,000 ft. (A, L, NY). Mt. Kinabalu, Gurulau Spur, *Clemens 51201* ♀ (L). Mt. Kinabalu, side of Granite Dome, *Clemens 29914* ♀ 12,500 ft. (K, L); S. slope, *Jacobs 5755* ♀ 3,600 m. (K, L, US). Mt. Kinabalu, *Clemens s.n.* ♀ 11,000 ft. (BM), *Nicholson SAN 17825* ♀ 10,000 ft. (BRI, K, L), *SAN 39766* ♀ 9,000 ft. (K), *Sinclair & Kadim 9146* ♀ 10,700 ft. (K, L), *Haviland 1094* j 11,000 ft. (K), *1095* ♀ 11,000 ft. (A, K), *Chew & Corner RSNB 868* ♀ 10,500 ft. (K), *RSNB 5887* ♀ 9–11,000 ft. (K), *Gibbs 4216* ♂ 12,000 ft. (K), *Anderson S27079* ♀ 11,300 ft. (K).

ILLUSTRATION. WASSCHER, J., Blumea **4**: *t. 4, fig. 2γ.* 1941, as *Podocarpus imbricata* var. *kinabaluensis.*

The robust form of this high-elevation species is characteristic of conifers in such places, and in general habit *Dacrycarpus kinabaluensis* resembles *D. compactus* from high mountains in New Guinea, although in detail their leaf form is, of course, quite different. *D. kinabaluensis* is most closely related to *D. cumingii*, differing in the markedly robust foliage leaves and distinctly shorter involucral leaves. The pollen cones also differ somewhat in shape. Perhaps it could be treated as a variety of *D. cumingii* but not, certainly, of *D. imbricatus.*

26. **Dacrycarpus cinctus** (Pilger) de Laubenfels, comb. nov.

Podocarpus cinctus Pilger, Bot. Jahrb. **69**: 253. 1938. Type: *Clemens 5261,* New Guinea, Busu River.

Podocarpus dacrydiifolia Wasscher, Blumea **4**: 410. 1941. Type: *NIFS bb13633,* Celebes, Pawreang Mts.

Shrub of less than 4 m. to a tree up to 30 m. high; bark brown to black, hard and uneven, inner bark reddish, breaking off in rough scales or plates; juvenile leaves slightly bilaterally flattened and distichous at first, the longest 12 mm. long and 0.8 mm. thick, falcate and bending upward to the pungent tip, gradually changing to resemble the mature leaves; mature foliage leaves of uniform size on a branch, slightly bifacially flattened, lanceolate, falcate, eventually reduced to 2–3 mm. in length and spreading at an angle to give the branch system a diameter of 3–4 mm., about 0.4–0.6 mm. wide, mature specimens including leaf sizes ranging up to 5 mm. in the center of a branch unit, often glaucous; leaves of non-foliage branches the same or more distinctly bifacially flattened, pollen cones terminal or lateral on a very short branch 2–3 mm. long, globular or oval, 4–10 mm. long and 2–3 mm. in diam., microsporophylls acuminate; seed cone lateral on a short branch or terminal, 5–15 mm. long, involucral leaves much longer than foliage leaves and clasping the young seed but generally not reaching past the middle of the mature seed, the longest 6–7 mm. long, the cone formed by a small warty receptacle 3–4 mm. long, with one or two projecting sterile bracts, seed and receptacle becoming red when ripe; mature seed with a small asymmetrical crest, 6–7 mm. in diam. and 6–7 mm. long. Fig. 9a.

Distribution. Mountain forests to high mountain shrubbery from 900 to 3,600 meters but mostly 2,200 to 3,200 meters, from the Celebes to the high mountains of New Guinea. Map 10.

Celebes. Masamba, *NIFS bb24958* s 900 m. (L). Pawreang Mts., Ulu Salu (Upper Binuang), *NIFS bb13633* ♀ 1,800 m. (L-holotype of *Podocarpus dacrydiifolia*). Pinapuang (Manado), *Eyma 3873* s (L). **Ceram.** G. Sofia, Central Mts., *Stresemann 125* j 1,300 m. (L). G. Pinaia, Middle Ceram, *Eyma 2276* s 3,030 m. (L), *Stresemann 251* s 3,010 m. (L), *276a* j 2,530–2,750 m. (L). **New Guinea.** Western Half: Mamberamo R. (Mt. Doorman), *Lam 1773* ♀ 3,260 m. (L). Hellwig Mts., *Pulle 964* ♀ 2,600 m. (K, L), *van Römer 736* s (L). Lake Habbema, *Brass 10513* ♀ 2,800 m. (A, K, L), *10514* j (A, L), *10675* ♀ 3,000 m. (A, K, L), *Brass & Versteegh 10447* ♀ 2,840 m. (A, L). L. Quarles, *Versteegh BW2537* s 3,600 m. (K, L). Terr. New Guinea: Wapu R. (Wabag), *Hoogland & Schodde 7166* s 9,500 ft. (A, L). Tomba, Mt. Hagen–Wabag Road, *Flenley ANU 2819* ♀ 8,900 ft. (K, L), *Robbins 238* ♀ 8,000 ft. (A, K, L, LAE, US). Lai Valley (Wabag), *Robbins 3112* ♀ 7,500 ft. (A). Minj-Nona Divide, *Pullen 5052* ♀ 10,600 ft. (L), *5267* s 9,500 ft. (K, L). Keglsugl (Chimbu), *Saunders 804* s 8,000 ft. (L, LAE). Toromambuno Mission (Upper Chimbu), *Pullen 313* ♀ 9,000 ft. (A, BRI, K, L, LAE, US), *313A* j (K, L, LAE). Mt. Wilhelm Track, Chimbu Valley, *Robbins 673* ♀ 9,000 ft. (A, BM, L, LAE). Mt. Wilhelm, *Brass 30412* s 2,770 m. (A, K, L, NY, US), *30707* ♀ 3,180 m. (A, K, L, LAE, NY, US), *Stauffer 5670* ♂ 3,250 m. (Z). Kerigomna Camp (Goroka), *Hoogland & Pullen 5574* ♂ 3,000 m. (A, BRI, K, L, US). Matalunga near Goroka, *Vink NGF 12430* ♀ 7,500 ft. (L, LAE). Marafunga (Goroka), *Womersley NGF 14018* ♀ 8,200 ft. (K, L, LAE), *NGF 24569* ♀ 7,700 ft. (K), *Havel NGF 17417* ♀ 8,000 ft. (LAE), *Hartley TGH 13263* ♀ 8,600 ft. (A, L), *Tuckwell W1553* s 8,400 ft. (LAE), *s.n.* ♂ 8,000 ft. (LAE). Finisterre Range, E., *Pullen 6116* j 8,100 ft. (L). Mannasat, Cromwell Mts., Huon Penins., *Hoogland 9386* ♀ 7,600 ft. (A, K, L), *9478* s (K), *9479* j (K). Busu R. (Mt. Sarawaket), *Clemens 5261* ♀ 9,000 ft. (A, LAE-isotypes of *Podocarpus cinctus*). Mt. Sarawaket, *Clemens 5562* ♀ 8–9,000 ft. (A, LAE), *5588* s (LAE), *6283* ♀ 7–8,000 ft. (A, LAE), *7559* ♀ 6–8,000 ft. (A). Rawlinson Range, *Clemens 12332* j 7–12,000 ft. (A). Samanzing, *Clemens 9387* ♀ 7–8,000 ft. (A, L). Papua: Mt. Kerewa, *Kalkman 4796* s, j 2,940 m. (L). Pass betw. Mt. Kerewa and Mt. Ne, *Vink 17188* j 2,890 m. (L). Mt. Ne, *Vink 17242* ♀ 2,880 m. (L). Mt. Giluwe, above Klareg, *Schodde 2021* ♀ 8,800 ft. (K, L, LAE), *2104* j 9,100 ft. (L, LAE). Woitapi-Kosipi Road (Cent. Div.), *Van Royen NGF*

20309 ♀ 6,300 ft. (K, L). Murray Pass, Wharton Range, *Brass 4688* ♀ 2,840 m. (A, K, L, NY, US).

ILLUSTRATIONS. WASSCHER, J., Blumea 4: *t. 4, fig. 6,* as *Podocarpus cincta,* and *fig. 7* as *Podocarpus dacrydiifolia.* 1941.

Confusion has existed between this species and *Dacrycarpus compactus* with which it overlaps in range, although they are not at all the same. The involucral leaves of *D. cinctus* are long and narrow, clasping the smaller seed, while those of *D. compactus* are short and triangular, barely reaching the base of the distinctly larger seed. Foliage leaves contrast in the same way. The terminal position of the pollen cone which is usual in *D. cinctus* is a character shared only with *D. compactus* and *D. dacrydioides.* The essential non-dimorphic quality of the mature foliage is shared only with *D. compactus, D. expansus,* and *D. imbricatus* (in part). There are several specimens of *D. cinctus* which differ from the typical form in the direction of *D. compactus* and could, perhaps, be recognized as forming a variety (FIG. 9b). These are: *Brass 4688, 10513, 10514, 10675, Brass & Versteegh 10447, Versteegh 2537, Pulle 964, Hoogland & Pullen 5574, Pullen 5052, 5267, Lam 1773, Schodde 2021, 2104, van Römer 736, Vink NGF 12430,* and *Womersley NGF 14018.* They differ in that the foliage leaves are somewhat broader (up to 0.8 mm.), as are the involucral leaves (up to 1.0 mm wide). The possibility exists that these are hybrids, being found at and not far below the lower elevation limit of *D. compactus.*

27. **Dacrycarpus expansus** de Laubenfels, sp. nov.

Arbor ad 25 m. alta; cortex squamosus. Folia plantarum iuvenilium dimorpha, ad ramulos breves compressa bilateraliter, patentia, falcata, pungentia, ad 12 mm. longa, 1.5 mm. lata, biseratim expansa; ad ramulos magis elongatos compressa bilateraliter, imbricata, lanceolata, pungentia, ad 4 mm. longa, in basi 0.8 mm. lata; folia plantarum adultarum compressa bifacialiter, expansa, falcata, acuta, dorso carinata, 2–4 mm. longa, 0.6–1.0 mm. lata. Strobili masculi laterales ad ramusculis 1–2 mm. longis, ovoidei, 6 mm. longi, 3 mm. crassi. Strobili feminei ad apicem ramulorum saepe brevi 4–5 mm. longi, foliis parvis; folia involucra longiora, 3–4 mm. longa, 0.6 mm. lata; receptaculum parvulum, verruculosum, 2–3 mm. longum; semen globosum, cristatum, 4 mm. diametro, 5–6 mm. longum. Holotypus: *Hoogland & Schodde 7463* (L), New Guinea, Yobobos Grassland. FIG. 7b.

DISTRIBUTION. Locally common in disturbed forests in the highlands of New Guinea at 2,600–2,670 meters.

New Guinea. TERR. NEW GUINEA: Yobobos Grassland, Laiagam Subdistrict (Wabag), *Hoogland & Schodde 7463* ♀ 8,500 ft. (L-holotype; BRI, LAE-isotypes), *7440* s (L, LAE), *7682* j (L, LAE), *Robbins 3214* ♂ 8,700 ft. (BRI, L, LAE). PAPUA: E. foot of Mt. Ambua, Tari Subdist., *Vink 17502* ♀, ♂ 2,670 m. (L), *17499* j (L), *17500* j (L), *17501* j (L).

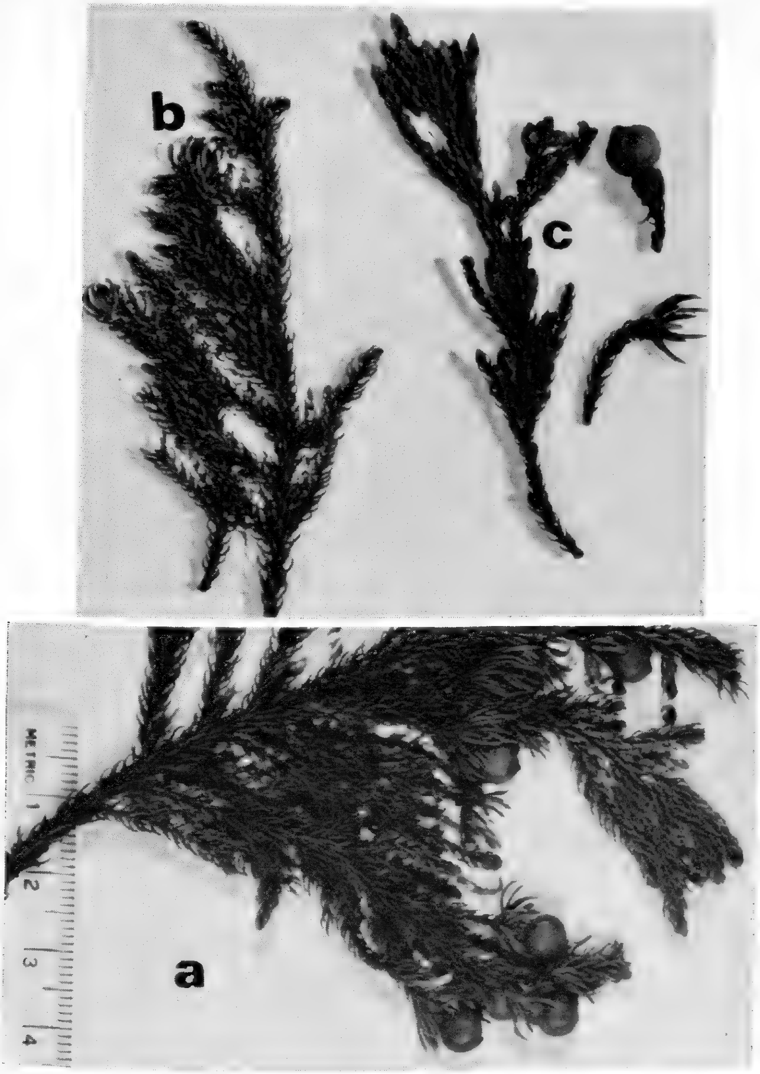


FIGURE 9. a, *Dacrycarpus cinctus* (Pilger) de Laubenfels, portion of *Hartley 13263* (A), typical form of the species; b, *the same*, fragments showing variation toward *D. compactus*; c, *D. compactus* (Wasscher) de Laubenfels, fragments.

The short distinctly bifacially flattened involucral leaves clasping the receptacle, but not the somewhat small seed, distinguish this new species from all others in the genus. The only other species which have distinctly bifacially flattened involucral leaves are *Dacrycarpus cinctus* and *D. compactus*. Those of *D. cinctus* are twice as long, clasping the seed, while those of *D. compactus* are up to twice as broad below a much larger seed. As in both of these species, *D. expansus* lacks dimorphic foliage when mature, contrasting in appearance because of the strongly spreading rather than imbricate leaves which are also distinctly broader than those of *D. cinctus.* The normally lateral pollen cones also distinguish *D. expansus* from these two species. Except for the great contrast in shape of the involucral and foliage leaves *D. expansus* resembles *D. steupii* in gross morphology, differing in habitat preference.

28. **Dacrycarpus compactus** (Wasscher) de Laubenfels, comb. nov.

Podocarpus compacta Wasscher, Blumea 4: 411. 1941. Type: *Brass 4284,* New Guinea, Mt. Albert Edward.

Small tree 2–15 m. high; bark hard, rough, warty, dark gray, breaking off in scales, inner bark reddish straw color; juvenile leaves bilaterally flattened, lanceolate, falcate and curved upward at the tip, acute, strongly keeled laterally, not distichous, 2.5 mm. long and 0.6 mm. thick; mature foliage leaves not dimorphic, bifacially flattened, spreading slightly, falcate, lanceolate, pungent, keeled on the back, 2–3 mm. long, 0.6–1.0 mm. wide (the wider probably on older plants); pollen cones lateral on a short branch about 3 mm. long or more usually terminal, 7–8 mm. long and 3 mm. in diam., microsporophylls lanceolate, acute; seed cone terminal, generally on a short branch 6–17 mm. long, involucral leaves robust, 4–5 mm. long and 0.8–1.2 mm. wide, clasping the receptacle, the cone itself made up of a small warty receptacle 3–4 mm. long with a sterile bract protruding; seed globular, with a blunt crest, 7–8 mm. long and 7 mm. in diam. FIG. 9C.

DISTRIBUTION. In high mountain forests and shrubberies often as an emergent, and sometimes the dominant tree at the tree line in New Guinea, from 3,200 to 3,900 meters. MAP 11.

New Guinea. WESTERN HALF: L. Habbema, *Brass 9291* ♀ 3,225 m. (A, K, L), *21104* ♀ 3,225 m. (A). TERR. NEW GUINEA: Mt. Kinkain, Cent. Kubor Range (Minj), *Saunders 708* ♀ 11,800 ft. (A, L), *Pullen 5111* ♂ 11,770 ft. (A, K, L), *5138* ♀ 12,000 ft. (K, L). Mt. Wilhelm, *Robbins 718* ♀ 12,000 ft. (L), *Brass 29861* ♀ 3,650 m. (A, K, L, NY, US), *29935* ♀ 13,100 ft. (A, K, L, NY, US), *s.n.* s 3,320 m. (US), *Millar NGF 14671* ♀ 12,000 ft. (K, L), *Womersley NGF 8852* ♀ 11,870 ft. (A, K, L), *8861* ♂ (A, K, L), *Pullen 338* ♀ 12,500 ft. (A, L), *Hoogland & Pullen 5650* ♂ 11,700 ft. (A, BRI, K, L, US), *5703* ♀ 12,500 ft. (A, BRI, K, L, US), *Havel NGF 17421* ♀ 11,500 ft. (K), *Stauffer 5670* ♂ 3,250 m. (K, L), *Balgooy 287* ♀ 3,650 m. (L). Mt. Otto (E. Highland), *Brass & Collins 31021* ♀ 3,460 m. (A, K, L, NY). Mt. Piora, Kaimantu Subdiv. (E. Highland), *Henty & Carlquist NGF 16566* ♀ 10,500 ft. (K, L). PAPUA: Mt. Dickson, Goilala Subdist., *Hartley TGH 12958* ♀ 11,500 ft. (L). Mt. Albert Edward, *Brass 4284* ♀ 3,680 m. (A, NY-isotypes), *4284A* j (A, NY), *4347* j (NY), *4348* s 3,680 m. (A, NY).

ILLUSTRATION. WASSCHER, J., Blumea 4: *t. 4, fig. 8.* 1941, as *Podocarpus compacta.*

The particularly large seed completely free of the involucral leaves and the small bifacially flattened not widely spreading leaves distinguish *Dacrycarpus compactus* from other species. *D. expansus*, with rather similar, though spreading leaves, has much smaller seeds and more lanceolate involucral leaves. The wild tree of *D. compactus* is a very striking plant, often rising above the other shrubs near the tree line and standing out with a dark green color. The short juvenile leaves are the most primitive in the genus and apparently only in this species are the juvenile leaves never distichous.

ADDITIONAL SPECIES:

Dacrycarpus dacrydioides (Rich.) de Laubenfels, comb. nov.

Podocarpus dacrydioides Rich. Essai d'une Flore de la Nouvelle Zéland, 358. *t. 39.* 1832. Type: *D'Urville* in 1827 (not seen).
Podocarpus thujoides R. Br. ex Mirb. Mém. Mus. Hist. Nat. Paris **13:** 75. 1825 (*nomen*).
Dacrydium excelsum Cunn. Ann. Nat. Hist. **1:** 213. 1838 (*nomen illeg.*, based on *Podocarpus dacrydioides*).
Nageia excelsa (Cunn.) Kuntze, Rev. Gen. Pl. 800. 1891.

Acmopyle Pilger, Pflanzenreich IV. **5** (Heft 18): 117. 1903. Type species: *Acmopyle pancheri* (Brongn. & Gris) Pilger.

Small trees; foliage leaves linear, bilaterally flattened, distichous, with more stomata on the underside, edges sometimes revolute; leaves on non-foliage branches (both fertile shoots and branches of the second order) scale-like, triangular and bifacially flattened; pollen cones terminal and lateral together; seed cones on short branches which are lateral or terminal or grouped together, becoming enlarged and warty as a receptacle with a single subterminal seed; the ovule at first inverted and partially covered by the epimatium, eventually becoming nearly erect, fused with the epimatium, and fleshy.

This genus is characterized by the unique combination of the seed fused with the epimatium (fertile scale), together with an inverted ovule which becomes gradually nearly erect as it matures. The seeds of other genera of Podocarpaceae which are fused with the fertile scale do not become erect. *Acmopyle* shares bilaterally flattened and distichous leaves with *Falcatifolium* and juvenile forms of *Dacrycarpus*. With the latter it also shares a warty receptacle. Two species are known, differing in the character of seed and receptacle as well as in size of the pollen cone and details of leaf-form. Both are island endemics.

29. **Acmopyle pancheri** (Brongn. & Gris) Pilger, Pflanzenreich IV. **5** (Heft 18): 117. 1903.

Dacrydium pancheri Brongn. & Gris, Bull. Soc. Bot. France **16:** 330. 1869. Type: *Pancher* in 1869, New Caledonia, Mount Mou.

Nageia pancheri (Brongn. & Gris) Kuntze, Rev. Gen. Pl. 800. 1891.
Podocarpus pectinatus Masters, Gard. Chron. III. **9**: 113. 1892. Type: *Hort. Sander s.n.*, of New Caledonian origin.
Acmopyle alba Buchholz, Bull. Mus. Hist. Nat. Paris II. **21**: 281. 1949. Type: *Buchholz 1704*, New Caledonia, Bois de Mois de Mai.

Tree from 5 to 25 m. high; bark hard and smooth, weathering to a gray color, brown to tan and fibrous within, with scales breaking off on older trees; foliage leaves bilaterally flattened and decurrent, distichous, linear and spreading 60° to 75° from the branch, tapering somewhat towards the apex which is turned slightly in the direction of the shoot apex, or slightly falcate, at first with two glaucous bands on each surface associated with the stomatiferous areas but with further development this condition suppressed on the upper surface but the white bands remaining prominent below, the midrib marked by a faint line on the upper surface and more pronounced below, leaves shorter at the beginning and end of a sequence of growth with the leafy shoots never producing a second cycle of leaves but commonly continued into fertile shoots; shade leaves spread out into a flat and almost solid plane, except for the smaller leaves at either end of the branch, 16–21 mm. long and 2.8–3.0 mm. wide, slightly revolute on the margins; leaves exposed to the sun less regularly placed and more noticeably keeled, often overlapping and weakly spread into a plane, 10–15 mm. long and 1.8–2.2 mm. wide, with intermediate forms sometimes found; non-foliage leaves scale-like, triangular, bifacially flattened, keeled on the back, less than 2 mm. long, on main branches bearing foliage shoots broadly decurrent and dispersed, on fertile branches (and occasionally at the base of a leafy shoot) more or less crowded; pollen cones terminal or often a pair (one of which is lateral) produced at the apex of a leafy shoot or on a scaly shoot which may itself be terminal or lateral either at the apex of a leafy shoot or a main branch bearing leafy shoots (on vigorous trees all of these together), subtended by a few small scales, 10–20 mm. long by 2–3 mm. in diam. (fide Hooker, 1902, to 35 mm. by 4 mm.), the microsporophylls small and triangular; seed cones terminal or lateral at the apex of a leafy shoot, or on a main shoot, or terminal or lateral on a scaly shoot which may be either terminal on a leafy shoot, or lateral on a main shoot (on vigorous trees a combination of these); the seed cone subtended by a peduncle 9–22 mm. long, densely covered by small overlapping scales and slightly enlarged toward the cone to a diameter of about 2 mm.; the cone formed by a fleshy warty receptacle 8–18 mm. long involving about 4 to 8 bracts whose free tips each surmount a bulge; one ovule inverted and protruding from the enveloping epimatium in the axil of a sub-apical bract, becoming almost erect and fleshy, the epimatium completely fused to the mature ovule and apparently attached for about half its length (marked by a roughened area on the seed and a characteristic ridge on the dried fruit); seed globular, 10–11 mm. in diameter, thick and hard.

DISTRIBUTION. Scattered in moist rainforest over serpentine rocks in most of New Caledonia from near sea level to at least 1,200 meters. Growing as a canopy tree in drier areas and sometimes found in the understory within the mossy forest where it is fully fertile.

New Caledonia. Upper Diahot, Tendé Forest, *McKee 17540* j 500 m. (P). Mt. Colnett, *Hürlimann 1964* ♀ 1,200 m. (P, Z). Mt. Paéoua, *McKee 17057* s 900–1,100 m. (P), *Bernardi 10151* ♀ 900–950 m. (P, Z). Mt. Boulinda, *Veillon 136* ♂ 1,200 m. (P), *Schmid 137* s (ORSTOM). Crest W. of Col de Rousettes, *de Laubenfels P429* s 700 m. (A, RSA). Me Arembo, *Bernier 1007* s (K, P). Mt. Koungouhaou N., *McKee 17954* ♀ 1,000–1,100 m. (P). Mt. Mou, *Pancher* (1869) ♀ 1,200 m. (P-holotype of *Dacrydium pancheri*), *Balansa 2862* ♀ (BM, K, NY, P), *Compton 485* ♀ (BM), *Franc 170* ♀ (A, BM, K, NY, P, Z), *Virot 10* s (A, P), *Le Rat 697* s (P), *980* ♀ (K, P), *2594* s (A, P), *Bernier 278* ♀ (P), *1309* ♀ (P), *Buchholz 1451* ♀ (ILL, K, P), *1587* ♀ (ILL, K, P), *1587S* j (ILL, P), *1593S* j (ILL, P), *1790* ♂ (ILL, K, P), *McMillan 5013* ♀ (P), *5014* s (P), *de Laubenfels P130* ♀, ♂ 1,140 m. (SBT), *P355* ♀ (A, K, RSA), *P356* ♂ (A, RSA), *Brousmiche s.n.* s (P), *Thorne 28704* s (P), *Baumann-Bodenheim & Guillaumin 11260* s (P, Z), *Baumann-Bodenheim 15632* s (P, Z), *15633* ♀ (P, Z), *McKee 3517* ♀ 1,100 m. (A, K, P). Mt. Ouin, *McKee 9795* s (K, P). Col de Mt. Dzumac, *McKee 9773* s (K, P), *9774* j (K, P), *12922* ♂ (P), *de Laubenfels P447* ♀ 900 m. (A, RSA), *Baumann-Bodenheim & Guillaumin 12714* s (P, Z), *Blanchon 930* s (P). Mt. Koghis, *Pancher s.n.* ♀ 800 m. (P), *Alleizette 142* ♀ (P), *Brousmiche 9* ♀ (with *Prumnopitys ferruginoides*), *Hürlimann 1657* s 1,050 m. (P, Z). Mt. des Sources, *Hürlimann 911* s (P, Z). Mois de Mai, *Bernier 276* s (P), *277* s (P), *279* s (P), *280* ♂ (P), *281* s (P), *321* j (P), *Buchholz 1354* s (ILL, P), *1388* s 200–250 m. (ILL, P), *1388A* j (ILL), *1388M* ♂ (P), *1698* s (ILL, P), *1698L* (shade) s (P), *1704* ♀ (ILL-holotype of *Acmopyle alba*; K, P-isotypes), *McKee 3454* s 200 m. (A, K, P), *Baumann-Bodenheim 13964* s (P, Z), *14258* ♂ (P, Z), *14263* ♀ (P, Z), *14988* s (P, Z), *14992* s (P, Z), *15096* ♂ (P, Z), *15097* ♀ (P, Z), *15098* s (P), *15130* s (P, Z), *15208* s (P, Z), *15213* s (Z). Slope N. of R. Bleue, *de Laubenfels P136* s 700 m. (SBT), *P382* ♀ 250 m. (A, RSA), *P383* ♂ (A, K, RSA, SBT), *P383A* (shade) s (A, RSA), *P446.5* ♀ 770 m. (A, RSA), *Baumann-Bodenheim & Guillaumin 10929* s (P, Z), *Baumann-Bodenheim 15043* j (Z), *15055* s (P, Z), *McKee 12653* s 200 m. (P). Bois Electrique, *Foster 206* ♀ (P), *de Laubenfels P377* ♀ 240 m. (A, RSA), *P378* s (A, RSA), *Hürlimann 3411* s 220 m. (Z). Without loc., *Mueller 44* s (ILL, P). Cult., *Hort. Sander s.n.* s (K-holotype of *Podocarpus pectinatus*).

ILLUSTRATIONS. HOOKER, J. D., Bot. Mag. *t. 7854.* 1902, as *Podocarpus pectinata*; PILGER, R., Pflanzenreich IV. **5** (Heft 18): *fig. 24.* 1903; Nat. Pflanzenfam. ed. 2. **13**: *fig. 128.* 1926; BUCHHOLZ, J. T., & N. E. GRAY, Jour. Arnold Arb. **28**: *t. 1B.* 1947; SARLIN, P., Bois et Forêts de la Nouvelle-Calédonie, *t. 22 & 23*, as *Acmopyle alba.* 1954.

The difference between shade and sun growth forms suggests that two entities are included under *Acmopyle pancheri* but this difference occurs regularly on single plants. *A. alba* differs from *A. pancheri* in having larger pollen cones (18–20 mm. long by 3 mm. in diam. in *A. alba* and 10–13 mm. long by 2 mm. in diam. in *A. pancheri*). There are absolutely no other differences between these two taxa, while even larger pollen cones are described by Hooker (1902). Because only a few examples of pollen cones are available to show variations in size and because specimens can not be distinguished in the absence of pollen cones, it is felt that *A. alba* should not be separated from *A. pancheri* at this time. In the future it might seem advisable to separate them at the varietal level.

30. **Acmopyle sahniana** Buchholz & Gray, Jour. Arnold Arb. **28**: 142. 1947. Type: *Gillespie 3273*, Fiji, Mt. Vakarogasiu.

Small and gnarled tree 3–5 m. high; leaves bilaterally flattened, distichous, spreading at an angle of 60° to 80°, linear, slightly tapering and curved in the direction of the branch apex near the blunt tip or falcate, decurrent, 10–19 mm. long and 2.0–3.2 mm. wide (wider according to Buchholz and Gray but not according to their illustrations or to herbarium specimens), glaucous on both surfaces at first but losing the glaucousness on the upper surface, mature leaves with two prominent glaucous and stomatiferous bands on the lower surface, very few stomata on the upper surface, midrib faintly marked on both surfaces, margin slightly revolute, leaves smaller at the begining and end of a sequence of growth with one sequence often continuing into a subsequent growth unit; nonfoliage leaves on main branches scale-like, bifacially flattened, long triangular, 1.5–2.5 mm. long, keeled on the back and broadly decurrent, more crowded at the base of a foliage branch and on the peduncle of the seed cone; pollen cones terminal, 5 mm. long and 2 mm. in diam.; microsporophylls triangular, acute; seed cones lateral or terminal on a foliage branch, with a short (5 mm.) scaly peduncle, the cone formed by a fleshy warty receptacle involving two bracts, the uppermost being fertile with a single inverted ovule partly covered by a broad epimatium; seed becoming nearly erect, rounded and elongated into a conical point, with the epimatium fused along one side, its margin forming a fringe about halfway to the micropyle, mature seed not known.

DISTRIBUTION. Known only from two isolated mountains on either side of Viti Levu in dense low forest 800 to 1,050 meters in elevation, where it is locally common.

Fiji. VITI LEVU: Mt. Vakarogasiu (Namosi), *Gillespie 3273* s 900 m. (A-holotype; K-isotype), *Koroiveibau 14598* ♀ 2,600 ft. (K). Mt. Koroyanitu (Mt. Evans Range), *Smith 4122* ♂ 950–1,050 m. (A, BRI, ILL, K). Without loc., *Horne s.n.* s (K).

ILLUSTRATION. BUCHHOLZ, J. T., & N. E. GRAY, Jour. Arnold Arb. **28**: *t.* IA. 1947.

This rare species is of interest because its only relative, *Acmopyle pancheri*, occurs in New Caledonia, not a common combination.

Decussocarpus de Laubenfels, gen. nov. Type species: *Decussocarpus vitiensis* (Seemann) de Laubenfels.

Nageia Gaertner, De Fruct. et Sem. 191. 1788. Type species: *Nageia japonica, nomen illeg.* (description confused).

Folia opposita, decussatim vel spiraliter inserta, lanceolata vel rotundata, ad basim contracta, uni- vel multinervata. Strobili masculi solitarii vel fasciculati. Strobili feminei pedunculati; pedunculi cum squamis (vel foliis); semina saepius singula, globosa, inversa, squama fertilia cum ovulo conjuncta.

The new genus *Decussocarpus* is composed of three sections formerly treated as a part of *Podocarpus*. A group of characters unite these three sections while distinguishing them from *Podocarpus*. Ovules are produced subterminally on a scaly shoot not divided into a naked peduncle and a specialized receptacle with elongated bracts as in *Podocarpus*, although in some species a part of the fertile shoot becomes fleshy. The micropylar end of the inverted seed extends distinctly downward (towards the base of the fertile complex) so that the mature seed appears to be attached at an angle on the end of the fertile shoot. As a result the seed displays a projecting curved beak in contrast with all related taxa. Associated with the elongated attachment is the tendency for the fruit to fall with the fertile shoot still attached. In contrast with *Podocarpus*, a cluster of five or more pollen cones may occur in some species on a single shoot.

The leaves of *Decussocarpus* have a number of distinguishing characteristics. Opposite decussate leaves are found throughout the genus with the exception that in the section AFROCARPUS some branches have spirally placed leaves (herbarium specimens therefore may lack this character which, nevertheless, can be readily found on any mature living specimen of § AFROCARPUS). A unique leaf orientation further occurs in all sections of the genus, although it may be absent in a few species of the section DAMMAROIDES. The distichous leaves being amphistomatic, instead of making unequal twists on opposing sides of the branch to bring the axial surface of the leaf upwards at all times, always turn in the same manner with respect to the axis so that on the left side the abaxial surface is uppermost. This can be seen in section AFROCARPUS even on branches without decussate leaves. Unlike *Podocarpus*, the leaves of *Decussocarpus* have no accessory transfusion tissue and unlike *Prumnopitys* they do have a hypoderm. Also unlike *Prumnopitys*, the leaves are not linear, but oval or lanceolate.

Most species of *Decussocarpus* are large trees, some of which are valuable timber trees and others are in demand for decorative planting in the warmer parts of the world. The genus is divided into three sections based on the relative width and venation of the leaves. Section DECUSSOCARPUS has single-veined but relatively wide leaves compared to section AFROCARPUS whose leaves are more than ten times as long as they are wide. Section DAMMAROIDES has broad multiveined leaves.

Section DECUSSOCARPUS.

Podocarpus section *Polypodiopsis* Bertrand, Ann. Sci. Nat. V. **20:** 65. 1874. Type species: *Podocarpus vitiensis* Seemann [*Decussocarpus vitiensis* (Seemann) de Laubenfels].

Trees with opposite decussate leaves which are ovate or lanceolate, sessile, sharply narrowed to a decurrent base, single veined, amphistomatic, and not more than about five times as long as wide; pollen cones sessile, solitary or grouped on a special scaly shoot; seed cones in the form of a scaly or leafy shoot with one or rarely two fertile subterminal bracts; ovule inverted and covered by the seed scale which makes an apical crest over the inverted base of the ovule; seed large, globular, blunt at one end but elongated into a curved beak at the micropylar end (at the base of the fruit) and covered by the fleshy seed scale.

An account of this section is given in Wasscher (1941), who shows some uncertainty about how to treat it. Once its characters were completely known, there was agreement that it is most closely related to section DAMMAROIDES (*Nageia* of most authors). The difference in leaf size and venation, however, made it advisable to separate these two taxa into different sections which have until now been treated as a part of the extensive genus *Podocarpus*. The new genus, *Decussocarpus*, is here being proposed to accommodate the two groups and the more recently named section AFROCARPUS in order to recognize the considerable morphological differences that previously have been merged in the one genus *Podocarpus*. Section DECUSSOCARPUS extends from eastern Indonesia to South America, and fossil specimens of it from Chile were once the basis of reports of *Sequoia* in the Southern Hemisphere (Florin, 1940). There are four species.

KEY TO THE SPECIES OF SECTION DECUSSOCARPUS

1. Non-foliage branches bearing scales.
    2. Scales on non-foliage branches appressed, thin; foliage leaves with a sharp narrow midrib; mature pollen cones elongated. .... 31. *D. vitiensis*.
    2. Scales on non-foliage branches spreading, thick; mature pollen cone globular (rarely elongated).
        3. Mature foliage leaves with a raised central band narrower than the broad leaf margins; forest tree. .... 32. *D. comptonii*.
        3. Mature foliage leaves with a broad raised central band broader than adjacent leaf margins; small tree at water's edge. .... 33. *D. minor*.
1. Both primary and secondary branches bearing leaves. .... (*D. rospigliosii*).

31. **Decussocarpus vitiensis** (Seemann) de Laubenfels, comb. nov.

Podocarpus vitiensis Seemann, Jour. Bot. **1**: 33. *t. II*. 1863. Type: *Seemann 576*, Fiji.

Podocarpus filicifolius N. E. Gray (in part), Jour. Arnold Arb. **43**: 74. 1962. Type: *Kostermans* in 1949, Morotai.

Tree to 43 m. high; bark brown to red brown, weathering to blackish or gray, fibrous, fissured and peeling in short vertical strips; foliage branches opposite or alternate on non-foliage branches and subtended by a short 1–2 cm. scaly base, sometimes with both lateral and terminal foliage branches together on the same base, the foliage branch not normally branching again; foliage leaves distichous and equally twisted at the base, lanceolate with a small blunt tip, a narrow but distinct rib marking the vascular bundle on both surfaces, juvenile leaves up to 40 mm. long by 8 mm. wide, adult leaves 15–25 mm. long and 3–5 mm. wide; non-foliage branches with appressed and thin scale leaves which are broadly decurrent and dispersed, 1–2 mm. long; pollen cones single and terminal or grouped with terminal and lateral cones together, either one to three at the apex of a foliage branch or one to three at the apex plus opposite pairs of groups of one to three along a scaly branch, cylindrical, 10–24 mm. long and 1.8–2.2 mm. in diam., microsporophylls triangular, about 1 mm. long; one or two ovules subterminal on a scaly shoot, 6–10 mm. long (which may be terminal or axillary on leafy or scaly branches and solitary or grouped); ovule inverted with the micropyle lying close to the attachment of the seed complex with the micropyle at the end of an elongated beak that may extend more than 2 mm. below the attachment, the fertile scale completely enveloping the ovule and forming over the young seed an apical crest which sometimes persists on the mature fruit; mature seed globular, pear shaped, 13–16 mm. long including the curved beak, 8–10 mm. in diam., covered by the deep red fleshy scale and usually accompanied when it falls by the fertile shoot on which some of the scales may still persist.

DISTRIBUTION. Scattered and locally common in a discontinuous series of regions from Morotai to the Fiji Islands in rainforests, from near sea level to 1,800 meters. MAP 12.

Moluccas. Morotai, *Kostermans* (1949) j (L[8]-holotype of *Podocarpus filicifolius*; (A, K-isotypes). **New Guinea.** WESTERN HALF: Wissel Lakes, Mt. Barara, *Eyma 5155* j (L). Wissel Lakes, Motito, *Vink & Schram BW 8730* j 1,800 m. (L). Barnhard Camp (Idenburg R.), *Brass & Versteegh 12534* s 1,200 m. (A, L), *Brass 12787* ♀ 1,200 m. (A, BM, K, L), *12787a* j (A, L), *12912* ♀ (L). Cycloop Mts., *Versteegh BW 913* ♀ 1,100 m. (K, L, LAE), *Van Royen & Sleumer 6073* s 1,220 m. (K, Z). PAPUA: Koroba Station, *Pullen 2840* ♀ 5,300 ft. (LAE). Alola, *Carr 14160* ♂ 6,000 ft. (A, BM, L, NY). Lala R., *Carr 15666* ♂ 5,000 ft. (A, BM, L). **New Britain.** Mt. Tangis, Talasea Dist., *Frodin NGF 26292* j 3,500 ft. (L, LAE), *NGF 26917* s 2,400 ft. (L). Benim, Kandarian Dist., *Henty & Frodin NGF 27359* ♂ 1,000 ft. (L, LAE). Fullerborn Harbor (Kandarian), *Hammermaster & Sayers NGF 21842* ♂ 100 ft. (L). **Santa Cruz Is.** Vanikoro, *Walker BSIP 1580* j (L). **Fiji.** VITI LEVU: Nandarivatu, *Degener 14483* j 750–900 m. (A, K, L, NY, US), *14496* ♀ (A, NY), *Gillespie 3865* ♀ (K, NY, US), *Gibbs 674* ♀, ♂ (BM, K), *Vaughn 3254* j (BM, K), *Mead 1964* j (K), *1974* ♂ (K), *1982* s (K). Nausori, *Damanu NH15* s (K). Namboutini (Serua), *de Laubenfels P309* j 1,000 ft. (A, RSA), *Damanu R10* s (K), *R15* s (K), *R32* s (K), *Qoro & Kuruvoli s.n.* (K). Serua, *Bola 10* s (K), *Damanu NL8* s (K), *NL10* s (K), *NL12* s (K), *G7* s (K), *G20* s (K). Ndakivuna E. of Wainimbuka R., *Smith 7076* s 100–200 m. (US).

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[8] The Leiden specimen is accompanied by an unattached seed of *D. wallichianus*, a species which was also collected in the area by Kostermans. *Podocarpus filicifolius* was based on the presumed pairing of the alien seed with the accompanying leaves (de Laubenfels, 1967).

Naikorokoro, *Damanu KU22* s (K). Galva Forest, *Damanu 152* ♀ (K). VANUA LEVU: Mt. Kasi (Thakaundrove), *Smith 1796* s 300–430 m. (A, K, US). Without loc.: *Seemann 576* j (K-holotype of *Podocarpus vitiensis*; A, BM-isotypes), *Horne 531* s (K), *Tothill 844* s (K), *845* s (K), *Graff 33* s (K).

ILLUSTRATIONS. SEEMANN, B., Jour. Bot. 1: *t. II.* 1863; Fl. Vitiensis, *t. 78.* 1868, as *Podocarpus vitiensis.*

While in most ways typical of the genus of which *Decussocarpus vitiensis* is the type species, the dimorphic foliage, shared by two other species in section *Decussocarpus* is rather unusual, found elsewhere in the family only in *Dacrycarpus* and *Acmopyle.* The compound clustering of the pollen cones is also unusual occuring sporadically among other genera as *Prumnopitys ladei* and *Acmopyle pancheri*, as well as in such genera as *Taxodium* and *Metasequoia* in the Taxodiaceae. The narrow midrib and the not coarse scales and foliage leaves serve to differentiate sterile specimens of *D. vitiensis* from other closely related species. It is of interest to note that *D. vitiensis* broadly overlaps *D. wallichianus* in its distribution; the latter extends throughout New Guinea as well as further west.

32. **Decussocarpus comptonii** (Buchholz) de Laubenfels, comb. nov.

Podocarpus comptonii Buchholz, Bull. Mus. Hist. Nat. Paris. II. **21:** 284. 1949. Type: *Buchholz 1684*, New Caledonia, Mt. Mou.

Tree to at least 30 m. high; bark tan to gray-brown, weathering to gray or dark gray, fibrous, becoming very rough and fissured on older trees, breaking off in short vertical strips or rough fragments; foliage branches opposite or alternate on non-foliage branches or one to several at the apex of an older foliage branch, subtended by one or two pairs of spreading scales; foliage leaves on young plants distichous and equally twisted at the base, lanceolate with a blunt tip, the midrib marked below by a sharp narrow ridge and above by a slight groove, up to 30 mm. long by 6 mm. wide; adult leaves becoming not distichous but still equally turned, coriaceous, the midrib marked by a raised strip narrower than the leaf margins, the edges of the strip when drying appearing as two parallel ridges on both leaf surfaces, ovate-lanceolate, 6–15 mm. long by 2.5–4 mm. wide; non-foliage branches with dispersed spreading scales which are coriaceous, rounded, 1–2 mm. long on young plants and up to 4 mm. long as reduced leaves on fertile specimens; pollen cones single in the axils of foliage leaves, or from one to five or more at the apex of a foliage branch, or in terminal or lateral groups on non-foliage branches (not in compound groups), ovate, 4–6 mm. long (rarely to 12 mm.) and 2.5–3 mm. in diam., microsporophylls short triangular with large spreading edges to the open spore sacs; seed complex terminal on foliage branches or on lateral scaly branches and involving 2–3 decussate pairs of spreading scales or bracts followed by two unequal bracts one of which is fertile, or rarely both are fertile and equal; micropyle of the inverted ovule at the end of an elongated beak extending about 2 mm. below the spreading fertile bract, the fertile scale completely enveloping the ovule and forming an apical crest which sometimes persists on the mature fruit; mature seed globular, pear shaped, about 20 mm. long including the curved beak and 13–15 mm. in diameter, covered by the glaucous fleshy scale some 2–3 mm. thick which ripens dark red and dries over the seed (if not eaten by some bird), the surface of the seed with low scallops and ridges.

DISTRIBUTION. In rainforests throughout New Caledonia mostly from 750 to 1,450 meters, but also lower where lower rainforests occur. Probably the most common conifer in New Caledonia but always scattered in the forest.

New Caledonia. Ignambi, *Compton 1524* s (BM), *1587* ♀ (BM), *Foster 160* j (P), *Hürlimann 1832* j 1,170 m. (P, Z), *1842* ♂ 1,250 m. (P, Z), *Däniker 2902a* s (Z), *Bernardi 10347* s 1,100–1,200 m. (P, Z). Mt. Colnett, *Hürlimann 1966* j (P, Z). Mt. Panié, *McKee 15594* ♀ 1,000–1,400 m. (P), *15639* j 800 m. (P). Mt. Tchingou, *Hürlimann 1220* j 1,250 m. (P, Z). Mt. Paéoua, *McKee 17032* j 900–1,100 m. (P), *17056* ♀ (P), *Bernardi 10131* s (P, Z), *10149* s 900 m. (P, Z). Mt. Boulinda, *McKee 17354* j 1,150–1,300 m. (P), *17357* ♂ (P), *Veillon 120* j 1,100 m. (P). Mt. Me Maoya, *McKee 13037* s 1,350 m. (P), *13492* j 1,400–1,450 m. (P). Ridge W. of Col des Rousettes (Me Maoya), *McKee 9886* ♀ 800–900 m. (K, P). Bourail, below Téné, *Balansa 1381* ♀ (K, P). Mt. Nekandi (Thio), *McKee 17908* j 1,200 m. (P). Dent de St. Vincent, *LeRat 11* j (P). Mt. Humboldt, *Schlechter 15331* ♂ 1,400 m. (BM, K, P, Z), *15332* ♀ (P), *Buchholz 1578* s 1,300 m. (ILL), *Baumann-Bodenheim 15393* s 1,400 m. (P, Z), *15411* s (Z). Mt. Mou, *Vieillard 3264* ♀ (GH, K, P), *Virot 8* j (A, P), *38* j (A, P), *s.n.* j (A, P), *White 2033* ♂ (A, K, P), *Buchholz 1085* j (ILL, K, P), *1449* ♀ (ILL, K, P), *1449S* j (P), *1452* s (ILL, K), *1684* ♀ (ILL-holotype; K-isotype), *1684S* j (ILL, P), *1791* ♀ (ILL), *de Laubenfels P129* ♂ 1,140 m. (SBT), *P360* s (A, RSA), *P361* j (A, RSA), *Skottsberg 202* j (P), *Alleizette 492* ♀ (P), *McMillan 5015* ♂ (P), *Däniker 2902* j (P, Z), *McKee 3516* j (A, P), *Baumann-Bodenheim 5654B* s (Z), *Baumann-Bodenheim & Guillaumin 11257* s (P, Z), *11261* s (P, Z), *11282* s (P, Z), *11299* s (P, Z), *11301* s (P, Z), *Bernardi 9879* s (P, Z), *Blanchon 341* s (P). Couvelée, *Brousmiche 697* s (P). Mt. Dzumac, *de Laubenfels P153* ♀ (SBT), *P415* ♀ 760 m. (A, K, RSA), *Baumann-Bodenheim & Guillaumin 12725* j (P, Z), *12727* j 1,000 m. (P, Z), *Aubréville & Heine 229* ♀ (P), *Barets 8* j (P), *Bernardi 9520* ♀ 800–900 m. (P). Upper Ouinné Valley, *Bernier 267* j 750 m. (P), *268* ♀ (P), *Baumann-Bodenheim & Guillaumin 12815* s 700 m. (Z), *12843* s 700 m. (Z), *12861* s (Z), *12960* s 900 m. (Z). Upper Dumbéa Valley, *Hürlimann 1062* s 730 m. (P, Z). Mt. des Sources, *Bernier 271* j (P), *Buchholz 1222* j 950 m. (ILL, K, P), *de Laubenfels P123* ♂ 1,000 m. (SBT), *Hürlimann 931* j 800 m. (P, Z), *1573* j 530 m. (P, Z), *Bernardi 9445* ♀ 600 m. (P, Z). Bois de Mois de Mai (Walker's Place), *Bernier 203* ♀, j (P), *269* j (P), *270* s (P), *Buchholz 1350* s (ILL, K, P), *1350A* j (ILL, K), *1359* j (ILL, K, P), *1359A* j (K, P), *1367* s (ILL), *1697* ♀ (ILL, K, P), *Baumann-Bodenheim 14057* s (P, Z), *15178* s (P, Z), *15197* s (P, Z). Bois Electrique, *Hürlimann 3173* ♀ (Z). Upper R. Bleue, *Baumann-Bodenheim 15028* s (P, Z). Inland from Bay of Pirogues, *White 2120* j (A). Without loc. *Sarlin 228* j (P), *Baudouin 552* j (P).

ILLUSTRATION. SARLIN, P., Bois et Forêts de la Nouvelle-Calédonie, *t. 26.* 1954, as *Podocarpus comptonii.*

The juvenile form of *Decussocarpus comptonii* has a great deal in common with the adult form of *D. vitiensis* and the ecology of the two is identical. The adult form of *D. comptonii* is in a number of ways different from its juvenile form. The fact that *D. comptonii* is strictly endemic to New Caledonia while *D. vitiensis* extends for several thousand miles and both to the east and to the west of New Caledonia is a clear illustration of the curiously isolated flora of New Caledonia. There are many closely related species of conifers between the two areas mentioned, but none are common to the two.

33. **Decussocarpus minor** (Carrière) de Laubenfels, comb. nov.

Nageia minor Carrière, Traité Conif. ed. 2. 641. 1867. Type: *Vieillard 1275*, New Caledonia, Lake Arnaud.
Podocarpus minor (Carrière) Parlatore in DC. Prodr. **16**(2): 509. 1868.
Podocarpus palustris Buchholz, Bull. Mus. Hist. Nat. Paris. II. **21**: 284. 1949. Type: *Buchholz 1421*, New Caledonia, Plaine des Lacs.

Small tree or shrub 2–3 m. high; bark tan to dark brown (often stained with iron oxide from flood waters), very rough, fissured, fibrous, slightly scaly, breaking off in short thick vertical strips or ragged fragments; foliage branches opposite or alternate on non-foliage branches or single to grouped at the apex of an older foliage branch, subtended by one or two pairs of spreading scales; juvenile leaves distichous, equally twisted at the base, not crowded, lanceolate, the midrib marked by a broad raised area that may appear as three ridges when dry, up to 39 mm. long by 3–4.5 mm. wide, on young plants smaller, more crowded, not distichous but still equally twisted; mature foliage leaves almost imbricate and crowded but still (in part) with a slight equal turning, coriaceous, the midrib marked by a broad raised area, wider than the not raised margins (the raised area upon drying either irregularly wrinkled or appearing as three ridges), ovate, blunt, 7–20 mm. long by 2.5–5 mm. wide; non-foliage branches with dispersed spreading scales which are thick, rounded, 1.5–2.5 mm. long, smaller on juvenile specimens; pollen cones solitary or clustered up to five or more, terminal and lateral in the axils of spreading scales on a deciduous shoot at the apex of foliage branches, ovate, 4–8 mm. long by 2–2.5 mm. in diam., microsporophylls triangular with an elongated point; seed complex terminal on foliage branches and involving 2–3 decussate pairs of crowded spreading scales or bracts fol-followed by two unequal bracts one of which is fertile (or rarely both fertile and equal); micropyle of the inverted ovule at the end of a blunt beak which extends up to 2 mm. below the fertile bract, the fertile scale completely enveloping the ovule and forming an asymmetrical apical crest which persists on the mature fruit; mature seed globular pear-shaped, about 20 mm. long including the curved beak and 11–12.5 mm. in diam., covered by the glaucous fleshy scale which sometimes becomes deep red when ripe and after drying tends to crack and flake off the seed (which may persist on the tree for some time or break off anywhere from the base of the fertile bract to the base of the fertile shoot), surface of the seed rough and porous (making it very buoyant).

DISTRIBUTION. Along lake and river banks in shallow water over soils derived from serpentine, in the headwaters of the Yaté River and along small streams closer to the coast in the southernmost part of New Caledonia, at low elevations (up to 200 meters).

New Caledonia. Pirogues R., *White 2261* ♀ (A, K, P, US). R. Blanche (Mois de Mai), *McMillan 5120* s 600 ft. (A, K, P), *Baumann-Bodenheim 13923* s (P, Z). Upper Yaté R. (22 km. station), *Bernier 204* ♂, j (P), *245* ♀, j (P), *251* s, j (P), *Buchholz 1347* s (P), *1348* ♀ (ILL, K, P), *1421* ♀ (ILL-holotype of *Podocarpus palustris*; K, P-isotypes), *1705* j (ILL, K, P), *Sarlin 73* ♀ (P), *de Laubenfels P112* ♀, ♂, j (SBT), *P160* ♀ (SBT), *Foster 200* ♂ (P). Marais Kiki (Yaté R.), *McKee 1118* s (A), *1119* ♀ (A, P), *Baumann-Bodenheim 6370* j (Z), *Hürlimann 3157* j (Z). Creek Pernod, *Guillaumin 8339* j (Z), *8345* ♀ (Z), *Blanchon 1160* ♂ (P). R. des Lacs, bridge, *Thorne 28565* ♀ (GH, P), *Baumann-Bodenheim & Guillaumin 6511* ♂ (Z), *6580*, j (P, Z), *6766* ♀ (P, Z), *Hürlimann 3113* s (Z). R. de Lacs (near Madeleine Falls), *Bernier 125* j (P), *246* s (P), *249* s (P), *250* ♂ (P), *Le Rat 2587* ♀ (P), *Buchholz 1474* ♀ (ILL), *1719* ♀ (ILL), *1729* ♀ (ILL, K, P), *Däniker 228* ♀ (P, Z), *228a* ♀ (Z), *de Laubenfels P340* ♀ (A, RSA), *P340A* ♂ (A, RSA), *Baumann-Bodenheim & Guillaumin 11749* s (P, Z), *11811* s (P Z), *Stauffer 5807* ♀ (P, Z), *Blanchon 736* s (P). Plaine des Lacs in general, *Le Rat 607* ♀ (BM, P), *751* ♀ (P), *1040* ♀ (K, P), *2621* ♀ (P), *McMillan 5139* ♂ 600 ft. (A, K, P), *Baumann-Bodenheim & Guillaumin 6582* j (P, Z), *6594* s (P, Z), *Aubréville & Heine 130* ♂ (P), *170* ♂ (P). Lac en Huit, *de Laubenfels P115* ♀, ♂ (SBT), *McKee 3382* ♀ (A, P, US), *Rohrdorf 178* ♀ (Z), *Bernardi 9369* ♂ (P, Z). Grand Lac, *Virot 658* s (A, P). Plaine des Lacs, lake bank, *Franc 207* s (A, BM GH, K, P, US, Z). L. Arnaud, *Vieillard 1275* ♂ (P-holotype of *Nageia minor*). La Chute, *Blanchon 208* s (P). Prony Bay (B. du Sud), *Vieillard 1275* (apparently not the same as the previous collection of the same number) ♂ (A, BM, GH, K, NY, P), *Pancher* (1864) ♀ (P), *Balansa 186* ♀ (P). *Le Rat 149* ♀ (P). Carenage, *McKee 2573* s just above the sea (P). R. du Kaoris (Prony), *Bernier 247* s 30 m. (P). Kue [Koue] Bay, *Cribs 1493* ♀ (P). Without loc., *Deplanche 170* s (P), *Raoul s.n.* s (P), *Petit 138* ♂ (P), *Brousmiche s.n.* s (P), *Baumann-Bodenheim 6378* s (P).

ILLUSTRATION. SARLIN, P., Bois et Forêts de la Nouvelle-Calédonie, *t. 27*. 1954, as *Podocarpus palustris*.

The peculiar habit of this species which grows in shallow water with a swollen base to the trunk (somewhat like a bald cypress), immediately sets it apart. In general morphology it strongly resembles *Decussocarpus comptonii*, but close inspection reveals a different leaf morphology and slight differences in the pollen cone and the seed. This general similarity prevented the recognition of *D. comptonii* as a species for many years.

ADDITIONAL SPECIES:

Decussocarpus rospigliosii (Pilger) de Laubenfels, comb. nov.

Podocarpus rospigliosii Pilger, Notizbl. Bot. Gard. Berlin **8**: 273. 1923. Type: *Esposto 556*, Peru, Oxapampa (not seen, A photo.).

Section **Dammaroides** (Bennett) de Laubenfels, comb. nov.

Podocarpus section *Dammaroideae* Bennett ex Horsfield, Pl. Jav. Rar. 41. 1838. Type species: *Podocarpus latifolia* Wallich [*Decussocarpus wallichianus* (Presl) de Laubenfels].

Podocarpus section *Nageia* Endlicher, Syn. Conif. 207. 1847. Type species: *Podocarpus nageia* R. Br. [*Decussocarpus nagi* (Thunb.) de Laubenfels].

Leaves opposite decussate or subopposite, multiveined with the veins converging to the apex, obovate to elliptic, acute, distichous, rather large; terminal buds small, bud scales acute; pollen cones linear, solitary or grouped in the axils of leaves; seed cone on a scaly shoot with one or two subterminal bracts fertile; ovule inverted and enveloped by the fleshy fertile scale; seed globular with a slight protrusion at the micropylar end close to the spreading fertile bract but on the opposite side from the fruit attachment.

The multiveined leaves immediately distinguish section DAMMAROIDES from the remainder of the genus but, without fruit, trees of this group are very similar to the genus *Agathis* of the Araucariaceae. These are distinguished by their globular terminal buds quite different from the acute scales of buds in the section DAMMAROIDES. It has been customary for some time to call this section *Nageia*, ignoring Bennett's name apparently because he used an improper ending. Bennett described his section quite adequately and both Pilger (1903) and Wasscher (1941) refer to his name without comment. Gordon (1858) and others treated this section as a genus, *Nageia* Gaertner, a name which if accepted would have priority not only for the genus being proposed here, but also in the genus *Podocarpus* (if the section were to be retained in that genus). Indeed, Kuntze (1891) did substitute *Nageia* for *Podocarpus* but Pilger (1903) pointed out that the original description of *Nageia* confused its characters with those of *Myrica* ("stam. quattuor et styl. duo.") and, therefore, the name must be rejected.

There are five species differing in the presence or absence of a fleshy receptacle, the number and position of the pollen cones, and the orientation and size of the leaves.

KEY TO THE SPECIES OF SECTION DAMMAROIDES

1. Seed with a fleshy receptacle.
    2. Pollen cones grouped on a peduncle; leaves at least 6 cm. long. .... 34. *D. wallichianus.*
    2. Pollen cones solitary, sessile; leaves usually less than 5 cm. long (rarely to 7.5 cm.). .... 35. *D. motleyi.*
1. Seed lacking a fleshy receptacle.
    3. Leaves amphistomatic and equally turned, 20–31 cm. long. .... 36. *D. maximus.*
    3. Leaves hypostomatic and unequally turned, less than 20 cm. long.
        4. Pollen cone cluster sessile; leaves at least 9 cm. long. .... 37. *D. fleuryi.*

4. Pollen cone cluster on a peduncle; leaves usually less than 6 cm. long (rarely to 9 cm.). . . . . 38. *D. nagi.*

34. **Decussocarpus wallichianus** (Presl) de Laubenfels, comb nov.

Podocarpus latifolia Blume, Enum. Pl. Javae **1**: 89. 1827, *nomen illegit.*, non (Thunb.) R. Br. Type: *Blume s.n.*, Java, Mt. Salak.

Podocarpus latifolia Wallich, Pl. As. Rar. 26. 1830, *nomen illegit.* Type: *Wallich 6050*, India, Mt. Sillet.

Podocarpus wallichianus Presl, Bot. Bemerk. 110. 1844, based on *Podocarpus latifolia* Wall., which is a later homonym.

Podocarpus blumei Endlicher, Syn. Conif. 208. 1847, based on *Podocarpus latifolia* Blume.

Podocarpus agathifolia Blume, Rumphia **3**: 217. 1849, based on *Podocarpus latifolia* Blume.

Nageia blumei (Endl.) Gordon, Pinetum 135. 1858.

Nageia latifolia (Wall.) Gordon, *ibid.* 138.

Nageia wallichiana (Presl) Kuntze, Rev. Gen. Pl. 800. 1891.

Podocarpus latifolia Blume forma *ternatis* De Boer, Conif. Archip. Ind. 14. 1866. Type: *Teysmann s.n.*, Moluccas, Ternate.

Tree up to 48 m. high; bark smooth, peeling in large, thin, very irregular plates, tan to brown within, weathering to dark brown or gray and developing scattered large lenticels and irregular longitudinal markings; leaves decussate, distichous, amphistomatic, equally turned so that the lower surface is exposed on the left and the upper surface is exposed on the right side of the branch, many parallel vascular veins, elliptic, acute to acuminate, sometimes abruptly narrowed to the short (5–10 mm.) petiole, mostly 9–14 cm. long by 3–5 cm. wide but sometimes smaller to 6 cm. long and 2 cm. wide or (particularly for juvenile and shade leaves) up to 23 cm. long and 6.8 cm. wide, the extreme sizes (both smaller and larger) mixed with more usual sizes on the same tree (both extreme width and extreme length not usually together, the ratio of length to width varying from 2 to 6, so that the narrowest leaves are not usually the shortest while the longest are not usually the widest); terminal buds often 2–3 mm. beyond the last pair of leaf bases (lateral buds sessile), abruptly but slightly wider than the stem and then tapering, bud scales acute-acuminate and erect; pollen cones 1–7 on an axillary scaly peduncle 2–10 mm. long with one cone terminal and the remainder in decussate pairs, cylindrical, 8–18 mm. long by 3–4 mm. in diam., microsporophylls lanceolate, 2–3 mm. long; seed cone on an axillary scaly peduncle, 8–20 mm. or more long, the lanceolate scales deciduous as on the pollen cone peduncle; receptacle enlarged and becoming blackish and very fleshy upon maturing, 7–18 mm. long, composed of 4 to 7 sterile bracts, the curled ends of which protrude from the receptacle, and 1 or 2 subterminal fertile bracts with inverted ovules; seed smooth, globular with a small beak next to the point of attachment, completely covered by the thin fertile scale which accompanies the ripe seed, 15–18 mm. in diam.

DISTRIBUTION. In rainforests from eastern India to Normanby Island east of New Guinea, often as a common forest element at low elevation and extending as high as 1,575 meters (one collection at 2,100 meters). MAP 13.

India. Mt. Sillet, *Wallich 6050* ♂ (A-isotype of *Podocarpus latifolia* Wallich). E. Bengal, *Griffith 3005* ♂ (GH, P). Khasia, *Hooker & Thompson s.n.* s 3,000 ft. (A, L), *Apan 191* ♀, ♂ (GH). Assam, *King s.n.* ♂ (A, L, US). **Thailand.** Tenasserim, *Falconer s.n.* s (L). Kao Luang, N. Stritamurat, *Kerr 15445* s 600 m. (K). Tamtieng, Ranaung, *Kerr 11770* ♀ 200 m. (K). Kapor, Ranaung, *Kerr 16703* ♀ 50 m. (K). Kumpuam, Ranaung, *Kerr 16864* ♀ 50 m. (K). Kuabun, Ranaung, *Kerr 16351* s 50 m. (K). Lem Dan, Kaw Chang, *Rabil 19* s (K). Klaung Non Si, Kaw Chang, *Kerr 9324* s 10 m. (K). Kao Kuap, Kuat, *Kerr 17714* s 500 m. (K). Kao Ri Yai, Kanburi, *Kerr 10400* s 1,400–1,500 m. (K). Baw Rai Kinat, *Kerr 9509* s 300 m. (K). Adang, Sulut, *Kerr 14132* s 500 m (K). Khas Yai, 105 km. E. of Saraburi, *King 555A* ♀ 780 m. (L). **Laos.** Pak Munung, Wengchau, *Kerr 21215* ♂ 1,400 m. (K, P). **Cambodia.** Phnom San Kas, *Müller 499* s (P). Elephant Mts., *Poilane 23216* s 200 m. (P). Kre-dek, *Poilane 14664* s 600 m. (P). **Cochin China.** Phu Quoc I., *Pierre 5529* s (A, NY, P), *5530* ♀ (A, P). **Annam.** Vinh, Linhcam, *Chevalier 38234* s (P); Ke Bon, *Chevalier 38127* s (P). Quang-nam (S. of Da Nang), *Poilane 31558* s 500 m. (P). Massif Ngok Guga near Dakto, *Poilane 35675* s 1,000 m. (P). Massif du Brian near Djiring, *Poilane 24234* s (P), *24314* s 1,500 m. (P). Phan Rang (Can-Wa), *Poilane 5963* ♀ 900 m. (A, P). W. of Ca Na, *Evrard 2422* s 1,200 m. (A, NY, P). **Malaya.** Jerai Reserve, Kedah, (*Mal.*) *17848* s (K). Kledang Saiang Reserve, Perak, *Mead 12828* ♀ (K), *Noakes 20133* ♀ (K), *22147* s (K). Kinta, Perak, *Low 64* ♀ (K). Perak, *Scortechini s.n.* j (A). Kebal Ayam, Kurantan, Pahang, *Loh 15065* s (K). B. Soga, Johore, *Ridley 11223* s (K). Labis, *Sinclair 38991* s (L). Johore, G. Pulai, *Sinclair 10578* j (K, L, NY). **Sumatra.** Mt. Sibajak, E. Coast, *Lörzing 7336* ♂ 1,200 m. (L), *11664* s 400–425 m. (L), *15531* ♂ 1,350 m. (L). Karo Plateau, Mt. Siosar, *Lörzing 8628* s 1,575 m. (L), *15657* s 1,525 m. (L). Bandar Betsy, Simelungun, *NIFS bbE1352* j 50 m. (L). E. Coast near Kisaran, *Krukoff 238* j (A, NY, US). E. Coast, Asahan, *Yates 2554* ♀ (A, NY). *Boeea 6255* j (A, L), *Bartlett 8108* s (US). Tapanuli, Sibolga, *NIFS bb1357* j 5 m. (L). Tapanuli, Angkola, *NIFS bb31536* s 600 m. (L). Benkulen, Redjang, *Endert bbE1084* s 800 m. (L), *Renwarin bb2450* ♀ (L), *NIFS bb8842* s 900 m. (L). Palembang, Banjuasin, *NIFS bbE1106* s 15 m. (L). Palembang, Pasemah land, *NIFS TB200* s 1,200 m. (L). Palembang, G. Pakiwang (Ranau L.), *Van Steenis 3754* s 1575 m. (L). **Java.** G. Lajung, *Koorders 1261* s 150–250 m. (L). G. Salak (Batavia), *Anon.* (1845) s (L), *Koorders 24181* s 1,000 m. (L). Preanger, Parakan Salak, *Koorders 39402* s (K, L), *39403* s 1,000 m. (A), *39404* s (L), *39406* s 1,100 m. (A), *39407* s 1,350 m. (A), *39409* s 1,000 m. (L), *39413* s 1,000 m. (L), *39415* s (A). G. Megamendong, *Junghuhn s.n.* s (L). G. Pangarango, *Junghuhn s.n.* ♀ 3,000 ft. (L). G. Gedeh, *Anon. 204* s (L), *Hasskarl 346* ♂ (L). Takokak, *Koorders 1262* s (L), *1264* s (L), *11909* s (L), *39592* s 1,200 m. (A), *39596* s (A, L). Preanger, Tjipatudja, *Backer 8866* s 450 m. (L). Without loc., *Blume s.n.* ♀ (L-lectotype, *Podocarpus latifolia* Blume), *s.n.* s (L), *Hasskarl s.n.* j (L), *Junghuhn s.n.* s (L), *Miquel s.n.* ♂ (L). **Karimata.** Sung Tajan, *Teysmann 11598* s (L). **Billiton.** *Riedel* (1876) ♀ (FI). **Sarawak.** Lundu, G. Gading, *Anderson 15391* ♀ 2,600 ft. (K, L). B. Mersing, in from Tatau, Luang *S22176* ♀ 900 m. (K). Bintulu, Merurong Plateau, *Brunig S9999* s 820 m. (L). Lawas, *Brunig S12083* s 1,000 m. (L). Mt. Majan, *Clemens 21822* j (NY). **North Borneo.** Penampang, *Leaño-Castro 5989* s, 5,000 ft. (K, L). Mt.

Kinabalu, *Clemens s.n.* j 7,000 ft. (NY), *Chew & Corner RSNB 4878* ♀ 5,000 ft. (K). Elopura, Sandakan, *Keith A7* s 10 ft. (K). Gompa, Kudat, *Balajadia 4055* s sea level (K). Tawau, *Ampon A1652* ♀ (K, US), *Martyn SAN 18453* ♀ 50 ft. (K, L, NY), *Meijer SAN 19547* s 30 ft. (L). Without loc. *Wood 1244* j (A, K), *s.n.* s (US), *Burbridge s.n.* j (K). **Borneo.** Tidung's Land (SE. Borneo), *NIFS bb18217* s 4 m. (A, L). G. Beratus (Balikpapan), *Kostermans 7464* s 900 m. (A, L), *7486* ♀ 900–950 m. (A, K, L). Samarinda, *Kostermans* (1956) ♂ low (L). Mahakam, *Amdjah 51* j (L). Mt. Palimasen (Cent. Kutei), *Kostermans* (1954) ♂ 900 m. (K, L). **Philippines.** Cagayan, *Curran 16738* ♀ (US), *17200* ♀ (NY, US). Mt. Sulu (Apayao Subprov.), *Fenix 28348* ♀ (A, NY, US). Mt. Moises (Isabella), *Ramos & Edaño 46333* ♀ (A, NY). Baguio, *Williams 1035* s (K, NY, US). Lamao R., Mt. Mariveles (Bataan), *Williams 399* s 2,200 ft. (NY, US), *624* ♀ 3,000 ft. (NY), *752* ♀ 2,000 ft. (NY), *753* ♀ 1,800 ft. (A, K, NY, US), *Barnes 147* ♀ (K, NY, US), *194* ♀ (K, NY, US), *Copeland 244* ♀ (K, NY, US), *Whitford 1353* ♀ (K, NY, US), *Curran 17616* s (L). Mt. Giting-Giting, Sibuyan I., *Elmer 12360* ♀ (A, K, L, NY, US). **Celebes.** Usu (Malili), *NIFS Cel/III–80* s (A, K, L), *Cel/III–143* s 10 m. (A, L), *Cel/III–146* s 25 m. (K). Tebetano (Malili), *NIFS bb24489* j 450 m. (A, L). Tawingana (Malili), *NIFS bb25541* s 120 m. (L). Tamborano (Malili), *NIFS bb9696* s 600 m. (L). Gorontalo Buladu (Manado), *NIFS bb15602* s 400 m. (L). Poso, Majoa (Manado), *NIFS bb31500* s 700 m. (L). Manado, Kolonodale, Bakomtefe, *NIFS bb31506* s 100 m. (A, L). Lapo Lapo, SE. of Kandari, *Beccari* (1874) s (FI). **Moluccas.** Obi, *Ahasrip 118* s (K, L, NY). Ternate, *Teysmann s.n.* j (L-holotype of forma *ternatis*). Morotai, *Kostermans 1660* s 50 m. (A, L). W. Ceram, *NIFS bb19647* s (L). **New Guinea.** VOGELKOP: Warsamson Valley (E. of Sorong), *Moll BW 11652* s 30 m. (L). Kebar Valley, Tobie, *Schram BW 7951* s 740 m. (L), *Smit BW 2314* s 650 m. (L), *Sijde BW 5579* s 750 m. (L). Nertoi, Kebar Valley, *Mangold BW 2350* ♀ 750 m. (L). Kebar Valley, *Van Royen 5058* ♀ 550–700 m. (K, L). Sidai (W. of Manokwari), *Schram BW 1785* s (L), *BW 6174* s 5 m. (L), *Koster BW 6705* s (L), *BW 6760* ♀ 10 m. (K, L), *BW 6922* s 10 m. (L), *BW 6977* s 5–10 m. (L). Manokwari, *Menusefer BW 8180* ♀ 140 m. (L). Baru (Teminabuan), *Hallewas BW 944* s 10 m. (L). Beriat (S. of Teminabuan), *Schram BW 6021* ♀ 10 m. (L). SERUI: Biak, *NIFS bb30717* s 50 m. (A, L), *bb30779* s 80 m. (A, L), *bb30813* ♀ 50 m. (A, L), *bb30887* s 50 m. (L), *Moll BW 9574* s 35 m. (L), *BW 9589* s 35 m. (L). Mios Num. I., *NIFS bb30939* s 200 m. (A, L), *bb30947* s 200 m. (A, L), *bb30961* s 200 m. (A, L). Japen, Sumberaba, *Koster BW 11121* s 8 m. (L). Japen, Aisao, *Schram BW 10596* s 200 m. (L). Japen, *NIFS bb30260* s 300 m. (L). WEST: Armina (Babo), *Moll BW 12968* s (L). Agondo (Babo), *Lundguist bb32983 (264)* s 20 m. (K, L). Esania, Borowai (Fak Fak), *Stefels BW 3147* s 20 m. (L). Tiwara, Arguni Bay, *Telussa BW 5158* s (L). Tairi, Kaimana, *Loupulua BW 5140* ♀ 230 m. (L). Najaja (Uta), *Lundguist bb32845 (126)* s 3 m. (K, L). Djera, near Uta, *Aet 271* s (L). CENTER: Barnhard Camp, *Brass & Versteegh 13175* ♀ 850 m. (A), *13555* ♀ 150 m. (A, L). Cycloop Mts., *Koster BW 4301* s 500 m. (L). Muju Subdiv. (near Papua, S. edge of mts.), *Kalkman BW 8502* ♀ 120 m. (L). TERR. NEW GUINEA: Yambi Yambi, Sepik, *Womersley NGF 3704* s (K). Sepik, *Ledermann 9027* s (K). Mt. Salall, Passir (Madang), *Zollinger 3025* s (A, FI). Oriemburg, *Clemens 1231* s 2,500 ft. (A, L, Z). Sattleberg, *Clemens 2172* s 2,000 ft. (A, Z). Near Lae, *Womersley NGF 17621* ♀ 500 ft. (K, L). Gabensis (Lae), *NGF W41* j (A). PAPUA: Fly R., *D'Albertis* (1877) s (FI). L. Daviumbu (Middle Fly), *Brass 7909* s (A, L). Sibium Range, *Pullen 5932* s 2,300 ft. (L). Oriomo R., *Hart 5005* ♀ (A, K, L), *Brass 5878* s (A, K, L, NY, US), *5880* j (A, NY, US), *5906* s 5–10 m. (A, NY), *White & Gray*

NGF 10415 ♀ 70 ft. (K, L). Sogeri, in from Port Moresby, *Forbes 911* s (L), *Anon. NGF 4503* j (A, K, L). Ramoi, *Beccari 365* ♀ (FI). Maipa (Kairuku), *Darbyshire 971* ♀, j 200 ft. (K, L), *Saunders 1088* s (L). Dieni, Ononge Road (Cent. Div.), *Brass 3962* j 500 m. (A, NY). Milne Bay Dist., *Womersley NGF 19298* ♀ 1,200 ft. (K, L). Normanby I., *Brass 25824* j 600 m. (A, L).

ILLUSTRATIONS. BLUME, C. L., Rumphia **3**: *t. 173.* 1849 (as *Podocarpus agathifolia*); PILGER, R., Pflanzenreich IV. **5** (Heft 18): *fig. 9A* (as *Podocarpus wallichianus*) & *fig. 9B* (as *Podocarpus blumei*). 1903; Nat. Pflanzenfam. ed. *2.* **13**: *fig. 134A* (as *Podocarpus wallichianus*) & *fig. 134B* (as *Podocarpus blumei*). 1926; KOORDERS, S. H., & TH. VALETON, Atlas der Baumarten von Java **3**: *t. 588.* 1915 (as *Podocarpus blumei*).

Podocarpus wallichianus and *P. blumei* have generally been treated as distinct species but are here being united under the name *Decussocarpus wallichianus*. Wasscher (1941), who treated *Podocarpus blumei*, analyzed the two taxa and concluded they were probably the same. The differences reported, as thickness of leaf and acuminate leaf tip, are variations that may occur even on a single plant depending on age and exposure. Further, considerable variation in leaf dimensions are frequently found on single herbarium sheets. By comparing the predominant sizes within any region, it appears that this species is, in fact, rather consistent throughout its considerable range.

35. **Decussocarpus motleyi** (Parlatore) de Laubenfels, comb. nov.

Dammara motleyi Parlatore, Enum. Sem. Hort. Bot. Mus. Florent. 26. 1862. Type: *Motley 1300*, Borneo, Bandjarmasin.
Podocarpus beccarii Parlatore in DC. Prodr. **16**(2): 508. 1868. Type: *Beccari 2649*, Sarawak, near Kuching.
Nageia beccarii (Parlatore) Gordon, Pinetum **2**: 186. 1875.
Agathis motleyi (Parlatore) Warburg, Monsunia **1**: 185. 1900.
Podocarpus motleyi (Parlatore) Dümmer, Jour. Bot. **52**: 240. 1914.

Tree up to 40 m. high; leaves opposite or subopposite, amphistomatic, distichous, coriaceous, elliptical, acute or with a small acuminate tip, narrowed at the base to a short thick petiole 2–3 mm. long, somewhat variable in shape, usually 3–5 cm. long and 15–22 mm. wide but reaching 7.5 cm. long and 28 mm. wide; terminal buds compact, tapering at first, the scales rounded to lanceolate, acute to acuminate, 3–5 mm. long; pollen cones axillary, solitary, sessile, cylindrical, 15–20 mm. long when mature and 5–6 mm. in diameter; microsporophylls lanceolate, keeled, 2 mm. long; seed cone on an axillary scaly peduncle 2–5 mm. long with 3–4 pairs of decussate deciduous scales, receptacle becoming fleshy (on some specimens with nearly fully developed seed there is no enlargement), 8–12 mm. long, composed of 5 to 9 spreading sterile bracts, the single subterminal fertile bract with an inverted ovule covered by the fertile scale; seed smooth, globular, with a small beak at the micropylar end near the point of attachment, 13–16 mm. in diam.

Distribution. Mostly in low poorly drained areas but extending to 500 meters elevation in rainforests, from Sumatra and Malaya to the southern part of Borneo. Map. 14.

Malaya. G. Tebu (Trengganu), *Sinclair & Salleh SFN 40798* s (L). Lumut, Dindings (Perak), *Hadden 16554* ♀ (K), *Symington 27841* s (K). Legari Melintang, Dindings, *Strugnell 16568* s (K). Johore, S. Kayu, Mawai-Temulang Road, *Corner 21341* s (K). **Sumatra.** Barus (Sibolga), Tapanuli, *NIFS bb29532* s 25 m. (A, L), *bb31596* s 1 m. (A, L). Near Banjunglintjir, Palembang, *NIFS 12T1P13* ♂ 15 m. (L), *12T1P185* ♀ 15 m. (L), *Thorenaar 12T13* s (L), *Grashoff 874* ♂ 20 m. (L). Rawas, Palembang, *Grashoff 1138* ♀ 150 m. (L). Riau Arch., Karimon, *NIFS bb17229* s 150 m. (A, L). Belimbing, *NIFS bb28495* s 6 m. (A, L). **Sarawak.** Near Kuching, *Beccari 2649* ♀ (FI-holotype of *Podocarpus beccarii*; K-isotype). G. Perigi (Lundu), *Anderson 13304* ♂ 1,000 ft. (A, K). Simunjan, *Drahman S0316* s sea level (L). Without loc., *Foxworthy 353* ♀ (K). **Borneo** (SE. part). Tidung's Land, S. Lebakis, *NIFS bb18328* s 5 m. (A, L). Bandjarmassing, *Motley 1300* s (K-isotype of *Dammara motleyi*). Puruk Tjahu, Tahudjan, *NIFS bb21151* ♀ 500 m. (A, L).

Illustration. Wasscher, J., Blumea **4**: *t. 4, fig. 11.* 1941, as *Podocarpus motleyi*.

The extremes of leaf sizes in *Decussocarpus motleyi* and *D. wallichianus* approach each other and the latter occurs throughout the range of the former so that the possibility of confusion exists. The pollen cones are diagnostic and the terminal buds lying directly above the last leaf attachment help to differentiate the two. By observing the most common leaf sizes of a tree (or even a specimen), however, the species can be readily separated. The lack of enlargement of the receptacle on some specimens (see *NIFS 12T1P185*) merits further observation.

36. **Decussocarpus maximus** de Laubenfels, sp. nov.

Arbor parva, 4.5 m. alta; folia magna, decussata, coriacea, elliptica, acuminata, basi magis rotundata, in petiolum perbrevem angustata, 20–34 cm. longa, 6–9 cm. crassa; gemmae parvae, acuminatae; strobili feminei ramunculum axillarem 12 mm. longum formantes; squamae ramusculi decussatae, 3–4 mm. longae, deciduae; receptaculum nullum; semen globosum, diametro ca. 16–18 mm. Holotypus: *Anderson 3361/7* (L), Sarawak, Sibu. Fig. 10.

Distribution. In low elevation swamp forest of Sarawak and possibly Sumatra.

Sarawak. Sg. Assan, Naman F. R. (Sibu), *Anderson 3361/7* ♀ 12 ft. (L-holotype; K-isotype). **Sumatra.** Silo Maradja (Ashan), *Bartlett 6805* s (K, L, NY, US). Between Djuma Tombak and Taratak, Tanah Djawa (Simelungun), *Bartlett 8226* s (NY, US). Bangka, Sungei liat, *Teysmann s.n.* s (L).

Decussocarpus maximus is unique in the genus in combining a lack of a fleshy receptacle with amphistomatic leaves, although, as mentioned above, some specimens of *D. motleyi* with very small leaves may also

FIGURE 10. *Decussocarpus maximus* de Laubenfels, photograph of the holotype, *J. A. R. Anderson 3361/7* (L).

combine these characters. The leaves of *D. maximus* are without question the largest of any conifer, being approached at their lower limits by juvenile leaves of *D. wallichianus* and of various species of *Agathis*. The largest leaves described above belong to a fertile specimen. Aside from leaf size, the leaf form and terminal buds correspond to *D. wallichianus* but the seed is produced on a shoot that is not fleshy. The range of *D. maximus* is included within the range of closely related species and the Sumatra specimens, being sterile, are distinguished by their leaf size only (*Bartlett 6805*: 15–20 by 6.5–9 cm. and blunt, possibly from damage; *Bartlett 8226* and *Teysmann* (Bangka): 20–22 by 7–8 cm.). In having neither hypostomatic leaves nor a fleshy receptacle, *D. maximus* (and perhaps a part of *D. motleyi*) exemplifies best, among the species in section *Dammaroides*, the special characteristics of the genus.

37. **Decussocarpus fleuryi** (Hickel) de Laubenfels, comb. nov.

Podocarpus fleuryi Hickel, Bull. Soc. Dendrol. France **75**: 75. 1930. Lectotype: *Fleury 38017*, Tonkin, Phu Tho.[9]

Tree to at least 10 m. high; leaves opposite, decussate, coriaceous, hypostomatic with unequal turning so that the upper surface of the leaf is always uppermost, elliptic, acuminate, narrowed at the base more or less to a petiole, 8–18 cm. long and 3.5–5 cm. wide; terminal bud large, somewhat beyond the nearest leaves, tapering sharply, but scales lanceolate, acute, erect; pollen cones grouped in an axillary sessile cluster of three and subtended by several pairs of overlapping, broad, keeled scales, long cylindrical, about 3.5 cm. long and 4 mm. in diam.; microsporophylls small, triangular, acute; seed cone on an axillary scaly not enlarged peduncle, 15–20 mm. long; ovule inverted in the axil of a subterminal bract; seed globular, 15–18 mm. in diam. FIG. 11.

DISTRIBUTION. In mountain forests from northern Annam to Kwangtung. MAP 14.

Kwangtung. Naam Kwan Shan (Tseng Shing Dist.), *Tsang 20123* ♂ (A, NA, NY, US), *25273* ♀ (A). **Tonkin.** Phu Tho, *Chevalier 38017* ♀ (P-lectotype). Hoa Binh, *Ste. forestier 8408* s (P-syntype). Phu Huo, *Chevalier 37512* s (P). **Annam.** Vinh, Nghe An, *Fleury 30180* s (P-syntype). Near Hue, *Poilane 29808* ♀ 1,300–1,400 m. (ILL, P). Mt. Bana (25 km. from Tourane), *Clemens 4190* s (A, K, NY, P).

The much larger leaves distinguish sterile specimens of *Decussocarpus fleuryi* from *D. nagi*, although both have hypostomatic leaves. Otherwise, the female peduncle of *D. fleuryi* is longer, the pollen cones are longer, and, particularly, the pollen cone cluster is sessile. The general form of the leaf corresponds with that of *D. wallichianus* and even Hickel, in the original description, included a specimen of the latter (*Poilane 5963*) among the specimens he listed. However, the stomatic condition and

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[9] Chevalier is given as the collector for this specimen on the sheet in Paris.

FIGURE 11. *Decussocarpus fleuryi* (Hickel) de Laubenfels, photograph of *Tsang 25273* (A).

orientation of the leaves at once distinguish even sterile specimens. The sessile pollen cluster and the lack of a fleshy receptacle also separate these two species.

38. **Decussocarpus nagi** (Thunberg) de Laubenfels, comb. nov.

Myrica nagi Thunb. Fl. Japon. 76. 1784. Type: ex herb Thunb., microfiche no. 23381 (A–GH).

Nageia japonica Gaertner, De Fruct. et Sem. **1**: 191. 1788 (in part, *nomen illeg.*, description confused).

Podocarpus nageia R. Br. ex Mirbel, Mem. Mus. Paris **13**: 75. 1825 (based on *Nageia japonica*).

Podocarpus cuspidata Endl. Syn. Conif. 207. 1847. Hort.

Nageia cuspidata (Endl.) Gordon, Pinetum 136. 1858.

Nageia ovata Gordon, Pinetum, Suppl. 42. 1862. Type: *Fortune* in 1861, Japan, Yeddo (not seen).

Podocarpus nageia R. Br. var. *rotundifolia* Maxim. Gartenflora **13**: 37. 1864 (based on *Nageia ovata* Gordon).

Podocarpus nageia R. Br. var. *angustifolia* Maxim. *ibid.* Hort.

Podocarpus ovata (Gordon) Henk. & Hoch. Syn. Nadelh. 381. 1865.

Dammara veitchii Henk. & Hoch. *ibid.* 216. Hort.

Podocarpus japonica (Gaertner) Nelson, Pinac. 155. 1866, *nomen illeg.*, non Siebold.

Podocarpus caesius Maxim. Mél. Biol. **7**: 561. 1870. Hort.

Nageia nagi (Thunb.) Kuntze, Rev. Gen. Pl. 798. 1891.

Podocarpus nagi (Thunb.) Makino, Bot. Mag. Tokyo **17**: 113. 1903.

Podocarpus nagi (Thunb.) Makino var. *rotundifolia* (Maxim.) Makino, *ibid.* 114.

Podocarpus nagi (Thunb.) Makino var. *angustifolia* (Maxim.) Makino, *ibid.*

Podocarpus formosensis Dümmer, Gard. Chron. III. **52**: 295. 1912. Type: *Schmüser 1357*, Formosa, S. Cape (not seen, photo of type accompanies descript.).

Podocarpus nankoensis Hayata, Ic. Pl. Formos. **7**: 39. 1918. Type: *Hayata* in 1916, Formosa, Nanko.

Podocarpus nagi (Thunb.) Makino var. *koshunensis* Kanehira, Trans. Nat. Hist. Soc. Formosa **21**: 145. 1931. Syntypes: *Mori 25075, Sasaki 25076, 25077, Kanehira 26078, 22239, Matsuda 2594* (not seen).

Podocarpus koshunensis (Kanehira) Kanehira, Formosan Trees. Rev. ed. 36. 1936.

Tree to 25 m. high; bark smooth, peeling in thin flakes, dark brown weathering gray; leaves decussate, distichous, hypostomatic, multiveined, elliptic, acuminate, to rounded at the tip, the apex often showing evidence of aborted growth, sometimes abruptly narrowed to a short wide petiole, often glaucous especially on the underside, 4.5–5 cm. long or sometimes longer, 10–20 mm. wide, somewhat variable in size and shape even on individual specimens; terminal bud often 1–2 mm. beyond the last pair of leaves, abruptly wider than the stem and then tapering to an acuminate apex, bud scales long lanceolate; pollen cones 1–5 on an axillary scaly peduncle 3–10 mm. long, subtended by a lanceolate scale up to 6 mm. long, cylindrical, 10–20 mm. long, the longer ones terminal in the cluster, microsporophylls small, acuminate, widely spreading and not crowded, about 1 mm. long; seed cone on an axillary peduncle with deciduous lanceolate scales, peduncle 5–10 mm. long, not enlarged; one or two seeds developing from inverted ovules (rarely there are 3 ovules) in the axils of subterminal bracts, completely covered by the seed scale, globular and elongated into a hooked beak at the micropylar end, smooth, glaucous, the seed itself 12–13 mm. wide and 15–16 mm. long, the fleshy bluish-black covering at least 2 mm. thick but drying on the seed and wrinkling, the seed often falling with the peduncle attached.

Distribution. Scattered from southeastern China and Hainan to southern Japan in forests at low elevation, up to 800 meters in more southerly parts. Because of the high degree of disturbance of forests almost throughout its range and its popularity in cultivation, it is most difficult to distinguish between plants naturalized from cultivated sources and truly native individuals. Probably some of the specimens cited are, in fact, cultivated even where not indicated as such. Map 15.

China. Hainan: Pak Shik Ling (Cheng Mai Dist.), *Lei 745* ♀ (A, L, NY, US). Pak Shek Shan (Lam Ko & Cheng Mai Dists.), *Tsang 681* (*L.U. 17430*) s (A, L, NY, US). Nodoa, Sha Po Ling, *McClure 8131* ♀ 800 m. (A). Manning, *How 73876* s 700 ft. (A, P). Kwangsi: Ta Tse Tsuen, Yung Hsien, *Steward & Cheo 728* ♀ 380 m. (A, NY, P). Sup-man-ta Shan, *Liang 69401* s (A). Wah Kong (Hing On Dist.), *Chung* (*Tsoong*) *83667* s (A), Kiangsi: Tung Lei (Kiennan Dist.), *Lau 3964* ♀ (A, US). Fukien: Hinghwa, *Chung 924* ♀ (A). Yenping, *Chung 2979* ♀ (A), *3570* s (A), *Dunn 3523* ♀ (A). Chekiang: Ping-yang Hsien, *Ho 1554* ♀ (A). Tsingtien, *Keng 99* ♀ (A), 20–40 miles W. of Wenchow, *Ching 1832* ♀ 250–450 m. (A, P, US). Yentang Shan, *Chiao 14685* s (A, NY, US, Z), *Hu 241* ♀ (A). Without loc., *Chen 4091* ♀ (A). **Formosa.** Southern: Koshun (=Hengchun), *Kanehira 28* s (A), *29* s (A). E. Coast: Hualien, *Kuntz 084* ♂ (US). Nanwo (Karenko Prov.), *Wilson 11109* s (A, US). Northern: Nanko, *Hayata* (1916) ♂ (A-isotype of *Podocarpus nankoensis*). Tamsui, Chapa, *Henry 1446* s (A, NY, US). Kankou (Taipei Co.), *Kao* (1960) ♀ (L). Kangu (Taipei), *Keng s.n.* s (US). Urai (Taihoku Prov. = Taipeh), *Wilson 10279* s (A, US). Herinki (Taihoku Prov.), *Wilson 10242* s 660 m. (A, US). Siusuie, *Kanehira 14* s 2,500 ft. (A). **Ryukyu Islands.** Ishigaki I., Kabira, *Smith 66* s (US). Okinawa, Mt. Kunchon, *Wilson 8064* s 0–200 m. (A); Linkin, *Kimura & Hurusawa 95* s (US); *Sonohara, Tawada & Amano 6290* s (US). **Japan.** Kyushu: Kagoshima, *Wilson 6262* s (A). Near Kumamoto, *Wilson* (1917) ♀ (A). Hondo: Kurashiki (Okayama), *Uno s.n.* ♀ (A). Kasugayama (Nara), *Kume s.n.* ♂ (A). Shizuoka, *Dorsett & Morse 763* ♂ (US). Between Kamakura & Zushi, *Beattie & Kurihara 10437* s (US). Toke (Chiba Pref.), *Walker 5649* ♂ (US). Tamato, *Wilson* (1904) ♂ (A). *Yakushima* (betw. Ambo & Kasugidani), *Moran 5351* s 350 m. (US).

Illustrations. Pilger, R., Pflanzenreich IV. 5 (Heft 18): *fig. 9C–E.* 1903; Nat. Pflanzenfam. ed. 2. **13**: *fig. 134C–E.* 1926, as *Podocarpus nagi*; Dümmer, R., Gard. Chron. III. **52**: *t. 132.* 1912, as *Podocarpus formosensis*; Kanehira, K., Formosan Trees, rev. ed. *t. 4.* 1936, as *Podocarpus koshunensis.*

The large number of specific names which have been applied to *Decussocarpus nagi*, including several horticultural names, result from long aquaintance with it in cultivation, and from its wide distribution. Most of the differences noted for the various units proposed are within the normal variation of a population or even of an individual. The variety *rotundifolia* (equals *Nageia ovata*) of *Podocarpus nagi* possibly is defensible as a distinct taxon, having leaves ovate, compared to the usual elongated outline.

Section **Afrocarpus** (Buchholz & Gray) de Laubenfels, comb. nov.

Podocarpus section *Afrocarpus* Buchholz & Gray, Jour. Arnold Arb. **29:** 57. 1948. Type species: *Podocarpus falcatus* (Thunb.) R. Br. [*Decussocarpus falcatus* (Thunb.) de Laubenfels].

Decussocarpus falcatus (Thunb.) de Laubenfels, comb. nov.

Taxus falcata Thunb. Prodr. Pl. Capensis, 117. 1800. Type: *Thunberg* in 1773–1774, Cape of Good Hope (not seen).

Podocarpus falcatus (Thunb.) R. Br. ex Mirb. Mém. Mus. Hist. Nat. Paris **13:** 75. 1825.

Podocarpus gracillimus Stapf, Fl. Trop. Afr. [ed. Prain] **6**(2): 343. 1917. Type: *Nelson 423*, Transvaal, Houtschberg.

Decussocarpus gracilior (Pilger) de Laubenfels, comb. nov.

Podocarpus gracilior Pilger, Pflanzenreich IV. **5** (Heft 18): 71. 1903. Type: *Schimper 1160*, Ethiopia, Chere.

Decussocarpus mannii (Hook.) de Laubenfels, comb. nov.

Podocarpus mannii Hook. Jour. Linn. Soc. **7:** 218. 1864. Type: *Mann 1065*, St. Thomas Island.

Nageia mannii (Hook.) Kuntze, Rev. Gen. Pl. 800. 1891.

Podocarpus usambarensis Pilger, Pflanzenreich IV. **5** (Heft 18): 70. 1903. Lectotype: *Holst 2467*, Tanganyika, Usambara.

Podocarpus dawei Stapf, Fl. Trop. Afr. [ed. Prain] **6**(2): 342. 1917. Type: *Dawe 961*, Uganda.

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The numbers in parentheses refer to the corresponding species in the text.

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Havel & Kairo *NGF 17341* (1)

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Tothill *553* (6a); *844*, *845* (31); *854* (6a)
Toxopeus *427* (3); *485* (21b)
Tsang *681*, *L.U. 17430* (38); *20123*, *25273* (37); *27332* (21b)
Tsang & Fung *L.U. 18100* (52)
Tuckwell *W1553* (26)

Van Römer *736* (26); *1233* (12c)
Van Royen *3721* (1); *3857* (3); *3873* (1); *3895* (21c); *5058* (34); *NGF 16182* (1); *NGF 20289* (23); *NGF 20309* (26)
Van Royen & Sleumer *6073* (31); *6246* (6a); *7219* (3); *7403* (1); *7948* (3); *7948A* (21c); *7948B* (3); *8203A* (19)
Van Royen, Sleumer, & Schram *7791* (12a)
Van Steenis *3754* (34); *8357* (12a); *8423* (21d); *17544*, *18267* (21a)
Vaughn *3254* (31); *3258* (21b)
Veillon *120* (32); *136* (29); *142* (22); *145*, *511* (7)
Versteegh *BW 248* (1); *BW 250* (21c); *BW 253* (1); *BW 269* (3); *BW 281* (1); *BW 913* (31); *BW 2537* (26); *BW 3009* (1); *BW 3041* (6b); *BW 4754*, *BW 4891*, *BW 4985*, *BW 7378* (6a); *BW 7596*, *BW 10407* (1); *BW 10411* (21c); *BW 12610* (21b); *BW 15249* (6a)
Versteegh & Kalkman *BW 5594* (6a)
Versteegh & Koster *BW 14* (21b)
Vidal *623* (24); *3910* (13)
Vieillard *1259* (18); *1260*, *1261*, *1262* (22); *1275* (33); *1277* (8); *1278*, *3262* (7); *3264* (32); *3265* (9)
Vink *NGF 12430* (26); *BW 15271* (6a); *17188*, *17242* (26); *17499*, *17500*, *17501*, *17502* (27)
Vink & Schram *BW 8620* (6b); *BW 8667* (23); *BW 8730* (31); *BW 8731* (21c); *BW 8746* (3); *BW 8764* (1); *BW 8796*, *BW 8914* (6b); *BW 8945* (1)
Virot *8* (32); *9* (9); *10* (29); *37* (7); *38* (32); *39* (18); *40* (9); *152* (8); *187* (7); *206* (22); *400* (7); *469* (18); *658* (33)

Wakau *4155* (2)
Walker, F. S. *BSIP 212* (31); *BSIP 247* (13)
Walker *70* (2); *ANU 859*, *ANU 859A* (1); *5649* (38); *7526* (21c)
Wallich *6045* (2); *6050* (34)
Wang *33651* (5a); *35591* (21b); *36532* (5a); *39608* (21b)
Warburg *11119* (21a); *14721* (21b)
White *2001* (7); *2033* (32); *2112* (22); *2120* (32); *2122* (8); *2238* (7); *2261* (33); *2285* (22)
White & Gray *NGF 10407* (6a); *NGF 10415* (34)
Whitford *951* (24); *1353* (34)
Whitmore *2368* (21b)

Williams *399*, *624*, *752*, *753*, *1035* (34); *1298*, *1299* (21c)
Wilson *6262*, *8064*, *10242*, *10279*, *11109* (38)
Winkler *512* (1); *1035* (21a); *1036* (1); *1037* (13); *1866* (21a)
Womersley *NGF 3704* (34); *NGF 4420* (3); *NGF 4428* (23); *NGF 4483* (19); *NGF 5338* (21c); *NGF 5351* (1); *NGF 5353* (21c); *NGF 5354* (19); *NGF 8852*, *NGF 8861* (28); *NGF 9419* (19); *NGF 9430* (21c); *NGF 11038* (19); *NGF 11067*, *NGF 11260* (21c); *NGF 13922* (19); *NGF 14018* (26); *NGF 14253* (21c); *NGF 17621* (34); *NGF 17902* (1); *NGF 17939* (23); *NGF 19298* (34); *NGF 24563* (21c); *NGF 24569* (26); *NGF 24928* (21b)
Womersley & deLaubenfels *NGF 19460* (21c)
Womersley & Floyd *NGF 6138* (21c)
Womersley & Millar *NGF 7680* (3); *NGF 8324* (21c)
Womersley & Sleumer *NGF 14013* (21c)
Wood *1244* (34); *SAN 4172* (5b); *SAN A4179* (17)
Wood & Wyatt-Smith *SAN A4493* (25)
Wray *1028* (2); *1198* (21b); *3875* (12b); *3899* (2)
Wray & Robinson *5354*, *5380* (2)
Wyatt-Smith *71650*, *80370*, *80371* (1); *93115* (17)

Yapp *493* (12a)
Yates *1987*, *2148* (21b); *2554* (34)

Zollinger *2262* (21a); *3025* (34)
Zwart *6517* (21d)

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THE VASCULAR SYSTEM IN THE AXIS OF DRACAENA FRAGRANS (AGAVACEAE),

1. DISTRIBUTION AND DEVELOPMENT OF PRIMARY STRANDS.

M. H. ZIMMERMANN AND P. B. TOMLINSON [1]

WE HAVE OUTLINED THE STATE of existing knowledge of the vascular anatomy of monocotyledons with secondary growth in a previous article which serves as an introduction to our present studies (Tomlinson & Zimmermann, 1969). These have been concerned with a number of genera in the Agavaceae. There are quantitative and often diagnostic anatomical differences between the plants we have studied, but we believe that fundamental principles of vascular distribution is the same in all of them. We have therefore restricted our description to one species, *Dracaena fragrans* (L.) Ker-Gawl., of which we had abundant living material available for a detailed study. The same species had also been used by earlier investigators of this problem (e.g., Cordemoy, 1894; Meneghini, 1836; von Mohl, 1824) although often under the older, now incorrect name of *Aletris fragrans* L. Where necessary, however, we shall refer to other plant species. For convenience, our results are presented as two separate articles, devoted to primary and secondary tissues respectively, although such a separation is somewhat arbitrary. Indeed, we will have cause to show that the two types of vascular tissue are interdependent and often continuous.

MATERIALS AND METHODS

Sectioning. Specimens investigated were collected from a large clump cultivated at the Fairchild Tropical Garden. Material was either sectioned freshly or after fixation in FAA and subsequent washing. For the study of the course of vascular bundles sequential series of tranverse sections were cut on a "Reichert" sliding microtome from two lengths of distal mature shoots, each representing a sympodium. Selection of material needed some care because in some shoots the central tissue is easily torn during sectioning. For the investigation of the vascular anatomy of leaf-trace departure a complete series of sections 40μ thick was prepared. For the analysis of longitudinal continuity of vascular traces sections 33μ thick at intervals of 100μ were used. These sections were stained in safranin and Delafield's haematoxylin and mounted permanently in "Piccolyte."

For the study of vascular development in the crown, serial transverse and longitudinal sections 10μ thick of shoot apices were cut on a rotary

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[1] Contribution to a study of the vascular system of monocotyledons by one of us (P.B.T.), supported by N. S. F. grant GB-5762-X.

microtome from material embedded in "Paraplast." Routine methods of embedding, staining and mounting were employed. Because of the wide diameter of these developing crowns, pieces of ribbon containing only four sections were mounted on each slide.

Serial analysis. Cinematographic analysis of the three-dimensional vascular structure was carried out with the series of sections from the mature stem. These methods have been described in ample detail in previous papers (Zimmermann & Tomlinson, 1965, 1966). The method of plotting provascular strands in the series of sections from the meristematic crown has also been described in previous papers (Zimmermann & Tomlinson, 1967, 1968). The optical shuttle was employed for plotting, according to the procedure described in the paper on the vascular development of *Prionium* (Zimmermann & Tomlinson, 1968). A slight methodical variation was necessary because each slide in this series contained four sections. Most strands can easily be followed by matching the corresponding section on two successive slides with an interval of 3 sections between. In areas where provascular strands make sharp turns (immediately below the apical meristem) and require the use of each section, optical alignment was achieved in the following way: *5d–6a*, 5d–*6b*, 5d–*6c*, 6c–7a, *6d–7a*, etc., whereby the number indicates the slide, the letter the section on the slide, and the italics mark the sequence of photography. The reader can easily appreciate that alignment had to be achieved over an interval of two sections (e.g., 5d–6c above) once every four sections. With the *Dracaena* crown this was just possible without losing continuity of the strand which was plotted. There is no question that the procedure is easier to follow when each slide contains only a single section.

GENERAL MORPHOLOGY AND ANATOMY

Growth habit. *Dracaena fragrans*, a native of tropical Africa, is a common ornamental in South Florida. It has apparently been known in cultivation in Europe at least since 1768 (Sims, 1808). In cultivation it forms a diffuse shrub or rarely a low tree. Basal shoots are straight and erect, but distal branches are often bent over by the weight of the terminal cluster of leaves. Leaves are lanceolate, up to 75 cm. long, and lack a petiole. Their insertion is open but broad and even overlapping. On vigorous shoots, leaves persist for a long time, so that leafy shoots up to 2 m. high may be present. Otherwise on suppressed and less vigorous shoots leaves form the distinct terminal cluster which is so common in many other woody monocotyledons. The longevity of leaves is of considerable anatomical significance, a point which will be discussed later. Each leaf subtends a minute axillary bud enclosed by its prophyll.

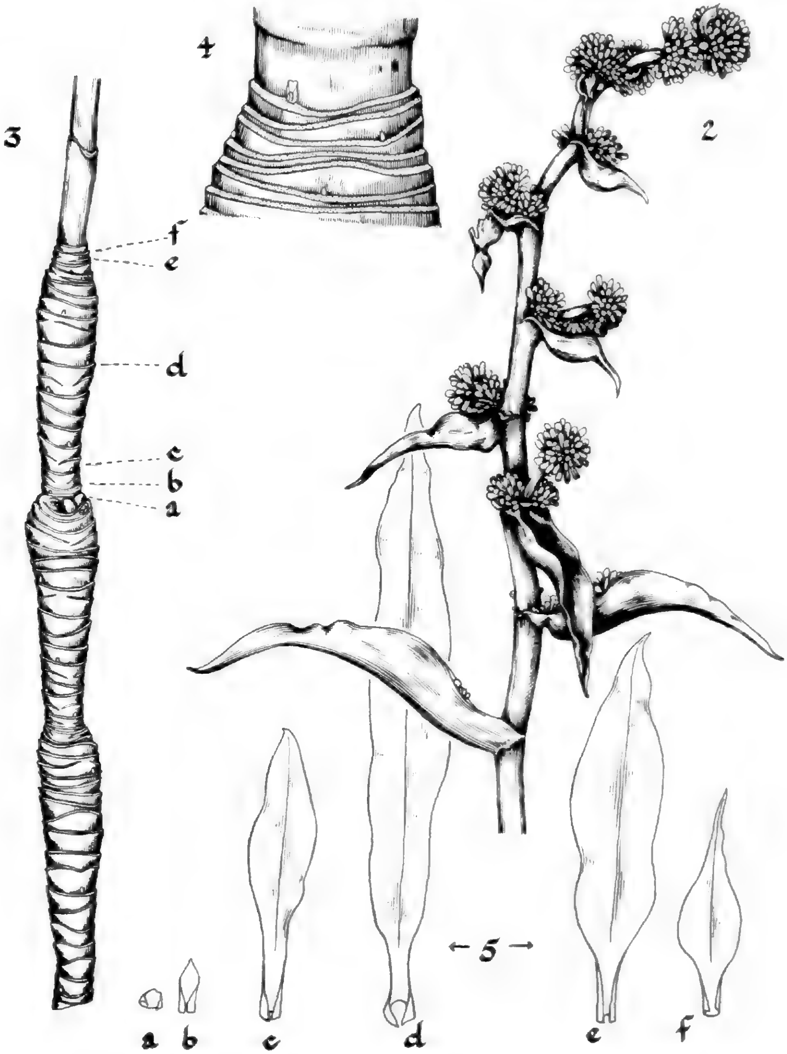
Inflorescences are always terminal (FIG. 1) and branching is closely associated with flowering. Flowering and resultant branching begins in plants 2 to 3 years old when they are about 1 m. high. The transition from vegetative to reproductive state of the axis is marked by a gradual reduc-

FIG. 1. *Dracaena fragrans.* Distal part of a flowering shoot, × 1/5.

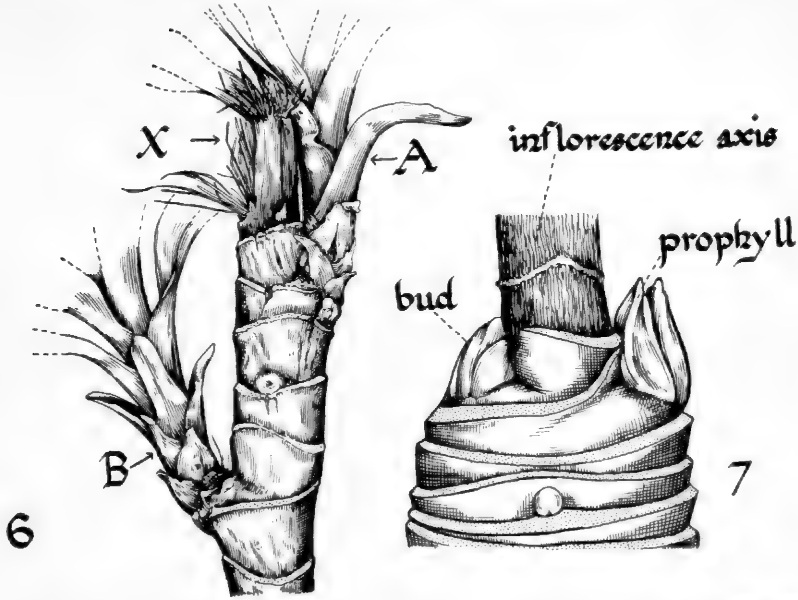
tion in leaf size associated with an abrupt elongation of internodes (FIGS. 2–5). Bracts which subtend the first-order flowering branches are white and caducous although it is obvious from the transition upwards along the shoot that they are homologous with foliage leaves. The detailed structure of the flower-bearing branches has been described by Troll (1962).

Branching is normally sympodial from a bud in the axil of one of the transitional leaves immediately below the inflorescence. At the time of anthesis this renewal bud is indistinguishable from other dormant buds (FIG. 4). After flowering it grows out rapidly (FIG. 7), pushing the terminal inflorescence into a pseudolateral position. Each axis branches in this way and is, therefore, a sympodium consisting of many successive growth units. The sympodium appears articulate both from the scars of the dried inflorescence stalks, and a swelling which marks each joint (FIG. 3). This articulation is most noticeable in distal, horizontal axes.

After flowering there is an evident competition among a number of potential renewal buds, because the inhibition of more than one is always released (FIG. 7). One of them usually becomes dominant and re-imposes inhibition upon the others. However, two (rarely more) buds may grow out simultaneously. This leads to a branched axis with an inflorescence scar in the crotch of the fork. Plants in South Florida flower several times in one year and although it is obvious that different axes flower at different times of the year it seems likely that a vigorous shoot can flower



FIGS. 2–5. *Dracaena fragrans*. Habit details. 2, Terminal inflorescence, × 1/2. 3, Flowering shoot with all leaves detached, showing 3 units of sympodium and base of inflorescence axis as a continuation of vegetative axis, × 1/2. Letters indicate levels of insertion of corresponding leaves shown in FIG. 5. 4, Detail of region of transition from vegetative to reproductive axis, × 2, leaves removed at their insertion; buds shown in axils of a number of leaves. 5, Series of leaves (a–f) from distal unit shown in FIG. 3, their levels of insertion indicated in that figure, beginning with prophyll (a) and ending with most distal transitional leaf (f), × 1/4.

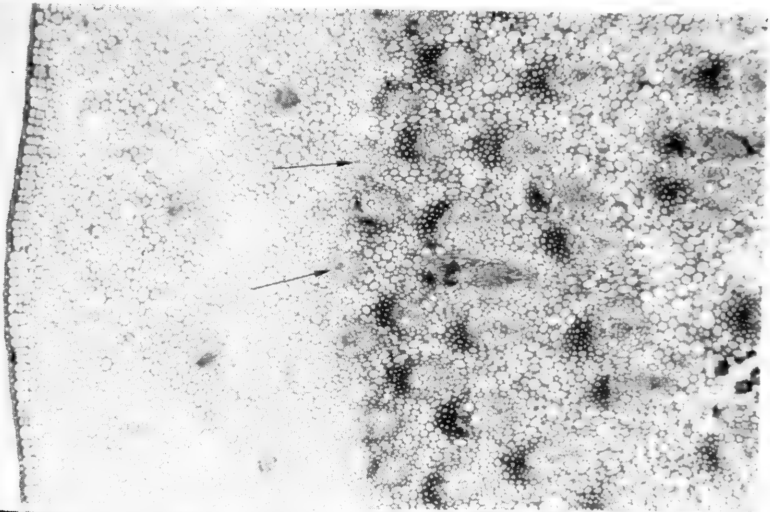


FIGS. 6 and 7. *Dracaena fragrans*. Branching. 6, Erect axis with 2 branches, renewal shoots at A and B from axillary buds whose inhibition is released by destruction of apex of parent shoot at X, × 2/3. 7, Normal renewal growth below old inflorescence axis, × 2. Buds developing in axils of two most distal leaves; prophylls conspicuous. This corresponds to FIG. 4 after lapse of 2 months.

two or three times each year. This is indicated by a close succession of inflorescence scars. For a further morphological description of flowering in arborescent Liliiflorae the reader is referred to the detailed work of Schoute (1903, 1918).

The release of apical dominance is normally the result of flowering but it may be induced in other ways. Decapitation releases from inhibition the dormant buds immediately below the injury (FIG. 6). Apical dominance is also released on the upper side of leaning stems where numerous dormant buds may grow out, much as in woody dicotyledons (see *Fig. 15* in Tomlinson & Zimmermann, 1969). Erect, rapidly growing suckers commonly develop from the base of old plants, presumably for the same reason. The influence of these various methods of growth on the distribution of vascular tissue is largely described in the second article of this series.

Primary tissues (FIG. 8). Epidermis slightly thick-walled, covered by a thin but conspicuous cuticle. Periderm in hypodermal or subhypodermal layers developing early by etagen-like divisions of cortical cells, the outermost derivatives suberized. Cortex, 1–3 mm. wide, of uniform and fairly compact parenchyma; no independent cortical vascular system



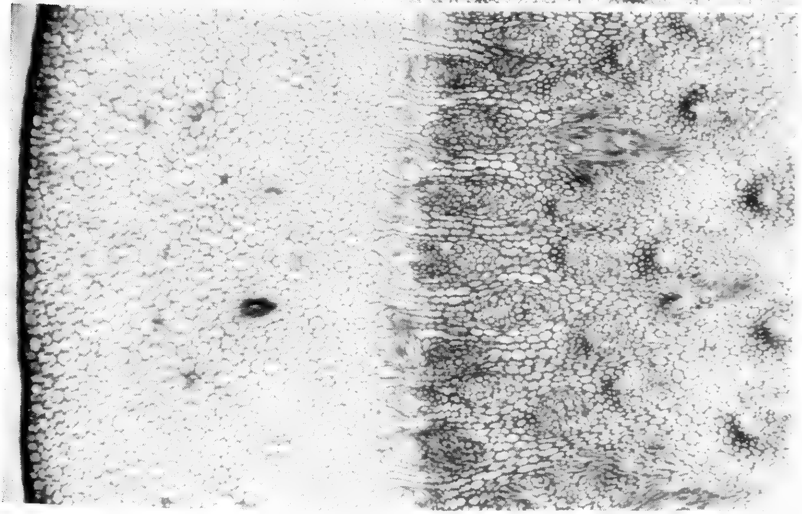


FIG. 8. (ABOVE). Transverse section of mature primary stem of *Dracaena fragrans*. × 36. All bundles in cortical area are leaf traces. Arrows point out vertical bundles immediately above point of branching from leaf trace. They appear small because they lack the fibrous sheath.

FIG. 9 (BELOW). Transverse section of mature stem of *Dracaena fragrans*, taken from the same stem, a few centimeters higher, below the sympodial branch. A small amount of secondary tissue has been formed by the cambium. × 36.

developed. Central cylinder delimited by compact, often lignified ground parenchyma and peripheral, congested vascular bundles. Central bundles more diffusely distributed among thin-walled ground tissue resembling parenchyma of cortex. Vascular bundles each with a sheath of narrow compact angular cells, the sheathing cells thick-walled around phloem but sheath becoming more uniformly sclerotic around peripheral bundles. Vascular tissues collateral, including a wide strand of angular metaxylem elements, V-shaped in transverse section, usually with narrow protoxylem elements at the apex of the V and a single phloem strand in the angle of the V. Peripheral vascular bundles with little or no protoxylem, the metaxylem scarcely V-shaped. Leaf traces conspicuous in outer part of central cylinder, the xylem represented largely by abundant protoxylem. Xylem including fairly wide angular tracheids with indistinct end walls and scalariform pitting. Protoxylem elements rounded, with annular or spiral wall thickening. Metaxylem tracheids of the order of 5–10 mm. long, and overlapping extensively. Phloem including long sieve-tube elements usually with transverse end walls and simple sieve plates, but sieve plates commonly compound on oblique or very oblique end walls. Raphide clusters common in otherwise unmodified parenchyma cells. Tannin cells infrequent.

Secondary tissues (FIG. 9). This arises from an etagen cambium of the type which has already been described in the earlier review (Tomlinson & Zimmermann, 1969). Ground tissue of compact tabular and radially-arranged cells about 120μ long, with slightly thickened and lignified cells, the walls with abundant simple pits. Tannin deposits and raphide clusters frequent. Secondary vascular bundles always amphivasal. Central phloem strand including short sieve-tube elements with simple, more or less transverse sieve plates. Phloem separated from xylem by short, thin-walled parenchyma cells. Secondary tracheids conspicuously different from those of primary vascular bundles; of the order of 3.6 mm. long and with indefinite end walls; walls thick; bordered pits with crossed slit-like apertures, more or less parallel to the axis of the cell. Short xylem parenchyma cells infrequent.

The difference in length between secondary ground tissue cells and secondary tracheids suggests that the latter undergo about a 30-fold extension during development since both arise from similar initials.

COURSE OF PRIMARY VASCULAR BUNDLES

The distribution of primary vascular tissue in *Dracaena fragrans* is similar to that of the palm *Rhapis excelsa* as described by us (Zimmermann & Tomlinson, 1965) with slight quantitative differences. Each leaf is supplied with a number of leaf traces which diverge from the stem at varying depths. Major bundles diverge from the center, minor bundles from near the periphery, and intermediate bundles from an intermediate area of the stem. Outgoing leaf traces produce a number of derivative bundles by branching. Most of these branches are short bridges which link in an upward direction with nearby vertical bundles. Axial continuity from each leaf trace is maintained by a continuing vertical bundle which

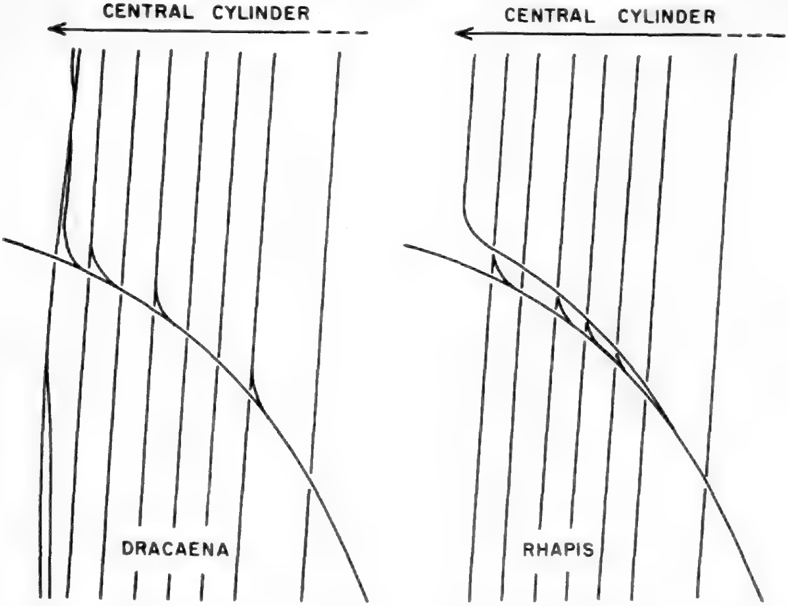


FIG. 10. Diagrammatic representation of leaf-trace departure in *Dracaena fragrans* (LEFT) and *Rhapis excelsa* (RIGHT). In *Rhapis* the vertical bundle is usually the lower- and innermost branch of the leaf trace. From the point of branching it follows the leaf trace to the periphery of the central cylinder. In *Dracaena*, the vertical bundle usually branches from the leaf trace outside and above the bridges. Newly released vertical bundles show a tendency to anastomose among themselves. For an unusual type of vertical-bundle branch see TEXT and FIG. 13.

usually diverges from the leaf trace at the very periphery of the central cylinder. The newly released vertical bundle is normally very narrow if the stem does not contain secondary tissue (FIG. 8). In this very peripheral position it readily splits or anastomoses with similar neighboring bundles on its way up the stem. This contrasts with the situation in *Rhapis* where the vertical bundle is released near the stem center and accompanies the parent leaf trace, on its outwardly diverging path, almost all the way to the periphery of the central cylinder (FIG. 10). The upwardly continuing vertical bundle, as in *Rhapis*, then gradually approaches, over a distance of many internodes, the center of the stem whereupon the process of bundle branching is repeated again in association with another, more distal leaf. Major bundles have the longest, minor bundles the shortest distances between two such successive leaf contacts. Thus, the overall course of vascular bundles is similar to that illustrated for *Rhapis* (Zimmermann & Tomlinson, 1965; *Fig. 3*, right). In *Dracaena*, in contrast with *Rhapis*, the central bundles have no helical path. Major dorsal bundles merely describe a turn of about 120° in the center, as described in the next section of this paper. This turn, as with the helical twisting in *Rhapis*, is in the direction of the phyllotactic spiral. This turn may be governed by the same developmental principle which causes phyllotaxis.

The distribution of protoxylem changes throughout each bundle in the same manner as in *Rhapis*. This change is less conspicuous in *Dracaena* than in *Rhapis* because protoxylem and metaxylem elements are more nearly of the same diameter. As one follows a vascular bundle of *Dracaena* in a distal direction one finds protoxylem first not very far above its divergence from the leaf trace as a vertical bundle. Continuing upwards, the number of elements further increases to reach a maximum where the bundle passes out into another leaf. Metaxylem is continuous into bridges as well as the continuing vertical bundle but the leaf trace contains only protoxylem. In this respect *Dracaena* is identical with *Rhapis* although the "loss" of metaxylem from the outgoing leaf trace is less obvious because the two tissues are not so clearly distinguished.

Irregularities in the course of bundles throughout the stem are somewhat more common than in *Rhapis*. The anastomosing tendency of the lower part of vertical bundles, at the periphery of the central cylinder, has been mentioned. If the stem consists of primary vascular tissue only, the vertical bundles are quite small in their lowermost portion, at the periphery, where they come off the leaf trace and without a well-developed fibrous sheath (FIG. 8). In places where the primary vascular cylinder is covered by a mantle of secondary tissue, the same vertical bundles are larger and more conspicuous, because the fibrous sheath is better developed (FIG. 9).

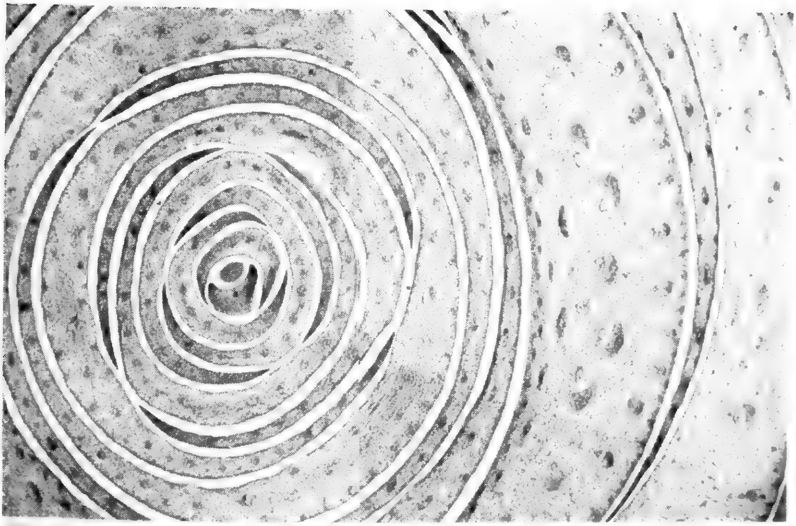
Another irregularity which has been observed is the occasional forking leaf traces. When such a bundle is followed upwards in the stem center, the two branches diverge along two different radii. From these observations it appears that developmental processes are somewhat less rigid in *Dracaena* than in *Rhapis*.

The important topic of the relation between primary and secondary vascular bundles is reserved for the second article in this series.

DEVELOPMENTAL PATTERN OF THE PRIMARY VASCULAR SYSTEM

Observations. General aspects of the anatomy of the meristematic crown are shown in the photomicrographs, FIGURES 11 and 12. Leaves and leaf primordia are arranged in a phyllotactic spiral with a divergence between 1/3 and 2/5, as can be seen from FIGURE 11. The approximately median longitudinal section through the crown shows the usual monocotyledonous organization (FIG. 12). It is obvious from this longitudinal section that primary thickening growth involves re-orientation of tissue through about 90° as we have described for *Rhapis* and *Prionium* (Zimmermann & Tomlinson, 1967, 1968).

The developing vascular system of the meristematic crown is far too complex to be demonstrated in individual microtome sections. Provascular strands were, therefore, followed throughout a series of transverse sections and their radial distance from the stem center plotted on graph paper as



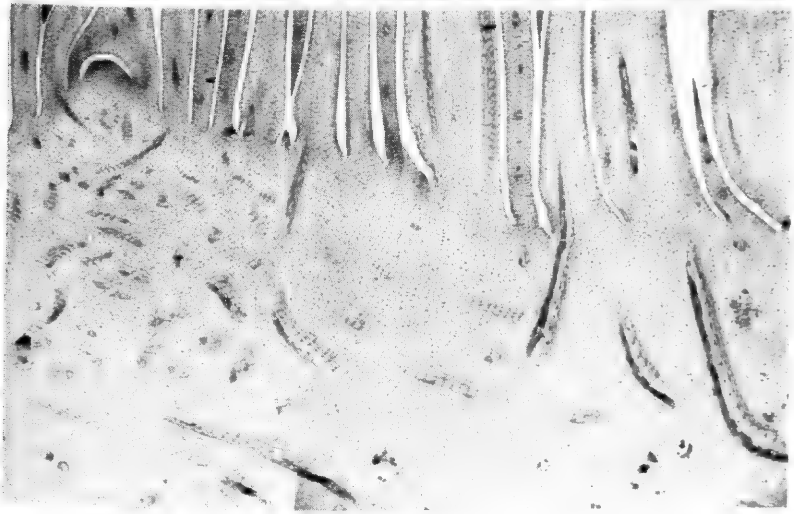


FIG. 11 (ABOVE). Photomicrograph of transverse section through the meristematic crown of *Dracaena fragrans* at the level of the apical meristem. × 26, showing the phyllotactic arrangements of the leaves. Note the symmetrical arrangement of the major leaf traces on the dorsal side.

FIG. 12 (BELOW). Approximate median longitudinal section through the meristematic crown of *Dracaena fragrans*, × 26. Because of their complex three-dimensional path, none of the individual provascular strands can be seen over more than a very short distance. A thorough knowledge of their path, gained through plotting (FIG. 13 and TEXT) enables us to interpret a single section like this quite easily. Note the sharp turns of the major strands below the apical meristem. Note also the minor leaf trace on the far right of the photograph.

had been done for *Rhapis* and *Prionium*. The results are shown in FIGURE 13. The three-dimensional arrangement of provascular strands in the crown is difficult to represent on paper, our representation is therefore simplified as follows. All radii are shown in a single plane. All leaves are rotated into the same plane. This eliminates the 120° turn of the major bundles. In order to reconstruct the three-dimensional pattern of the crown from FIGURE 13, the reader has to go through a mental exercise which first involves rotating leaves back to their proper position, and second involves re-establishing the 120° turn of the major bundles. This process of simplification is very similar to the one used in our description of the *Rhapis* crown. It has the advantage that one can more easily appreciate the re-orientation of a major dorsal bundle during successive developmental stages.

FIGURE 13 shows the major dorsal leaf trace in leaf primordia P 1 to P 17, P 1 being the youngest visible primordium. The pattern of vascular development appears to be the same as the one found in *Rhapis* and *Prionium*. Vertical bundles originate from major leaf traces of P 17. Approximately below the base of P 14 they fuse into the meristematic cap into which all blind-ending vertical bundles converge (cf. Zimmermann & Tomlinson, 1967, 1968). From the diagram one can extrapolate that the leaf-contact distance for a major bundle is about 20 to 25 internodes, although the series of sections was too short to show this directly. If the section series had been longer and had included the insertions of older (lower) leaves, the major leaf trace of P 1 would have been seen originating as a vertical bundle from a leaf trace diverging into a leaf at about the level of P 20–25.

A rather unusual type of vertical-bundle branch was found in two major leaf traces to P 11. Both vertical bundles ended distally immediately below the apical meristem in what might be a leaf primordium younger than P 1 and represented by an indistinct ridge. If this interpretation is correct there would be a leaf-contact distance of 11 internodes between P 0 and P 11. Only two such centrally located vertical bundle branches were found and one of them is shown in FIGURE 13. The developmental meaning of this rare type of vertical bundle is unknown.

FIGURE 13 shows some further irregularities which are of no fundamental significance, such as the apparent crossing over of the lower portions of the major leaf traces of P 1 and P 2, P 5 and P 6, P 7 and P 8. They could have resulted by comparing bundles on different radii of the stem (the crown is not perfectly circular in transverse section), from slight irregularities of development, or indeed, from the process of plotting.

The meristematic cap is similar in position and extent to that described in the apices of *Rhapis* and *Prionium*. It is recognized as the umbrella-shaped meristematic area, below the shoot apex proper, into the periphery of which the blind-ending vertical bundles fuse. It is pierced by leaf traces already connected to vertical bundles.

The primary vascular connection between an axillary bud and the vascular system of the central cylinder has also been traced in this series

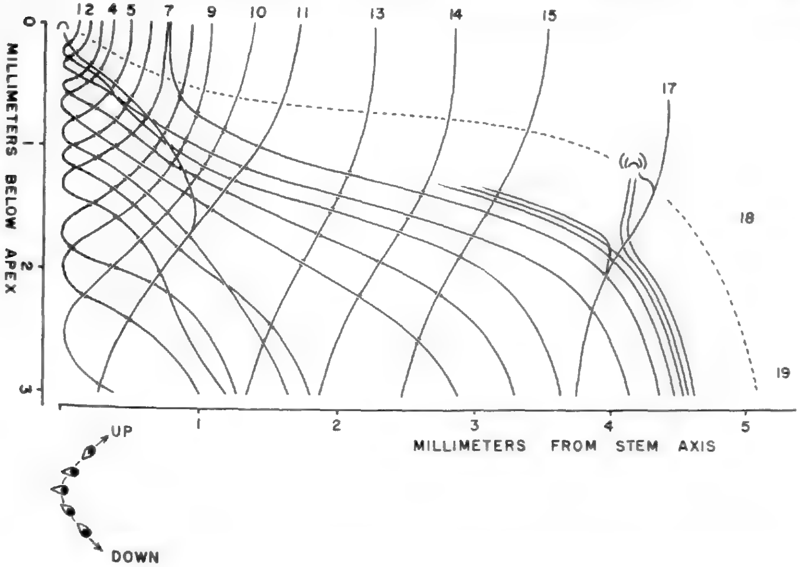


FIG. 13. The path of major leaf traces from leaf primordia 1 through 17, obtained from plotting each individual bundle through a series of transverse sections. In this diagram, all radial distances are plotted within a single radial plane regardless of position in the third dimension. The diagram therefore does not represent a real radial section as in FIG. 12. Major leaf traces P 1 to P 17 are shown, for P 7 also a minor one. The reader has to visualize that there are numerous intermediate leaf traces between these two extremes, from each leaf. Vertical bundle branches normally appear from leaf traces of P 17. The one shown from leaf trace P 11 appeared unusually early (see text). Vascularization of the axillary bud of P 17 includes two vertical bundles and one satellite bundle. The dashed line marks the approximate level of leaf insertion. INSET BELOW. The 120° turn of the major leaf traces in the stem center, as seen in successive transverse sections.

of sections. The provascular connection between axillary bud and stem was established only in P 17 and older leaves. In P 15 the axillary bud meristem was apparent but still entirely without discernible procambial strands. This suggests that vascular continuity between axillary buds and main axis is established late, in the manner of minor leaf traces. A more detailed discussion of the development of the vascular system of axillary buds will follow in the second paper of this series.

Developmental inferences. The sequence of vascular development is thought to be as follows. Leaf traces link up with a potential vertical bundle in the cap, then differentiate out below the cap. Leaf traces which develop early, i.e., those arising in a position near the center of the cap, become major bundles; those developing further out, near the cap periphery, become minor bundles. For comparison both a major and a minor trace from P 7 are shown in FIGURE 13.

These developmental processes have been discussed in detail in our articles on the developmental pattern of the vascular system of *Rhapis* and *Prionium*. We may merely point out here that there are no cortical bundles in *Dracaena*, a fact which is of utmost significance as we shall see in the next paper of this series.

DISCUSSION

In a previous review (Tomlinson & Zimmermann, 1969) we have noted that von Mohl (1824) equated the primary vascular system of "*Aletris fragrans*" and other species which he studied with that of a palm, in so far as he understood the course of vascular bundles in the palm stem. Von Mohl's contemporaries and all subsequent investigators who studied arborescent Liliiflorae at first hand claim to have confirmed his observations (e.g. Meneghini, 1836; Millardet, 1865; de Cordemoy, 1894; and others). However, our own more recent investigation of the palm stem (Zimmermann & Tomlinson, 1965) has shown that von Mohl's understanding was incomplete, because he overlooked the axial continuity of vascular bundles which is so important in long-distance transport. We have already given our historical interpretation of the topic (Tomlinson & Zimmermann, 1966) and need not discuss it any further. The present study of *Dracaena fragrans* has confirmed that von Mohl was right in principle. The primary vascular anatomy of the axis of this plant does indeed correspond in all essentials with that of a palm, but we now have a much more complete understanding of the anatomy of the palm and its development. *Dracaena* conforms in the pattern of primary vascular differentiation, a pattern which we believe is fundamental for monocotyledons as a whole (Zimmermann & Tomlinson, 1965, 1967, 1968).

Our cinematographic analyses have included other species and genera of arborescent Liliiflorae. Analysis of the mature axis of *Cordyline terminalis*, *Dracaena marginata* and *Pleomele* (*Dracaena*) *reflexa* confirms the course of vascular bundles described for *Dracaena fragrans*. Single sections which we have prepared from the stems of several other genera and species can also be interpreted according to our three-dimensional analysis. This additional evidence puts our interpretation on firm ground.

SUMMARY

The primary vascular system of arborescent Liliiflorae was thought by von Mohl and subsequent investigators to be equivalent in principle to that of palms. An analysis of the system in the vegetative axis of *Dracaena fragrans* with the aid of cinematographic methods confirms this. In addition, however, it also shows that axial continuity of the palm type, overlooked by these early anatomists, which has only recently been demonstrated, also occurs in *Dracaena* and related plants. The origin of the primary vascular system has been traced by plotting the course of provascular strands in the developing crown. We regard, on the basis of

similar studies of other plants, this pattern as fundamental for the monocotyledons. The basis has thus been laid for a future investigation of secondary vascular tissues in these plants.

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COMPARATIVE MORPHOLOGICAL STUDIES IN DILLENIACEAE, IV. ANATOMY OF THE NODE AND VASCULARIZATION OF THE LEAF

WILLIAM C. DICKISON

IN A CONTINUING EFFORT to provide comprehensive anatomical information which might prove useful in elucidating taxonomic and phylogenetic relationships of the Dilleniaceae, an extensive investigation of nodal and leaf vasculature was undertaken.

Aside from remarks pertaining to ovular structure by Cordemoy (1859), and an occasional reference to internal structure by various other workers, the earliest comprehensive anatomical investigations on Dilleniaceae are the contributions of Baillon (1866–67, 1871) and Hitzemann (1886, cited by Ozenda, 1949).

The first comparative morphological studies on the family to appear were those of Parmentier (1896), who found the leaf to contain characters of diagnostic value, and Steppuhn (1895) who made an extensive investigation of stem, leaf, and root of some one hundred fifty dilleniaceous species.

Solereder (1908) and Metcalfe and Chalk (1950) published additional anatomical information, but contributed little to help clarify the phylogenetic position of the group. The most recent study on comparative vegetative anatomy of the family was by Ozenda (1949) whose observations on seedling, nodal, and leaf anatomy were scattered among seven genera.

All researches referring to the Dilleniaceae, therefore, are either incomplete, or else were produced in the last century and thus warrant reinvestigation. This paper describes heretofore unreported anatomical data of both taxonomic and phylogenetic significance.

MATERIALS AND METHODS

Material of over one hundred dilleniaceous species was examined. Specimens studied were received from, or are housed in: the Arnold Arboretum, Harvard University (A); State Herbarium of South Australia, Adelaide (AD); Arizona State University, Tempe (ASU); Botanic Museum and Herbarium, Brisbane (BRI); Commonwealth Scientific and Industrial Research Organization, Canberra (CANB); Royal Botanic Garden, Edinburgh (E); Gray Herbarium, Harvard University (GH); Royal Botanic Gardens, Kew (K); Botanical Survey of India, Southern Circle, Coimbatore (MH); Missouri Botanical Garden, St. Louis (MO); Animal Industry Branch, Northern Territory Administration, Alice Springs (NT); Western Australian

Herbarium, Perth (PERTH); Rancho Santa Ana Botanic Garden, Claremont (RSA); Sarawak Museum, Kuching (SAR); Botanic Gardens, Singapore (SING); University of California, Berkeley (UC); and the United States National Museum, Washington (US). The assistance of the curators of these collections is gratefully acknowledged. I also wish to thank Doctors R. D. Hoogland, H. Keng, and C. R. Metcalfe for providing seed used in this study.

The study of lamina vascularization was accomplished entirely through the use of cleared leaves. Clearing was carried out using the standard NaOH method followed by safranin stain. Dried materials were initially re-expanded in 5 percent NaOH prior to fixation and sectioning. Nodes were serially sectioned and stained with a combination of safranin-fast green. Petiole vasculature was followed by obtaining sections throughout the length of the petiole as well as midway through the midrib.

NODAL ANATOMY

No detailed, comprehensive study of nodal anatomy in the Dilleniaceae has previously been undertaken. Sinnott (1914) attempted to utilize the nodes of several genera within the family (*sensu* Gilg, 1893) as evidence to support his idea that the trilacunar node was primitive; furthermore, that the unilacunar and multilacunar node was derived by reduction or amplification. This author listed six genera of the Dilleniaceae (*sensu stricto*) as having tri- or pentalacunar nodes.

Ozenda (1949) after an examination of *Hibbertia, Dillenia, Schumacheria, Tetracera, Curatella,* and *Davilla* also concluded that the mature nodes of the family were tri- or multilacunar; however, he was of the opinion that the multilacunar condition was the primitive pattern. The primitive nature of the multilacunar node in the Dilleniaceae has also been advocated by Meeuse (1966, p. 49).

As a result of comparative morphological data from both fossil and extant plants, in addition to ontogenetic considerations, the primitive nature of the trilacunar node was questioned by Marsden and Bailey (1955) and Canright (1955). These authors suggested that the unilacunar two-trace system represented the primitive condition. The unilacunar two-trace node is characteristically described as having two vascular traces which arise from independent primary bundles and, therefore, do not represent the dichotomy of a single median trace.

Pant and Mehra (1964) re-evaluated nodal anatomy in many Pteropsida, and concluded that the statements of Marsden and Bailey (*loc. cit.*) concerning nodal patterns in fossil ferns and gymnosperms were not always substantiated. They then advised caution in accepting the unilacunar two-trace node as primitive for all Pteropsida. Results from a study of developmental patterns in stem primary xylem indicated to Benzing (1967a, b) that the odd-numbered trace, unilacunar one-trace or trilacunar, was more likely to be primitive in angiosperms. A recent paper by Namboodiri and

Beck (1968b) supports this view and regards the unilacunar one-trace node as the primitive condition in the Coniferales.

My observations reveal that mature nodes of *Dillenia* (FIG. 8), *Didesmandra*, and *Schumacheria* (FIG. 7) are exclusively multilacunar.[1] The numerous leaf traces are associated with a corresponding number of parenchymatous gaps in the cauline stele. The number of traces in *Schumacheria* and *Didesmandra* was found to be stable at nine and seventeen respectively. The number in *Dillenia*, however, varies from as few as seven (*D. pulchella*) to as high as twenty-seven (*D. suffruticosa*). Variability is also evident within a single species, the number of traces apparently reflecting the age and size of the node. The manner in which bundles depart the stele was found generally to be correlated with the presence or absence of sheathing leaf bases. If the petiole does not sheath the stem, all traces tend to depart simultaneously. If the leaves are amplexicaul, the median trace passes out initially, with laterals departing in succession at higher levels.

The leaves examined of the semi-herbaceous, rhizomatous genus *Acrotrema* were supplied by three traces; i.e., the node was trilacunar (FIG. 4). The median trace departs first with the resulting gap remaining open above the level at which the two lateral gaps close. Large-leaved species (e.g., *A. arnottianum*) should be studied when available to determine to what extent leaf size affects the nodal pattern in this extremely variable genus.

In contrast to the information presented by Ozenda (1949), all hibbertias are not uniformally trilacunar. Numerous species with reduced, needle-like leaves possess unilacunar nodes (FIG. 2). In these cases, the primary stele is composed of a continuous cylinder of vascular tissue with no discrete bundles discernible. At the unilacunar node, a single trace passes directly into the leaf. All broad-leaved hibbertias from New Caledonia and Fiji are trilacunar. Leaf size is not always indicative of nodal patterns, however. Trilacunar *Hibbertia huegelli* (FIG. 45) and *H. monogyna* (FIG. 46), for example, possess smaller leaves than *H. nitida* (FIG. 47) which is unilacunar.

The most reduced leaves in the family are encountered in the genus *Pachynema*. The small, scale-like, lateral appendages were found to be vascularized by a single prominent trace with a well defined gap in the stele. From the flattened stem of *P. dilatatum*, leaves may be secondarily supplied by weak cauline traces (FIG. 34).

The New World genera *Curatella*, *Davilla* (FIG. 6), and *Doliocarpus* are mostly pentalacunar; but seven-trace nodes occur in *Davilla aspera*, and *Doliocarpus major* is trilacunar. Trilacunar, three-trace nodes are also uniform throughout the genus *Tetracera* where special effort was made to examine representative species from the Old and New World tropics. In *Tetracera*, three bundles are associated with three widely separated

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[1] The report by Benzing (1967a) of unilacunar one-trace nodes in the mature stems of *Dillenia indica* is in error. I have personally examined the sections used in this study and conclude that they were not taken from any member of the Dilleniaceae.

gaps (FIG. 3). The lateral bundles arc up and through the cortex where they enter the petiole. This contrasts with the condition in the trilacunar hibbertias with sheathing leaf bases, where the laterals enter the leaf directly from the stele (FIG. 5).

The seedling anatomy of *Dillenia indica*, *Tetracera indica*, *Hibbertia dentata*, and *H. scandens* was examined. The cotyledonary nodes in the first two species are of the 2:1 type, viz., two traces departing from a single gap (FIGS. 1, 40). My observation of the 2:1 cotyledonary nodal pattern in *Dillenia indica* once again contradicts the information presented by Ozenda (1949) who illustrated a single cotyledonary trace. Particular attention was paid to the double traces at subnodal levels and in all instances they originated from independent parts of the stele. In *Dillenia indica*, a species with multilacunar nodes in the mature stem, the first formed seedling leaves possess a trilacunar node (FIG. 41). Numerous examples can be found in other dicotyledonous families of a similar progression, as in Magnoliaceae, Degeneriaceae, etc.

The cotyledonary node of *Hibbertia dentata* and *H. scandens* differs by being of the unilacunar one-trace type (FIG. 12). No evidence of doubleness could be observed in the single, broad strand of vascular tissue which passes into the cotyledon. The occurrence of a 1:1 cotyledonary node in *Hibbertia* is of particular interest, since it is a genus with trilacunar mature nodes, and is generally considered to be more primitive in its characters than either *Dillenia* or *Tetracera*. The question again arises whether an even or odd number of nodal traces represents the primitive condition. A thorough study of the cotyledonary node in other Dilleniaceae would be worthy of careful attention.

It is perhaps significant, that more than one case was observed among the seedling and mature nodes of *Dillenia* where an even number of traces prevailed. This condition resulted from suppression of one of the lateral bundles with the result that an even number of traces departed the stele. Although this might be dismissed as abnormal, the fact that it was observed more than once indicates that it may be of some significance.

Although the majority of plant families exhibit a combination of unilacunar and trilacunar, or trilacunar and multilacunar nodes, it is relatively uncommon for a single family to possess all three types (Bailey & Nast, 1944). The Dilleniaceae are, therefore, unusual in possessing four patterns: unilacunar two-trace, unilacunar one-trace, trilacunar, and multilacunar. Bailey (1956) points out that transitions from trilacunar to unilacunar nodes may occur as the result of anatomical specialization in response to the environment. The reduction of leaf size in *Hibbertia* is such an adaptation. Thus, the mature foliage nodes in Dilleniaceae (*sensu stricto*) demonstrate two distinct trends of specialization: (1) secondary reduction and elimination of the lateral strands of the trilacunar nodes; and (2) amplification of the trilacunar node by the addition of laterals.

Bailey and Howard (1941) note that trends of specialization in nodal anatomy are not infrequently correlated with specializations elsewhere in the plant (e.g., wood). No such direct correlations were noted in the dillenias. In fact, those genera having the least advanced wood generally possess the more highly evolved nodes.

It is not possible to construct relationships within the family solely on the basis of nodal structure due to the presence of a similar anatomy in both Old and New World genera. Likewise, nodal anatomy is of limited value in determining relationships beyond the family. When the nodes of putatively related families are compared, it is evident that they are all essentially tri- or multilacunar. There is, accordingly, no basis for accepting or rejecting alliances from this information alone.

A significant exception to the above generalizations is found in the Theaceae where the node is uniformly characterized by a broad trace which departs from a single gap. Keng (1962) agreed with Canright (1955) in considering this pattern to be the result of phylogenetic fusion of several separate traces. If Canright's (*loc. cit.*) suggested trends of nodal specialization are accepted, it leads one to the conclusion that the nodal anatomy in the two families represents the culmination of distinct lines of evolution. Therefore, although the wood and pollen of these groups is similar (Dickison, 1967a, b), nodal anatomy suggests they may in fact be only distantly related.

A similar conclusion might be reached regarding the predominantly unilacunar, one-trace nodes of Ericaceae; however, the report by Philipson and Philipson (1968) of trilacunar nodes in *Rhododendron* gives cause for re-evaluation.

PETIOLE VASCULARIZATION

An attempt to define the range of variability in petiolar anatomy of Dilleniaceae disclosed the following major patterns:

Species with Unilacunar Nodes (1:1).

(1) A single, slender, unbranched trace enters the lamina: numerous hibbertias (FIG. 27).

Species with Trilacunar Nodes (3:3).

(1) Traces fuse and form a flattened arc: *Hibbertia quadricolor.*

(2) Traces fuse and form "V" shaped arc: *Hibbertia coriacea* (FIG. 17).

(3) Traces fuse and form cylindrical, flattened, or concave vascular ring, either confluent or slightly dissected: *Doliocarpus major*; *D. olivaceus*;[2] *Hibbertia dealbata*; *H. oubatchensis*; *H. patula* (FIG. 14); *H. trachyphylla*; *Tetracera akara*; *T. arborescens*; *T. daemeliana* (FIG. 16); *T. korthalsii*; *T. macrophylla*; *T. ovalifolia*; *T. portobellensis*; *T. scandens*; *T. volubilis.*

(4) Traces form a closed cylindrical ring with one or more medullary bundles produced by invagination: *Hibbertia lucida* (FIG. 13).

(5) Traces form an abaxial arc of fused or dissected collateral bundles with a separate adaxial trace derived from the inrolling and/or division of the lateral bundles. The adaxial trace may be lost in the lamina: *Acrotrema*

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[2] Nodes were not examined.

sp.; *A. bullatum*; *A. gardneri*; *A. lanceolatum*; *A. uniflorum*; *A. walkeri*; *Hibbertia banksii*; *H. pancheri*; *H. wagapii*; *Tetracera boiviniana*; *T. masuiana*.

(6) Traces form an abaxial arc of fused or dissected collateral bundles with a separate adaxial trace derived from division of the median bundle. The adaxial trace may be lost in the lamina: *Hibbertia scandens*; *Tetracera indica*.

Species with Multilacunar Nodes (five to many traces from an equal number of gaps).

(1) Traces remain free forming a ring of widely dissected collateral bundles (bundles are often of unequal sizes): *Acrotrema costatum*;[2] *Didesmandra* (FIG. 15); *Dillenia excelsa*; *D. luzoniensis*; *Schumacheria angustifolia*.

(2) Traces fuse to form confluent or only slightly dissected ring, often "U" or "V" shaped in outline: *Davilla* (FIG. 22); *Dillenia bolsteri* (FIG. 19); *D. eximia*; *D. indica*; *D. ovata*; *D. pentagyna*; *D. salomonensis*; *D. suffruticosa; D. turbinata*.

(3) Traces fuse to form confluent or only slightly dissected ring with an arc (rarely superimposed) of fused or dissected medullary bundles: *Curatella americana* (FIGS. 10A,B,C); *Dillenia alata*; *D. beccariana* (FIG. 20); *D. castaneifolia* (FIG. 18); *D. megalantha*; *D. papuana*; *D. philippinensis*; *D. reifferscheidia*.

(4) Traces form an abaxial arc of fused or dissected collateral bundles with an adaxial enclosed siphonostele. The adaxial ring may subsequently open laterally or invaginate to produce additional free bundles: *Doliocarpus coriaceus*; *D. dentatus*; *D. guianensis* (FIG. 21); *D. rolandri*.

It is evident that petiole vascularization in Dilleniaceae is quite diverse both between and within genera. In the present study, subtle deviations in vascularization pattern, the general outline of the vascular cylinder, and small, adaxial, subsidiary wing traces were ascribed little importance. Despite acknowledged incompleteness, I feel the descriptions outlined above will prove useful in future comparative studies relating to the family.

It should be emphasized, that the descriptions presented are not based entirely upon observations from a single "characteristic" region. Wherever possible, sections were examined throughout the petiole and midrib as suggested by Howard (1962). The importance of determining the entire sequence of petiole vascularization is well exemplified in study of the Dilleniaceae. Not only are there significant fluctuations within a single petiole, but patterns which appear superficially similar between genera can be shown to have different origins. An example of the latter situation is illustrated by *Hibbertia scandens* and the Ceylonese acrotremas, both of which possess petioles with an abaxial arc and adaxial strand of vascular tissue. However, the adaxial bundle is derived from the median trace in *H. scandens* (FIGS. 11A,B,C), whereas it originates from the lateral nodal bundles in *Acrotrema* (FIGS. 9A,B,C,D).

The diversity present at the species level indicates that the petiole may be of taxonomic significance in the family. In the New World genus *Do-*

liocarpus, *D. major* and *D. olivaceus* are distinguished by their pubescent ovaries and fruits. An absence of medullary bundles in the petiole was also found to separate these taxa readily from all other species examined in the genus. Hunter (1966) considers *Doliocarpus rolandri* Gmel. to be a synonym of *D. major* Gmel. I have studied a collection from Brazil cited as *D. rolandri* (*Pires & Cavalcante 52254*, US) and found the petiole to possess medullary bundles, a character which is not encountered in *D. major*. A re-examination of this genus taxonomically might yield additional basis for separation of the species. Other specific variation is found in *Acrotrema* (where *A. costatum*, from Thailand and Malaya, is quite distinct from the Ceylonese species), *Hibbertia*, and *Dillenia*, though much more material must be studied before the true value of these data can be realized.

Petiole structure cannot be used to separate the Dilleniaceae into subfamilies or tribes. Moreover, there is little or no correlation between petiole vascularization and nodal anatomy. When considered as a whole, the vascular pattern in species with trilacunar nodes cannot be considered more primitive than that in species with multilacunar nodes.

In plants with multilacunar nodes, petioles with widely dissected cylinders tend to be correlated with slender venation lacking massive bundle sheathing, which I consider primitive. With intensification of leaf venation and bundle sheathing, the complexity of the petiolar anatomy also increases. I believe, therefore, that unfused bundles represent the primitive condition in multilacunar dillenias. Subsequent evolutionary progression has produced fusion of traces and the formation of more complex medullary bundle patterns. These specializations have apparently occurred more than once, since the same apparent trends are also evident in species with trilacunar nodes.

These ideas of nodal and petiolar evolution in Dilleniaceae do not agree with the conclusions of Decker (1967) who worked on the Luxemburgieae (Ochnaceae). Within the Luxemburgieae, Decker considers the multilacunar node more primitive than the trilacunar, and petioles with numerous, unfused bundles (some of which may be medullary), more primitive than petioles with fused traces devoid of medullary bundles. In view of the frequent derivation of the Ochnaceae from the Dilleniaceae, such contrasting opinions are of special interest.

A foliar character of debatable morphological derivation is the presence of petiolar wings in some Old World dilleniaceous species. Hoogland (1952) attaches taxonomic importance to the presence of completely amplexicaul petiolar wings in certain species of *Dillenia*. Morphologically, these wings are frequently considered to be stipules. Hoogland (*loc. cit.*) does not accept this interpretation for the following reasons: (1) there is often no sharp distinction between the petiolar wings and lamina, (2) stipules of the usual morphological type do not occur in the dillenias, (3) in caducous wings, separation from the petiole begins from the base of the petiole and not from the apex as one would expect, and (4) Ozenda (1949) describes the wings as being weakly vascularized in contrast to the situation in the Magnoliaceae where the stipules receive a separate trace from the cauline stele.

I have found vascularization of the wings in *Dillenia* to vary from weak (e.g., *D. albiflos*) to rather strong (e.g., *D. philippinensis*; *D. suffruticosa*). In the latter case the venation is highly reticulate. In either situation the wings are never supplied by independent traces from the cauline stele. Although I do not have any original interpretation for these structures, they do not appear comparable to true stipules.

VASCULARIZATION OF THE LAMINA

Major Venation. Although the prevailing type of major foliar venation in the Dilleniaceae is pinnate, with the secondary veins proceeding to the margin of the blade, wide variation in leaf size, shape, and vascularization is encountered in the genus *Hibbertia.* A study of leaf vasculature in this genus showed that three basic venation patterns can be recognized: (1) pinnate leaves in which the numerous, strong, parallel, lateral veins extend diagonally outward from the midvein toward the margin of the lamina where they are interconnected by curved peripheral venation (FIG. 43); (2) pinnate leaves in which the principal lateral veins are fewer in number, irregular in their occurrence, more tenuous, and tend to sweep upward upon departure from the midvein (FIGS. 42, 44); and (3), a pattern where two or more strong, terminal, lateral veins reflex back after departure from the midrib to terminate, often very massively, at the leaf base. A varying number of prominent lateral veins may connect the midrib with the reflexed lateral (FIG. 49). This specialized venation pattern is exclusively associated with those hibbertias with reduced, needle-like leaves. The physiological significance of this type of vasculature is not clear.

Concomitant in *Hibbertia* with a general trend toward reduction in leaf size as a response to xerophytic conditions, is a trend in reduction of leaf vascularization. Theoretically, this specialization commences with the progressive loss of the basal lateral veins connecting the midrib and reflexed laterals (FIGS. 47, 48) so as eventually to reach a situation where the reflexed veins are without major interconnecting venation (FIG. 49). The ultimate reduction is represented in *H. fasciculata* where only a small number of very weak reflexed apical veins are present; the lower one-half of the leaf is entirely devoid of venation, excepting the midvein (FIG. 50).

Cotyledons of *Dillenia indica*, *Tetracera indica*, and *Hibbertia dentata* differ in shape from ovate, to oblong-elliptical, to linear-lanceolate, but all exhibit fundamentally similar venation. The vasculature is characterized by the presence of strongly accentuated, arcuate basal lateral veins which terminate in, or near, the cotyledon apex. Several less prominent veins diverge from the midrib to connect with the strongly ascending basal veins (FIG. 40). Another feature of cotyledonary vasculature is the "feathery" termination of the midvein and arcuate laterals. Feathery termination of the midrib was also observed in the mature leaves of the family.

The first-formed seedling leaves of *Dillenia indica*, with their strong, parallel, pinnate veins and serrate margins are sharply distinguished from the cotyledons (FIG. 41).

Minor Venation. In addition to noteworthy features of major venation, the pattern and diameter of the minor veins, in association with bundle sheathing, is often of diagnostic and perhaps of taxonomic significance in the Dilleniaceae.

The occurrence of bundle sheaths around the veins is almost a universal feature of dilleniaceous leaves. Sheathing is noticeably absent only in some hibbertias and *Acrotrema*. When present, the sheath cells are either unlignified and parenchymatous in nature, or lignified, pitted, sclerenchymatous elements.

Parenchymatous sheaths typically surround both the major veins and terminal veinlets. These sheaths usually consist of cells elongated parallel to the vascular bundles; however, occasionally they become considerably lobed and oriented at right angles to the veins (FIG. 33). Sclerotized bundle sheathing is recognized by the presence of lignified, extensively pitted cells. When sclerenchyma occurs, it may form massive sheaths over the veins and veinlets as in *Hibbertia* (FIG. 30), *Tetracera* (FIG. 32), and some species of *Doliocarpus*. The formation of sclerified bundle sheaths enclosing the terminal tracheids is an uncommon feature in dicotyledonous leaves (Esau, 1965). Of more frequent occurrence in the family is sclerenchyma around the major veins, but with veinlets devoid of sheathing or possessing only an incomplete sheath. The most striking pattern is seen in *Hibbertia banksii* where the mature leaves exhibit an interrupted sclerenchymatous sheath (FIG. 29).

Parenchymatous sheath cells were observed in *Curatella* (FIG. 31) and all species of *Dillenia* (FIG. 23), except *D. philippinensis* and *D. reifferscheidia* where pitted elements are found. Also, the presence of lobed parenchymatous sheathing around the terminal veinlets in *Doliocarpus dentatus* (FIG. 33) and *D. rolandri* readily distinguishes them from all other species of the genus. The variation present in *Doliocarpus* in the node, petiole, and minor venation warrants further study.

Distinctions can also be made between genera and species on the basis of the diameter of veins and veinlets. Very slender venation is present in *Acrotrema*, *Didesmandra* (FIG. 26), *Schumacheria*, and some hibbertias (*H. scandens*, *H. dentata*, *H. tetrandra*, etc.). Associated with slender vascularization is weak bundle sheathing or its complete absence. Only in *Hibbertia* is massive venation sometimes devoid of sheathing (FIG. 28). There appears, nevertheless, to be in the family a rather distinct trend toward increased vein size accompanied by intensification of the amount of vein sheathing.

A restricted trend was observed in *Dillenia* toward the formation of vein islets devoid of free vein endings. It is possible to trace this progression from species with slender veins and numerous free vein endings (e.g.

D. salomonensis and FIG. 23) through species with an intermediate pattern (e.g. *D. quercifolia, D. ovalifolia, D. nalagi*) to a pattern illustrated by *D. papuana* (FIG. 24) where free vein endings are scarce. The terminal condition in this sequence is seen in the massive, closed venation of *D. schlechteri* (FIG. 25).

A taxonomic correlation of minor venation patterns in *Dillenia* is illustrated by similar closed venation types occurring in *D. papuana, D. cyclopensis*, and *D. schlechteri*, all of which are considered closely related by Hoogland (1959) on the basis of floral structure. The only other species which were observed to possess comparable vasculature were *D. beccariana*, and *D. turbinata*. On the basis of leaf venation, I was not able to segregate *Wormia* as a distinct genus from *Dillenia*.

The leaves of the Dilleniaceae appear to display a rather distinct phylogenetic trend of specialization toward more massive vascularization, accompanied by an increase in bundle sheathing. The same fundamental trends have also been described for the Winteraceae (Bailey & Nast, 1944). When the venation pattern, size, type, and degree of bundle sheathing, as well as petiole vasculature, are considered together, they offer excellent diagnostic leaf characters at the family, genus, and in some instances, species level. Additional material in all stages of maturity will have to be examined to understand fully the taxonomic significance of this information.

TERMINAL IDIOBLASTS

The occurrence of specialized terminal-veinlet elements in several widely diverse dicotyledonous families has been well established. In a recent review of the literature, Tucker (1964) describes their presence in the Magnoliaceae. The occurrence of terminal idioblasts is now reported for the first time in the Dilleniaceae.

Specialized terminal cells were observed only in relatively few species of *Hibbertia*. The diversity in vein endings is thus in accordance with variation in leaf shape and venation. The terminal cells are all of the basic tracheoid type (see Foster, 1956). Employing the classification of Tucker (*loc. cit.*), one can recognize tracheoidal elements, viz. scalariform or scalariform-reticulate pitted cells, and dilated tracheids. Leaves of *H. scandens* (cult. K, *s.n.*) and *H. dentata* (cult. K, *s.n.*) were found to contain terminal elements which closely resemble tracheary cells in general morphology. The elements in *H. dentata* (FIG. 36) tend to occur singly and have exclusively scalariform pitting whereas the idioblasts of *H. scandens* (FIG. 35) often occur in clusters where they assume more irregular shapes and have reticulate pitting.

The terminal elements of *Hibbertia pachyrhiza* (*C. L. Wilson 861*, FIG. 38), although of the basic tracheoid type, differ considerably in their morphology. The latter cells are thick-walled, pitted to a much less degree, and are characteristically spherical in outline. In comparison with surrounding parenchyma these elements are significantly larger (75–140 μ in diameter). They occur singly or in clusters of three to four on each vein ending.

Terminal elements in *Hibbertia huegelli* (*C. L. Wilson 777*), *H. monogyna* (*Maiden s.n.*), *H. elata* (*Ingram 19852*), *H. billardieri* (*Clemens 42584a*), and *H. linearis* (*White 8580*) tend to be intermediate between the elongated tracheoid element and the spherical one (FIG. 37).

Dilated tracheids were found in *Hibbertia scandens* (FIG. 39), *H. dentata*, *H. nymphaea* (*Morrison s.n.*, A), and *H. amplexicaulis* (*Pritzel 531*). In *H. scandens* and *H. dentata* they were often in the same leaf with tracheoidal elements, and several veins were noted where the two types were present at the same vein endings. Generally, however, dilated tracheids seem to occur rather sparsely throughout the leaf and are not present at every vein terminus.

The taxonomic usefulness of terminal idioblasts in the Dilleniaceae appears limited in view of their rather infrequent occurrence. Phylogenetically it is of interest that the most diverse vein endings are found in *Hibbertia*, which on the basis of other criteria, is considered rather primitive. A similar situation has been reported in the Magnoliaceae (Tucker, *loc. cit.*). The full phylogenetic value of terminal idioblasts still remains to be developed; however, the trend toward the formation of specialized terminal cells appears to be a distinct one, subsequently leading toward the reduction in size of the elements and in the amount of pitting on the wall surface.

SUMMARY

A comprehensive study of nodal and leaf vascularization in Dilleniaceae has led to the following fundamental conclusions:

(1) The mature foliar nodes of Dilleniaceae (*sensu stricto*) are unilacunar one-trace, trilacunar, and multilacunar. The unilacunar and multilacunar patterns are both derived from the trilacunar condition. The cotyledonary node is unilacunar two-trace or unilacunar one-trace. Evidence from nodal anatomy appears to discredit a close relationship between the Dilleniaceae and Theaceae.

(2) The petiolar anatomy of the family shows considerable diversity. Descriptions of major venation patterns reveal that, in general, vascular cylinders composed of widely dissected bundles are more primitive than petioles with fused bundles and more complex medullary traces.

(3) The vascularization of the lamina displays fundamental phylogenetic trends of specialization in both major and minor venation. Bundle sheath cells are either parenchymatous or sclerenchymatous and may enclose the terminal tracheids. Slender venation patterns lacking bundle sheathing are less specialized than coarser-veined leaves with massive bundle sheathing.

(4) When considered together, nodal anatomy and foliar vasculature are of excellent diagnostic value and frequently of taxonomic and phylogenetic significance in the Dilleniaceae.

(5) The presence of specialized terminal idioblasts in the leaves of *Hibbertia* is a character of which the importance is yet to be determined.

MATERIAL EXAMINED

Acrotrema sp. **Ceylon:** *Thwaites CP3899* (US). *A. bullatum* Thw. **Ceylon:** *Thwaites CP239* (US). *A. costatum* Jack. **Thailand:** *Smitinand 2999* (US). *A. gardneri* Thw. **Ceylon:** *Thwaites CP253* (US). *A. lanceolatum* Hook. **Ceylon:** *Thwaites CP2660* (US). *A. uniflorum* Hook. **Ceylon:** *Thwaites CP1014* (US). *A. walkeri* Wight. **Ceylon:** *Thwaites CP694* (US).

Curatella americana L. **Brazil:** *Irwin 5470* (NY); **Nicaragua:** *Van der Sluijs s.n.* (preserved material).

Davilla aspera (Aubl.) Benoist. **Trinidad:** *Howard 10502* (GH); **Brazil:** *N.T. Silva 16*. *D. multiflora* (DC). St. Hil. **Panama:** *Dodge & Allen 17360* (MO). *D. rugosa* Poir. **Brazil:** *A. de Mattos Filho s.n.* (preserved material). *Davilla* sp. **Brazil:** *Irwin 5570* (NY).

Didesmandra aspera Stapf. **Sarawak:** *Burtt & Woods B.2540* (E); *S.18297* (SAR); Native collector (SAR) *s.n.* (preserved material).

Dillenia alata (R.Br. ex DC.) Mart. **New Guinea:** *P. van Royen 4677* (A, US). *D. albiflos* (Ridl.) Hoogl. **Malaya:** *Corner SING F 29369* (A). *D. beccariana* Martelli. **Sarawak:** *SAR 16272* (A). *D. biflora* (A. Gray) Martelli ex Dur. & Jacks. **Fiji:** *Gillespie 2182* (GH); *A. C. Smith 8762* (US). *D. bolsteri* Merr. **Philippines:** *Wenzel 3112* (GH). *D. castaneifolia* (Miq.) Martelli ex Dur. & Jacks. **New Guinea:** *Womersley NGF 3768* (A). *D. cyclopensis* Hoogl. **New Guinea:** *van Royen & Sleumer 5812* (A). *D. excelsa* (Jack) Gilg. **North Borneo:** *Ramos 1379* (A). *D. eximia* Miq. **Borneo:** *NIFS bb 16830* (A). *D. indica* L. **Australia:** Cult. BRI *s.n.* (preserved material); **India:** *Sastri s.n.* (preserved material); Cult. E *C4388*. *D. luzoniensis* (Vidal) Martelli ex Dur. & Jacks. **Philippines:** *J. V. Pancho s.n.* (preserved material). *D. megalantha* Merr. **Philippines:** Quezon. *M. Q. Lagrimas s.n.* (preserved material). *D. monantha* Merr. **Philippines:** Herre *1010* (A). *D. montana* Diels. **New Guinea:** *Hoogland & Pullen 6265* (A). *D. nalagi* Hoogl. **Papua:** *Hoogland & Taylor 3438* (A). *D. ochreata* (Miq.) Teysm. & Binn. ex Martelli. **Celebes:** *NIFS bb 18085* (A). *D. ovalifolia* Hoogl. **New Guinea:** *van Royen 3012* (A). *D. ovata* Wall. ex Hook.f. & Thoms. **Indo-China:** *Squires 320* (A); Cult. SING *s.n.* (preserved material). *D. papuana* Martelli. **Papua:** *Womersley NGF 3926* (A); *NGF s.n.* (preserved material). *D. pentagyna* Roxb. **India:** *Ellis 23815* (MH). *D. philippinensis* Rolfe. **Philippines:** Makiling. *M. Q. Lagrimas s.n.* (preserved material). *D. pulchella* (Jack) Gilg. **Singapore:** Cult. SING *s.n.* (preserved material). *D. quercifolia* (White & Francis ex Lane-Poole) Hoogl. **Papua:** *Hoogland 3286* (A). *D. reifferscheidia* Villar. **Philippines:** Quezon. *Lagrimas s.n.* (preserved material). *D. reticulata* King. **Sarawak:** *SAR 16655* (A). *D. salomonensis* (White) Hoogl. **Solomon Islands:** *Walker & White 145* (A). *D. schlechteri* Diels. **New Guinea:** *Womersley & Millar NGF 7000* (A). *D. suffruticosa* (Griff.) Martelli. **Singapore:** Cult. SING *s.n.* (preserved material); *Canright 978* (ASU). *D. turbinata* Fin. & Gagnep. **Hainan:** *How 72058* (A).

Doliocarpus coriaceus (Mart. & Zucc.) Gilg. **British Honduras:** *Gentle 2892* (US); **Colombia:** *Cuatrecasas 16556* (US). *D. dentatus* (Aubl.) Standl. **Bolivia:** *Krukoff*

10088 (UC). *D. guianensis* (Aubl.) Gilg. **Surinam:** UC *947180*. *D. lasiogyne* Benoist. **Brazil:** *Klein 1.281* (US). *D. major* Gmel. **Panama:** *von Wedel 2860* (MO); *I. M. Johnston 1694* (MO). *D. olivaceus* Sprague & Williams ex Standl. **Panama:** *Stern et al. 11* (US). *D. rolandri* Gmel. **Brazil:** *Pirés & Cavalcante 52254* (US).

Hibbertia acicularis (Labill.) F. Muell. **Australia:** Queensland. *Clemens 43622* (A); *C. T. White 9466* (A). *H. altigena* Schlechter. **New Caledonia:** *H. S. McKee 3709* (A). *H. amplexicaulis* Steud. **Australia:** *Pritzel 531* (A). *H. aspera* DC. **Australia:** New South Wales. *Constable 42837* (A). *H. aurea* Steud. **Australia:** *C. L. Wilson 843* (US). *H. australis* Wakefield. **Australia:** *Aston 359* (A). *H. banksii* Benth. **Papua:** *L. J. Brass 8431* (A). *H. baudouinii* Brongn. & Gris. **New Caledonia:** *Baumann-Bodenheim 11203* (A). *H. bracteata* (R.Br.) Benth. **Australia:** New South Wales, *C. T. White 5012* (A). *H. billardieri* F. Muell. **Australia:** Queensland. *Clemens 42584a* (US). *H. brongniartii* Gilg. **New Caledonia:** *Thorne 28580* (RSA). *H. cistiflora* Wakefield. **Australia:** New South Wales. *Helms 1290* (A). *H. cistifolia* R.Br. **Australia:** *Specht 843* (US). *H. coriacea* (Pers.) Baill. **Madagascar:** *Humbert 5866* (US). *H. crenata* Andr. **Australia:** *C. L. Wilson 851* (US). *H. cuneiformis* (Labill.) Gilg. **Australia:** Cult. K, *s.n.* (preserved material); *E. H. Wilson 297* (US). *H. dealbata* Benth. **Australia:** *Specht 844* (A). *H. dentata* R.Br. Cult. K, *s.n.* (preserved material). *H. deplancheana* Bur. ex Guillaum. **New Caledonia:** *Thorne 28232* (GH). *H. depressa* Steud. **Australia:** *Royce 5760* (US). *H. ebracteata* Bur. ex Guillaum. **New Caledonia:** *H. S. McKee 3697* (A). *H. elata* Maiden & Betche. **Australia:** New South Wales. *Ingram 19852* (US). *H. exutiacies* Wakefield. **Australia:** *Eichler 17965* (AD). *H. fasciculata* R.Br. ex DC. **Australia:** *Aston 387* (A). *H. furfuracea* Benth. **Australia:** *C. T. White 5382* (A). *H. gilgiana* Diels. **Australia:** *C. L. Wilson 856* (US). *H. glaberrima* F. Muell. **Australia:** *Perry 5379* (US). *H. gracilipes* Benth. **Australia:** *Royce 5792* (US). *H. huegelli* F. Muell. **Australia:** *C. L. Wilson 777* (US). *H. hypericoides* (DC.) Benth. **Australia:** *E. H. Wilson 454* (A). *H. lasiopus* Benth. **Australia:** *C. L. Wilson 781* (US). *H. linearis* R.Br. ex DC. **Australia:** Queensland. *C. T. White 8580* (A); *Hoogland 7747* (CANB). *H. lucens* Brongn. & Gris. **Fiji:** *A. C. Smith 6494* (A); *A. C. Smith 1877* (GH). *H. lucida* Schlechter ex Guillaum. **New Caledonia:** *C. T. White 2210* (A). *H. melhanioides* F. Muell. **Australia:** *C. L. Wilson 740* (US). *H. microphylla* Steud. **Australia:** *C. T. White 5317* (A). *H. miniata* Gard. **Australia:** *C. L. Wilson 782* (US). *H. monogyna* R.Br. ex DC. **Australia:** New South Wales. *J. H. Maiden s.n.* (GH). *H. montana* Steud. **Australia:** *C. L. Wilson 839* (US). *H. mucronata* (Turcz.) Benth. **Australia:** *C. L. Wilson 792* (US). *H. nana* Däniker. **New Caledonia:** *Baumann-Bodenheim 15358* (A). *H. nitida* (R.Br.) F. Muell. **Australia:** Fl. Novae Holl. *141* (GH). *H. nymphaea* Diels. **Australia:** *Morrison s.n.* (A). *H. obtusifolia* DC. **Australia:** New South Wales. *Pullen 3882* (A). *H. oubatchensis* Schlechter. **New Caledonia:** *McKee 3306* (A). *H. pachyrhiza* Steud. **Australia:** *C. L. Wilson 861* (US). *H. pancheri* (Porch. & Seb.) Briq. **New Caledonia:** *Thorne 28585* (RSA). *H. patula* Guillaum. **New Caledonia:** *H. S. McKee 3543* (A). *H. procumbens* DC. **Australia:** *Long 209* (A). *H. pulchella* Schlechter. **New Caledonia:** *H. S. McKee 2381* (A). *H. pungens* Benth. **Australia:** *Royce 7640* (PERTH). *H. quadricolor* Domin. **Australia:** *C. L. Wilson 853* (US). *H. racemosa* (Endl.) Gilg. **Australia:** *C. L. Wilson 811* (US). *H. rhadinopoda* F. Muell. **Australia:** *Pritzel 97* (A). *H. salicifolia* F. Muell. **Australia:** Queensland. *C. L. Wilson 625* (US). *H. saligna* R.Br. ex DC. **Australia:** New South Wales. *Constable 43107* (NSW). *H. scabra* Brongn. & Gris. **New Caledonia:** *Thorne 28545* (RSA).

H. scandens (Willd.) Dryand. **Australia:** Cult. BRI, *s.n.* (preserved material); Cult. K, *s.n.* (preserved material). *H. sericea* (R.Br.) Benth. **Australia:** *Muir 855* (A). *H. serrata* Hotchkiss. **Australia:** *C. L. Wilson 855* (US). *H. stirlingii* C. T. White. **Australia:** *C. L. Wilson 757* (US). *H. stricta* (DC.) R.Br. ex F. Muell. **Australia:** *Hoogland 8420* (CANB). *H. subvaginata* (Steud.) Ostenf. **Australia:** *C. L. Wilson 764* (US). *H. tetrandra* (Lindl.) Gilg. **Australia:** *C. L. Wilson 848* (US); Cult. K, *s.n.* (preserved material); Cult. E, *C3544*. *H. tomentosa* R.Br. **Australia:** *Specht 638* (A). *H. tontoutensia* Guillaum. **New Caledonia:** *McMillan 5060* (A). *H. trachyphylla* Schlechter. **New Caledonia:** *Hürlimann 846* (A). *H. uncinata* (Benth.) F. Muell. **Australia:** *E. H. Wilson 155* (A). *H. vaginata* (Benth.) F. Muell. **Australia:** *C. L. Wilson 859* (US). *H. vestita* A. Cunn. **Australia:** New South Wales. *NSW 55998* (A). *H. wagapii* Gilg. **New Caledonia:** *Thorne 28266* (GH).

Pachynema dilatatum Benth. **Australia:** Northern Territory. NT *6129*. *P. junceum* Benth. **Australia:** Northern Territory. NT *6750*.

Schumacheria castaneifolia Vahl. **Ceylon:** *Abeywickrama s.n.* (preserved material). *S. angustifolia* Hook. f. & Thoms. **Ceylon:** US *597415*.

Tetracera akara (Burm. f.) Merr. **Borneo:** *Elmer 21314* (A). *T. arborescens* Jack. **Sumatra:** *Toroes 5293* (A). *T. asiatica* (Lour.) Hoogl. **Hainan:** *Lau 3875* (A). *T. asiatica* (Lour.) Hoogl. ssp. *asiatica* Hoogl. **China:** *Liang 69507* (A). *T. boiviniana* Baill. **Tanganyika:** *Tanner 2548* (UC). *T. daemeliana* F. Muell. **Australia:** *C. T. White 11690* (A). *T. euryandra* Vahl. **New Caledonia:** *Taylor 2* (A). *T. indica* (Houtt. ex Christm. & Panz.) Merr. **Singapore:** *H. Keng s.n.* (preserved material). *T. korthalsii* Miq. var. *subrotunda* (Elm.) Hoogl. **Borneo:** *Elmer 21376* (GH). *T. leiocarpa* Stapf. **Liberia:** *Cooper 45* (GH). *T. macrophylla* Wall. ex Hook. f. & Thoms. **Singapore:** *Canright 1127* (ASU). *T. masuiana* De Wild. & Th. Dur. **Congo:** *Becquaert 37* (GH). *T. nordtiana* F. Muell. var. *nordtiana*. **New Guinea:** *L. J. Brass 7480* (A). *T. ovalifolia* DC. **Panama:** *Johnston 1140* (GH); **Brazil:** *Dusén 14630* (MO). *T. portobellensis* Buerling. **Bolivia:** *Steinbach 7229* (MO). *T. scandens* (L.) Merr. **Philippines:** *Lagrimas s.n.* (preserved material). *T. volubilis* L. **Mexico:** *Purpus 7647* (MO).

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EXPLANATION OF PLATES

PLATE I

FIGS. 1–8. Dilleniaceae, nodal anatomy. 1, *Tetracera indica* (seed received from *H. Keng*, Singapore), transverse section of cotyledonary node showing unilacunar two-trace condition (c.t., cotyledonary trace), × 32. 2, ***Hibbertia pungens*** (*Royce 7640*), transverse section of unilacunar node, × 32. 3, *Tetracera boiviniana* (*Tanner 2548*), transverse section of trilacunar node illustrating widely separated gaps, × 13. 4, *Acrotrema* sp. (*Thwaites CP3899*), transverse section through rhizome in region of leaf trace (lt) and adventitious root departure, × 13. 5, *Hibbertia scandens* (cult. BRI, *s.n.*), transverse section of node illustrating trilacunar condition with widely separated gaps and sheathing petiole, × 13. 6, *Davilla rugosa* (*de Mattos Filho s.n.*), tranverse section of pentalacunar node, × 13. 7, *Schumacheria castaneifolia* (*Abeywickrama s.n.*), transverse section of multilacunar node. Note the median trace departs before laterals (lt, leaf trace), × 13. 8, *Dillenia ovata* (cult. SING, *s.n.*), transverse section of multilacunar node illustrating simultaneous departure of leaf traces, × 13.

PLATE II

FIGS. 9, 10. Dilleniaceae, petiolar anatomy. 9A, B, C, D, *Acrotrema* (*Thwaites CP3899*), transverse sections of the petiole and midrib illustrating derivation of abaxial arc and adaxial bundle, × 32. 10A, B, C, *Curatella americana* (*Irwin 5470*), transverse sections of petiole illustrating formation of medullary bundles, × 13. 10D, *the same*, transverse section of petiole at base of lamina showing medullary bundles (indicated by arrows), complete fusion of vascular cylinder, and extraxylary fibers, × 30.

PLATE III

FIGS. 11–14. Dilleniaceae, petiolar and nodal anatomy. All figures × 30. 11A, B, C, *Hibbertia scandens* (cult. BRI, *s.n.*), transverse sections of petiole illustrating origin of abaxial arc and adaxial bundle. 12, *H. dentata* (seedling grown from K seed *2264*), transverse section of cotyledonary node showing a single broad trace departing the vascular cylinder. 13, *H. lucida* (*C. T. White 2210*), transverse section of petiole at base of lamina showing formation of medullary bundles by invagination. 14, *H. patula* (*McKee 3543*), transverse section of petiole at base of lamina depicting confluent vascular cylinder. Note sclerotic nature of pith and well developed extraxylary fibers.

PLATE IV

FIGS. 15–22. Dilleniaceae, petiolar anatomy. 15, *Didesmandra aspera* (Sarawak, *s.n.*), transverse section of petiole at base of lamina showing widely dissected vascular cylinder, × 15. 16, *Tetracera daemeliana* (*C. T. White 11690*), transverse section of petiole at base of lamina showing flattened, slightly dissected vascular cylinder, × 32. 17, *Hibbertia coriacea* (*Humbert 5866*), transverse section of petiole at base of lamina showing arc of vascular tissue, × 32. 18, ***Dillenia castaneifolia*** (*Womersley NGF 3768*), transverse section of petiole at base of lamina showing arc of medullary bundles, × 15. 19, *D. bolsteri*

(*Wenzel 3112*), transverse section of petiole at base of lamina showing confluent "V" shaped vascular cylinder, × 32. 20, *D. beccariana* (*SAR 16272*), transverse section of petiole at base of lamina showing superimposed medullary bundles (indicated by arrows), × 17. 21, *Doliocarpus guianensis* (UC *947180*), transverse section at base of petiole showing abaxial arc of dissected bundles and adaxial siphonostele, × 17. 22, *Davilla aspera* (*Howard 10502*), transverse section of petiole at base of lamina showing nearly complete vascular cylinder. Note abundant sclereids in cortex, × 32.

PLATE V

FIGS. 23–26. Dilleniaceae, minor venation. All figures × 25. 23, *Dillenia megalantha* (*M. Q. Lagrimas s.n.*), note prominent parenchymatous bundle sheath and numerous free vein endings. 24, *D. papuana* (*Womersley NGF 3926*), note almost complete absence of free vein endings. 25, *D. schlechteri* (*Womersley & Millar NGF 7000*), note complete absence of free vein endings accompanied by massive venation and bundle sheathing. Sheath cells extend into vein islets. 26, *Didesmandra aspera* (*SAR S.18297*), note weak, slender venation and incomplete bundle sheathing.

PLATE VI

FIGS. 27–30. Dilleniaceae, minor venation. 27, *Hibbertia exutiacies* (*Eichler 17965*), base of leaf showing single leaf trace and termination of reflexed lateral veins, × 35. 28, *H. subvaginata* (*C. L. Wilson 764*), note massive venation lacking bundle sheathing, × 35. 29, *H. banksii* (*Brass 8431*), venation showing characteristic interrupted sclerotized sheathing, × 25. 30, *H. wagapii* (*Thorne 28266*), note terminal veinlets are completely enclosed by sclerenchymatous bundle sheathing, × 25.

PLATE VII

FIGS. 31–34. Dilleniaceae, minor venation. 31, *Curatella americana* (*Irwin 5470*), minor venation showing abundant parenchymatous bundle sheathing, × 25. 32, *Tetracera macrophylla* (*Canright 1127*), note sclerenchymatous bundle sheathing completely surrounds terminal tracheids, × 25. 33, *Doliocarpus dentatus* (*Krukoff 10088*), terminal veinlet with abundant parenchymatous sheathing. Note sheath cells often orientated at right angles to vein, × 54. 34, *Pachynema dilatatum* (NT *6129*), scale-like leaf vascularized by weak cauline traces, × 54.

PLATE VIII

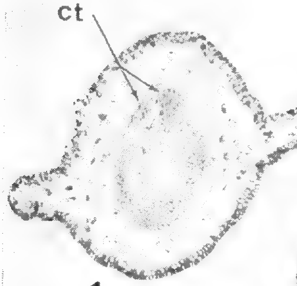
FIGS. 35–39. Terminal veinlet idioblasts in *Hibbertia*. 35, *H. scandens* (cult. K, *s.n.*), × 130. 36, *H. dentata* (cult. K, *s.n.*), × 120. 37, *H. huegelli* (*C. L. Wilson 777*), × 100. 38, *H. pachyrhiza* (*C. L. Wilson 861*), × 130. 39, *H. scandens* (cult. K, *s.n.*), × 120.

PLATE IX

FIGS. 40–44. Dilleniaceae, major venation. 40, *Dillenia indica* (seed received from *H. Keng*, Singapore), cotyledonary node and vascularization of cotyledon. 41, *the same*, vascularization of first foliage node and leaf. 42, *Hibbertia dentata* (cult. K, *s.n.*), natural size. 43, *H. tontoutensia* (*McMillan 5060*), × 1.2. 44, *H. cuneiformis* (*Wilson 297*), × 2.5.

PLATE X

FIGS. 45–50. Leaf vascularization in *Hibbertia*. Due to fluctuations in leaf size, magnifications given are intended to indicate only general size ranges. 45, *H. huegelli* (*C. L. Wilson 777*), × 3.5. 46, *H. monogyna* (*Maiden s.n.*), × 4. 47, *H. nitida* (Fl. Novae Holl. *141*), × 5. 48, *H. vestita* (*NSW 55998*), × 13. 49, *H. exutiacies* (*Eichler 17965*), × 9. 50, *H. fasciculata* (*Aston 387*), × 9.



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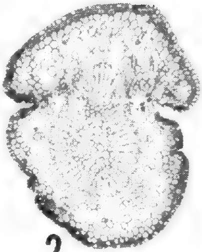

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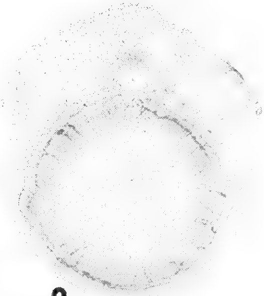

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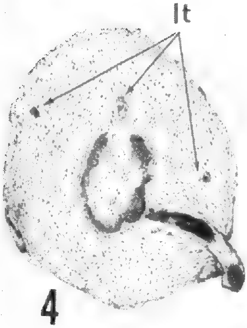

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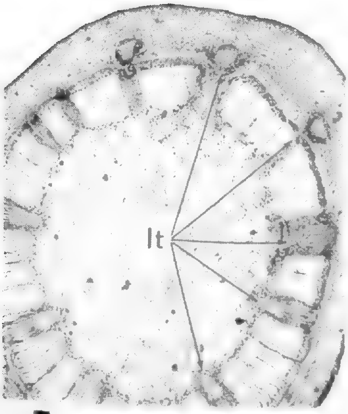

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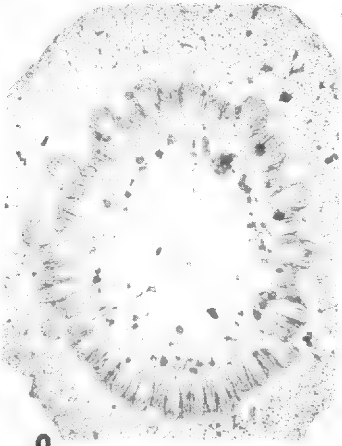

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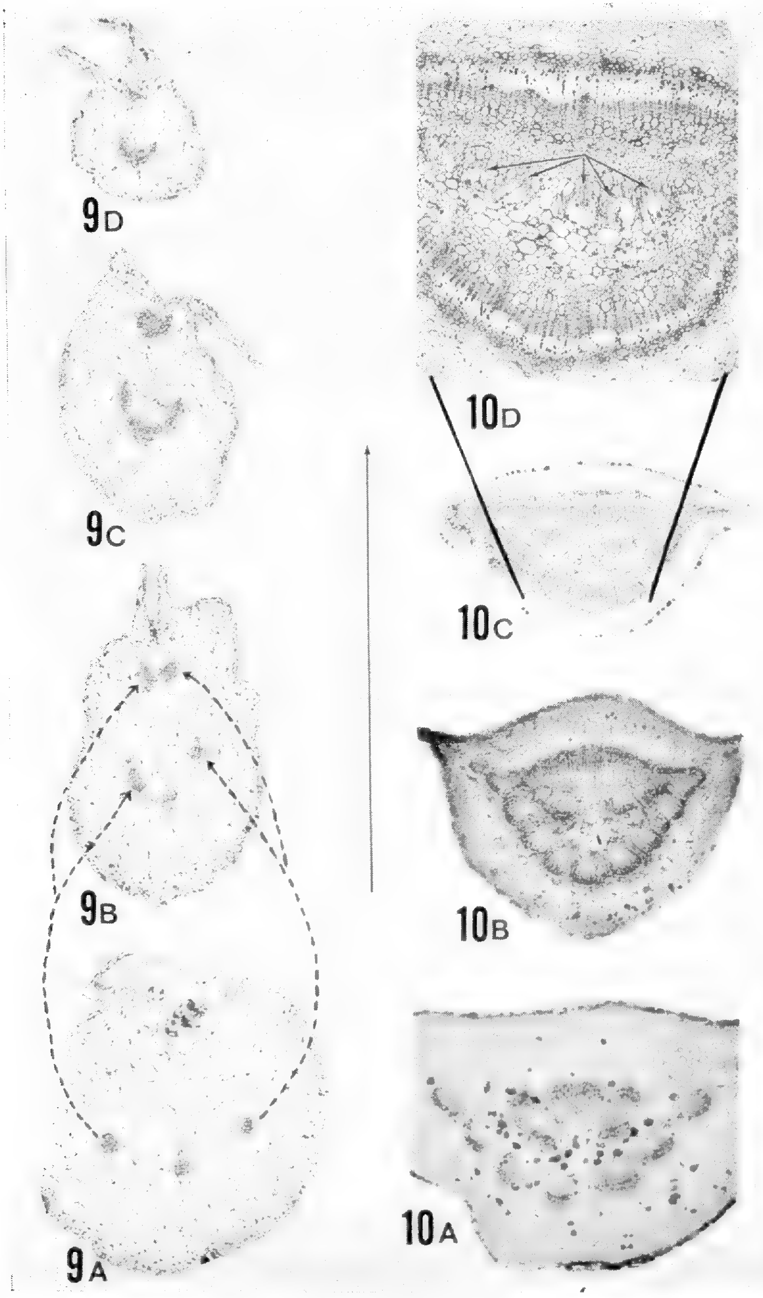

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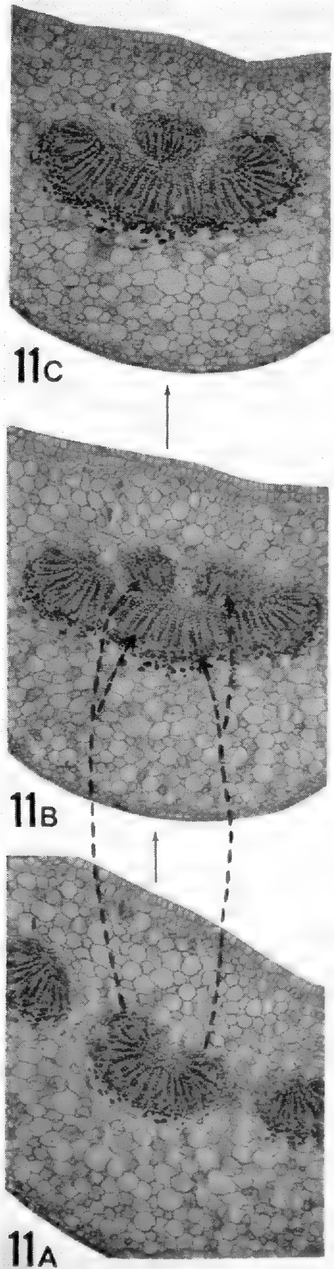

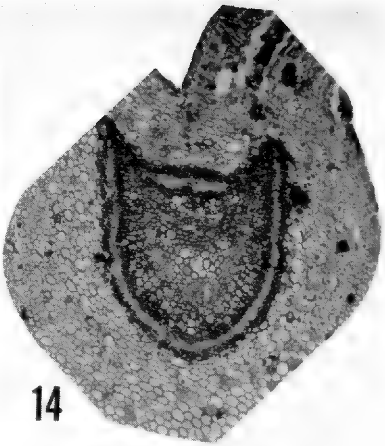

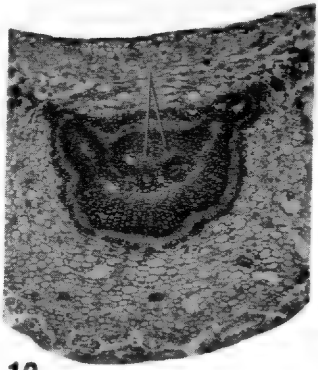

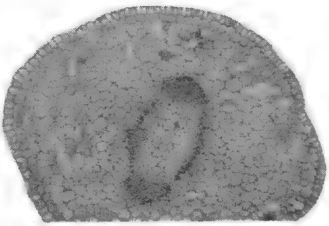

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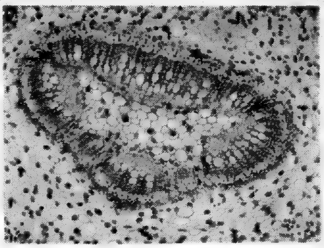

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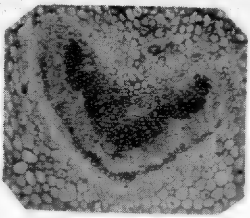

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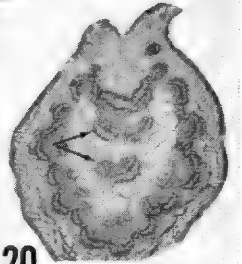

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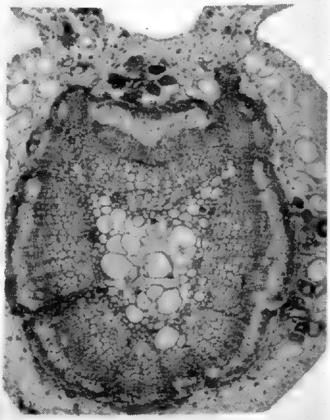

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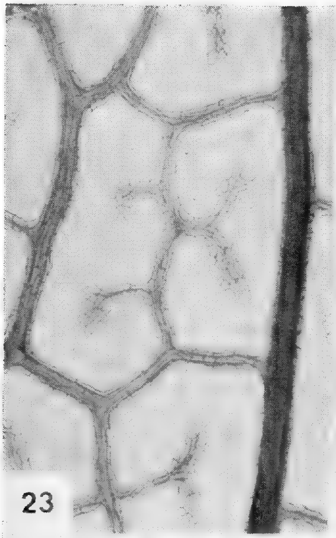
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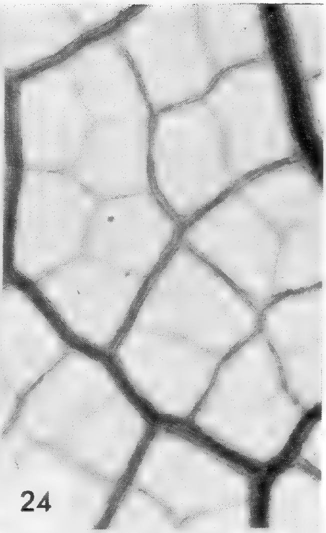
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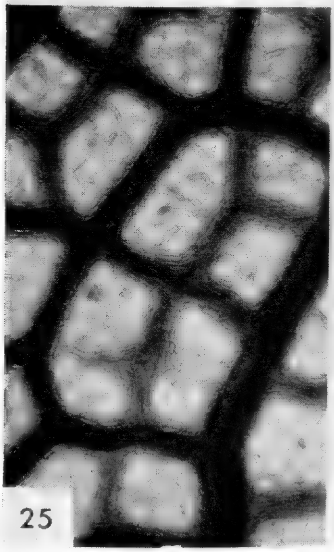
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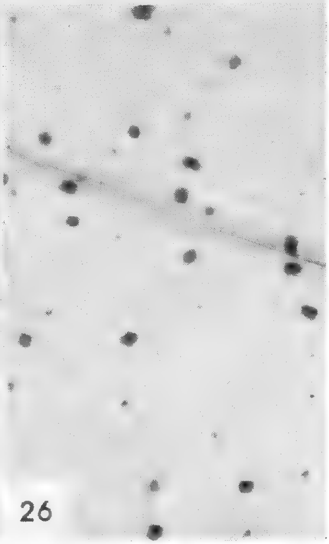
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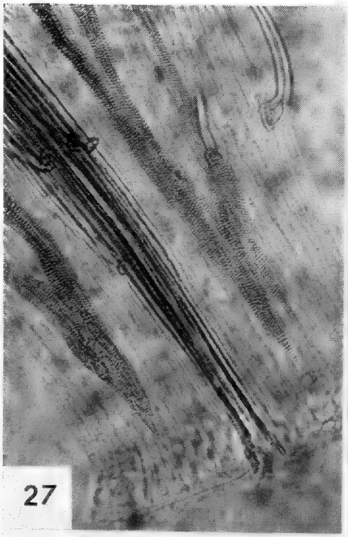
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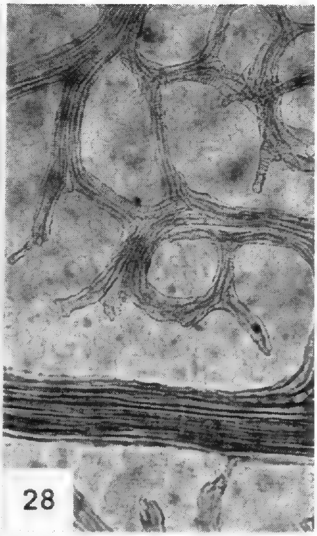
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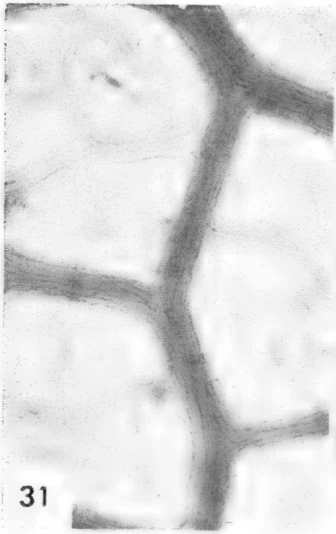
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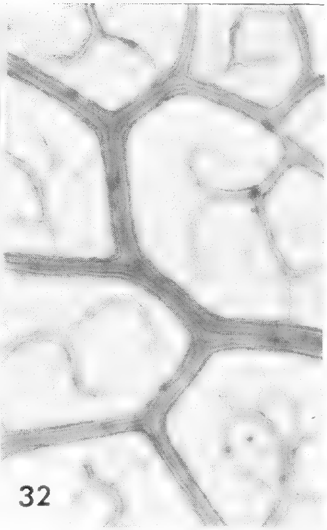
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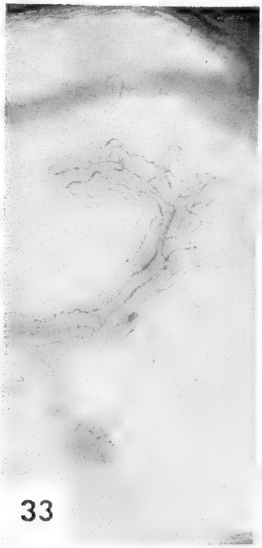
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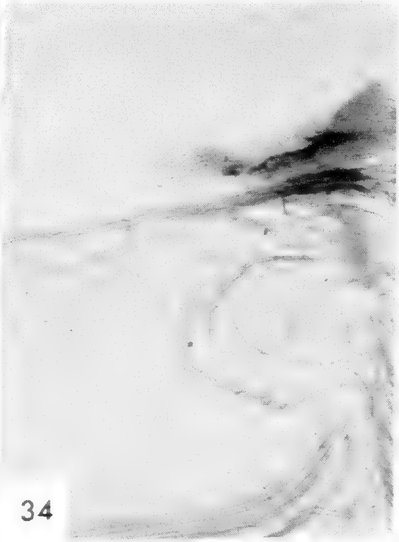
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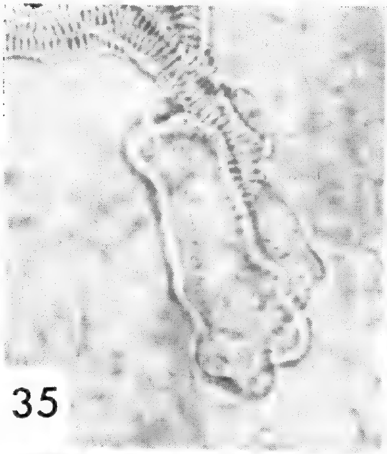
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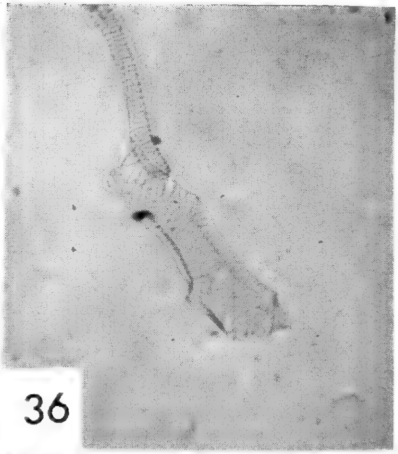
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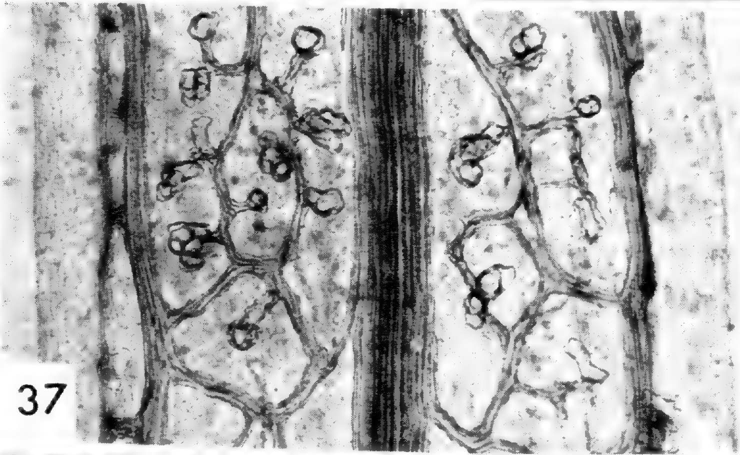
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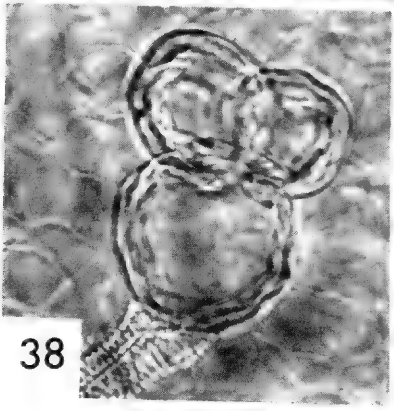
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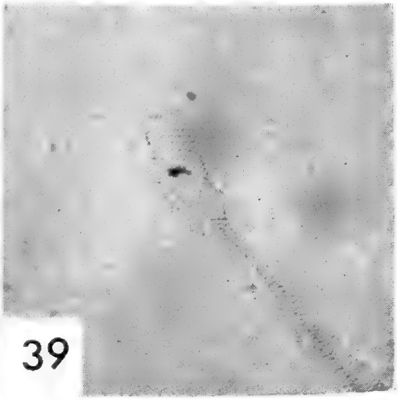
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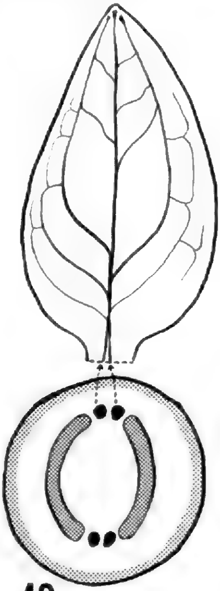

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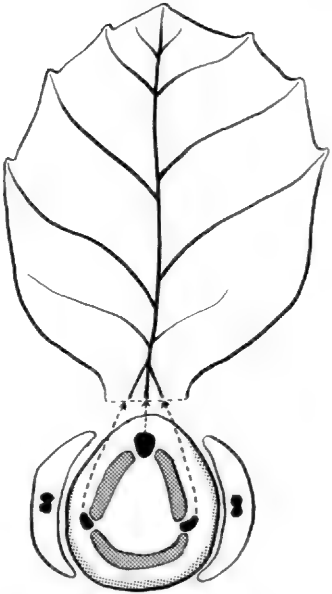

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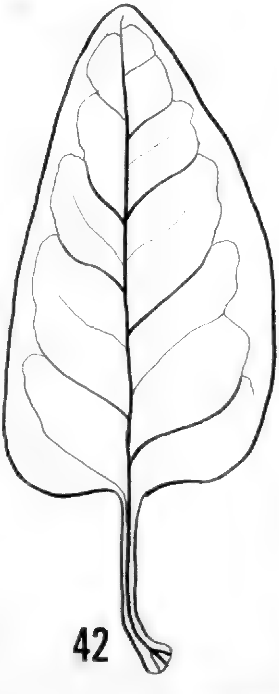

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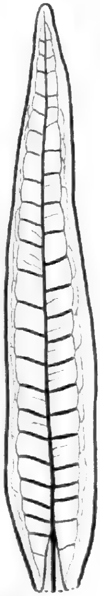

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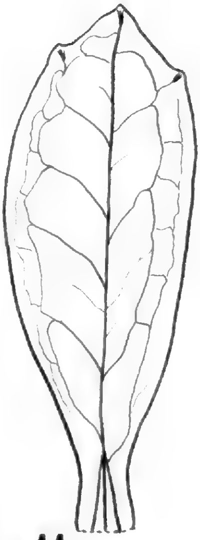

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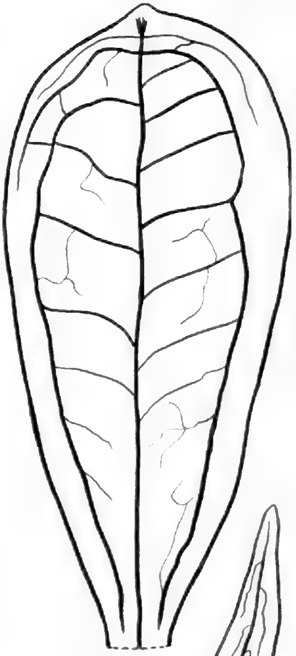

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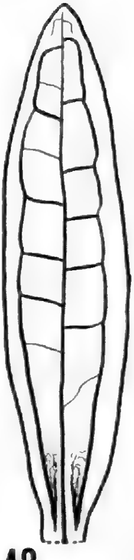

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ANATOMY AND ONTOGENY OF THE CINCINNI AND FLOWERS IN NANNORRHOPS RITCHIANA (PALMAE)[1]

NATALIE W. UHL

THE LARGE, TERMINAL, compound inflorescence of *Nannorrhops ritchiana* (Palmae-Coryphoideae) is composed of unspecialized branch systems (Tomlinson & Moore, 1968) which may serve as a model for the derivation of more specialized types of palm inflorescence. Observations on the inflorescence of *Nannorrhops ritchiana* are continued here with a description of the anatomy and some aspects of the ontogeny of the rachillae, of the ultimate flowering units, and of the flowers. *Nannorrhops* is especially important because completely sheathing and vasculated bracteoles are present throughout the ultimate flowering unit. Detailed studies confirm Tomlinson and Moore's tentative designation of this unit as a cincinnus and reveal basic constructional principles that apply to many, if not all, of the varied flowering units found in palms; e.g. the triad of a pistillate and two staminate flowers, where interpretation has been difficult because bracts are absent or lack vasculature (Uhl, 1966). The form and anatomy of the carpel may also illustrate some primitive features for palms.

MATERIAL AND METHODS

Inflorescence branches from plants at the Fairchild Tropical Garden, Miami, Florida, were available in various stages of development from the following collections: *Moore 6009*, *Read 735*, and *Tomlinson* 14.XI.63 and 14.XI.66. These were fixed in formalin-acetic acid-ethanol, desilicified for 1 to 2 weeks with approximately 1/3 commercial strength hydrofluoric acid, and embedded in Paraplast. Serial sections of flowers and rachillae were made at 5, 7, 10, and 15 microns and were stained with safranin and fast green or safranin and aniline blue. Cincinni and flowers were also cleared as described previously (Uhl, 1966), the number of cleared flowers examined exceeding 50. Two films were prepared for cinematographic analysis (Tomlinson & Zimmermann, 1965) of rachillae and mature flowers. Some observations and photographs (FIGS. 8–19) were made in polarized light. Since growth is continuous, but not uniform, dimensions of the material examined are included below.

RACHILLAE

Morphology. Structural patterns are simple despite the large size of the inflorescence in *Nannorrhops* (Tomlinson & Moore, 1968, *Fig. 42*). Up

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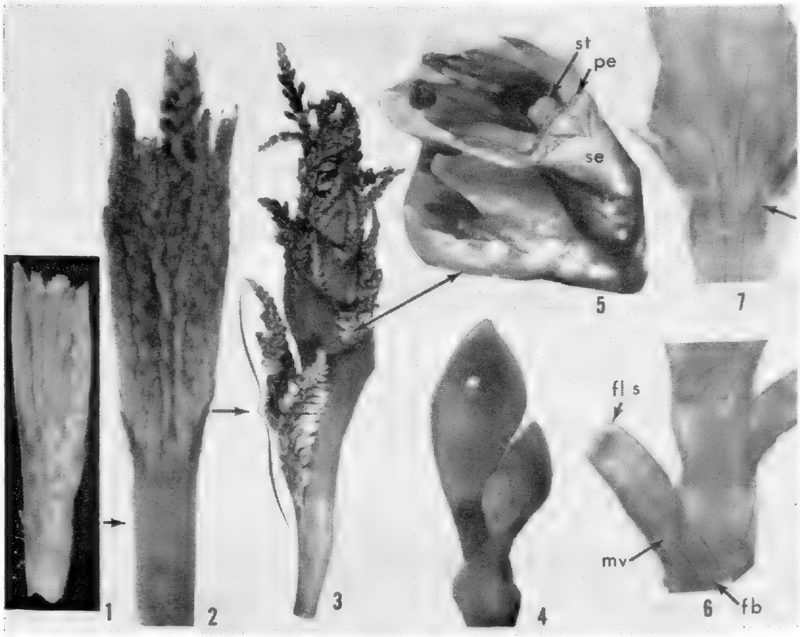
[1] From work supported by National Science Foundation Grant GB–7758; principal investigator, Harold E. Moore, Jr.

to five orders of branches are formed monopodially. The visible flower-bearing axes or rachillae are mostly branches of the fourth order, but whatever the order, they are similar in size and in the number of flower-clusters or cincinni produced. Rachillae taper slightly in diameter (from 1.5 mm. to 0.75 mm.) and are indeterminate in length and in potential number of flower clusters. Fully expanded rachillae in the material examined range from 5 to 12 cm. in length and bear from about 20 to 45 cincinni. A few distal cincinni are usually abortive.

Development. Maturation of flowering axes within the inflorescence is complex. Four different patterns can be recognized: one with reference to the inflorescence as a whole, a second in the sequence of development of lateral branches, a third on individual rachillae, and a fourth within each flower cluster.



FIGS. 1–7. FIGS. 1–3, Three successive developmental stages of a third order branch, arrows indicate sequence, further explanation in text. FIG. 1, immature third order branch, × 1.5; FIG. 2, third order branch, later stage than FIG. 1, some fourth order branches much larger than others, × 1.5; FIG. 3, third order branch (bracketed) on second order branch, subtending bract removed, × 0.5; FIG. 4, a cincinnus, flowers in bud, all bracts removed, × 6; FIG. 5, open flowers, upper with one petal and one stamen removed, × 5; FIG. 6, part of a cleared rachilla to show bundles in bracts subtending stalks of first flowers of cincinni, × 4; FIG. 7, central part of a cleared flower to show vascular system and five bundles in stalk, arrow indicates large, fused bundles opposite sepal insertion. DETAILS: fb, fibrous bundle in bract; fl s, stalk of first flower of a cincinnus; mv, midvein of the bract; pe, petal (removed); se, sepal tube; st, stamen (removed).

Maturation is basipetal in the inflorescence as a whole. Upper first and second order branches produce the first flowers (Tomlinson & Moore, 1968, *Fig. 40*).

The further expansion of specific lateral branches is not uniform but can be related to the order of the branch. Third order branches mature acropetally, but development of fourth order branches is irregular. Mature flowers are produced on some fourth order axes when others are still in early stages of development as illustrated by FIGS. 1–3. In early stages of growth, some fourth order branches are equal in size to the main branch (third order axis) on which they are borne (FIG. 1). The result is a digitate configuration, which may be useful in interpreting digitate branching in mature inflorescences elsewhere in palms. In a later stage (FIG. 2) some of the fourth order branches have matured while others are still undeveloped.

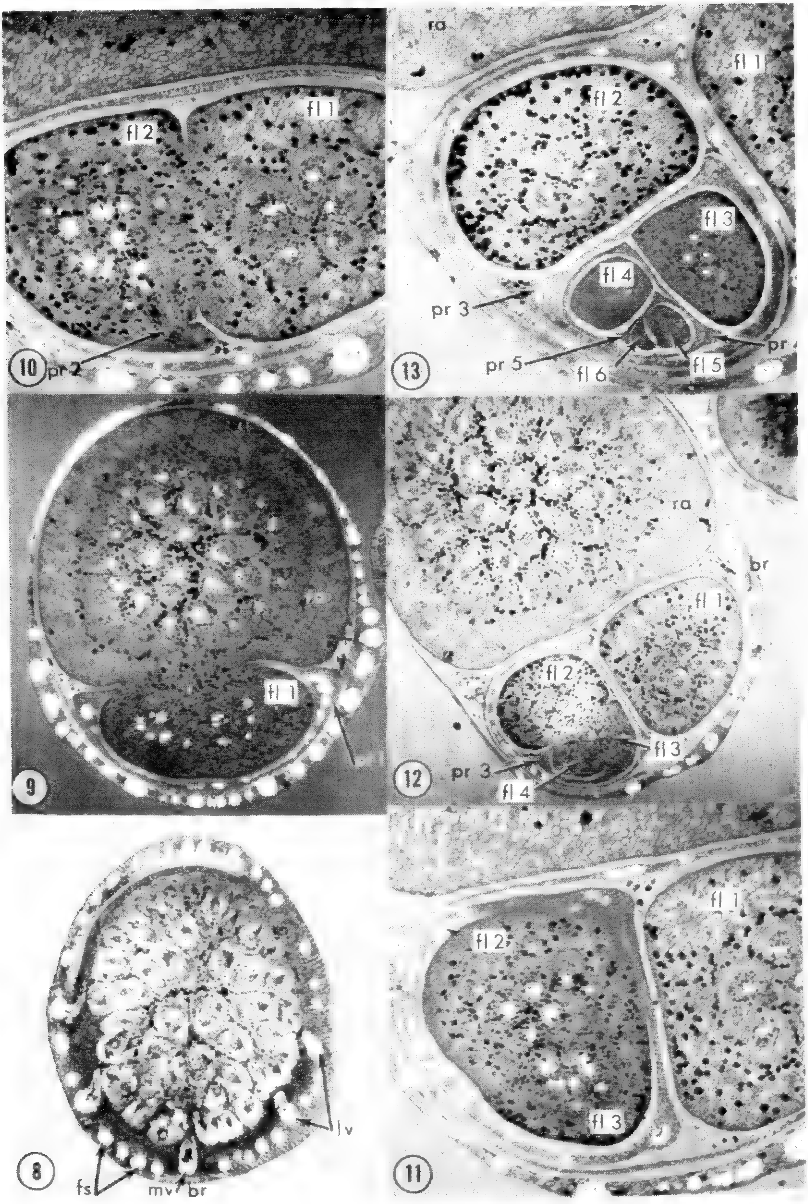
Flowers may mature irregularly on a specific rachilla. Those in cincinni at the middle of the rachilla often develop before those in cincinni nearer the base or the apex (FIG. 3), but in general the order of development is acropetal. Within each cincinnus there is still another acropetal series in the maturation of individual flowers (FIG. 4).

Anatomy. The vascular system in rachillae is composed of a central or subcentral group of about 10 (8–12) large vascular bundles with a number (ca. 13) of intermediate and smaller bundles peripheral to them (FIGS. 8, 9, 12). The peripheral bundles represent strands which supply cincinni, and they vary in number and position depending on the proximity of the level examined to a cincinnus. Each large bundle has 1 to 4 large vessels (FIG. 12) and a complete fibrous sheath which is approximately 5 to 7 cells wide over the xylem. Most commonly there are two large vessels per bundle, but bundles about to branch have three large vessels and small branch bundles only one. The narrow cortex is of small unspecialized parenchyma 6 to 8 cells in width, and the epidermis is of smaller isodiametric cells.

BRACTS

Morphology. Two types of bracts may be present on rachillae. On first, second, and third order branches there is usually an irregularly bicarinate prophyll which is inserted basally in an adaxial position. This bract is commonly empty on first and second order branches but on third order branches it subtends the first lateral branch.

Flower clusters are subtended not by prophylls but by irregularly funnel-shaped bracts with attenuate dorsal tips. Similar but larger bracts borne on one axis and subtending branches of the next order occur throughout the inflorescence and may be arranged in a reduction series from a foliage leaf (Tomlinson & Moore, 1968). Bracts subtending cincinni are the smallest of the series and are all equal in size and shape at maturity. On fully expanded rachillae, each bract is about 3 mm. long, the sheathing part extending for ca. 2 mm. of this.



FIGS. 8–13. Successive transections of a cincinnus, taken in polarized light. FIG. 8, transection of rachilla and bract subtending a cincinnus, × 18; FIG. 9, transection of rachilla and axis of the first flower, × 18; FIG. 10, transection at level of origin of lower trace to prophyll on second flower, × 36; FIG. 11, transection at level of origin of upper trace to prophyll on second flower, × 36; FIG. 12, transection of rachilla and stalks of first, second, third, and fourth

Anatomy. Each bract subtending a cincinnus is supplied by five vascular bundles and by a large number of fibrous strands (Figs. 6, 8, 9). The vascular bundles, which may be designated as a midvein and two pairs of lateral bundles, originate as small branches of peripheral stelar strands. The continuing vertical bundles (Zimmermann & Tomlinson, 1965) from which the midvein and first pair of lateral bundles originate usually enter the stalk of the first flower. Vertical bundles providing the second pair of laterals, however, continue in the rachilla. Lateral vascular bundles branch and anastomose distally in the bract (Fig. 6). The numerous fibrous strands (Figs. 6, 8) are wide tangentially and also branch and anastomose distally. They are tapered somewhat proximally but are not connected to the vascular cylinder of the rachilla.

FLOWERING UNITS

Morphology. With the initiation of the first flower, the growth pattern of the inflorescence shifts from monopodial to a sympodial elaboration of clusters, each consisting of five or six successively younger flowers (Fig. 4). The bract on the rachilla subtends the first flower. The stalk of this flower in turn bears an adaxially situated bracteole which is completely sheathing and has two subequal adaxial tips, thus differing from the bract subtending the first flower and definable as a prophyll. The prophyll subtends the second flower of the cluster. The stalk of the second flower bears a similar bracteole which subtends the third flower. This pattern is repeated up to five or six times in *Nannorrhops* (Figs. 8–13). Each floral primordium is initiated on the opposite side of the appropriate floral stalk and at an angle of approximately 75°. Although five or six buds are present in the cluster, only three flowers usually mature. Because flowers are successively younger and pedicels elongate successively during maturation, the two-rowed condition of a cincinnus, though structurally present, is not readily evident macroscopically. Left-handed and right-handed cincinni occur, depending on whether the second flower is initiated on the left or right side of the first floral axis. A specific rachilla usually bears predominantly left- or right-handed clusters — e.g. on a right-handed rachilla only one or two basal and one or two median cincinni are left-handed.

Anatomy. Bundles which supply the first flower of a cincinnus originate as branches of major axial bundles in the rachilla. The first such branch originates at about the level of insertion of the second cincinnus

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flowers, × 18; Fig. 13, transection through all flowers of a cincinnus, × 36. Details: br, bract subtending first flower of a cincinnus; fl 1 to fl 6, successive flowers of a cincinnus; fs, fibrous bundles of bract; mv br, midvein of bract; lv, lateral vascular bundles of bract subtending first flower; pr 1, prophyll borne on axis of the first flower; pr 2, prophyll of second flower, arrow points to lower trace; pr 3, prophyll of third flower; pr 4 and pr 5, prophylls of fourth and fifth flowers respectively; ra, rachilla.

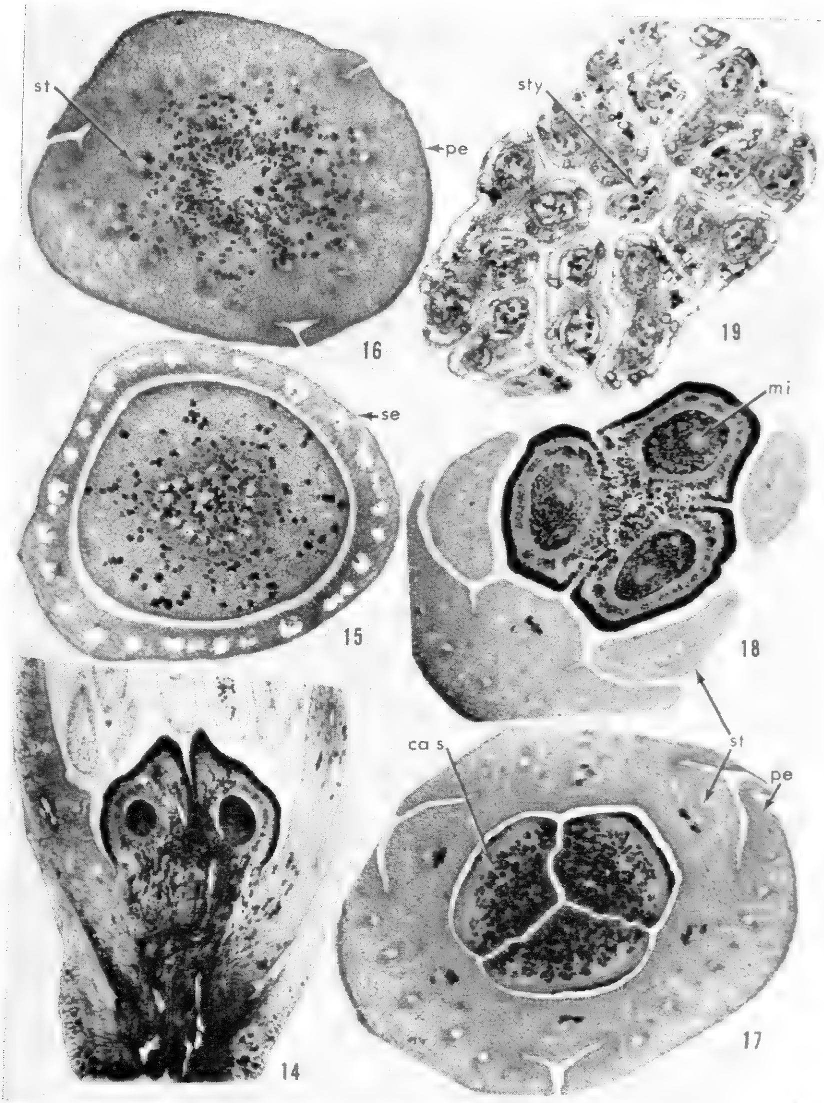
below. About three more branches are derived from axial bundles at higher levels, and further branching of these provides the complete supply to the first flower. At the level of origin of the midvein of the subtending bract, this supply consists of a group of about 16 bundles. The exact number of bundles is somewhat subjective unless the level is carefully indicated, since bundles are frequently small, especially near their origin, and fibrous bundle sheaths are often confluent for some distance.

Anatomically as well as morphologically prophylls are different from other bracts in the inflorescence. The main vascular complement of each prophyll is two vascular bundles, one supplying each tip (FIGS. 9, 11, 13). These traces are derived as small branches of marginal stelar bundles of the floral stalk. The bracteole is obliquely inserted and irregularly bicarinate, one tip being slightly longer than the other. The trace to the longer tip originates at a slightly lower level than that to the shorter (FIG. 11), and is a somewhat larger bundle which often branches distally. Unconnected fibrous strands are also present in the prophyll (FIG. 11) and occasionally a third vascular bundle (FIG. 11) is seen.

Above the origin of the traces to the first bracteole, the stelar bundles of the first flower provide the vascular supply to the second floral stalk (FIGS. 8, 9, 20). Two of the ensuing bundles produce small branches, each supplying one tip of the second prophyll (FIGS. 10, 11), and the pattern is repeated until up to five or six floral primordia are formed (FIGS. 8–13, 20). Thus anatomically each flower, its axis, and bracteole are identical to the others making up the cincinnus. Transections of the floral axes of the first, second, third, and fourth flowers may be compared in FIGURES 10, 12, and 13 and their similarity noted. The pattern of origin of the vascular supply to each floral stalk is also similar as can be seen in FIGURE 20 which is a camera lucida drawing of the major bundles in a cleared cincinnus.

THE FLOWER AT ANTHESIS

Morphology. Among the palms, approximately 165 genera are monoecious, about 39 are dioecious, and some 34 genera bear perfect flowers. *Nannorrhops* belongs among the last, having perfect flowers with three sepals, three petals, six stamens, and a tricarpellate gynoecium. Open flowers (FIG. 5) are approximately 6 mm. long. The sepals are 3 mm. long and are connate for two-thirds this length forming a sheath, above which the membranaceous tips are free. Petals are ca. 5 mm. long, ovate, somewhat fleshy, shortly imbricate near the base and then valvate. Stamen-filaments are wide and fleshy basally (FIGS. 5, 18), but taper to the attachment of the versatile anthers which are subequal, basally divergent, and laterally dehiscent. The three carpels are free in young stages, but in mature flowers are connate by ventral faces through the ovarian and stylar regions. Thus at anthesis the gynoecium is syncarpous with definite external grooves showing the limits of each carpel. Each carpel has a distinct stalk, an ovoid fertile part, and a long attenuate style through which



FIGS. 14–19. Sections of mature flowers, taken in polarized light. FIG. 14, tangential longisection with two carpels, × 20; FIG. 15, transection through sepal tube and floral axis at level of origin of petal traces, × 36; FIG. 16, transection through base of flower above FIG. 15, × 36; FIG. 17, transection at higher level where carpel stipes are distinct, × 36; FIG. 18, transection of ovarian part of gynoecium, carpels connate, × 36; FIG. 19, transection of anthers and style, × 36. DETAILS: ca s, carpel stipe; mi, micropyle; pe, petal; se, sepal tube; st, stamen trace; sty, style.

a locular canal extends to open distally. There is no connection (compitum, Carr & Carr, 1960) between locular canals of adjacent carpels. No definite stigmas are present. Papillose stigmatoid tissue is apparently present at anthesis around the stylar opening but is not developed until the flower opens. An anatropous ovule is attached ventrally and basally in each locule and is turned so that the micropyle is lateral rather than dorsal in respect to the funiculus.

At anthesis about one-third the length of the flower consists of a tapered solid basal part (FIG. 5) sheathed by the sepal tube and representing the region of insertion of petals, stamens, and carpels. A very short petal-stamen tube surrounds the free carpel stalks (FIGS. 14, 17) but since all organs are free just *below* the ovary in the mature flower, the short petal-stamen tube does not seem to justify the term "perigynous."

Anatomy. Floral anatomy in *Nannorrhops ritchiana* has been described by Morrow (1965) and Gupta (1960). The present study confirms most of the observations of these authors and provides further details of carpel anatomy, organogeny, and histogenesis. The general outlines of the floral vascular system can be seen in FIG. 7 which is a cleared preparation of the central part of a flower. Just below sepal insertion, bundles present in the floral stalk enlarge, extend peripherally, and branch forming a group of bundles which provide traces to the floral organs. Further details of this pattern are presented in a radial plot of one of the large axial bundles (FIG. 23). The pattern is irregular in that traces to floral organs are branches originating near the insertion of the organ *or* at a lower level.

Gupta (1960) reports two rings of bundles in the floral pedicels: an outer of 11 or 12 and an inner of three larger ones. Morrow (1965) states that 9 (8 to 10) strands enter the base of the flower. Three central strands do mature first in floral stalks and are often larger (FIGS. 12, 13). In mature pedicels both large and small bundles are present with a gradual transition in size. The number of bundles is somewhat subjective because of the difficulty of getting exactly comparable levels. In the material I studied, 10 to 15 bundles were present, five or six showing birefringent xylem (FIGS. 10, 12, 13).

Just below sepal insertion, larger bundles of the stalk extend toward the periphery, become larger, and branch (FIG. 7). Smaller bundles may fuse with larger ones or also branch. The floral stele, at the level of sepal insertion, consists, therefore, of about 20 to 25 medium to small bundles, arranged in a thick ring, the larger bundles toward the center. Fifteen (14 to 18) small sepal traces originate as branches of peripheral bundles of this stele. Sepal traces near their origin consist of a few sieve elements and two to four xylem elements and are very easily overlooked; but slightly higher in the sepal-tube, fibrous caps are present on these bundles and unconnected fibrous bundles are present between vascular strands. Thus a ring of approximately 28 bundles is present in a transection of the sepal-tube (FIG. 15). Five vascular bundles with four to six interspersed

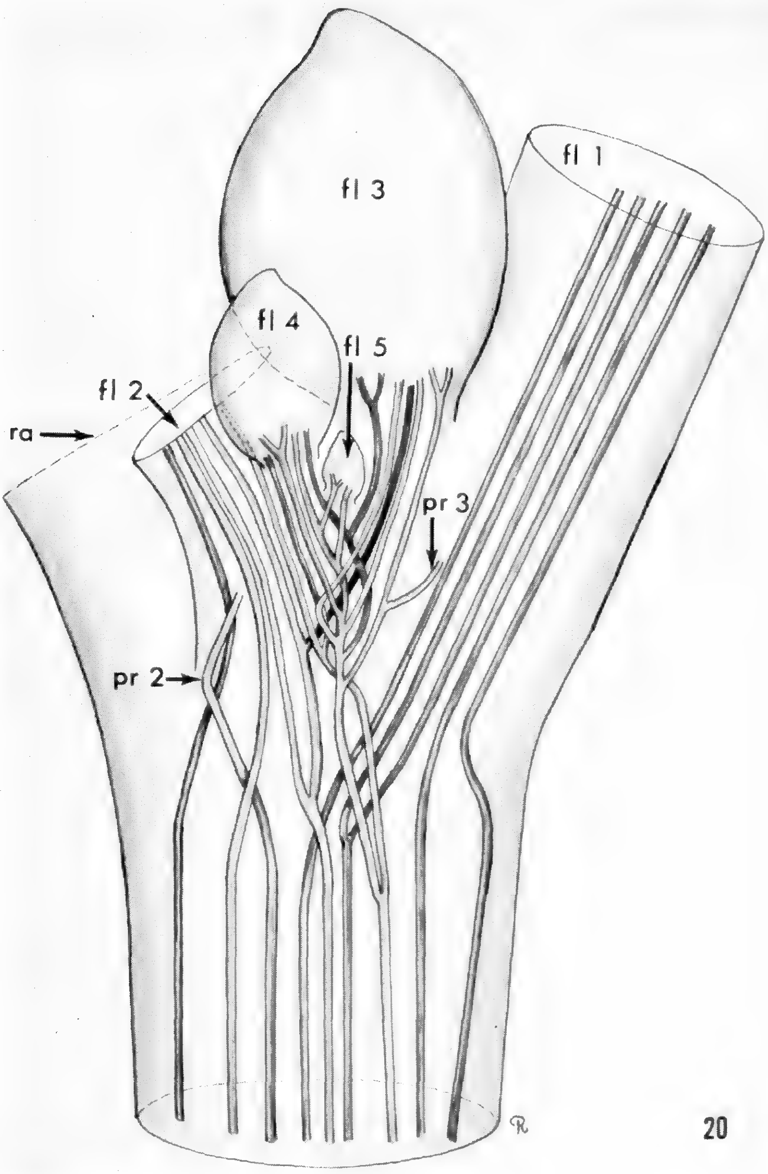


FIG. 20. Wash drawing of a cleared cincinnus, done with Wild M5 stereomicroscope and drawing attachment, to show major vascular supply to flowers. First two flowers, fl 1 and fl 2, abscissed; younger flowers, fl 3 to fl 5, in bud; pr 2, one trace to the prophyll borne on the second flower; pr 3, one trace to the prophyll of the third flower; ra, rachilla.

fibrous strands represent the supply to each sepal, a midstrand and two laterals reaching the tip.

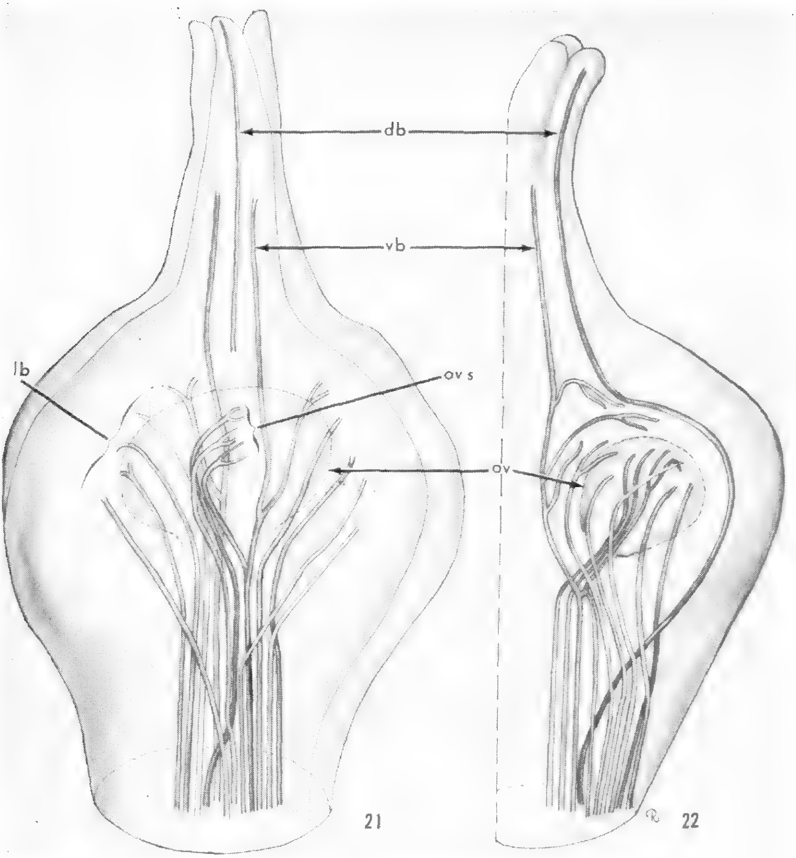
There are six to nine traces, situated in a median row, in the base of each petal (FIG. 16). These may be stelar bundles extending directly into the petal or they may be branches of a stelar bundle. The number of traces varies slightly. Morrow (1965) reports three and Gupta (1960) five from receptacular strands and one from a perianth-stamen bundle. A single median procambial strand develops first in each petal followed by three strands at a later stage in ontogeny. The two laterals from this group of three divide very near the central stele and with the midvein and one or more small traces from the receptacle form the seven major strands (FIGS. 16, 17). These often produce parallel branches at higher levels.

Traces to stamens arise in two whorls in the same manner as petal supplies by the branching or direct conversion of a vertical bundle into a stamen trace. Antipetalous traces may arise as a branch of the same vertical bundle which formed the median petal trace, or as a branch or conversion of an adjacent bundle. Stamen traces are large bundles which divide in the base of the filament (FIGS. 17, 18) into two traces which are oriented xylem to xylem in the filament with the phloems lateral in position, but which reunite in the distal part of the filament.

In the receptacle below the gynoecium, about ten large vertical bundles (bright spots, FIG. 16) are arranged in a central ring with smaller strands external to them. Slightly higher, all stelar bundles are divided into three groups, one of which supplies each carpel stalk. Some 14 bundles are present in a close group in the lower part of each stalk. One of the larger bundles becomes the dorsal bundle of each carpel and the others form the lateral and ventral bundles. There are usually four major pairs of lateral bundles and two ventrals (FIG. 21). The latter may be distinguished by position and by their extension with the dorsal bundle higher into the style. Other small bundles are aligned along the ventral face of the locule and at anthesis extend about one-half the length of the ovary. Branches of the ventral bundles and the dorsal bundle extend into the style while lateral bundles and branches of the ventrals and the dorsal vascularize the ovary wall around the locule (FIGS. 21, 22). Two or three small bundles from the carpellary stele remain in median positions and, with a branch from one ventral bundle, form the ovular supply. In the funiculus these bundles are nearly confluent but divide into separate bundles in the chalazal region (FIGS. 21, 22).

ORGANOGENY

The value of broadening surveys of floral anatomy to include organogeny and histogenesis has been emphasized recently (Tepfer, 1953; Esau, 1965; Kaplan, 1968). Gupta (1960) includes a brief description of organogeny in *Nannorrhops*, but floral histogenesis has not previously been done for a palm. The difficulty of obtaining suitable stages for such



FIGS. 21, 22. Wash drawings of cleared gynoecia, prepared as for FIG. 20. FIG. 21, entire gynoecium showing only bundles of the nearest carpel in dorsal view, dorsal bundle (db) not completed for clarity; FIG. 22, lateral view of part of a cleared gynoecium showing traces of one carpel, one ventral and the corresponding lateral bundles omitted for clarity. DETAILS: db, dorsal bundle; lb, lateral bundles; ov, ovule; ov s, ovular supply.

studies in most palms is obvious. In *Nannorrhops*, however, particularly fortunate sequences in maturation of both inflorescence branches and flowers occur. FIGURE 4 shows a cincinnus made up of five successively younger flowers. Cincinni mature acropetally on their respective branches (FIG. 3). Further, there is a lag in maturation of basal branches, so that rachillae with young stages and others with flowers at anthesis may be present on the same branch. Thus, because of a developmental pattern that results in mature flowers over a long period of time, necessary material for ontogenetic investigations of flowers up to anthesis may be found on a single inflorescence branch.

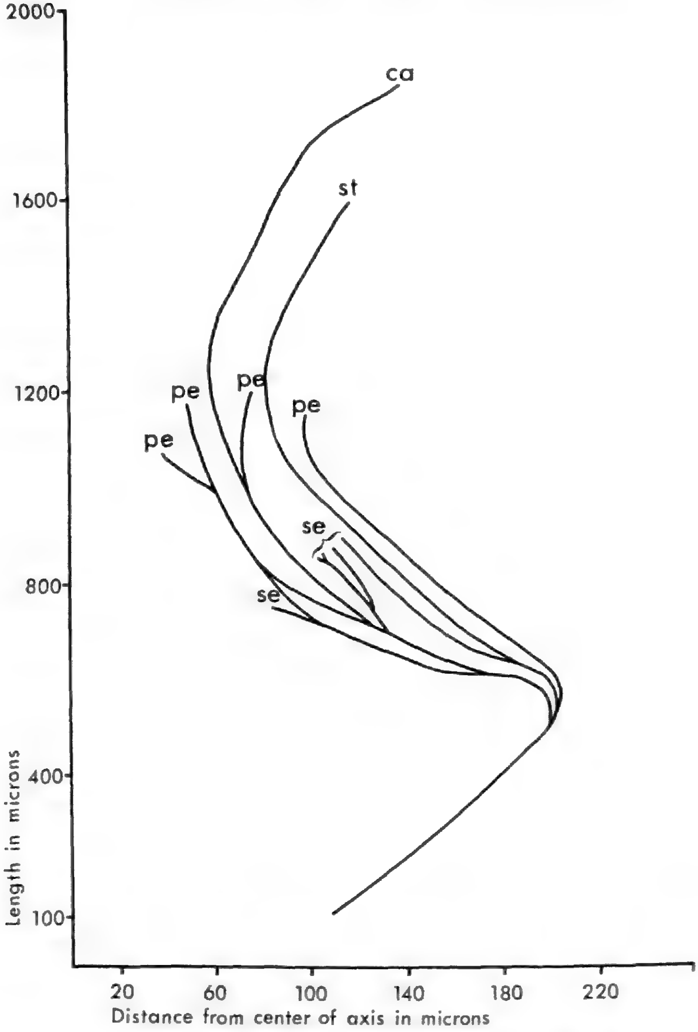


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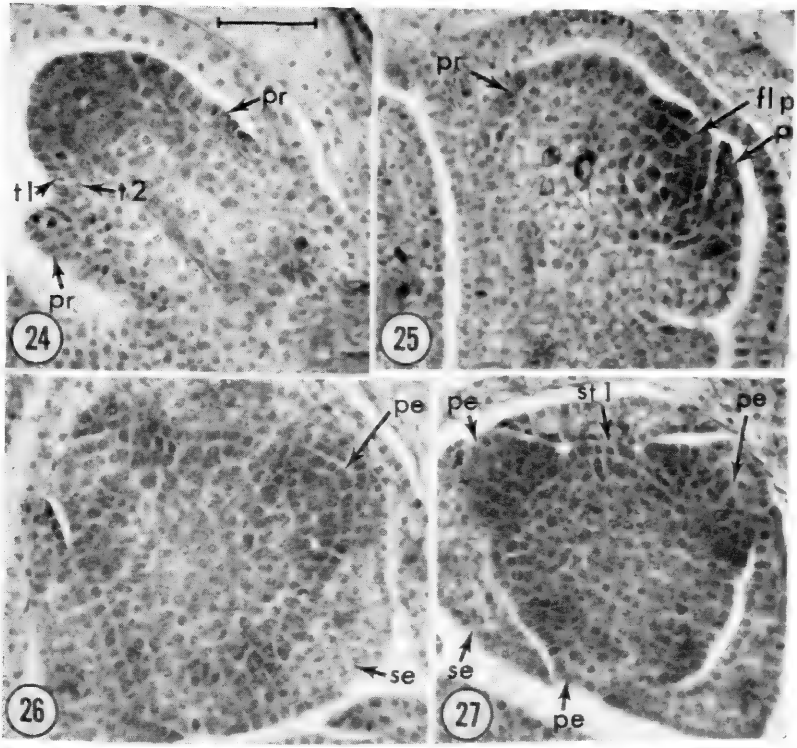
FIG. 23. Plot of the radial path of a major bundle of the floral axis. DETAILS: ca, carpel trace; pe, petal trace; se, sepal trace(s); st, stamen trace.

Above the insertion of the bracteole and subtended floral axis, floral organs arise in acropetal succession on the flanks of the apex. The floral apex is relatively long and is broadly ovate in outline; the one illustrated in FIGURE 24 is ca. 50μ long and 60μ wide. Floral organs are similar in shape in earliest stages and are developed in whorls of three, but each whorl is actually a low spiral since no three organs are at exactly the same level.

Sepals are essentially triangular in outline and slightly narrower than



FIGS. 24–27. HISTOGENESIS. FIG. 24, near-median longisection of a floral apex; FIG. 25, transection showing the primordium of a floral apex and the prophyll (pr) subtending it; FIG. 26, transection of a floral apex showing initiation of petal primordia; FIG. 27, transection of an older floral apex showing young primordia of the lower whorl of stamens. All referable to scale, FIG. 24; scale equals 50μ. DETAILS: fl p, floral primordium; pe, petal; pr, prophyll; se, sepal; st 1, stamen of lower whorl; t 1 and t 2, first and second tunica layers.

other appendages. After initiation, the separate sepal primordia increase in size by apical and marginal growth (FIGS. 26, 27) until the margins of adjacent sepals overlap slightly (FIG. 26). The connate sepal base arises as a unit showing no indication of ontogenetic fusion. Sepals enlarge by subsequent intercalary growth to a length of 3 mm. and envelop all other floral organs until they exceed this length.

Young petal primordia are not initiated until the sepals are approximately 80μ in length. Petal primordia are round to triangular in outline (FIG. 27) and like the sepals develop rapidly at first by apical and marginal meristematic activity. Marginal growth is more extensive in petals than in sepals (FIGS. 28, 31) and in addition an adaxial meristematic region produces thickened tips (FIG. 28). As the flower gradually increases in size (FIG. 5), closed petals protrude farther from the sepals reaching a length of 5 to 6 mm. in late bud. The thickened apical regions of the petals mature first. Later elongation is by a basal meristematic region (FIG. 37).

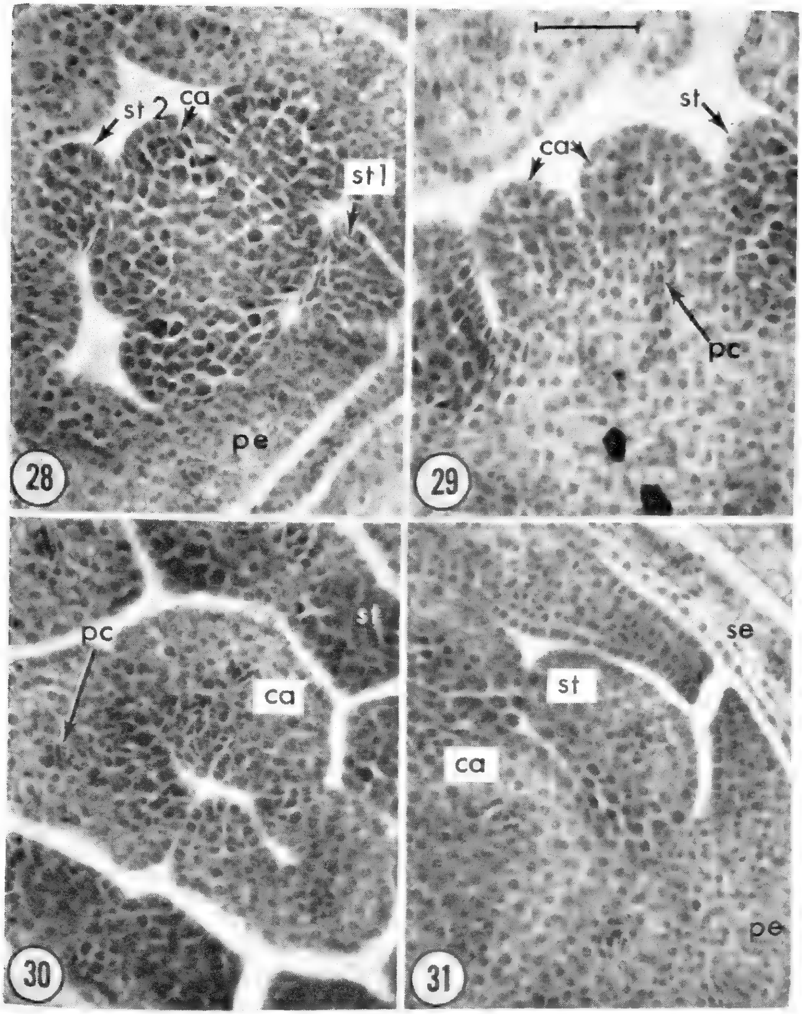
Stamen primordia are initiated in two whorls of three and are elliptic to triangular in outline. FIGURE 27 shows the lower whorl in early stages and FIGURE 28 a later stage of the upper whorl. Initial growth is by apical and marginal meristematic areas. Anther sacs develop in adaxial and lateral positions (FIG. 30). Development of other aspects of the anther is similar to but not as regular as that described by Boke (1949) for *Vinca rosea* (= *Catharanthus roseus*). Sporogenous cells are formed by divisions of primary parietal cells. The tapetum develops later and is one to two cells wide (FIG. 36). In mature stages the endothecium is a single layer of large cells (FIG. 19).

The three carpels are separate in origin (FIGS. 28, 30) and show the familiar crescentic shape illustrated for developing carpels by other authors (Tepfer, 1953; Esau, 1965). In early stages carpels resemble stamens in size and shape (FIGS. 28, 29). Marginal and adaxial growth (FIG. 30) provide the horseshoe-shaped primordium with a solid base and develop what has been called an adaxial lip (Tucker, 1959). The ovule primordium arises ventrally on one side in the base of the shallow cup-like lamina. Directly above the insertion of the ovule, ventral sutures of the carpels are open (FIG. 33). The submarginal position of the ovule can be seen in a young carpel (FIG. 33).

Fusion of the three carpels is ontogenetic and begins in the style. FIGURES 32 to 34 are a series of transections of a gynoecium 230μ in height. Only the upper 130μ of the styles are connate. FIGURE 34 is the first section (proceeding distally) which shows connation. Fusion is by meristematic activity along the appressed ventral faces of the carpels. Initially epidermal cell walls become pointed and interlock (FIG. 35). Subsequent cell divisions produce a solid zone of tissue with no evidence of epidermal layers (FIG. 18). This zone closes the ventral suture of each carpel and joins the three carpels. Fusion progresses gradually toward the base of the gynoecium so that in the flower at anthesis, stylar and ovarian parts are connate but stipes are still separate (FIGS. 17, 18).

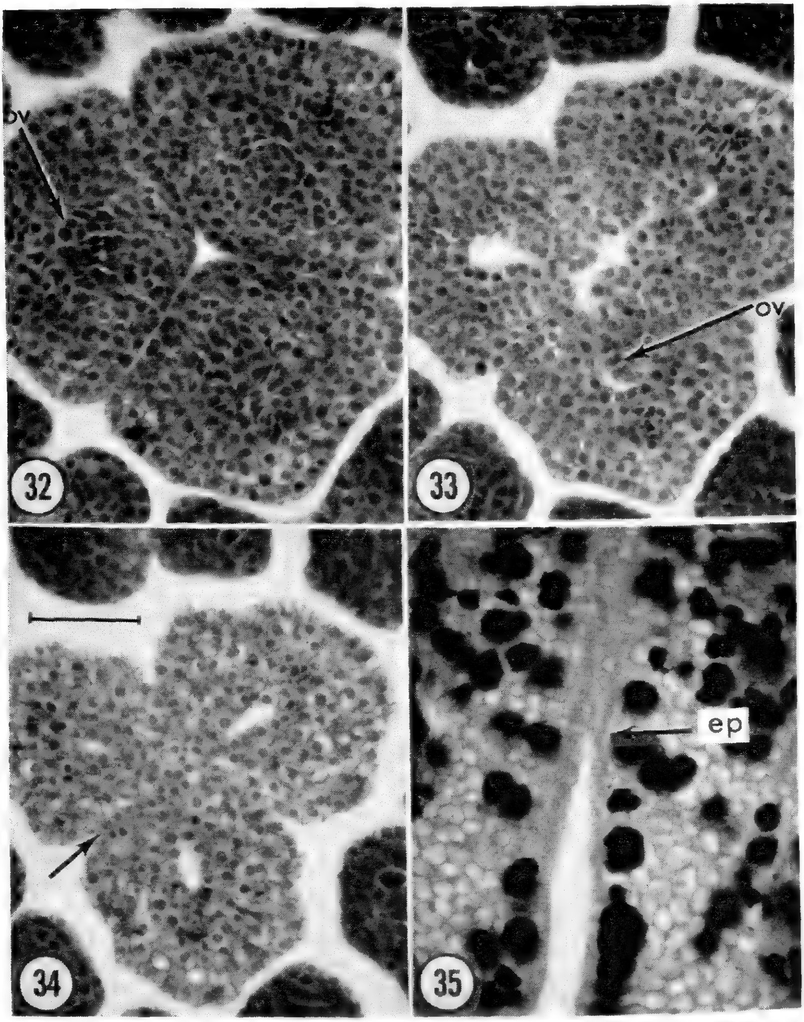
HISTOGENESIS

The floral apex. Esau (1965) states that the amount of zonation of a floral apex may depend on its "determinateness," zonation being lost or obscured in more determinate apices. This applies well to the floral apex of *Nannorrhops* which is relatively indeterminate and shows distinct zonation. The apex (FIG. 24) is zonate with a two-layered tunica, a central group of large corpus initials, and a rib meristem. Barnard (1960) states that two-layered tunicas are relatively common in both floral and vegetative apices of monocotyledons and lists them in the Gramineae, Cyperaceae, Juncaceae, and Liliaceae. Rohweder (1963) has since demonstrated two-layered tunicas in the floral apices of Commelinaceae.



Figs. 28–31. Histogenesis, continued. Fig. 28, transection of a floral apex showing carpel primordia; Fig. 29, longisection of a young flower, stamen, and carpel primordia approximately equal in length; Fig. 30, transection of a young flower, meristematic activity adaxial in two upper carpels, marginal in lower; Fig. 31, transection of base of an older flower showing adnate carpels, stamens, and petals. All referable to scale Fig. 29; scale equals 50μ. Details: ca, carpel; pc, procambial strand; pe, petal; se, sepal; st, stamen; st 1, stamen of lower whorl; st 2, stamen of upper whorl.

Prophyll and floral primordium. The prophyll is inserted obliquely on the floral axis. The tip adjacent to the subtended floral axis is lower and is initiated first (Fig. 24, right). In early stages it is triangular in outline. There appear to be oblique or periclinal divisions in the dermat-



FIGS. 32–35. DEVELOPMENT OF SYNCARPY. FIGS. 32–34. Successive transections through a young gynoecium ca. 230μ long. FIG. 32, ovarian part of gynoecium, 30μ above base, carpels free; FIG. 33, transection 30μ above FIG. 32, near top of ovules, carpels free, ventral sutures open; FIG. 34, 40μ above FIG. 33, first section showing fusion of carpels; FIG. 35, transection of epidermal layers between two carpels in mature flower to show the pointed and interlocked epidermal cells. All referable to scale FIG. 34; scale equals 50μ. DETAILS: ep, epidermis; ov, ovule; unlabeled arrow, FIG. 34, indicates area of fusion of carpel faces.

ogen in the initiation of the tips of the prophyll. This is the only place where periclinal divisions were observed in the first tunica layer. After initiation, each segment of the prophyll is extended by marginal growth, the two extensions meeting to complete the abaxial sheathing part of the prophyll. The adaxial part of the sheath is adnate to the axis to a slightly higher level and apparently develops by intercalary growth.

Floral organs. All floral organs are initiated by periclinal divisions in the second tunica and usually only one underlying corpus layer. Initiation of petals is illustrated in FIG. 26, stamens in FIG. 27, and carpels in FIG. 28. Only anticlinal divisions were observed in the first tunica layer during the development of floral organs.

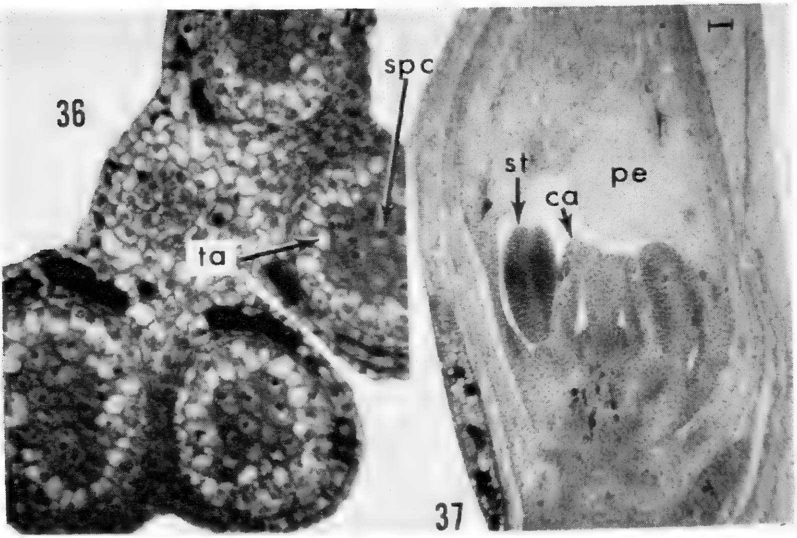
Procambium. The difficulties of determining direction of maturation of procambium are well recognized. In all organs studied for *Nannorrhops*, development of the first procambial strands appears to be acropetal. The first recognizable procambium in a floral stalk is in the form of three central strands. In all floral organs, a single median strand of procambium develops first. This is present in sepals when they are about 160μ high. Stamens and carpels are about 40μ in length when the median strand is recognizable. A single procambial strand is present in petals when they are about 250μ long and three strands are developed when the petals are approximately 330μ in length. The seeming lag in the formation of procambium in the sepals and petals might be accounted for by the rapid early elongation of these organs to enclose developing stamens and carpels which achieve more maturity before elongation.

DISCUSSION

The cincinnus. For obvious reasons the sometimes huge inflorescences of palms have not been readily available for detailed studies. Within the family much diversity is found in both major axes and ultimate flowering units. Evolution in the inflorescence of *Nannorrhops* appears to have resulted in complex patterns of maturation rather than in extreme condensation and/or fusion. Consequently study of this genus is particularly helpful in understanding other genera where more reduction is present. The monopodial systems of major axes are described in a previous paper (Tomlinson & Moore, 1968). With the initiation of the first flower, growth in the inflorescence changes abruptly from monopodial to sympodial.

Designation of the flowering unit in *Nannorrhops* as a cincinnus is not readily evident macroscopically because the five to six flowers within each cluster are successively younger. Details of anatomy and ontogeny, however, show that the basic unit in each flower cluster is a single flower bearing a distinctive bracteole on its axis. In the axil of the bracteole, a new floral primordium is initiated at an angle of approximately 75° on the alternate and abaxial side of each successive floral stalk. Thus the theoretical main axis of the unit is reversed at each primordium and the result is a short scorpioid cyme or cincinnus (Rickett, 1955).

Comparison of the ultimate units of *Nannorrhops* and *Aristeyera* (a



FIGS. 36, 37. FIG. 36, transection of part of anther, for magnification refer to scale FIG. 34; FIG. 37, near-median longisection of young flower; scale equals 50μ. DETAILS: ca, carpel; pe, petal; sp c, sporogenous cells; st, stamen; ta, tapetum.

triad of flowers, Uhl, 1966) suggests that the angle of divergence and position of the bracteole and its subtended primordium determine the shape and consequent definition of the flower cluster. In *Aristeyera*, each floral primordium is borne on the adaxial side of the axis rather than the abaxial as in *Nannorrhops* and the angle of divergence is approximately 25° to 45°. This type of analysis seems to be applicable to many of the diverse ultimate units in palms which are to be treated in detail elsewhere.

Realization that the bract on the flower may be distinctive in shape and anatomy is also useful in interpreting other units. In *Aristeyera* no vascular bundles are present in the bracteole. The second bracteole is bicarinate, however, suggesting a prophyll as in *Nannorrhops*. The significance of the prophyll, a bract which is morphologically and anatomically different from other bracts in the inflorescence, is not apparent at this time.

The flower. Barnard (1955, 1957a,b, 1958) found that in the Gramineae, Cyperaceae, and Juncaceae, stamens were initiated in deeper layers of the floral meristems than other floral organs and, therefore, more closely resembled axial buds. Sharman (1960) also thought stamens (Gramineae) were cauline since they are more like buds in initiation and shape. Other workers (Boke, 1947, 1948, 1949; Tepfer, 1953; Kaussmann, 1963; Kaplan, 1968) have found all floral organs homologous to leaves in patterns of initiation and growth. Because of the nature of palm leaves, developmental patterns are obviously complex and cannot be compared to those of floral organs except in very earliest stages. Leaf primordia in some palms as described by Periasamy (1962) seem similar to those of floral organs in *Nannorrhops* but histogenesis has not been studied.

Evidence from organogeny and histogenesis in *Nannorrhops* suggests that all floral organs are homologous. Stamens and all other floral appendages arise by periclinal divisions in the T_2 and one or more corpus layers. In early stages organs are similar in form and all receive an initial median procambial strand. Later growth patterns differ according to the whorl involved. Sepals develop rapidly and enclose other organs, but remain separate from other floral whorls; while petals, stamens, and carpels become briefly adnate showing zonal growth for a short distance at the base of the flower (FIGS. 14, 31). In addition to evidence from histogenesis, the shape and anatomy of the mature stamens suggest a laminar or foliar nature. The filaments are very wide at the base (FIG. 5). Further the large vascular bundle divides near the base of the filament suggesting the multiple trace condition of foliar stamens (Canright, 1952; Moseley, 1958).

In general the vascular system of the *Nannorrhops* flower is similar to that of *Rhapis* (Uhl, Morrow, & Moore, 1969) and differs from that of the arecoid palms, *Juania, Ravenea,* and *Ceroxylon* (Uhl, in press). Major differences are in the vascular supply to the sepals which is much smaller in the latter genera, and in the type of connation and vascular supply of the carpels. In *Juania, Ravenea,* and *Ceroxylon,* carpels are connate peripherally and ventral sutures are not completely closed at anthesis; in *Rhapis* carpels are separate and those of *Nannorrhops* are connate by ventral faces. Ventral sutures are closed at anthesis in both the latter taxa. The ovular supply in the arecoid genera is a single bundle formed by fusion of a branch from *each* ventral bundle. In both *Rhapis* and *Nannorrhops*, a branch from *one* ventral and branches of several other bundles form the ovular supply.

Within the palms the *Nannorrhops* flower is relatively unspecialized but within the Coryphoideae, it is one of a few in which extensive syncarpy is developed. Ontogenetic development of syncarpy would seem to relate *Nannorrhops* to other Coryphoideae with separate carpels, and stylar origin of the fusion suggests further connection to a group of coryphoid genera in which the carpels are connate by the stylar regions only. A second type of fusion is seen in the sepals. The connate base arises as a unit with no evidence of union during ontogeny. Many coryphoid genera have connate sepals (Morrow, 1965), the significance of connation here is not understood at the present time.

Much has been written and argued about the basic nature of the angiosperm carpel (Eames, 1961; Tucker, 1959). Consideration of many aspects of carpel structure in palms is beyond the scope of this paper and will be considered in a later survey. It is tempting, however, to point out here that certain features of carpels in the monocotyledons (*Rhapis, Nannorrhops, Juania, Ravenea, Ceroxylon*) seem equally and, perhaps, more primitive than those of the Ranales (*sensu* Eames, 1961). In early stages, carpels of *Nannorrhops* are separate, stipitate, and conduplicate, with open ventral sutures. These are features considered primitive in carpels (Bailey & Swamy, 1951; Baum, 1961). The ovule, in both *Nannorrhops* and *Rhapis*, is attached basally and submarginally to one side of the laminate region. The large vascular supply to the ovule and its origin in both genera, when considered with the unspecialized form, lead to the surmise that a single ovule may possibly be primitive in palms.

ACKNOWLEDGMENTS

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ASPECTS OF MORPHOLOGY OF AMENTOTAXUS FORMOSANA WITH A NOTE ON THE TAXONOMIC POSITION OF THE GENUS

HSUAN KENG

THE GENUS *Amentotaxus* was established by Pilger in 1916 (Bot. Jahrb. **54**: 41), based on the type species, *A. argotaenia* (Hance) Pilger. This species, described from sterile material only, was originally designated as a member of the genus *Podocarpus*. As soon as its compound staminate strobilus became known, it was transferred to *Cephalotaxus*, and finally to a separate genus, *Amentotaxus*.

The genus *Amentotaxus* is endemic to eastern Asia. It was first collected from a small islet near Hongkong and also from southern Kwangtung. Subsequently it was reported from southern Formosa, western Hupeh and Szechuan, and from southern Yunnan and northern Tonkin (see FIG. 1). Fossil remains have been recorded from Europe and western America (Sporne, 1965). It was generally considered as a monotypic genus; Li (1952), however, recognizes that there are at least four distinct entities (which he considered species) involved, based on color and relative width of the stomatal bands, and geographic distribution. Chuang and Hu (1963), on the other hand, point out that the characters of the stomatal band appear to be less constant, and maintain that there is only one species, namely *A. argotaenia* (Hance) Pilger.

It is rather difficult to make a judgment on this controversial issue without thoroughly examining suitable materials with reproductive structures, which unfortunately, are not available. For simplicity of nomenclature, since all the materials used in this study are from a small locality in southern Formosa, the binomial *Amentotaxus formosana* Li is, accordingly, adopted. It would be interesting to have reports on the strobilate structures based on the materials from other parts of the geographical range of the genus.

The plants of *Amentotaxus* are small to medium-sized, dioecious, evergreen trees. A limited number of them are perhaps in existence, and they grow in almost inaccessible places. Moreover, they are not represented in any botanical garden or arboretum in the world. Owing to the scarcity of material, *Amentotaxus* is among the least known of the gymnosperms. A comprehensive taxonomic description, the only one available, was prepared by Yamamoto (1927); an amendment with a note on leaf anatomy was presented by the same author a few years later (1931). The stomatal and ovulate structures were reported by Florin (1931, 1938–45); his interpretation of the latter, as indicated in a drawing reproduced in 1951, p. 375, *fig. 64*, was apparently based on poorly preserved herbarium material, and is inadequate. Only fragments of the embryonic

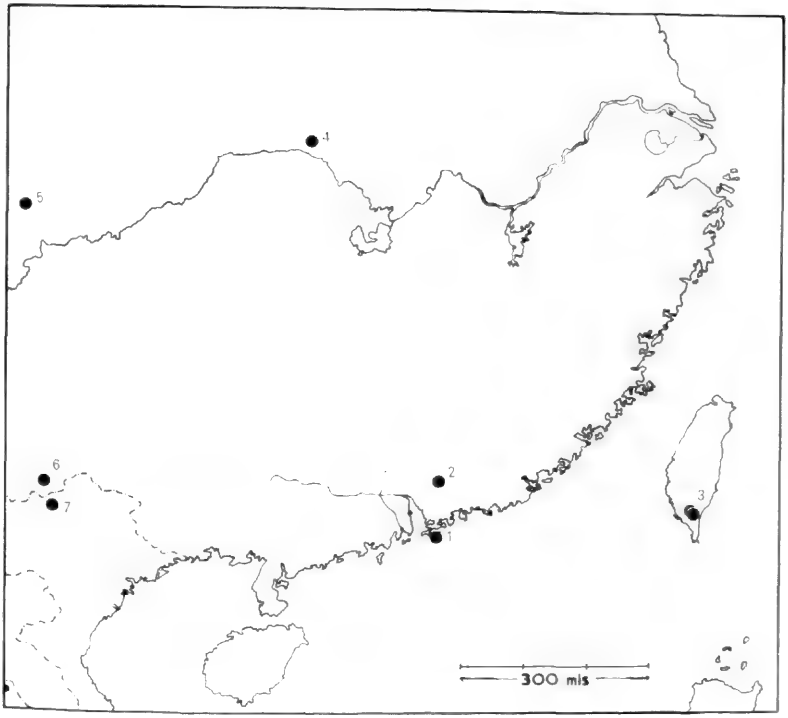

FIGURE 1. Geographic distribution of the genus *Amentotaxus*. 1, Lantao Island, near Hongkong; 2, Mt. Lo-fau-shan, Kwangtung; 3, Taitung and S. Kaohsiung, Taiwan (Formosa); 4, Hsing-shan, Hupeh; 5, Mt. Omei-shan, Szechuan; 6, Makwan, Yunnan; 7, Cha Pa, Tonkin (based on the herbarium specimens cited in Li, 1952).

development were given by Sugihara (1943); and his chromosome number, $n = 11$, on the basis of counts from the female gametophyte, is incorrect, as pointed out by Chuang and Hu (1963). The pollen morphology has been carefully investigated by Erdtman (1957).

MATERIALS AND METHODS

Material preserved in FAA (including leaves, staminate strobili, ovulate strobili, seeds, and seedlings), and dried material (including young ovulate strobili, seeds, and seedlings) taken from herbarium specimens, were received from Professor Ching-en Chang of the Pingtung Agriculture College, Taiwan. All the materials were collected by Professor Chang from near Shin-Huah Farm, Shaw-Jia, Dah-Wu, Taitung, between 1965 and 1968. Clearings of materials were made with 5 percent NaOH at room temperature. Microtome sections 10 to 12 μ thick were stained with a safranin-fast green combination.

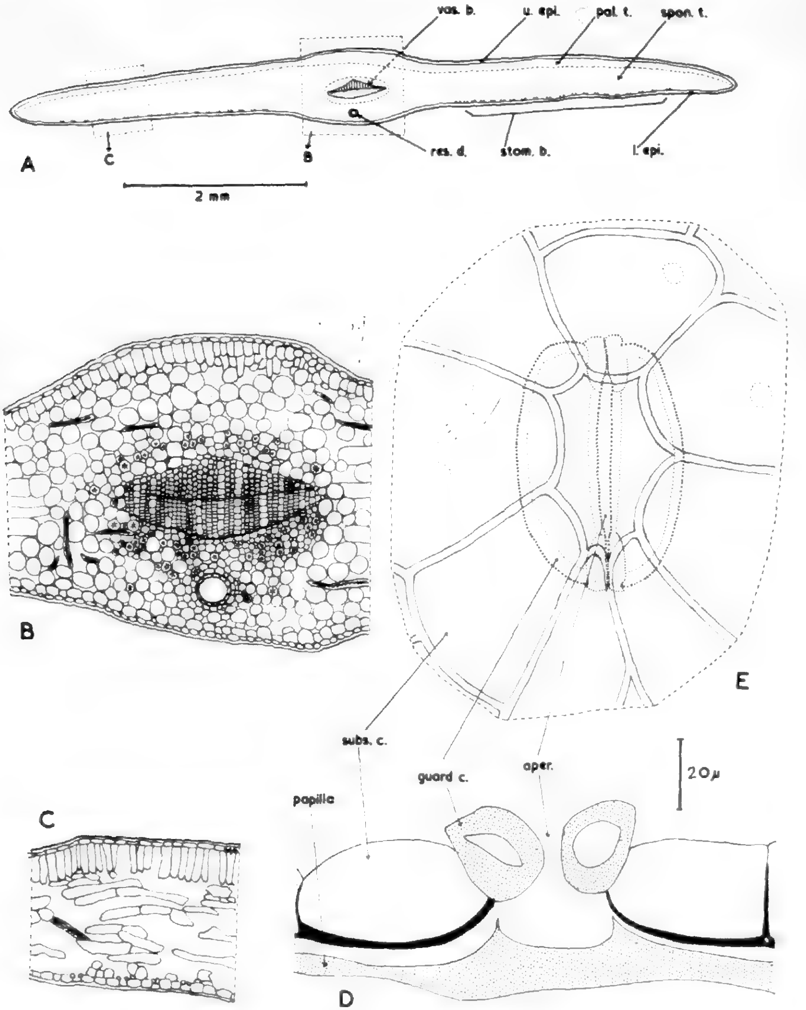

FIGURE 2. Transverse section of a leaf, and surface and sectional views of a stoma. A, Diagram of the transverse section of a leaf; B and C, portions of A, enlarged, showing the cellular details; D, sectional view (across the axis) of a stoma; E, surface view of a stoma (the broken lines marked *guard cells* are drawn at a different focus). NOTE: *aper.* = apertures; *guard c.* = guard cells; *l. epi.* = lower epidermis; *pal. t.* = palisade tissue; *res. d.* = resin ducts; *spon. t.* = sponge tissue; *stom. b.* = stomatiferous band; *subs. c.* = subsidiary cells; *u. epi.* = upper epidermis; *vas. b.* = vascular bundle.

Leaves. Foliage leaves are persistent, spirally arranged on the branchlets but twisted at the base into two rows in one plane. Internodes are 6 to 7 mm. long (average). Each leaf consists of a lamina and a very short petiole. Laminae are coriaceous, bifacially flattened, with the adaxial surface upward. They are linear, often strongly falcate, acute or more often acuminate at apex and slightly oblique at base, 5–7 cm. long, 0.5–1 cm. broad. Two very prominent stomatiferous bands are present on the abaxial surface and run parallel to the elevated midrib, one on each side of it (see PLATE I, a & b). Petioles are strongly decurrent on the branchlets.

Anatomically, each lamina possesses only one large, median vascular bundle with a resin canal beneath (see FIG. 2, A & B). The assimilatory tissues consist of one to two (near and at the midrib) rows of palisade cells and numerous polygonal, elongate, and dissipated spongy cells. The upper and lower epidermis are both well defined, the former with slightly more thickened cuticle layer. Stomata are arranged in longitudinal rows, their axes oriented more or less parallel to the midrib of the leaf. Each stoma (see PLATE II, b; FIG. 2, E) is encircled by 7 to 9 subsidiary cells. Strong papillae of the subsidiary cells surround the orifice of the stomatal apparatus like a wall, while the guard cells are also heavily cutinized. Sclereids are abundant, slender, branched or unbranched at one or both ends, and generally lying between the midrib and leaf-margins and perpendicular to them (see PLATE II, b).

Staminate strobilus. The compound staminate strobili are produced within the large winter bud which is borne on the top of the previous year's branchlets. They are short-stalked, usually four (sometimes three, rarely two or five) together, subtended by four rows of imbricate bud-scales (see PLATE I, a; FIG. 3, A). These scales are leathery, strongly keeled and more or less pointed. The true terminal bud of these branchlets is generally in the center and is further protected by small, thin scales (FIG. 3, B); it remains dormant and resumes its activity only after expansion and withering of the surrounding compound staminate strobili.

Each compound staminate strobilus is spike- or catkin-like, from which is derived the generic name *Amentotaxus* (FIG. 3, C). When fully expanded, the compound strobilus can reach a length of 2.5 to 3 cm. or more. It consists of approximately 20 to 30 globular staminate strobili somewhat decussately arranged (though not quite regular), growing along the main axis in four rows. These globular staminate strobili are clearly recognizable especially in the middle portion of the spike, since the distal ones are overcrowded and fused, and the lowermost ones are sometimes adherent to the side (secondary) branches rather than being on the main axis itself.

The staminate strobilus is globular or ovoid, 2.5 to 3 mm. in diameter in bud (see FIG. 3, D). It is composed of 9 to 12 closely compacted microsporangiophores,[1] which are peltate, with four or five (varying from

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[1] Since the homologous structure in *Taxus* is peltate which is strongly suggestive of *Equisetum*, and since it is subtended by a bract in *Austrotaxus* (Saxton, 1934, p. 243, *f. 20 & 21*) and *Pseudotaxus* (Florin, 1948 a, p. 389, *f. 2*), microsporangiophore is perhaps preferable, as a designation, to microsporophyll; although no trace of the subtending bracts has been found at the base of the stalk in *Amentotaxus*.

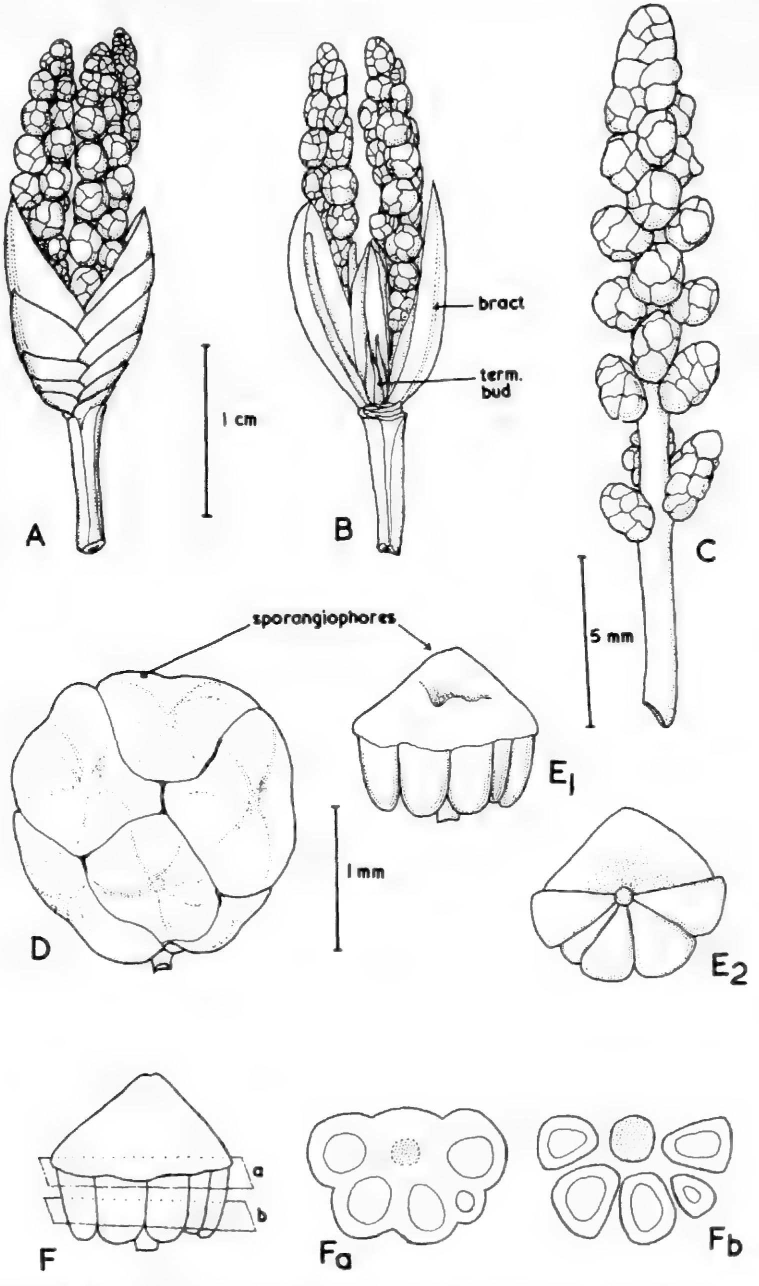

FIGURE 3. Compound staminate strobilus, staminate strobilus and microsporangiophore. A, External view of an unfolded winter bud, showing a cluster of four (one is not seen) compound staminate strobili; B, *the same*, with half

two to eight) microsporangia hanging underneath in a semicircle and with a short stalk near the center (see PLATE II, e; FIG. 3, E). The outline of the peltate microsporangiophores, as seen from the outer surface, varies from round to deltoid, to more commonly polygonal, due to mutual compression.

At maturity the thickened outermost layer and one or two (in part) inner layers of the microsporangial walls are retained (see PLATE II, d & e). The microspores are wingless.

Ovulate strobilus. The ovulate strobilus is globular to ovoid, flattened dorsiventrally (see PLATE I, b; FIG. 4, A_1, A_2, B_1, B_2, C_1, C_2). These strobili are situated singly in the axils of foliage leaves. The ovule is solitary, terminal on the strobilate axis, and subtended below by five (or six) pairs of opposite and decussate, sterile bracts; three pairs of which are lateral and prominently keeled, and the other two (or three) pairs are dorsiventral and only slightly curved (FIG. 4, A_4). The stalk of the strobilus is slender, about 1–1.5 cm. long, more or less flattened and narrowly winged.

Young ovules, at the stage of about 3 mm. in length (excluding the sterile bracts) (FIG. 4, A_3), possess an elongate conical nucellus, of which the upper part is loosely enveloped by a single layer of integument, the lower half, however, is seemingly associated only with the cupular arillus primordium. The integument (if it is interpreted as confined to the portion above the arillus only) and the arillus, at this stage, appear to be completely separated. The vascular supply to the ovule, as seen in cross section, consists of 8 to 10 normally oriented vascular bundles. They terminate at the end of the ovule far below the nucellus — neither the integument nor the arillus primordium is visibly vascularized.

In the slightly older ovules at the stage of about 5 mm. in length (FIG. 4, B_3), as a result of the enlargement of both the nucellus and the integument, these two parts become approximate. Also, owing to the intercalary growth of the lower half of the ovule, the integument becomes evidently embedded in the cupular arillus. The vascular supply can be observed near the base of the ovule.

In the still older ovules, at the stage of about 6.5 cm. in length (FIG. 4, C_3; FIG. 5), the nucellus is enveloped by and fused with the integument except for the uppermost part which remains free. Nearly two-thirds of the integument, in turn, is embedded in and completely united with the arillus. Isolated tracheids may be found in the lower part of the ovule at a fairly high level in the region where the fusion of aril and integument occurs.

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of the bracts and compound staminate strobili removed, showing the hidden terminal bud inside; C, a compound staminate strobilus, showing a number of ovoid to globular staminate strobili more or less decussately arranged on an axis; D, a globular staminate strobilus (taken from the median of C), enlarged; E_1 and E_2, two views of a sporangiophore showing five microsporangia arranged in a semicircle below; F_a and F_b, two diagrammatic sectional views of the sporangiophore.

A general outline of the tissues in the largest ovule available is shown in FIGURE 5. The arillus consists of 10 to 15 layers of parenchyma cells with rows of resinous cells lining the epidermis near the rim. The cuticle is thin. The lower portion of the integument is composed of 12 to 20 layers of small, partly closely packed, and partly loosely dissipated parenchyma cells. There is no clear distinction of the arillus from the integument below the level of fusion. The upper portion of the integument is heavily cuticularized. The cells near the micropyle are enlarged, sclerenchymatous, and oriented horizontally. The nucellus is prominently beaked; the beak is hemispheric, and composed of numerous small polygonal cells with moderately heavy walls rather loosely arranged especially towards the micropylar end. A large portion of the nucellus at this stage, is digested and replaced by the multicellular megagametophyte. Isolated tracheids and short rows of tracheids are observed at the lower part of the peripheral region where the integument and arillus are merged.

The ovular structure of *Amentotaxus* in general, as noted by several authors (e.g. Florin and others), is rather similar to that of *Torreya*; but its vasculature is very much simpler. In *Amentotaxus*, although there are 8 to 10 vascular strands entering the base of the ovule, only the isolated tracheids are present in the lower part of the ovule, in the region where the integument and arillus meet. In *Torreya*, however, there are two vascular strands running up inside the arillus nearly to the apex of the seed, each of which then sends a branch through a foramen in the stony layer of the integument; each branch forks, forming a loop which encircles the seed. Oliver (1903) proposed the "hyposperm theory" to explain this peculiar vascular structure. According to this theory, all the basal part (the "hyposperm") of the ovule is an intercalated growth and phylogenetically younger than the extreme tip (the "archisperm"). The branching of the integumental vascular bundles inwardly is also reported in *Austrotaxus* (Saxton, 1934, p. 419, *fig. 18*) and *Cephalotaxus* (Singh, 1961, p. 160, *fig. k*). In the case of *Amentotaxus*, no traces of such branching are present. With the intercalary growth of the lower part of the integument and arillus concomitantly with the enlargement of the nucellus, the integument becomes evidently embedded in the arillus and fused with it. There seems to be no evidence to prove that the lower part of the *Amentotaxus* ovule is a "hyposperm," or is phylogenetically younger than the upper part.

Seed and seedling. The seed is ellipsoid-oblong, drupe-like (PLATE I, c), 3.2 to 3.6 cm. long, 1 to 1.2 cm. broad, and slightly flattened dorsiventrally. The outer part of the seed coat is completely covered and fused with the arillus, except the extreme tip which is exposed (FIG. 6, A & B). The merged structure is soft-leathery in texture although the outer portion is easily blistered and disintegrated when soaked in water. The nucellus is almost entirely replaced by the ivory female gametophyte ("endosperm") which has an entire rather than ruminate margin (as in *Torreya*). The embryo is linear, lying in the center of the gametophyte.

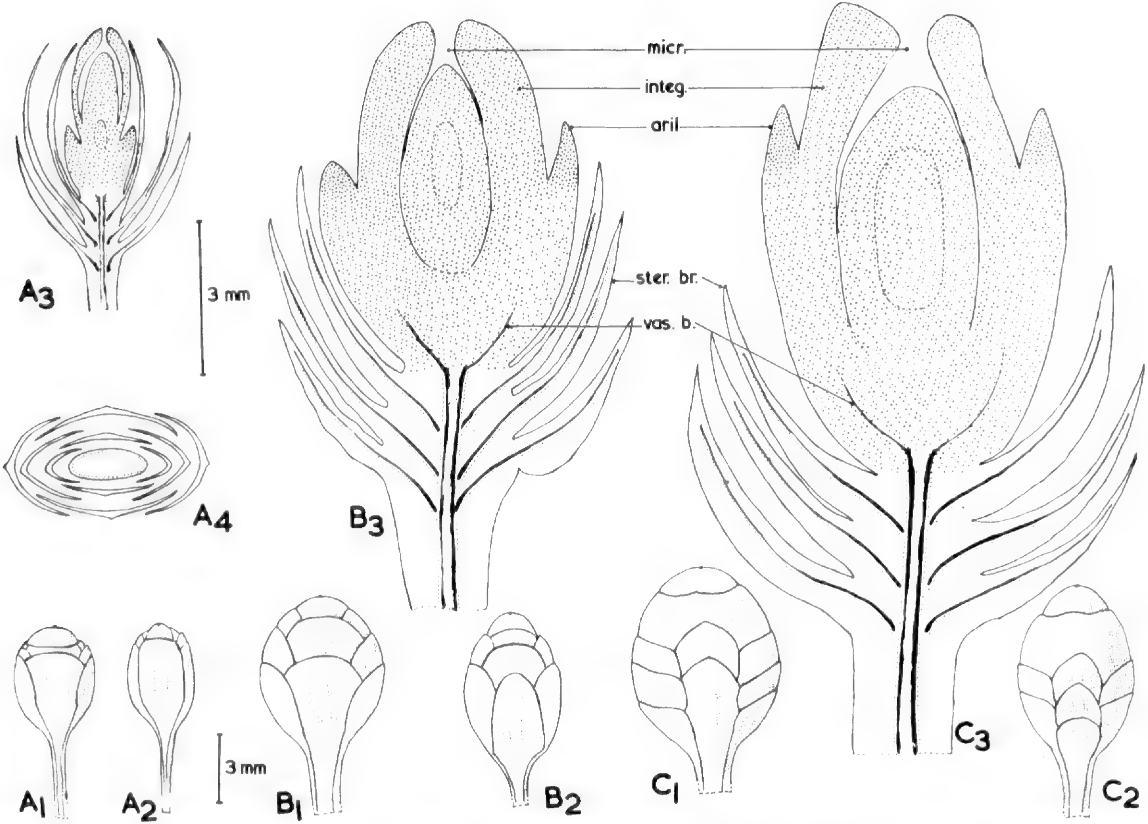

FIGURE 4. External and sectional views of three ovulate strobili. A_1 and A_2, two views of a young strobilus; A_3 and A_4, longitudinal and transverse sections of the same strobilus; B_1 and B_2, two views of a slightly older strobilus; B_3, longitudinal section of *the same*; C_1 and C_2, two views of an older strobilus; C_3, longitudinal section of *the same*; NOTE: *micr.* = micropyle; *integ.* = integument; *ster. br.* = sterile bract; *vas. b.* = vascular bundle.

In common with other conifers, germination is of epigeal type. In the one year old seedling examined (PLATE I, d), the cotyledons have dropped, but the two cotyledonary scars are clearly evident. The juvenile leaves are 3.5 to 4 cm. long, 3.5 to 4 mm. wide, with two glaucous stomatiferous bands underneath. Fundamentally of spiral arrangement, since the internodes are of variable length, the juvenile leaves appear subopposite or rarely subverticillate.

TAXONOMIC POSITION OF AMENTOTAXUS AND THE CLASSIFICATION OF THE CONIFERALES

Pilger (1926) assigns *Amentotaxus*, together with *Cephalotaxus*, to the Cephalotaxaceae on the basis of the compound nature of their staminate strobili. Kudo (1931), after seeing the ovulate strobilus, hitherto unknown, maintains that "it (*Amentotaxus*) must be included in a new family Amentotaxaceae, or in a new subfamily or tribe of Taxaceae, but not in Cephalotaxaceae" (p. 311). As a result, a new family Amentotaxaceae was proposed by Kudo and Yamamoto (in Kudo, 1931). Koidzumi (1932) strongly felt that the new family was not necessary. He, therefore, established a subfamily Amentotaxoideae (including both *Amentotaxus* and *Austrotaxus*) within the Taxaceae. Later on, following his enumeration of various similarities and dissimilarities among the Taxaceae, Cephalotaxaceae, and *Amentotaxus*, he (1942), recognized that *Amentotaxus* and *Cephalotaxus* are in fact related, and moreover, suggested that Taxaceae and Cephalotaxaceae should be merged into one family and both reduced to subfamilial status. Florin (1948, 1951) emphasized the differences of ovulate strobili and stomatal structures between *Cephalotaxus* and *Amentotaxus*, and thus sustained the transference of *Amentotaxus* from Cephalotaxaceae to Taxaceae. Chuang and Hu (1965) report the chromosome number of *Amentotaxus argotaenia* (Hance) Pilger (or *A. formosana* Li) to be $x = 7$, which is different from those reported from *Taxus* ($x = 12$), *Torreya* ($x = 11$), and *Cephalotaxus* ($x = 12$). They, therefore, support Kudo and Yamamoto in maintaining *Amentotaxus* in a separate family, the Amentotaxaceae. The present writer is inclined to think that (1) *Amentotaxus* is probably better placed in the Taxaceae than in the Cephalotaxaceae or in a separate family; (2) the Taxaceae are not isolated, but are likely allied to the Cephalotaxaceae, probably through *Amentotaxus*. These two points are elaborated in the following paragraphs.

Features which distinguish *Amentotaxus* from other members of the Taxaceae such as the spicate compound staminate strobili, the peculiar stomatal structure (with larger number of subsidiary cells, thickened papillae, etc.), etc., appear to be insufficient to warrant a separate family status. The difference in chromosome number is probably inadequate to be cited as a justification for the establishment of the Amentotaxaceae.[2]

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[2] For example, in a recent report (Hair & Beuzenberg, 1958) on the chromosome numbers of the Podocarpaceae, the following two closely related genera possess such

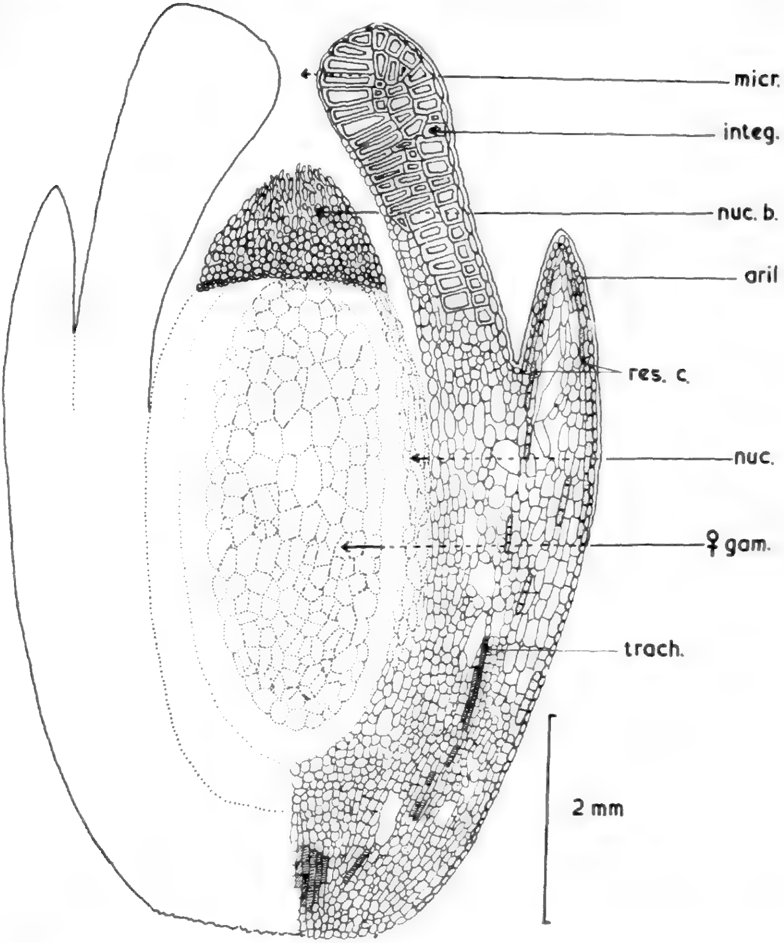

FIGURE 5. Longitudinal section of an ovule, details of Figure 4C₃. NOTE: *nuc. b.* = nucellus beak; *res. c.* = resin cells; *nuc.* = nucellus; ♀ *gam.* = megagametophyte; *trach.* = tracheids.

On the other hand, the resemblance of *Amentotaxus* to the Taxaceae, especially to the genus *Torreya*, in the general structure of staminate strobili, ovulate strobili, microsporangiophores, ovules, etc. is overwhelming. Therefore, Janchen's (1949) treatment including both *Amentotaxus* and *Torreya* in the Tribe Torreyeae under the Taxaceae appears to be a logical one.

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a range of variation: *Dacrydium* ($x = 15, 12, 11, 10, 9$), *Podocarpus* ($x = 19, 18, 17, 13, 12, 11, 10$); whereas other members of the family also have various different basic numbers: *Acmopyle* ($x = 10$), *Microcachrys* ($x = 15$), *Pherosphaera* ($x = 13$), *Phyllocladus* ($x = 9$), and *Saxagothaea* ($x = 12$).

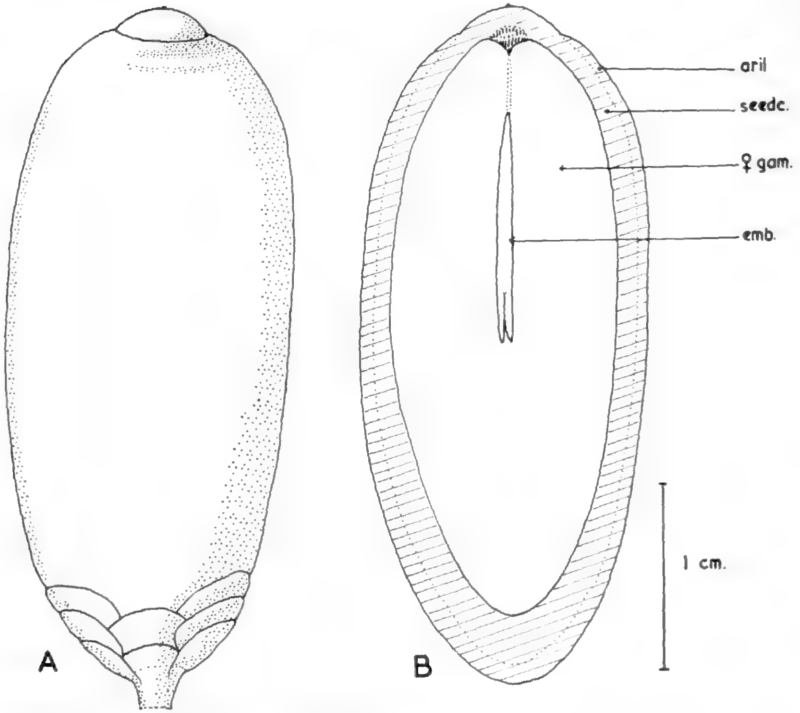

FIGURE 6. External and sectional views of a seed.

A more or less similar view is held by Kudo (1931), Koidzumi (1932), Li (1952), and others.

Florin in a series of papers (1948, 1951, 1954) strongly advocated separation of Taxaceae (which includes the following five genera: *Taxus, Amentotaxus, Torreya, Austrotaxus,* and *Pseudotaxus* [=*Nothotaxus*]) from the rest of the Coniferales to form a separate order, the Taxales, a view originally expressed by Sahni (1920) but modified by Florin with the exclusion of *Cephalotaxus.* A quite different scheme proposed by Buchholz (1934), was summarized by Chamberlain (1935, pp. 229, 230) as follows: The order Coniferales can be divided into two suborders: one the Pinineae (as Phanerostrobilares or Pinares) with an obvious cone, includes the Pinaceae, Taxodiaceae, Cupressaceae and Araucariaceae; the other, Taxineae (as Aphanostrobilares or Taxares) without such an obvious cone, contains the Podocarpaceae, Taxaceae, and Cephalotaxaceae.

Florin (1951, pp. 363, 364) fully endorsed Wilde's (1944) postulation that in *Podocarpus,* the species with 1-ovulate strobili are independently derived from those with multiovulate strobili, and represent the ultimate stage of reduction. In addition, his own interpretation (1951, 1954) of the ovulate strobilate structures of the modern conifers as possibly evolved from a much more complicated structure of fossil groups such as found in the palaeozoic *Lebachia*, *Ernestiodendron*, *Walchia*, and *Pseudovoltzia*, has been widely appreciated. Paradoxically, he insists that the 1-ovulate strobilus of the Taxaceae is a primitive rather than a derived condition; therefore the family Taxaceae is of entirely different origin from the rest of the other Conifers. This is mainly because of his emphasis on the finding of 1-ovulate *Palaeotaxus* in the Triassic and *Taxus jurassica* in the Jurassic rocks. "Because of its high geological age" he noted (1951, p. 349), "*Palaeotaxus* can hardly derive from any cone-bearing type." It seems he does not realize the possible existence of the exceptionally fast rate of evolution, designated by Simpson (1944) as tachytelic evolution. Many authors, such as Chamberlain (1935, p. 439), Pulle (1937), Takhtajan (1953, p. 34), etc. express their notions that the single ovulate strobilus of taxads is most likely derived from the multi-ovulate cones. The present writer (Keng, 1963) also points out that the evolution of the ovulate strobili in the genus *Phyllocladus* (belonging to the Podocarpaceae, or according to some authors, the monogeneric family, Phyllocladaceae) might indicate the possible mode of how the single, pseudo-terminate ovule of taxads could have been achieved. Incidentally, *Phyllocladus* is somewhat intermediate between the Taxaceae and Podocarpaceae; on morphological ground it is probably correct for it to be placed in the Podocarpaceae (Maheshwari, 1962).

Although, as discussed above, *Amentotaxus* should be better classified in the Taxaceae rather than Cephalotaxaceae, it does not mean that the Taxaceae and Cephalotaxaceae are totally unrelated as suggested by Florin. The present writer agrees with Saxton (1934), Pulle (1937), Koidzumi (1942), and many others that these two families are in fact related. In this connection, it is rather interesting to mention the views of Singh (1961) who has contributed an excellent account on the life history of *Cephalotaxus drupacea* Sieb. & Zucc. In his discussion of the relationships of the Cephalotaxaceae and Taxaceae, he pointed out a number of similarities between these two families and noted that they "resemble each other in wood structure, pollen structure, and to some extent embryogeny" (p. 193). He was, unfortunately, dominated by Florin's misconception that the Taxaceae are isolated and reached the contradictory conclusion that "it appears best to regard the Taxaceae and the Cephalotaxaceae as unrelated" (p. 193).

If we accept the general view that the compound staminate strobilus is a primitive condition (Wilde, 1944), that the peltate sporangiophore is more antiquated than the dorsiventral ones (Florin, 1948), and that the one-ovulate strobilus is derived from a multiovulate strobilus (Pulle, 1937), and also if we assume that the Taxaceae and Cephalotaxaceae are phylogenetically affiliated, then an ideal ancestral form of *Taxus-Amentotaxus-Cephalotaxus* complex would hypothetically possess the following synthetic strobilate features.

Staminate or microsporangiate strobili — a cluster of spike-like compound strobili surrounding a terminal bud and enveloped by numerous bud-scales (cf. *Amentotaxus*); each compound strobilus composed of many ovoid or globular strobili; each strobilus consisting of many peltate, spirally arranged sporangiophores with a number of sporangia on the undersurface around the stalk (cf. *Taxus, Pseudotaxus*); each peltate sporangiophore further subtended by a leafy bract (cf. *Pseudotaxus*, see Florin, 1948a, p. 389, *fig. 2*; or *Austrotaxus*, see Saxton, 1934, p. 423, *figs. 20 & 21*).

Ovulate or megasporangiate strobili — a strobilus composed of many imbricate ovuliferous scales each with several to two (or one) ovules on its upper surface (cf. *Cephalotaxus*); ovules erect, with only one integument and surrounded by a cupular arillus but free from it (cf. *Taxus, Pseudotaxus*); the integument supplied by a number of lengthwise vascular bundles, each of which gives a horizontal branch in the middle of the integument, toward the inner part of the ovule to supply the nucellus and gametophyte (cf. *Torreya*, see Oliver, 1903; *Austrotaxus*, see Saxton, 1934, p. 419, *fig. 18*; *Cephalotaxus*, see Singh, 1961, p. 160, *fig. k*).

To summarize, firstly, since the resemblance of *Amentotaxus* to *Torreya* (Taxaceae) is so overwhelming, it seems logical to include *Amentotaxus* in the Taxaceae; secondly, since the family Taxaceae is intricately affiliated to the Cephalotaxaceae on the one hand and possibly to the Podocarpaceae on the other, Buchholz's scheme of classification of the Coniferales, therefore, appears to be sound.

ACKNOWLEDGMENTS

I am most grateful to Professor Ching-en Chang, who kindly made several trips to the southern part of Taitung District, Formosa, to collect the materials for this study, and to Dr. H. L. Li and Dr. Gloria Lim for reading the manuscript. My thanks are also due to Professor B. Y. Yang, Dr. Ding Hou, and Mr. M. C. Kao for supplying some of the literature; to Dr. C. C. Hsü for translating several paragraphs from the Japanese literature; and to Mr. D. Teow for taking the photomicrographs.

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EXPLANATION OF PLATES

PLATE I

(Scale in each figure in 1 mm. divisions.)

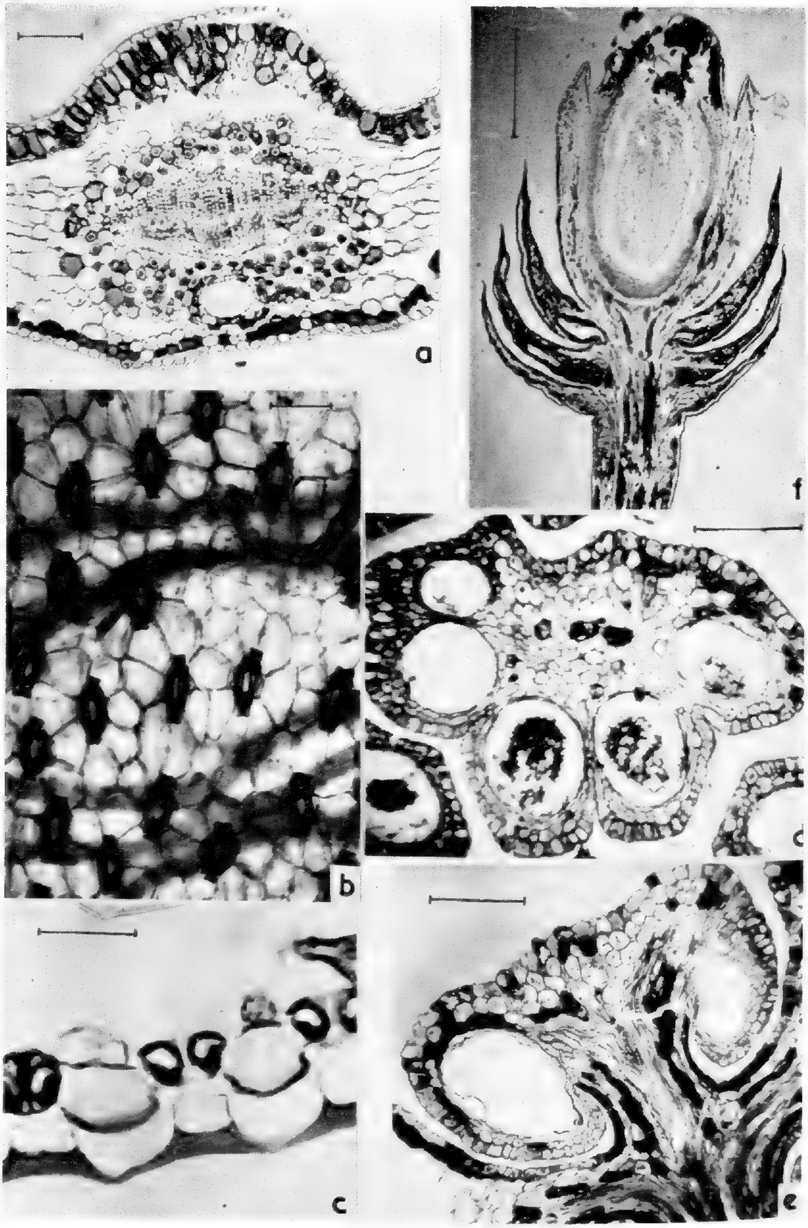
Amentotaxus formosana Li. a, Cluster of compound staminate strobili from an unfolded winter bud borne on the tip of a branchlet (cf. FIG. 3A); b, solitary ovulate strobilus borne in the axil of a leaf (which has dropped off) (cf. FIG. 4, C_2); c, one fully mature and three young seeds (cf. FIG. 6A); d, seedling, of which the two cotyledons (on the first node) have dropped off.

PLATE II

(Scales: in a, 150 μ; in b and c, 50 μ; in d and e, 200 μ; in f, 2 mm.)

Amentotaxus formosana. a, Transverse section of a leaf showing the midrib region (cf. FIG. 2B); b, lower (abaxial) surface of a leaf (after clearing) showing the stomata and sclereids; c, stomata in transverse section (cf. FIG. 2D); d, transverse section of a microsporangiophore (cf. FIG. 3, F_a); e, longitudinal section of a microsporangiophore; f, longitudinal section of an ovulate strobilus (cf. FIG. 4, C_3).

KENG, AMENTOTAXUS FORMOSANA



KENG, AMENTOTAXUS FORMOSANA

A KARYOLOGICAL SURVEY OF LONICERA, II

LILY RÜDENBERG AND PETER S. GREEN *

IN THE FIRST PAPER presenting the results of this survey, all the chromosome numbers recorded for the genus *Lonicera*, to that date, were assembled, together with many new counts. Since that time the study of *Lonicera* has continued, but to bring the investigation to a conclusion all the additional counts that have been made using the Arnold Arboretum collections are presented below (together with three further records that have appeared in the literature).

Cytological methods, documentation and nomenclature used here follow those of the first paper, to which reference should be made.[1]

An attempt was made to note differences in karyotype morphology and, certainly, differences in the overall size of chromosome complements were observed between different species. Also, variation in individual chromosomes, their size, centromere position, and the presence and size of satellites were noted, but considering the relatively large number of species in the genus and the few individuals investigated, it has not proved possible to compare and correlate these differences, and their groupings, with the infrageneric classification proposed by Rehder (1903).

At metaphase the chromosomes, in many cases, were so contracted that two satellites were not always visible. Thus, it was not possible to determine whether or not *Lonicera modesta* had a satellited chromosome pair. More details of morphology could be observed at late prophase. In some cells, pretreatment with oxyquinoline (Tjio & Levan, 1950) caused a structural differentiation of the chromosomes by revealing positively and negatively heteropycnotic segments. Homologues of similar size could then be identified by the location of the centromere and by the individual distribution of these segments. A comparable pattern has been observed in several homologues of different species of *Lonicera*. FIGURES 1 to 10 present examples which were encountered of nuclei in mitosis (most examples taken from species in different subsections of Rehder's classification).

A few comments may be made. In four cases both diploid and tetraploid plants have been recorded within the same species. In *Lonicera ferdinandii* Franch., the earlier undocumented counts and all the plants at the Arnold Arboretum appear to be diploid, except for one (AA 21595) which is tetraploid. This particular bush is an old one, raised from seed of *Rock 13519* collected in S.W. Kansu, China, in 1925, yet phenotypical-

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* In this survey, the cytological investigations have been carried out by one of us (L.R.), and the complementary taxonomy by the other (P.S.G.).

[1] Part I was published in Jour. Arnold Arb. **47**: 222–247. 1966.

ly it does not appear to differ significantly from the diploid. In *L. alpigena* L., Poucques (1949, pp. 129 & 186) has recorded $n = 9$ and $2n = 18$, both of which numbers were confirmed by counts on a plant in the Arnold Arboretum (AA 91–60) which, unfortunately, died before an authenticating herbarium specimen was collected. However, in this species, the tetraploid number, $2n = 36$, has been found in two plants of f. *nana* (Carr.) Zabel (see below). In *L. maximowiczii* (Rupr.) Maxim. var. *sachalinensis* Fr. Schmidt we can now document a tetraploid ($n = 18$ and $2n = 36$), in contrast to the diploid number of $2n = 18$ recorded for the species by Janaki Ammal & Saunders (1952, p. 540). The plant on which their count was based does not appear to have been documented and it is now impossible to know which variety may have been involved, or to confirm its identity. Lastly, in our first paper we recorded a plant of *L. modesta* Rehd. var. *modesta* as diploid ($n = 9$ and $2n = 18$) and of var. *lushanensis* Rehd. as tetraploid ($n = 18$ and $2n = 36$), both plants having been raised from seed sent from the Lushan Botanic Gardens in China. Here, however, there is need for taxonomic reassessment, as we have pointed out (Rüdenberg & Green, 1966, p. 225). Available herbarium material has proved inadequate to enable one to come to a sound conclusion, but it may well prove that two species are involved where diagnostic distinctions need careful delineation.

It is, perhaps, worth drawing attention to the fact that in the whole of both subsections TATARICAE and OCHRANTHAE, including many cultivars and hybrids, but with one exception, no polyploid plants have been observed. The exception is *Lonicera floribunda* Boiss. & Buhse (AA 341–44) which is tetraploid. Within and between these subsections hybridization takes place readily, yet meiosis in most of these diploid hybrids is, with the exception of some plants with bridges, perfectly normal. A few of the plants studied at the Arnold Arboretum form bridges at anaphase I, especially *L.* × *bella*; meiosis was, therefore, checked the next year to determine its constancy and whether or not the frequency of these bridges could be correlated with the seasonal variation in climate. It was found that the number of cells showing bridges was not the same for the two years. It was smaller after the more normal spring, in contrast to one with especially cold nights and periods of drought.

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TABLE. **Additional chromosome numbers in Lonicera**

SPECIES	*n*	*2n*	DOCUMENTATION AND COLLECTOR	GENERAL DISTRIBUTION
Subgenus LONICERA (Subgen. *Chamaecerasus* (L.) Rehd.) SECT. ISOXYLOSTEUM Rehd.				
Subsect. MICROSTYLAE Rehd.				
L. angustifolia Wall. ex DC.	9		See Mehra & Gill in Löve (1968, p. 576). Based on *Mehra & Gill 1291* (PUNJAB), Simla, W. Himalayas	Himalayas
**L. syringantha* Maxim.	18		AA 405–35, *Palmer*, 1 June & 26 Aug. 1936	North & West China
*var. *wolfii* Rehd.	18	36	AA 4992–2, *Allen*, 1 June 1927, also *Dudley & Dodd*, 28 May 1965	West China
*cv. Grandiflora		36	AA 1089–61, *Rüdenberg*, 18 May 1966	
Sect. ISIKA (Adans.) Rehd.				
Subsect. CAERULEAE Rehd.				
L. villosa (Mich.) Roem. & Schult.		18	See Löve & Löve (1966, p. 51). Based on *Löve & Löve 7496* & *7591*, Mt. Washington, New Hampshire	Northeastern North America
Subsect. PILEATAE Rehd.				
**L. pileata* Oliv.		18	AA 151031–B, *Dudley & Dodd*, 28 May 1965	Central and western China
	9		AA 225–28–E, *Green*, 4 Nov. 1965 and (as 225–28) *Kobuski & Roush*, 14 Sept. 1931	
**L. nitida* Wils.		18	AA 923–49, *Green*, 4 Nov. 1965	Western China
Subsect. VESICARIAE (Komar.) Rehd.				
L. ferdinandii Franch.	18		AA 21595 (*Rock 13519*, Kansu, 1925), *Kreps*, 25 May 1964	Northern China
Subsect. BRACTEATAE (Hook. f. & Thoms.) Rehd.				
L. altmannii Reg. & Schmalh.				
*var. *pilosiuscula* Rehd.		18	AA 14999, *Rehder*, 5 May 1927	Turkestan
Subsect. DISTEGIAE (Raf.) Rehd.				
L. involucrata (Richards.) Banks ex Spreng.	9	18	See Taylor & Mulligan (1968, p. 109). Based on *CTS 35077* & *CT 35434*, Graham Is., British Colombia	Northern America and south into Rocky Mts.
Subsect. ALPIGENAE Rehd.				
L. alpigena L.				
f. *nana* (Carr.) Zabel		36†	AA 14994–1, *Allen*, 13 August 1927	Central and southern European Mts.
		36	AA 803–35, *Green*, 26 May 1965	

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* This is the first publication of a documented count for this taxon.

† Due to an error *2n* 18 was incorrectly recorded for this plant in part I, p. 234.

Subsect. PILEATAE Rehd.				
**L. pileata* Oliv.		18	AA 151031–B, *Dudley & Dodd*, 28 May 1965	Central and western China
	9		AA *225–28–E*, *Green*, 4 Nov. 1965 and (as *225–28*) *Kobuski & Roush*, 14 Sept. 1931	
**L. nitida* Wils.		18	AA 923–49, *Green*, 4 Nov. 1965	Western China
Subsect. VESICARIAE (Komar.) Rehd.				
L. ferdinandii Franch.	18		AA 21595 (*Rock 13519*, Kansu, 1925), *Kreps*, 25 May 1964	Northern China
Subsect. BRACTEATAE (Hook. f. & Thoms.) Rehd.				
L. altmannii Reg. & Schmalh.				
*var. *pilosiuscula* Rehd.		18	AA 14999, *Rehder*, 5 May 1927	Turkestan
Subsect. DISTEGIAE (Raf.) Rehd.				
L. involucrata (Richards.) Banks ex Spreng.	9	18	See Taylor & Mulligan (1968, p. 109). Based on *CTS 35077* & *CT 35434*, Graham Is., British Colombia	Northern America and south into Rocky Mts.
Subsect. ALPIGENAE Rehd.				
L. alpigena L.				
f. *nana* (Carr.) Zabel		36†	AA 14994–1, *Allen*, 13 August 1927	Central and southern European Mts.
		36	AA 803–35, *Green*, 26 May 1965	

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* This is the first publication of a documented count for this taxon.

† Due to an error $2n = 18$ was incorrectly recorded for this plant in part I, p. 234.

TABLE. **Additional chromosome numbers in Lonicera** (*Continued*)

SPECIES	*n*	2*n*	DOCUMENTATION AND COLLECTOR	GENERAL DISTRIBUTION
Subsect. RHODANTHAE (Maxim.) Rehd.				
**L. tatarinowii* Maxim.		18	AA 17–44–B (*Meyer 1938a*, China, 1913), *Palmer*, 27 May 1936	Northern China & Korea
L. maximowiczii (Rupr.) Maxim.				
*var. *sachalinensis* Fr. Schmidt		36	AA 10102–C (*Wilson 8875*, Korea, 1917), *Dudley*, 4 June 1965, and *Rüdenberg*, 25 May 1966	Saghalin and Korea
	18		AA 598–38–B, *Dudley*, 4 June 1965, and *Rüdenberg*, 25 May 1966	
L. orientalis Lam.		18	AA 201–38–A, *Dudley*, 4 June 1965	Asia Minor to western China
	9		AA 956–34 (*Balls 1656*, Turkey, 1934), *Green*, 2 June 1964	
*var. *longifolia* (Dipp.) Rehd.		18	AA 15102, *Palmer*, 13 June 1940	
Sect. LONICERA (Sect. *Coeloxylosteum* Rehd.)				
Subsect. TATARICAE Rehd.				
L. tatarica L.		18	AA 288–41–A, *Green*, 31 May 1965	Eastern Europe to Turkestan
	9		AA 69–64, *Rüdenberg*, 10 May 1968	

TABLE. **Additional chromosome numbers in Lonicera** (*Continued*)

SPECIES	*n*	*2n*	DOCUMENTATION AND COLLECTOR	DISTRIBUTION GENERAL
L. × *muendeniensis* Rehd.	9		AA 1314–62, *Rüdenberg*, 10 May 1968	Cultivation
	9		AA 793–64, *Rüdenberg*, 10 May 1968	
		18	AA 1193–65, *Rüdenberg*, 10 May 1968	
f. *xanthocarpa* Hort.		18	AA 188–36–A, *Kreps*, 25 May 1964	
L. xylosteum L.	9		AA 765–34, *Rüdenberg*, 26 May 1966	Europe to Altai Mts.
	9		AA 358–62, *Gibson*, 17 May 1968	
*f. *mollis* (Regel) Rehd.	9		AA 66–37, *Kreps*, 26 May 1964	
*cv. Nana	9		AA 626–62, *Rüdenberg*, 16 May 1968	
L. chrysantha Turcz.	9		AA 1044–37–A, *Green*, 31 May 1965	Northeast Asia and Japan
f. *regeliana* (Kirchn.) Rehd.	9		AA 587–54, *Green*, 20 May 1965	
**L.* × *pseudo-chrysantha* Braun ex Rehd.	9		AA 686–54, *Rüdenberg*, 18 May 1966	Cultivation
L. koehneana Rehd.	9		AA 632–64, *Rüdenberg*, 10 May 1968	Western China

L. maackii (Rupr.) Maxim.	9	18	AA 15109–2, *Palmer*, 13 June & 7 Oct. 1940, and *Flint*, 19 Sept. 1966	Manchuria and China
f. *podocarpa* Franch. ex Rehd.		18	AA 7190–B (*Wilson 194*, W. Hupeh, 1907), *Dodd*, 28 June 1965, and *Flint*, 19 Sept. 1966	China
		18	AA 12319 (*Hers 1358*, China, 1919), *Palmer*, 27 May & 9 Sept. 1936, and *Flint*, 19 Sept. 1966	
		18	AA 15050–B (*Wilson 194bis*, W. Hupeh, 1907), *Palmer*, 24 Sept. 1936, and *Dudley & Dodd*, 28 June 1965, and *Flint*, 19 Sept. 1966	
		18	AA 23153–A, *Dudley & Dodd* 28 June 1965, and *Flint* 19 Sept. 1966	
L. quinquelocularis Hardw.				
f. *translucens* (Carr.) Zabel		18	AA 213–59–A, *Green*, 21 June 1965	Afghanistan to the Himalaya
		18	AA 213–59–B, *Appenzeller*, 9 June 1966	
		Sect. NINTOOA (Sweet) Maxim.		
Subsect. LONGIFLORAE Rehd.				
L. japonica Thunb.				
*var. *halliana* (Dippel) Nicholson		18	AA 953–1, *Sargent*, 12 July 1884	Eastern Asia

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* This is the first publication of a documented count for this taxon.

TABLE. **Additional chromosome numbers in Lonicera** (*Continued*)

SPECIES	*n*	2*n*	DOCUMENTATION AND COLLECTOR	GENERAL DISTRIBUTION
*var. *repens* (Sieb.) Rehd.	9	18	AA 897–49, *Appenzeller*, 20 June 1966	
*cv. Aureo-Reticulata		18	AA 1445–63, *Fordham*, July 1965	
Subgenus CAPRIFOLIUM (Adans.) Dippel (Subgen. *Periclymenum* (Mill.) Rehd.)				
Subsect. CYPHEOLAE (Raf.) Rehd.				
**L. glaucescens* Rydberg	9	18	AA 1031–52–A, *Appenzeller*, 9 June 1966	Northeastern North America
Subsect. EUCAPRIFOLIA (Spach) Rehd.				
**L. caprifolium* L.	9		AA 699–62, *Dudley*, 10 July 1965	Europe and western Asia
**L.* × *heckrottii* Hort. ex Rehd.		ca. 45	AA 113–49–A, *Rüdenberg*, 8 June 1966, and *Gibson*, 14 June 1968	Cultivation

* This is the first publication of a documented count for this taxon.

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EXPLANATION OF PLATES

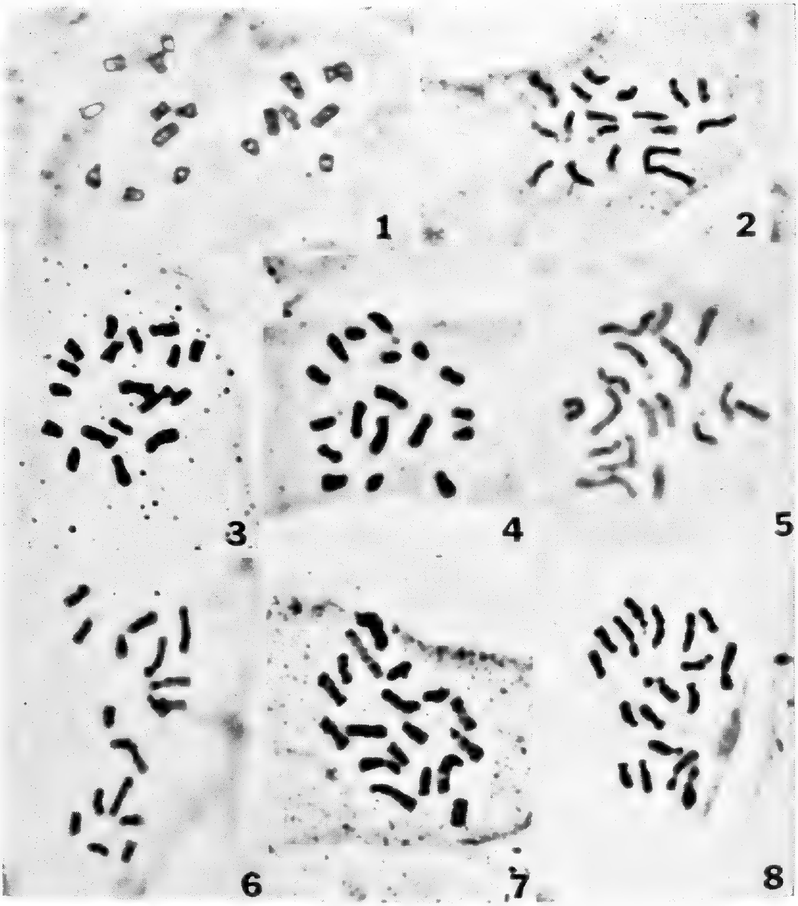
FIGURES 1–10. Mitotic divisions in species of *Lonicera*. All photomicrographs (× ca. 1800) show cells at metaphase with the exception of FIG. 9, which is at late prophase.

PLATE I

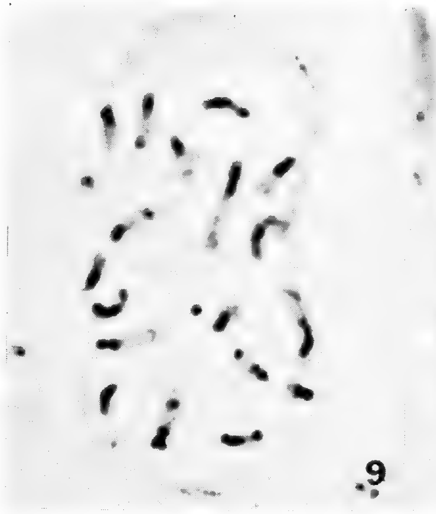
FIG. 1, *L. altmannii* var. *pilosiuscula* (AA 14999); FIG. 2, *L. involucrata* (AA 16–44); FIG. 3, *L. modesta* (AA 24–36); FIG. 4, *L. morrowii* (AA 1283–65); FIG. 5, *L.* × *bella* (AA 48–42–B); FIG. 6, *L. chrysantha* (AA 1044–37–A); FIG. 7, *L. japonica* cv. Aureo-Reticulata (AA 1445–63); FIG. 8, *L. etrusca* (AA 231–46).

PLATE II

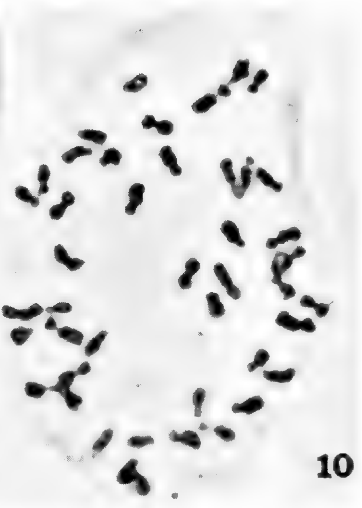
FIG. 9, *L. etrusca* (AA 231–46), note differentially stained chromosome segments at end of prophase. FIG. 10, *L.* × *heckrottii* (AA 113–49–A), ca. pentaploid.



RÜDENBERG & GREEN, LONICERA, II



9



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RÜDENBERG & GREEN, LONICERA, II

NOTES ON WEST INDIAN ORCHIDS, I

LESLIE A. GARAY

DURING THE COURSE of routine identifications of collections from various parts of the West Indies, several new species as well as a number of nomenclatorial changes have been noted. A study of the flora of the West Indies is currently under way by Dr. Richard A. Howard of Harvard University, which will document both the distribution and diversity of all orchid species known in that floristic region. In the mean time, notes, similar to this one, will be published seriatim.

Habenaria Dussii Cogn. in Urb. Symb. Antill. **6**: 307. 1909.

There is a flower from the holotype of *H. Dussii* Cogn. given by Professor Cogniaux to the collections of the Orchid Herbarium of Oakes Ames. Since then the type specimen has been destroyed in Berlin during World War II. This single flower enabled me to identify the following two collections reported for the first time outside the island of Guadeloupe.

Puerto Rico: Sierra de Luquillo, open grass-sedge savannah, wet, in cloud forest along El Toro trail, south side of El Yunque, *R. A. Howard & G. Taylor 18701* (AMES).

St. Vincent: St. David Parish, Soufrière Mountain, in tundra-like growth at elevation of 2800 ft. Entire plant green, *G. R. Cooley 8446* (AMES).

Cryptophoranthus erosus Garay, sp. nov. FIG. 1a–d.

Epiphytica, caespitosa, usque ad 3 cm. alta; radicibus crassiusculis, elongatis, satis profusis, flexuosis, glabris; caulibus secundariis erectis, abbreviatis, vaginis infundibuliformibus obtectis, usque ad 5 mm. longis; foliis oblongo-lanceolatis, carnosis, acutis, basin versus sensim in petiolo 1–2 mm. longo attenuatis, margine erosis, usque ad 2.5 cm. longis, 5 mm. latis; inflorescentiis abbreviatis, sessilibus, unifloris; bracteis ovato-cucullatis, dorsaliter carinatis, 4 mm. longis; floribus satis magnis, carnosulis, atropurpureis; sepalo postico spathulato-rhombeo, valde concavo, 3-nervio, dorsaliter apicem versus carinato mucronatoque, 14 mm. longo, 6.5 mm. lato; sepalis lateralibus usque ad apicem in synsepalo conniventibus, valde concavis, dorsaliter carinatis, acutis, 15 mm. longis, inter se 6 mm. latis; petalis carnosis, subfalcato-lanceolatis, acuminatis, uninerviis, 4 mm. longis, 1 mm. latis; labello breviter angusteque unguiculato, deinde suborbiculari expanso, margine valde eroso; disco utrinque carnoso carinato in medio, antice pectinato, 4.5 mm. longo, 3 mm. lato;

columna clavata, late alata, clinandrio lacero; ovario cylindrico, verrucoso, 2 mm. longo.

Dominican Republic: in the vicinity of Constanza. Flowers deep purple. Collected by Rev. Donald Dod and cultivated by him for Bro. *Alain H. Liogier 13508* (NY, type!).

This new species vegetatively resembles *C. sarcophyllus* (Rchb.f.) Schltr. from Venezuela, but the latter has broader, entire leaves, as well as dissimilar petals and lip.

Pleurothallis Dodii Garay, nom. nov.

Basionym: *Pleurothallis cryptantha* Cogn. in Urb. Symb. Antill. **7**: 176. 1912, not Barb. Rodr. 1877.

A recent collection by *Rev. D. Dod*, s.n. (NY), of this rare species in the **Dominican Republic**: Las Abejas, Cabo Rojo, has shown that the disc of the lip is covered with fine, but sparsely distributed, hairs as are the margins. This character, although not mentioned in the original description by Cogniaux, is present on the holotype which I have recently examined in Bruxelles.

Lepanthopsis Dodii Garay, sp. nov. FIG. 2e–f.

Epiphytica, caespitosa, usque ad 8 cm. alta; radicibus filiformibus, flexuosis, glabris; caulibus secundariis erectis, gracilibus, vaginis satis distantibus, adpressis, sursum dilatatis hispidulisque omnino obtectis, usque ad 4 cm. longis; foliis tenuibus, ellipticis, acutis vel obtusiusculis, margine muricato-denticulatis, usque ad 2 cm. longis, 6 mm. latis; inflorescentiis capillaribus, subdense multifloris, usque ad 4 cm. longis; bracteis infundibuliformibus, acuminatis, 1 mm. longis; floribus tenuibus, diaphanis, patentibus, glabris; sepalo postico ovato-lanceolato, acuminato, uninervio, 2 mm. longo, 1 mm. lato; sepalis lateralibus inter se usque ad medium connatis, ovato-lanceolatis, acuminatis, uninervis, 2 mm. longis, inter se 1.5 mm. latis; petalis ellipticis vel subrhombeis, acutis vel obtusis, 1 mm. longis, 0.5 mm. latis; labello carnoso, triangulari-cordato, 3-nervio, 1 mm. longo latoque; columna humili, crassa, apoda; ovario pedicellato 2 mm. longo.

Dominican Republic: Polo, epiphytic on trees, *Rev. D. Dod 43* (AMES, type!).

Lepanthopsis Dodii Garay differs from *L. acuminata* Ames in having smaller flowers, proportionately shorter and broader sepals, and differently shaped petals.

Since my revision of the genus in The Orchid Journal **2**: 467–469. 1953, I have examined the types of all West Indian *Pleurothallis* species. Among these species the following need to be transferred to the genus ***Lepanthopsis.***

Lepanthopsis barahonensis (Cogn.) Garay, comb. nov.

Basionym: *Pleurothallis barahonensis* Cogn. in Urb. Symb. Antill. **7**: 177. 1912.

Lepanthopsis blepharophylla (Griseb.) Garay, comb. nov.

Basionym: *Pleurothallis blepharophylla* Griseb. Cat. Pl. Cub. 260. 1866.

Lepanthopsis dentifera (L. O. Wms.) Garay, comb. nov.

Basionym: *Pleurothallis dentifera* L. O. Wms. in Ceiba **1**: 227. 1951.

Lepanthopsis Fuertesii (Cogn.) Garay, comb. nov.

Basionym: *Pleurothallis Fuertesii* Cogn. in Urb. Symb. Antill. **7**: 178. 1912.

Brachionidium ciliolatum Garay, sp. nov. FIG. 3g–j.

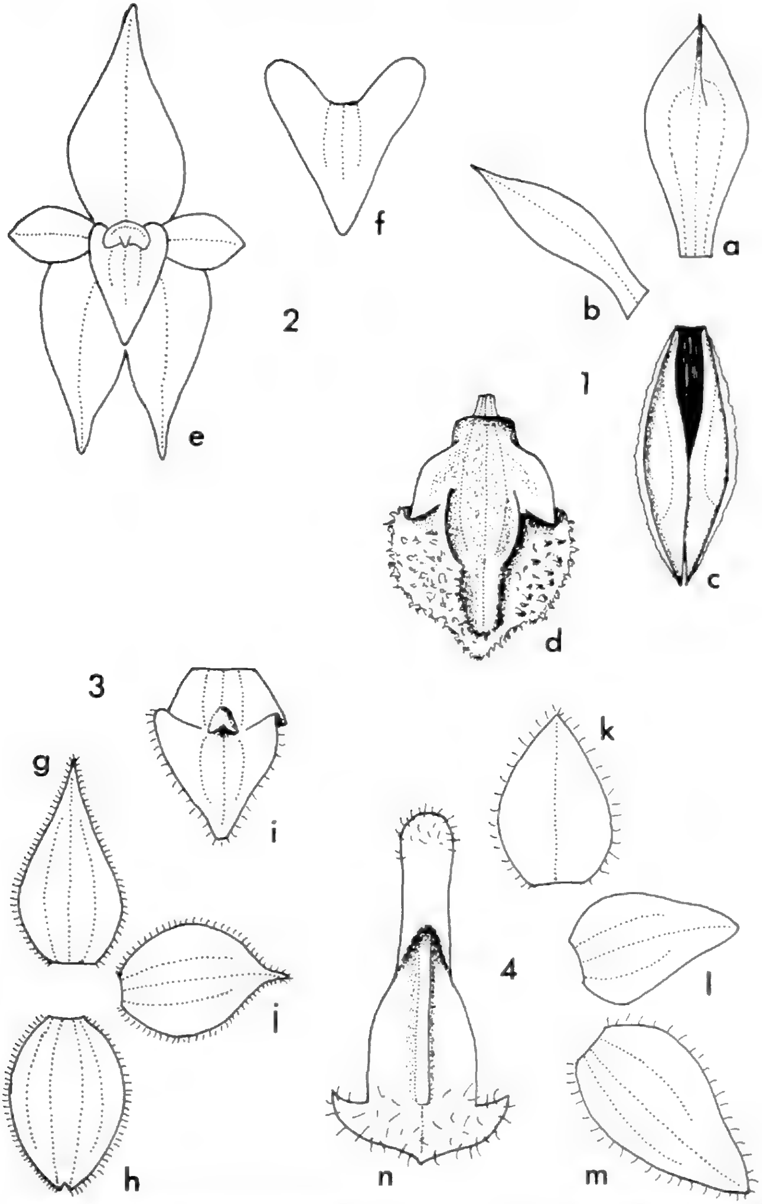
Epiphytica, parvula, ascendenti, usque ad 7 cm. alta; radicibus filiformibus, glabris; rhizomate ascendenti, cauliformi, vaginis scariosis, infundibuliformibus imbricantibusque omnino obtecto; caulibus secundariis vix ullis, monophyllis; foliis pergameneis, oblongo-ellipticis, acutis, subpetiolatis, usque ad 2 cm. longis, 5 mm. latis; inflorescentiis singulis, unifloris; pedunculo capillari, in medio univaginato, usque ad 3 cm. longo; bracteis infundibuliformibus, ovariis pedicellatis aequilongis; floribus pro genere satis parvulis, ciliolatis; sepalo postico ovato-lanceolato, subacuminato, 3-nervato, margine ciliolato, 7 mm. longo, 4 mm. lato; sepalis lateralibus usque ad apicem connatis, ibi bidentatis, ellipticis, obtusis, 4-nervatis, margine ciliolatis, 6 mm. longis, 4 mm. latis; petalis ellipticis, apice subito in apiculo triangulari-subfalcato, acuminato productis, 3-nervatis, margine ciliolatis, 6 mm. longis, 4 mm. latis; labello carnoso, e cuneata basi subsigmoideo, antice triangulari, acuto, 3-nervato, margine valde ciliolato; disco callo pulvinari, antice exciso ornato; toto labello 3 mm. longo, 2.5 mm. lato; columna humili, crassa, vix 1 mm. alta; ovario pedicellato ca. 2 mm. longo.

Puerto Rico: Pico del Oeste, Sierra de Luquillo, 1020 m. alt. Epiphytic orchid, plants with 3–4 leaves; flowers yellow-green, apparently do not open. Study trail area. *R. A. Howard & L. I. Nevling 16929* (AMES, type!).

This new species closely resembles *B. parvum* Cogn. both in size and in general appearance. It differs, however, in the shape of the floral segments which are not caudate. Both *B. tetrapetalum* (Lehm. & Krzl.) Schltr., and *B. simplex* Garay, although similar in appearance to *B. ciliolatum* Garay, have dissimilar and eciliate lips.

Epidendrum isochilum var. **tridens** Rchb. f. in Ber. Deutsch. Bot. Ges. **3**: 277. 1885.

Syn.: *Epidendrum belvederense* Fawc. & Rendle in Jour. Bot. **47**: 123. 1909.



FIGURES 1–4, West Indian orchids. FIG. 1, a–d, *Cryptophoranthus erosus* Garay; FIG. 2, e–f, *Lepanthopsis Dodii* Garay; FIG. 3, g–j, *Brachionidium ciliolatum* Garay; FIG. 4, k–n, *Campylocentrum constanzense* Garay. All figures greatly magnified.

There appears to be no distinction between *Epidendrum belvederense* Fawc. & Rendle and *E. isochilum* var. *tridens* Rchb. f. as a study of the holotypes indicates. Judging from the number of specimens which I have examined of this species from the Dominican Republic, this variety seems to be much more common than the typical variety, which is described as having an entire lip.

Epidendrum neoporpax Ames in Bot. Mus. Leafl. Harvard Univ. **2**: 112. 1934.

Basionym: *Epidendrum Porpax* Rchb. f. in Flora **48**: 278. 1865 not Rchb. f. 1855.

Syn: *Epidendrum vestitum* Ames in Sched. Orch. **4**: 51. 1923.
Epidendrum Porpax var. *domingensis* Cogn. in Urb. Symb. Antill. **7**: 181. 1912.

This rather rare Cuban species has been found recently in Costa Rica, and rediscovered by Mr. *Ariza Julia*, s.n., in the **Dominican Republic**: Sabaneta de Yasica, Puerto Plata Province. An examination of the type of *Epidendrum Porpax* var. *domingensis* Cogn. in the Bruxelles herbarium convinces me that it is identical with *E. neoporpax* Ames.

Epidendrum Sintenisii Rchb. f. in Ber. Deutsch. Bot. Ges. **3**: 277. 1885.

Syn.: *Epidendrum monticolum* Fawc. & Rendle in Jour. Bot. **47**: 124. 1909.

Recently I had the opportunity to examine and to compare the holotypes of *E. Sintenisii* Rchb. f. and *E. monticolum* Fawc. & Rendle. As a result of this study, I am convinced that they are conspecific. *Epidendrum Sintenisii* is now recorded from Puerto Rico and Jamaica.

Stellilabium minutiflorum (Krzl.) Garay, comb. nov.

Basionym: *Telipogon minutiflorus* Krzl. in Ann. Nat. Hist. Mus. Wien **33**: 14. 1919.

Syn.: *Telipogon Lankesteri* Ames Sched. Orch. 3: 23. 1923.
Stellilabium Helleri L. O. Wms. in Brittonia **14**: 443. 1962.

This rather rare Costa Rican species has recently been found in the **Dominican Republic**: Casalito Bonao by *Rev. D. Dod*, s.n. (NY). This is also a new record for the West Indies. *Stellilabium Helleri* L. O. Wms., of which I also have studied the holotype, agrees in every respect with Kraenzlin's type material which I examined in Vienna. *Telipogon Lankesteri* Ames likewise, does not offer any criterion by which it could be kept separate from *S. minutiflorum* (Krzl.) Garay.

Polyradicion Garay, gen. nov.

Pfitzer in describing the genus *Polyrrhiza* stated that it consists of four West Indian species. Of these four he mentioned only one in making an official transfer, namely *P. funalis* (Sw.) Pfitz. Thus, the genus *Polyrrhiza* is typified by this species. In *Flora of Jamaica,* Fawcett and Rendle regard *P. funalis* (Sw.) Pfitz. to be a synonym of *Dendrophylax funalis* (Sw.) Benth., a judgment which I consider to be correct. Since *Polyrrhiza* automatically becomes a synonym of *Dendrophylax* through this transfer, it leaves the other species without a validly published generic name. Since there are only two species involved I reject the idea of conservation in favor of a new name which I propose here with the same etymological meaning as was used by Pfitzer. The genus is, thus, characterized as follows:

Sepala petalaque simillima, aperta, lanceolata; labellum maximum, 3-lobum, lobi laterales quam lobum intermedium multoties breviores, basi in calcari valde evolutum producta; columna humilis, crassa, apoda, basi labellum adnata; clinandrium humile; anthera incumbens, opercularis; pollinia 2, stipiti nudi, distincti glandulae affixa.

Plantae epiphyticae, aphyllae; radices crassae, valde evolutae; caules vix ulli; pedunculi laterales, graciles, arcuati, abbreviati, semper uniflori; flores majusculae.

Species 2, Indiae Occidentalis incolae.

Typus: *Angraecum Lindenii* Lindl.

Polyradicion Lindenii (Lindl.) Garay, comb. nov.

Basionym: *Angraecum Lindenii* Lindl. in Gard. Chron. 135. 1846.
Syn.: *Aeranthus Lindenii* Rchb. f. in Walp. Ann. Bot. Syst. **6**: 902. 1864.
Dendrophylax Lindenii Benth. ex Rolfe in Gard. Chron. ser. 3. **4**: 533. 1888.
Polyrrhiza Lindenii Cogn. in Urb. Symb. Antill. **6**: 680. 1910.

Distribution: Florida, Cuba.

Polyradicion Sallei (Rchb. f.) Garay, comb. nov.

Basionym: *Aeranthus Sallei* Rchb. f. in Walp. Ann. Bot. Syst. **6**: 902. 1864.
Syn.: *Dendrophylax Sallei* Benth. ex Rolfe in Gard. Chron. ser. 3. **4**: 533. 1888.
Polyrrhiza Sallei Cogn. in Urb. Symb. Antill. **6**: 680. 1910.

Distribution: Dominican Republic, Haiti.

Dendrophylax gracilis (Cogn.) Garay, comb. nov.

Basionym: *Polyrrhiza gracilis* Cogn. in Urb. Symb. Antill. **6**: 679. 1910.

An examination of the holotype, *Wright 3300,* in the Orchid Herbarium of Oakes Ames has shown clearly that it is referable to the genus *Dendrophylax* Rchb. f. It is closely allied to *D. hymenantha* Rchb. f., differing in its shorter, 1-flowered peduncle and in the size of its flowers which are twice as large. *Dendrophylax hymenantha* Rchb. f., however, has been united with *D. varius* (Gmel.) Urb., but this decision requires further study.

Campylocentrum constanzense Garay, sp. nov. FIG. 4k–n.

Epiphytica, caespitosa, aphylla, usque ad 4 cm. alta; radicibus numerosis fasciculatis, filiformibus, flexuosis, glabris; caulibus nullis vel vix ullis; inflorescentiis numerosis, fasciculatis, erectis, capillaribus, simplicibus vel dichotome ramosis, supra laxe plurifloris, omnino setaceo-hirsutis, usque ad 4 cm. longis; bracteis ovato-cucullatis, acutis vel obtusiusculis, extus setaceo-hirsutis, 1 mm. longis; floribus minimis, hyalinis; sepalo postico ovato, acuto vel obtusiusculo, uninervio, extus sparse setaceo-hirsuto, 1.5 mm. longo, 1 mm. lato; sepalis lateralibus oblique ovatis, obtusiusculis, extus setaceo-hirsutis, 3-nerviis, 2 mm. longis, 1 mm. latis; petalis subfalcato-ovatis, obtusiusculis, 3-nerviis, glabris, 1.5 mm. longis, 1 mm. latis; labello anchoriformi-lobato, antice breviter apiculato, basi calcarato, calcari cylindrico obtuso, setaceo-hirsuto; disco in medio longitudinaliter carinato, antice setaceo-hirsuto; toto labello 3 mm. longo, antice 1.5 mm. lato; columna humili, crassa, vix 1 mm. alta; ovario cylindrico, muricato-hispidulo, cum pedicello 2 mm. longo.

Dominican Republic: Constanza, epiphytic on trees, *Rev. D. Dod 66* (AMES, type!).

This species is quite unique in the Section DENDROPHYLOPSIS Cogn. because of the anchor-shaped lip and a distichously branching, setaceous inflorescence.

BOTANICAL MUSEUM
HARVARD UNIVERSITY

POLLEN CHARACTERISTICS OF AFRICAN SPECIES OF VERNONIA

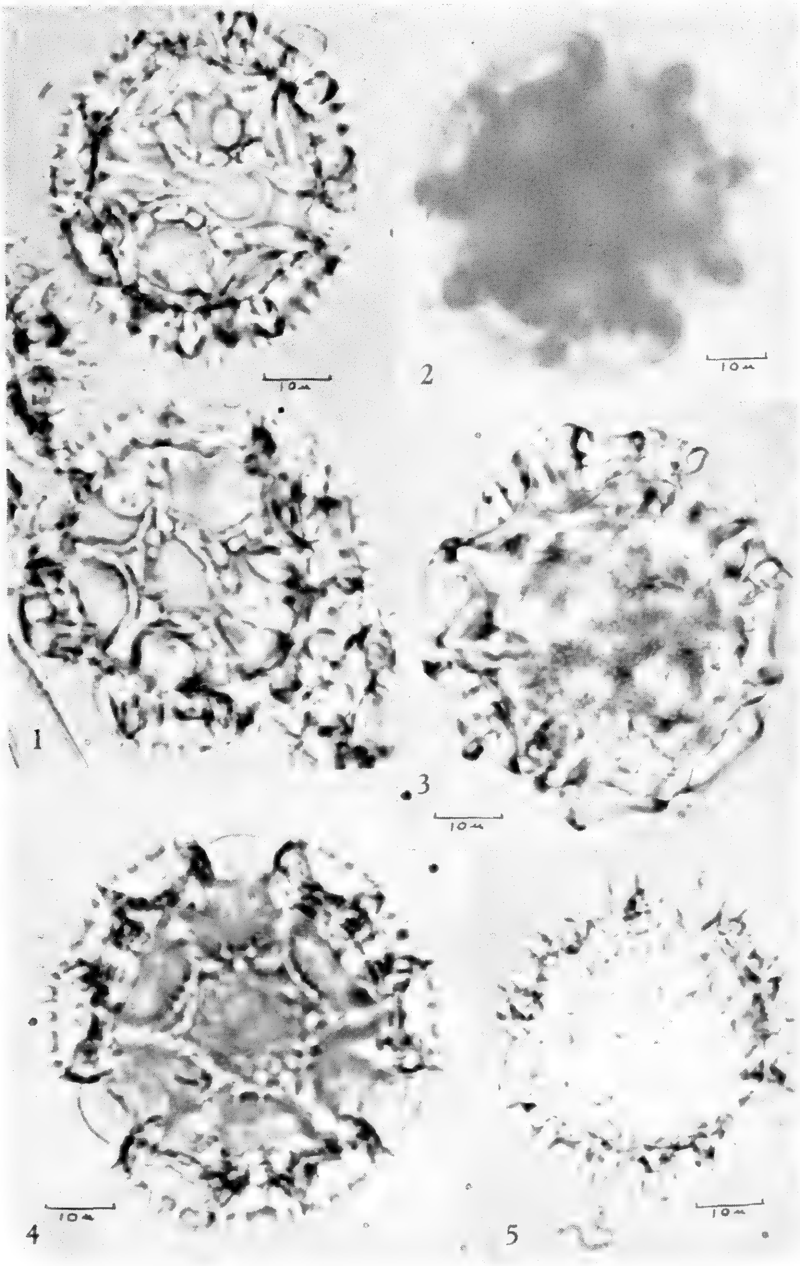
C. EARLE SMITH, JR.

DURING A TAXONOMIC STUDY of the species of section STENGELIA of the Composite genus, *Vernonia*, pollen of a number of species was examined. Whenever possible, a floret from a specimen of the type collection was dissected and the anthers macerated in lacto-phenol and methylene blue. A single grain from each slide was photographed. Size was determined by measurements of ten grains from each slide, after scanning to ascertain whether the grains measured fell into more than one size class. Measurements were made to the outside of the reticula, but did not include the length of spines.

Obviously, not all of the specimens examined belong to section STENGELIA, although all of the species have been assigned here because of thin terminal appendages on otherwise firm or chartaceous phyllaries. Perhaps a future student of the genus will find corollary characters on which the sections of the genus can be more firmly based. The large number of species involved in Africa alone precludes this in my short-term examination of the section STENGELIA.

Pollen sizes range from an average of 29.1 μ for *Vernonia praecox* Welw. ex O. Hoffm. to 69.5 μ for grains of *V. wittei* Hutch. & Burtt (FIG. 6). The average pollen diameter is 51.9 μ. The largest number of species with a similar pollen size fall into the next highest size class, 53.3 μ. A total of seven species have an average pollen size of 51.7 μ. Twenty-six species fall into larger pollen-size classes and 24 species fall into smaller pollen-size classes than the 15 species in the median groups. Thus, except for the few plants having either very large pollen grains or very small pollen grains in relation to the average pollen size for this group of species, the species are well clustered with the greatest number falling centrally.

No attempt was made to study the anatomy of the pollen grains of this group. Morphologically, all of the grains examined are similar. All are nearly spherical and are evidently tricolporate, although this sometimes is difficult to determine (FIG. 4). In all of the pollen examined, the outside of the grain is marked by a raised reticulum. This may be thin, but in the majority of the species the surface reticulum is moderately to heavily thickened. Often, the pattern of the reticulum is very regular with polar alveoli surrounded by a ring from which radiate, at regular intervals, a series of bars. These are crossed on the sides of the grains at regular intervals by bars of equal size. On one side of the grain a longitudinal alveolus extends from pole to pole and one of the pores occurs in this at the equator (FIG. 1). Frequently, the polar rings are



FIGURES 1–5. pollen grains of *Vernonia* species. FIG. 1. *Vernonia guineensis* var. *cameroonica*, average pollen diameter 51.7μ; the lower grain, in polar view, shows the regularity of the reticulation common to many of the upright or shrub-

broken by this longitudinal opening so that if flattened, the total open area would resemble a dumbbell. On the sides of the grain, the alveoli do not appear to be geometrically balanced in any of the species. Where the reticulation follows a similar pattern in all of the grains examined, I have called it regular in spite of a lack of an exact geometric pattern. In many species, polar areas may be defined or not, but the reticulation over the remainder of the surface of the pollen grain appears to be randomly placed (FIG. 5). I have called this type of reticulation irregular.

In most of the species, the reticulation is further decorated by spines arising from the top and sides. The spines all appear to be simple conical protuberances of the same material from which the reticulum is formed. *V. albo-violacea* De Wild. has almost no spines on the reticulum. The spines on pollen grains of other species vary from small to large, but they are uniform in size for a species. Only *V. bojeri* Less., *V. gerberiformis* Oliver & Hiern, *V. mandrarensis* Humbert, and *V. prolixa* S. Moore lack spines completely.

The reticulation of *V. gerberiformis* is unusual among the species examined. The reticulation is relatively narrow and produced upward from the surface of the grain in a wing-like projection (FIG. 3). I shall make no attempt to formulate an adaptive advantage for this deviation from the usual pattern among the *Vernonia* pollen grains studied. With an average pollen diameter of 66.3 μ (measured at the outside of the reticulum), this is the second largest grain examined.

The surface of the pollen grains was examined under oil immersion (485 ×) in order to study the surface details. In none of the grains was a regular pattern or design seen. Some of the reticula and pollen surfaces are not smooth. The roughness is not readily discernible and does not appear to be produced in a regular pattern. However, the reticulation on some of the species (for example, *V. adoensis* Sch.-Bip. ex Walp., *V. gerberiformis*) is not completely contiguous with the surface of the pollen grain. When the reticulum is heavy, it frequently stands above the grain surface on a series of pedestals which may be relatively far apart or rather close together (FIG. 2). The presence of the pedestals negates the possibility that this is an artifact created when the surface of the grain shrinks away from the reticulum. In the pollen grains of other species with an equally heavy reticulum, the elevation of the reticulation above the surface does not seem to be present.

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by species; the upper grain shows the elongate alveolus connecting the poles; note the pore at the equator. FIG. 2, *Vernonia adoensis* (oil immersion). note the spaces between the reticulum and the pollen grain surface on the upper left quarter. FIG. 3, *Vernonia gerberiformis*, average pollen diameter 66.3μ; the wing-like extension of the reticulum has been observed only in this species. FIG. 4, *Vernonia adoensis*, average pollen diameter 59.8μ; note the three pores in the median section. FIG. 5, *Vernonia castellana*, average pollen diameter 48.5μ; this shows the thin, irregular reticulum common to several species with a basal rosette of leaves.

On the basis of the gross morphological characteristics of specimens and on a detailed study of the achenes and flowers, the species have been grouped into clusters which show similarities. Pollen grain data have been regrouped (TABLE 1) on this basis (excluding species which apparently do not belong to section STENGELIA). In general, the characteristics of the pollen grains seem to support the groupings by overall morphology. For instance, the first group of three species, *V. lasiopus* O. Hoffm. in Engl., *V. brownii* S. Moore, and *V. albo-violacea*, varies relatively little in average pollen grain diameter; the grains have reticula of medium thickness with short or nearly absent spines.

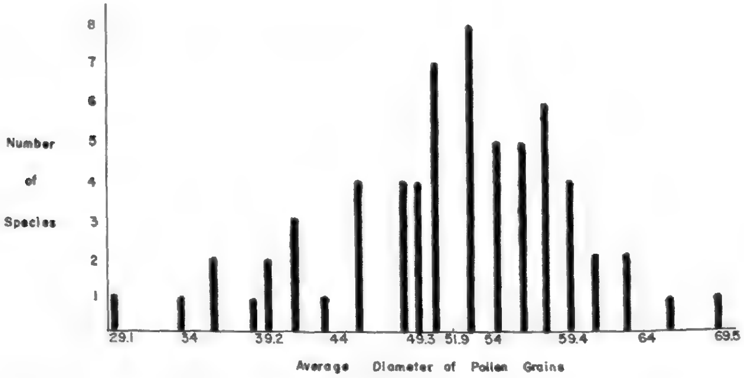

FIGURE 6. Graph illustrating the number of species of *Vernonia*, section STENGELIA, with pollen falling into each size class. Note that pollen size for most of the species falls near the median, 51.9μ.

The second group of species, *V. polyura* O. Hoffm., *V. filigera* Oliver & Hiern, *V. longipetiolata* Muschler, and *V. oxyura* O. Hoffm. in Engl., again agree well in pollen characteristics as well as in overall morphology, except for grain size in one species. The pollen grain size of three of the species ranges from an average diameter of 40.4 μ to 46.9 μ. The average pollen grain size of grains of *V. filigera* is 56.6 μ. It is hardly desirable to exclude the species from this grouping on this one feature alone, but it does necessitate another careful look at the specimens to be included here.

The break in size observed in the example cited above is perhaps better illustrated in the group of species clustered around the type species of the section, *V. adoensis* Sch.-Bip. ex Walp. On the basis of their gross morphology, these species fall readily into a group. An examination of the details of the achenes and flowers discloses no major discrepancy in the pattern. For the most part, the morphology of the pollen grains of these species supports the grouping. Average pollen diameters for most species of the group range between 56.6 μ and 63.0 μ. However, the average pollen grain diameters of *V. shirensis* Oliver & Hiern and *V. woodii* O. Hoffm. (which are now considered synonymous) are 46.9 μ.

The species of section STENGELIA fall into two distinct groups on the basis of plant habit. The bulk of the species are rank-growing upright sub-shrubs from a perennial base, or upright shrubby plants. A few may become tree-like. The pollen of many of these species has an average diameter of 50.1 μ or more, except for the species grouped around *V. polyura*. The reticulum on the grains is generally heavy.

The other group of species is distinguished by a rosette habit with flowers borne on a, usually, leafless scape. The scape may be unbranched and support a single head or it may support several heads. Many of the average pollen grain diameters for this group are less than 50 μ. The reticulation on the grains is often thin and very irregular. However, more exceptions occur among the species with basal rosettes than among the species with an upright habit. For example, the pollen of *V. gerberiformis*, which was previously described, is very different from the usual pattern of grain size and morphology. The grains of *V. nyassae* Oliv. in Hook., *V. pumila* Kotschy & Peyr. and *V. anandrioides* S. Moore have a heavy, regular reticulum. Furthermore, the grains of the last two have an average diameter of 53.3 μ. The pollen grains of the species with a basal rosette are more variable in size and morphology than are the pollen grains of the other species assigned to section STENGELIA.

In only three of the species examined, pollen grains of two size classes occurred. Both *V. calvoana* (Hook. f.) Hook. f. and *V. insignis* (Hook. f.) Oliver & Hiern have pollen grains similar in size and morphology. In both, the larger grains appeared to be normal. The smaller pollen grains appear to have been aborted. Because they were removed from herbarium specimens, it was impossible to apply germination tests for viability of the grains to confirm my assumption that the smaller grains are not functional. About half the pollen grains of *V. achyrocephaloides* Hutch. & Bruce were also smaller than the grains measured, and appeared to be nonfunctional. So little is yet known about the biology and genetics of species of section STENGELIA that I can make no assumptions as to the cause of the difference in pollen grain sizes. It is, perhaps, significant that all of the species have average pollen diameters near the upper limit of pollen size for this group of 64 species.

SUMMARY

A total of 64 species of *Vernonia*, purportedly belonging to section STENGELIA, were examined for pollen size and shape. Preparations from anthers, from herbarium specimens, macerated in lacto-phenol and methylene blue were examined and ten pollen grains from each slide were measured. Grouping in size from the smallest to the largest observed indicates that the largest number of species fall close to the average pollen diameter of 51.9 μ. Homogeneity is further emphasized by the reticulation, usually spiny, which covers the outer surface of all of the grains seen. When the species are regrouped on the basis of their gross morphological characteristics and detailed observations on

achenes and floral morphology, pollen morphology and average pollen diameter confirms the groupings for the most part.

The species traditionally included in section STENGELIA can be divided into a group with basal rosettes and heads borne on scapes versus a group of upright sub-shrubs or shrubs (rarely tree-like) with heads on the sides or ends of branches. In general the first group has smaller pollen grains with thin, irregular reticula. The second group generally has larger pollen grains with heavy, more regular reticula. The group with basal rosettes is less homogeneous than the other in regard to pollen size and morphology.

In only three species of the 64 examined were pollen grains of two size classes found. In all instances, the smaller grains appeared to be nonfunctional. All three species have pollen diameters in the upper size range. Insufficient knowledge of the biology and genetics of these species precludes an explanation.

TABLE 1. **Comparison of pollen characters with gross morphology of species of Vernonia section Stengelia**

SPECIES	POLLEN SIZE μ	RETICULATION THICKNESS	PATTERN	SPINES LENGTH	DISTRIBUTION	PROVENIENCE
V. albo-violacea	51.7	Medium	Regular	Almost none		*Bequaert 492*, Congo
V. brownii	56.6	"	Irregular	Short	Frequent	*Brown 2656*, Uganda
V. lasiopus	53.3	"	Regular	"	Occasional	*Volkens 444*, Tanzania
V. oxyura	40.4	Thin	±Regular	Medium	Numerous	*Buchanan s.n.*, Malawi
V. longipetiolata	42.0	Medium	Regular	"	Occasional	*Kassner 2746*, Congo
V. polyura	46.9	Thin	Irregular	Large	"	*Goetze 866*, Tanzania
V. filigera	56.6	Medium	"	Medium	Numerous	*Schimper 1530*, Ethiopia
V. nyassae	48.5	Heavy	Regular	Small	Frequent	*Thomson s.n.*, Zambia?
V. swynnertonii	51.7	"	Irregular	Short	±Numerous	*Swynnerton 1908*, Rhodesia
V. gerberiformis	66.3	Winged	"	None		*Schweinfurth 2688*, Sudan?
V. wittei	69.5	Medium	"	Short	Frequent	*de Witte 543*, Congo
V. chthonocephala	35.6	Thin	"	"	"	*Welwitsch 3886*, Angola
V. subaphylla	38.8	"	"	"	Few	*Carson 10*, Zambia
V. praemorsa	40.4	Medium	"	"	Occasional	*Stolz 104*, Malawi
V. agricola	43.6	Thin	"	Medium	Numerous	*Kassner 2136*, Zambia
V. castellana	48.5	"	"	"	"	*Gossweiler 2883*, Angola
V. anandrioides	53.3	Heavy	Regular	Short	Occasional	*Gossweiler 2132*, Angola
V. pumila	53.3	Medium	±Regular	"	Frequent	*Elliot 7037*, Kenya?
V. homilocephala	54.9	±Heavy	Irregular	"	Numerous	*Elliot 7058*, Kenya?
V. longepedunculata	50.1	Heavy	"	Short	Few	*Homblé 881*, Congo
V. pleiotaxoides	51.7	"	"	"	Frequent	*Quarré 2654*, Congo
V. procera	53.3	"	"	"	Numerous	*Chevalier 7899*, Congo?
V. lancibracteata	58.2	"	Regular	"	Frequent	*Eyles 291*, Zambia
V. firma	50.1	Medium	Regular	Short	Frequent	*Schweinfurth 3153*, Sudan?
V. vallicola	58.2	Heavy	"	Medium	"	*Gossweiler 3781*, Angola

TABLE 1. **Comparison of pollen characters with gross morphology of species of Vernonia section Stengelia** (*Continued*)

	POLLEN	RETICULATION		SPINES		
SPECIES	SIZE μ	THICKNESS	PATTERN	LENGTH	DISTRIBUTION	PROVENIENCE
V. braunii	51.7	Heavy	Irregular	Medium	Numerous	*Braun 1979*, Tanzania
V. calvoana var. *microcephala*	53.3	Medium	Regular	Short	Frequent	*Lightbody 26259*, Cameroon
V. iodocalyx	53.3	"	"	Medium	"	*Holst 4327*, Tanzania
V. leucocalyx var. *acuta*	54.9	"	"	Short	"	*Keay & Lightbody 28366*, Cameroon
V. ruwenzoriensis	54.9	"	"	"	Numerous	*Elliot 7673*, Uganda
V. saltuarii	54.9	±Heavy	±Regular	Medium	Frequent	*Swynnerton 827*, Tanzania
V. leucocalyx	58.2	Medium	Irregular	Short	Occasional	*Goetze 928*, Tanzania
V. shirensis	46.9	Heavy	±Regular	Medium	Numerous	*Meller s.n.*, Mozambique
V. woodii	46.9	"	Regular	"	"	*Wood 8155*, South Africa
V. polymorpha var. *ambigua*	56.6	"	±Regular	"	"	*Schimper 817?*, Ethiopia
V. kotschyana	58.2	"	Irregular	"	"	*Kotschy 290*, Ethiopia
V. adoensis	59.8	"	Regular	"	Frequent	*Schimper 318*, Ethiopia
V. buchingeri	59.8	"	"	"	Numerous	*Schimper 386*, Ethiopia
V. polymorpha var. *adoensis*	59.8	"	"	"	"	*Schimper 823*, Ethiopia
V. grantii	63.0	"	Irregular	"	"	*Grant s.n.*, Uganda
V. rothii	48.5	Medium	"	"	"	*Roth 346*, Ethiopia
V. stenostegia	48.5	"	"	"	Occasional	*Robins s.n.*, Nigeria
V. stenolepis	53.3	Heavy	Regular	Short	Numerous	*Johnston s.n.*, Tanzania?
V. hymenolepis	58.2	Medium	Irregular	Medium	"	*Petit s.n.*, Ethiopia
V. calvoana	59.8	Heavy	Regular	Short	Occasional †	*Mann 1238*, Cameroon
V. insignis	61.4	"	"	"	" †	*Mann 1925*, Cameroon
V. polymorpha var. *microcephala*	50.1	Heavy	Regular	Medium	Occasional	*Schimper 581*, Ethiopia
V. tigrensis	51.7	"	"	Short	"	*Schimper 817*, Ethiopia
V. abyssinica	54.9	"	Irregular	"	"	*Schimper 389*, Ethiopia
Species not morphologically compatible with above groups						
V. praecox	29.1	Thin	Irregular	Short	Numerous	*Welwitsch 3330*, Angola
V. mandrarensis	33.9	Heavy	"	None		*Humbert 6724*, Madagascar
V. denudata	35.6	Thin	"	Long	Few	*de Witte 588*, Congo
V. crataegifolia	42.0	Medium	"	Medium	Occasional	*Tyson 1188*, South Africa
V. prolixa	42.0	Heavy	"	None	Occasional	*Elliot 8383*, Uganda?
V. anthelmintica *	46.9	"	Regular	Short	"	*Wight 3868*, India
V. bojeri	50.1	Medium	Irregular	None		*Bojer s.n.*, Madagascar
V. chevalieri	51.7	Heavy	"	Short	Frequent	*Chevalier 5505*, Congo?
V. guineensis var. *cameroonica*	51.7	"	Regular	"	"	*Latilo & Daramola 34467*, Cameroon
V. ulophylla	53.3	"	Irregular	Medium	Numerous	*Welwitsch 3279*, Angola
V. cardiolepis	56.6	"	Regular	"	"	*Welwitsch 3280*, Angola
V. rotundisquama	56.6	"	Irregular	Long	Frequent	*Gossweiler 1228*, Angola
V. incompta	58.2	Medium	"	Medium	Occasional	*Kassner 2261*, Rhodesia
V. hierniana	61.4	Heavy	"	"	Numerous	*Welwitsch 3278*, Angola
V. achyrocephaloides	63.0	Medium	"	Short	Occasional †	*Walter 4*, Zambia

* An Asiatic species all of whose relatives are African.

† Pollen of 2 size classes; largest measured, smallest apparently nonfunctional.

Total — 64 species examined.
Average pollen diameter — 51.9.

NEW CROPS RESEARCH BRANCH
CROPS RESEARCH DIVISION, ARS
U.S. DEPARTMENT OF AGRICULTURE
BELTSVILLE, MARYLAND 20705

A NEW SPECIES OF FICUS FROM SURINAME

GORDON P. DEWOLF, JR.

IN THE PROCESS of revising the genus *Ficus* for the *Flora of Suriname*, three specimens (taken from the same tree) were found which did not seem to match any of the previously known forms of the genus. Further study has convinced me that this tree represents an entity, sufficiently distinct from all others to be considered a species which has not been previously described.

It is perhaps of some interest to note that in the course of twelve years of intermittent study of *Ficus* in tropical America, this is the first time that it has been necessary for me to describe a new species in this group. Other undescribed taxa undoubtedly exist in tropical America — the highlands of Brazil probably harbor a few — but their numbers are unlikely to be large.

Ficus Lanjouwii, sp. nov.

Arbor, ramulis ca. 3–4 mm. diametro, crassis, brunneis, dense pubescentibus; stipulae 6–8 mm. longae, caducae, triangulares, acuminatae, dense adpressi-pubescentes; lamina oblanceolata 2.5–5 cm. lata × 7–14 cm. longa, acuminata, basi ima acuta, nervis lateralibus utrinsecus ca. 10–15, petiolo ad 5–15 mm. longo, adpressi-pubescente; receptacula globosi-pyriformia 8–9 mm. diametro; pedunculi geminati, 1–2 mm. longi, dense pubescentes; involucrum bilobum 1 mm. latum, dense pubescente; ostiolo haud prominente, 1 mm. lato.

Tree. Twigs 3–4 mm. in diameter, densely pubescent with ascending trichomes on new growth. Stipules 6–8 mm. long, acuminate, deltoid, densely appressed pubescent. Lamina 2.5–5 cm. wide × 7–14 cm. long, oblanceolate, apex acuminate, base cuneate; lateral veins 10–15 pairs, departing from the midrib at an angle from 20° to 30°; basal veins 1 pair, departing from the midrib at an angle from 50° to 60°; intercostals very slightly raised. Petiole 5–15 mm. long, 1/13–1/15 the length of the lamina, densely appressed pubescent. Figs 8–9 mm. in diameter ± globose-pyriform, borne in pairs among the leaves; peduncles 1–2 mm. long, densely appressed pubescent; basal bracts semicircular, about 1 mm. across, densely appressed pubescent; ostiole plane with the surface of the fig, about 1 mm. in diameter. Female and gall flowers about 1–1.2 mm. long, with 3 narrowly lanceolate tepals with hyaline margins. Scales present between the flowers.

Leaf structure: cystoliths few on the upper surface, more abundant on the lower surface; sclereids present generally along the veins; lower

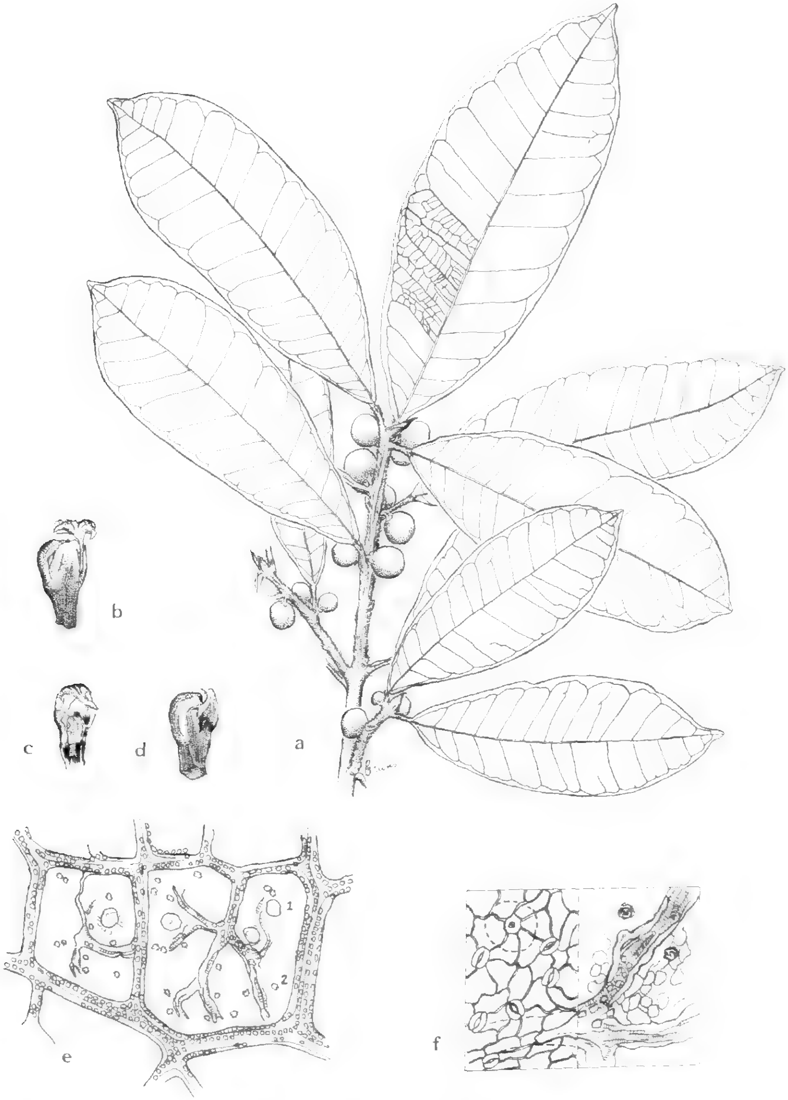

FIGURE 1. *Ficus Lanjouwii.* a, twig, × 1; b, female flower, × 15; c, d, male flower, × 15; e, lower surface of leaf, × 600, without cellular detail, showing tabular crystals of calcium oxalate along the veins, cystoliths (1) and druses of calcium oxalate (2); f, lower surface of leaf, × 600, showing cellular detail, at left, view of epidermis showing stomates and (top) a cystolith; at right, subepidermal view showing sclereids along the veins, tabular crystals of calcium oxalate along the veins, and druses of calcium oxalate (upper center and upper right).

epidermal cells plane; stomates superficial; druses present in the mesophyll cells; tabular crystal cells present.

This species appears to be allied to the widespread *Ficus trigona* L. f. It differs from that species in the greater number of lateral veins in the leaves (10 to 15 pairs *vs.* 3 to 9 pairs) and their lower angle of departure from the midrib; in the orifice of the fig not being surrounded by a raised rib of receptacular tissue; and in having the tepals of the flowers narrowly lanceolate (not hooded).

The species is known from three collections taken from a single tree between 1918 and 1922. I take pleasure in commemorating the name of the Senior Editor of the *Flora of Suriname*, who has been connected with studies of the Moraceae for more than thirty years.

TYPE SPECIMEN: Plantae Surinamenses, communicatae ex Herb. Acad. Rhenotraiect. Hab. Sectie O. Arbor no. 790, Coll. *B.W.*[1] no. *4639*, d. d. 21-iv-1920 (A, holotype; U, isotype).

Additional specimens: data as above, *B.W. 3639* (A, U); *B.W. 5859* (A, U).

[1] B.W. = Collection made by the Forestry Bureau (Boschwezen).

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A REVISION OF THE GENUS FLINDERSIA (RUTACEAE) *

Thomas G. Hartley

The genus *Flindersia* R. Br. is known to occur naturally in the Moluccas (Ceram and Tanimbar Islands), New Guinea, New Caledonia, and eastern Australia south to southcentral New South Wales. It may be distinguished from other known genera of the Rutaceae in that area by the fruit, which is a 5-carpellate, septicidal capsule with two to six winged seeds per carpel. The genera *Coombea* and *Tetractomia*, both of which occur in New Guinea, also have winged seeds but the fruits tend to be subapocarpous and are 4-carpellate. Also, the endocarp detaches in the mature fruits of these two genera and does not in *Flindersia*. The monotypic genus *Chloroxylon*, of southern India and Ceylon, is apparently more closely related to *Flindersia* than any other genus of the Rutaceae. It differs markedly, however, having two whorls of five stamens each, a pulvinate disc, and a 3-carpellate, loculicidal capsule. It is similar to *Flindersia* in having winged seeds and an embryo that is much like that of *F. fournieri*, *F. laevicarpa* and *F. brayleyana*.

The basically New Guinean-New Caledonian-eastern Australian distribution of *Flindersia* is not unusual and quite closely parallels the distributions of *Bubbia* (Winteraceae), *Stenocarpus* (Proteaceae), *Geijera* (Rutaceae), *Halfordia* (Rutaceae) and *Sphenostemon* (Aquifoliaceae). The distribution of *Geijera* is especially similar in that it, too, extends into the drier country of Queensland and New South Wales.

The family affinity of *Flindersia* has long been in question. It was initially placed in the "Natural Order" Cedreleae, apparently because of the resemblance of its fruits to those of *Cedrela* and *Toona*. Several authors, including DeCandolle (1878), Bentham and Mueller (1863) and Bailey (1899) have essentially followed this classification, placing *Flindersia* in the Meliaceae, tribe Cedreleae. The leaves, cotyledons and perianth of *Flindersia* are often pellucid-dotted, however, and it was on this basis that Engler (1896 and 1931) placed it, along with *Chloroxylon*, in the Rutaceae, subfamily Flindersioideae. White (1921) and Francis (1929 and 1951) have also placed it in the Rutaceae. Erdtman (1952, p. 388) stated

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* This is the third of a series of studies on the Rutaceae of Malesia.

that the structure of the pollen of *Chloroxylon* favors its assignment to the Rutaceae rather than to the Meliaceae and he also placed *Flindersia* in the Rutaceae. The wood anatomy, although closer to the Rutaceae, is apparently somewhat intermediate between that family and the Meliaceae. On this basis White (quoted by Record in Welsh, 1931), Harrar (1937), and Dadswell (cited in Metcalfe & Chalk, 1950, p. 314) have suggested placement in a separate family.

The family Flindersiaceae, including *Flindersia* and *Chloroxylon*, was published by Airy-Shaw (1965). His basis for the creation of the new family was that the two genera are more or less intermediate between the Rutaceae and the Meliaceae. With regard to *Flindersia*, he states ". . . occupies an almost exactly midway position between the two large families Rutaceae and Meliaceae, agreeing with the former especially in the possession of pellucid oil-glands in the leaves, and with the latter in the structure of the capsule."

I have not found any definite evidence that the structure of the capsule of *Flindersia* or *Chloroxylon* indicates a relationship to the Meliaceae. There is clearly no close relationship to *Toona* or *Cedrela*, the capsules of which are a rather highly derived syncarpous type with a large, persistent central axis that is lacking in both *Flindersia* and *Chloroxylon*.

There may be significant similarities between *Chloroxylon* and the meliaceous genera *Cedrelopsis* and *Ptaeroxylon*, but they are not strong and more comparative studies will be needed in order to assess their significance, if any. Both of these genera, which are endemics of Madagascar and South Africa, respectively, have winged seeds and capsules that slightly resemble those of *Chloroxylon*.

It seems that the structure of the capsule of *Flindersia*, in which the carpels separate in the mature fruit to form distinct or nearly distinct, boat-shaped valves, each with a separate placenta (dissepiment), may indicate a relationship to the subapocarpous condition that prevails in the Rutaceae, subfamily Rutoideae. Furthermore, in the Rutoideae it is not uncommon for capsular fruits to have evolved in basically subapocarpous genera, as evidenced by species of *Esenbeckia, Evodia, Bonina, Melicope, Tetractomia, Pelea*, and *Myrtopsis*.

Further data pertinent to this problem are available from chemistry. J. R. Price, of the Commonwealth Scientific and Industrial Research Organization, Melbourne, and E. Ritchie, of the University of Sydney, have long been interested in the chemical taxonomy of the Rutaceae. They have shown quite conclusively, I believe, that chemical evidence strongly favors placement of *Flindersia* and *Chloroxylon* in the Rutaceae. The relevant points from two of their papers dealing with this (Price, 1963; Ritchie, 1964) are listed below.

1. Twelve species of *Flindersia* and the single species of *Chloroxylon* have been found to synthesize alkaloids known as furoquinolines. These compounds are known to occur only in the Rutaceae where they have been identified in 31 genera including all of the subfamilies of Engler (1931) except the Spathelioideae and Rhabdodendroideae.

2. There has not yet been a definite identification of any alkaloid in the Meliaceae.[1]
3. Both *Flindersia* and *Chloroxylon* contain coumarins, as do several other genera of the Rutaceae and several other angiosperm families, but not the Meliaceae.
4. Five species of *Flindersia* have been found to contain the flavanone glycoside hesperidin, which, Price points out, is ". . . . . a characteristic metabolite of *Citrus* species, also reported from *Zanthoxylum* but not, I think, from outside the family."

Thus it seems that the bulk of evidence available at the present supports the position of *Flindersia* and *Chloroxylon* in the Rutaceae.

I was able to collect and study three of the New Guinean species of *Flindersia* while with the Australian Commonwealth Scientific and Industrial Research Organization, Phytochemical Survey of New Guinea, 1961–1965. This study is otherwise based on herbarium specimens. The contributing herbaria are listed below, with abbreviations from Lanjouw and Stafleu's Index Herbariorum, Part I. Ed. 5 (Regnum Vegetabile, 31. 1964).

A	Arnold Arboretum of Harvard University, Cambridge
BM	British Museum (Natural History), London
BO	Herbarium Bogoriense, Djalan Raya, Bogor, Indonesia
BRI	Botanic Museum and Herbarium, Brisbane
CANB	C.S.I.R.O. Division of Plant Industry, Canberra
GH	Gray Herbarium of Harvard University, Cambridge
K	Royal Botanic Gardens, Kew
L	Rijksherbarium, Leiden
LAE	Department of Forests, Lae, Territory of New Guinea
MEL	National Herbarium of Victoria, Melbourne
MICH	University Herbarium, University of Michigan, Ann Arbor
NSW	National Herbarium of New South Wales, Botanic Gardens, Sydney
NY	New York Botanical Garden, New York
P	Muséum National d'Histoire Naturelle, Paris
US	U.S. National Museum (Department of Botany), Smithsonian Institution, Washington

I wish to thank the directors and curators of these herbaria for making specimens in their care available to me. Thanks are also extended to Lindsay Smith for many helpful notes on the specimens loaned from Brisbane, and to Lily M. Perry, who translated into Latin the description of the single new species, *Flindersia unifoliolata*.

Flindersia R. Br. in Flinders' Voyage **2**: 595. 1814. Type species: *Flindersia australis* R. Br.

Oxleya A. Cunn. ex Hook. in Hooker's Bot. Misc. **1**: 246. 1830. Type species: *Oxleya xanthoxyla* A. Cunn. ex Hook. [*Flindersia xanthoxyla* (A. Cunn. ex Hook.) Domin].

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[1] Identified alkaloids are listed for *Melia azadirachta* L. and *Naregamia alata* Wight & Arn. by Willaman and Schubert (1961, p. 146).

Strzeleckya F. Muell. in Hooker's Jour. Bot. Kew Gard. Misc. **9**: 308. 1857. Type species: *Strzeleckya dissosperma* F. Muell. [*Flindersia dissosperma* (F. Muell.) Domin].

Small to large trees; branchlets, leaves, inflorescences, and fruits glabrous or variously covered with simple, stellate, or scale-like trichomes. Leaves alternate, subopposite or opposite, paripinnate, imparipinnate, trifoliolate, unifoliolate, or simple; leaflets 1–8 pairs, opposite or subopposite, usually pellucid-dotted, entire. Inflorescence terminal, terminal and upper-axillary, or upper-axillary, paniculate, usually densely flowered. Flowers bisexual, functionally staminate or (rarely) functionally carpellate or functionally neutral; sepals 5, distinct or connate basally, usually imbricate basally, often pubescent abaxially, glabrous adaxially, occasionally pellucid-dotted; petals 5, distinct, slightly to strongly imbricate in bud, glabrous to pubescent abaxially and adaxially, often pellucid-dotted; stamens 5, opposite the sepals, inserted on the disc near or at the base, inflexed apically or declinate, filaments glabrous or pubescent abaxially, anthers 2-celled, cordate, basifixed to dorsifixed; staminodes 5, without anthers, together with the stamens forming one androecial whorl, generally somewhat reflexed, glabrous, otherwise like the filaments in each species; disc cupular, between the stamens and the ovary, glabrous, deeply to shallowly folded-crenulate to folded-lobed in the plane of attachment of each stamen and staminode; gynoecium a single, 5-carpellate, 5-loculate pistil, ovary usually globose and shallowly 5-lobed, densely pubescent, usually with 5 apical glands around the base of the style, placentation axile, the placentae protruding into each locule and each with 1–3 superposed ovules on each side (2–6 per locule), style short, stigma capitate or peltate, 5-ridged and often 5-angled or -lobed. Fruit a 5-valved, 5-loculed, septicidal capsule, without a persistent axis; pericarp sub-woody to woody, the exocarp coarsely muricate or with low, mound-like excrescences. Seeds flat, oblong to elliptic, 2–6 per locule, 1–3 attached on each side of each of the placentae (dissepiments) which are much enlarged and persistent in the fruit; testa light to dark brown, forming a terminal wing or a wing that extends around the entire embryo and is elongated at both ends; endosperm absent; embryo elliptic to oblong, the cotyledons flattened, broadly to narrowly cordate, usually pellucid-dotted, the hypocotyl terminal or lateral.

The presence, abundance, and size of trichomes on the leaves and branchlets is variable and in several of the species these parts may range from glabrous to rather densely pubescent. Trichomes are consistently present on at least the youngest inflorescence branches or axils of inflorescence branches of all of the species except possibly *Flindersia unifoliolata*, where the inflorescence is not known. In species 1 through 5 only simple trichomes are known. In the remaining species stellate and/or lepidote trichomes are consistently present, at least in the inflorescence, and may or may not be mixed with simple trichomes.

Leaf arrangement is also variable. *Flindersia fournieri* has basically alternate leaves but occasional opposite leaves also occur. The same is true of *F. amboinensis*. *Flindersia australis* also seems to have basically alternate leaves but specimens (and perhaps even trees?) may be found with entirely opposite leaves. Of the species that have basically opposite leaves, several vary to subopposite but none to alternate.

Four of the species, *Flindersia fournieri*, *F. laevicarpa*, *F. brayleyana* and *F. ifflaiana*, have leaves that are consistently paripinnate. Most of the other species with basically imparipinnate leaves often have occasional leaves, or even a majority of leaves, in some specimens, that are paripinnate. This is especially true in *F. pimenteliana*, *F. amboinensis*, *F. acuminata*, *F. schottiana*, *F. bourjotiana* and *F. australis*.

The simple leaves of *Flindersia unifoliolata*, *F. laevicarpa* var. *heterophylla* (where they occur only rarely), *F. maculosa* and *F. dissosperma* (where they occur only rarely) are obviously derived from compound leaves. I have only referred to the first two as unifoliolate, however, since they are the only ones in which the petiole is clearly homologous to a rachis.

Flower sex and the distribution of sexes varies considerably. The major trend, noted in *Flindersia pimenteliana*, *F. bourjotiana*, *F. bennettiana*, *F. collina*, *F. dissosperma*, *F. ifflaiana*, and *F. australis*, is for the replacement of many of the bisexual flowers in an inflorescence with functionally staminate flowers. In view of the fact that the fruits are usually large and heavy, and that rarely does more than one ever fully develop from a single inflorescence, this may be interpreted, from the standpoint of adaptation, as a means of reducing the number of potential fruit-forming flowers while still maintaining a large attractive inflorescence.

Separation of the valves of the fruit is essentially complete (two or sometimes three may remain attached basally, but are easily separated) in species 1 through 14. In the two remaining species, *Flindersia ifflaiana* and *F. australis*, all five valves remain attached basally and are relatively difficult to separate. This is apparently an important taxonomic character since it correlates, logically, I think, when seed dispersal is considered, with the type of wing formed by the seed: in those species in which valve separation is complete the seeds are winged at both ends whereas in *F. ifflaiana* and *F. australis* the seeds have a terminal wing only.

The position of the hypocotyl of the embryo is unusually variable in the genus but is apparently consistent for each species. In three species, *Flindersia fournieri*, *F. laevicarpa*, and *F. brayleyana* it is terminal, located at the apex of the embryo as it is oriented in the fruit. In the remaining species it is lateral, located at the adaxial margin of the embryo. In four of these species, *F. pimenteliana*, *F. unifoliolata*, *F. bourjotiana*, and *F. ifflaiana*, it is ascending at approximately a 45° angle, while in the remainder it is horizontal. Two of the species with the lateral-ascending type of hypocotyl, *F. pimenteliana* and *F. unifoliolata*, also have exclusively simple trichomes as do the four species with the terminal type of hypocotyl. This indicates, perhaps, that the lateral-ascending type is phylogenetically intermediate.

As far as I have been able to determine, chromosome numbers have been published for only four species (Smith-White, 1954). These were based on counts from germinated seeds and are as follows: ***Flindersia bourjotiana, F. xanthoxyla*** (publ. as ***F. oxleyana***), and ***F. schottiana*** (and "***F. pubescens***"): $2n = 36$. ***Flindersia australis***: $2n = 108$.

Most of the species are important economically as commercial timbers. The woods have a number of uses ranging from general building to cabinet-making.

The general relationships of the sixteen species are presented in the following outline. I am reasonably confident that the species in each of the groups are more closely related to one another than to any of the other species. Between the groups, however, the only assumption I would make is that the species in Groups I and II are more closely related to one another than they are to any of the species in Groups III through VI.

OUTLINE OF SPECIES RELATIONSHIPS

Trichomes simple; hypocotyl terminal or lateral-ascending.	
Leaves paripinnate; hypocotyl terminal.	Group I 1. *F. fournieri* 2. *F. laevicarpa* 3. *F. brayleyana*
Leaves basically imparipinnate; hypocotyl lateral-ascending.	Group II 4. *F. pimenteliana* 5. *F. unifoliolata*
Trichomes (at least some of them) stellate and/or lepidote; hypocotyl lateral or (in two species) lateral-ascending.	
Valves of fruit separating completely at maturity; seeds winged at both ends.	
Ovules 6 in each locule.	
Leaves alternate.	Group III 6. *F. amboinensis* 7. *F. acuminata*
Leaves opposite or subopposite.	Group IV 8. *F. schottiana* 9. *F. bourjotiana* 10. *F. xanthoxyla*
Ovules 4 in each locule.	Group V 11. *F. bennettiana* 12. *F. collina* 13. *F. dissosperma* 14. *F. maculosa*

Valves of fruit not separating completely at maturity; seeds winged at one end only.	Group VI

15. *F. ifflaiana*
16. *F. australis*

In the citation of collections, where applicable, the abbreviations listed in the initial paper of this series (1966, p. 175) are used for collections numbered in sequence. There is one addition:

SN Australian Phytochemical Survey Number

KEY TO THE SPECIES [2]

1. Trichomes exclusively simple; flowers (not known for *F. unifoliolata*) 2–4.2 mm. long; ovules 1 or 2 on each side of the placentae; exocarp of mature capsule with low, smooth, mound-like excrescences or coarsely muricate with excrescences to 4 mm. long; seeds 1 or 2 on each side of the dissepiments, winged at both ends. . . . . 2.
    2. Leaves paripinnate or imparipinnate or (occasional leaves) unifoliolate; leaflets 1–5 pairs. . . . . 3.
        3. Leaves paripinnate or (occasional leaves) unifoliolate; petals pubescent adaxially; exocarp of mature capsule with low, smooth, mound-like excrescences or, if muricate, then capsule less than 5.5 cm. long; seeds 1 on each side of the dissepiments. . . . . 4.
            4. Leaves 6–30 cm. long; petiolules 2–13 mm. long; leaflets 1–4 pairs, 4–15 cm. long; capsule 2.9–5.2 cm. long; exocarp with low, smooth, mound-like excrescences or coarsely short-muricate. . . 5.
                5. Leaves alternate, subopposite or (occasional leaves) opposite; flowers 3.8–4 mm. long; exocarp coarsely short-muricate. . . . . 1. *F. fournieri*.
                5. Leaves opposite; flowers 2–3 mm. long; exocarp with low, smooth, mound-like excrescences or (rarely) coarsely short-muricate. . . . . 2. *F. laevicarpa*.
            4. Leaves 27–45(–75) cm. long; petiolules 10–25 mm. long; leaflets 3–5 pairs, 8–18.5(–22) cm. long; capsule 6–10 cm. long; exocarp with low, smooth, mound-like excrescences. . . 3. *F. brayleyana*.
        3. Leaves imparipinnate or (occasional leaves) paripinnate; petals glabrous adaxially; exocarp of mature capsule coarsely muricate, capsule 5.5–11.5 cm. long; seeds 2 on each side of the dissepiments. . . . . 4. *F. pimenteliana*.
    2. Leaves unifoliolate or (occasional leaves) imparipinnate with a single pair of lateral leaflets. . . . . 5. *F. unifoliolata*.
1. Trichomes predominantly stellate or lepidote, not exclusively simple; flowers 2.5–10 mm. long; ovules 2–3 on each side of the placentae; exocarp of mature capsule coarsely muricate with excrescences to 10 mm. long; seeds 2–3 on each side of the dissepiments, winged at one end only or at both ends. . . . . 6.

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[2] This key is intended to work with either flowering or fruiting material. It has been necessary, in its construction, to use statements in many of the couplets that are not completely contradictory, and it is, therefore, especially important for the user to follow through each couplet in its entirety.

6. Leaves opposite or subopposite, simple, trifoliolate, or imparipinnate, 1–36 cm. long; rachises (compound leaves) often winged laterally; leaflets (compound leaves) 1–3(–4) pairs; filaments glabrous; ovules 2 on each side of the placentae; capsule 2.3–7 cm. long; exocarp glabrous or glabrate; seeds 2 on each side of the dissepiments, winged at both ends. .... 7.
   7. Leaves imparipinnate or trifoliolate (occasional leaves may be simple in *F. dissosperma*). .... 8.
      8. Leaves 8.5–36(–45) cm. long; lateral leaflets with petiolules 1–6 mm. long; terminal leaflet on an extension of the rachis 0.9–3.5 cm. long; leaflets 6–18.5 cm. long; petals glabrous adaxially; capsule 4–7 cm. long; excrescences of the exocarp to 4 mm. long. .... 11. *F. bennettiana.*
      8. Leaves 1.5–14 cm. long; lateral leaflets sessile; terminal leaflet sessile (often narrowly attenuate at the base); leaflets 0.6–9 cm. long; petals short-pubescent in the basal half or glabrous adaxially; capsule 2.3–5 cm. long; excrescences of the exocarp to 2 mm. long. .... 9.
         9. Leaves 5–14 cm. long; leaflets 1–3 pairs; lateral leaflets 2–7 cm. long; main veins of leaflets 12–16 on each side of the midrib; inflorescence to 17 cm. long; flowers 4.7–5.3 mm. long; sepals appressed-pubescent; petals glabrate to appressed-pubescent abaxially, short-pubescent in the basal half adaxially; staminodes 2 mm. long; capsule 2.8–5 cm. long. 12. *F. collina.*
         9. Leaves 1.5–6.3 cm. long; leaflets 1–2 pairs; lateral leaflets 0.6–3.7 cm. long; main veins of leaflets 8–10 on each side of the midrib; inflorescence to 7.5 cm. long; flowers 4–4.5 mm. long; sepals glabrous except for ciliate margin; petals glabrous on both sides; staminodes 0.5 mm. long; capsule 2.3–2.7 cm. long. .... 13. *F. dissosperma.*
   7. Leaves simple. .... 14. *F. maculosa.*
6. Leaves alternate, opposite or subopposite, imparipinnate or paripinnate, (5.5–)8–57 cm. long; rachises angular to subterete; leaflets (1–)2–8 pairs; filaments pilose subapically to glabrous; ovules 2–3 on each side of the placentae; capsule 3.2–21 cm. long; exocarp minutely pubescent to glabrous; seeds 2–3 on each side of the dissepiments, winged at one end only or at both ends. .... 10.
   10. Leaves opposite, subopposite or alternate (if alternate, then the flowers not more than 5 mm. long); leaflets 2.2–22 cm. long; petals glabrous to sparsely or densely pubescent abaxially; ovules 3 on each side of the placentae; capsule 6.5–21 cm. long; seeds 3 on each side of the dissepiments, winged at both ends. .... 11.
      11. Leaves alternate. .... 12.
         12. Leaves 18–57 cm. long; leaflets broadly elliptic to (rarely) elliptic-lanceolate, 8–20 cm. long, apex acuminate to acute or obtuse; sepals densely appressed-pubescent; stamens 2.2–3.6 mm. long, filaments pilose subapically to glabrous. .... 6. *F. amboinensis.*
         12. Leaves 12.5–25(–35) cm. long; leaflets lanceolate to elliptic-lanceolate or narrowly elliptic, 5–10(–15) cm. long, apex narrowly long-acuminate to (occasionally) short and bluntly acuminate; sepals sparsely appressed-pubescent;

stamens 1.5–2 mm. long, filaments glabrous. .... 7. *F. acuminata.*

11. Leaves opposite or subopposite. .... 13.
    13. Leaflets (1–)2–8 pairs, chartaceous to subcoriaceous, not unusually brittle when dry, densely pellucid-dotted, (lateral leaflets) equal-sided to strongly oblique at the base; flowers 4–10 mm. long; petals sparsely appressed-pubescent abaxially, villous in the basal one-third to one-half or glabrous adaxially; exocarp glabrous to glabrate. .... 14.
        14. Leaves 19–54 cm. long; leaflets (4–)5–8 pairs; bases of lateral leaflets narrowly to broadly rounded to cordate, unequal-sided and often strongly oblique; flowers 4–6 mm. long; petals villous in the basal one-third to one-half adaxially; excrescences of the exocarp rather thick-conical. .... 8. *F. schottiana.*
        14. Leaves 9–33 cm. long; leaflets (1–)2–4 pairs; bases of lateral leaflets acute to obtuse, equal- or slightly unequal-sided; flowers 6–10 mm. long; petals glabrous adaxially; excrescences of the exocarp slender. .... 9. *F. bourjotiana.*
    13. Leaflets (2–)3–5 pairs, membranaceous to chartaceous, very brittle when dry, sparsely pellucid-dotted or without pellucid dots, (lateral leaflets) often oblique at the base; flowers 4–5 mm. long; petals glabrous on both sides; exocarp minutely and densely pubescent. .. 10. *F. xanthoxyla.*

10. Leaves opposite, subopposite or alternate (if alternate, then the flowers 6.5–7.5 mm. long); leaflets (2.4–)3–13.5 cm. long; petals densely to sparsely pubescent abaxially; ovules 2 on each side of the placentae; capsule 3.2–8 cm. long; seeds 2 on each side of the dissepiments, winged at one end only. .... 15.
    15. Leaves opposite, paripinnate; petiolules 4–9 mm. long; flowers 2.5–3 mm. long; petals glabrous or with a few papillae adaxially; staminodes 0.5 mm. long; capsule 3.2–5.5 cm. long; exocarp short-muricate, the excrescences (often becoming blunt with age) to 2 mm. long. .... 15. *F. ifflaiana.*
    15. Leaves alternate, subopposite or opposite, imparipinnate or (occasional leaves) paripinnate; petiolules of lateral leaflets obsolete to 3(–5) mm. long; flowers 6.5–7.5 mm. long; petals sparsely pubescent in the basal one-half to two-thirds adaxially; staminodes 1.5 mm. long; capsule 4.6–8 cm. long; exocarp long-muricate, the excrescences to 10 mm. long. .... 16. *F. australis.*

1. **Flindersia fournieri** Panch. & Sebert, Bois Nouv. Caléd. (part 2) 228. 1872. Type: *Fournier & Sebert 22,* New Caledonia.

Medium to large trees; outer bark dark brownish black, finely fissured; heartwood reddish brown; branchlets, leaves, and inflorescences glabrous to puberulent or short-pubescent with simple trichomes. Leaves alternate or (occasional leaves) subopposite or opposite, paripinnate, 6–13 cm. long; rachis glabrous to puberulent; petiolules 4–9 mm. long; leaflets 1–2 pairs, coriaceous, with or without scattered pellucid dots, glabrous or sparsely puberulent below, glabrous above, elliptic to elliptic-oblong, equal- or occasionally slightly unequal-sided, 4.3–8.2 cm. long, 1.8–3.8 cm. wide, base obtuse to cuneate, main veins 14–16 on each side of the midrib, apex obtuse to rounded, usually retuse. Inflorescence upper-axillary, to 10 cm. long, about as wide as long, axes and branches puberulent. Flowers bisexual, 3.8–4 mm. long; pedicels 0.5–2 mm. long; sepals puberulent, ciliolate, broadly obovate to suborbicular, 1–1.5 mm. long; petals white, densely appressed-pubescent abaxially, tomentose adaxially, elliptic with a rather abruptly narrowed base, 3.5–4 mm. long; stamens declinate, about 2.2 mm. long (elongating considerably after anthesis), filaments sparsely to rather densely villous, anthers dorsifixed, mucronulate, about 0.5 mm. long; staminodes 1 mm. long; disc 1.3 mm. high; gynoecium about 2 mm. high and about 1 mm. wide, ovules 2 on each side of the placentae (one of each pair is smaller and apparently aborts). Capsule separating (or easily separable) into 5 distinct valves at maturity, elliptic to elliptic-oblong, 4–4.7 cm. long; exocarp drying medium to dark reddish brown, glabrous, muricate, the excrescences to 2 mm. long; endocarp yellow-brown to brown. Seeds 1 on each side of the dissepiments, winged at both ends, about 3.5 cm. long; hypocotyl terminal.

DISTRIBUTION. New Caledonia; rain forests at lower elevations.

New Caledonia. Baie de Couaoua, *Balansa 1769* (A, BM, BO, K, NY); inland from Baie de Pirogues, *White 2125* (A, US); N de la Baie de Prony, *Balansa 163* (K); Prony, *Franc 1738* (A, NSW 99637, US), *1738A* (A, BM, BO, GH, K, NY); without definite locality, *Fournier & Sebert 22* (BM-isotype).

Apparently most closely related to *Flindersia laevicarpa* but differing rather strongly in having mostly alternate leaves.

2. **Flindersia laevicarpa** White & Francis, Queensl. Agr. Dept. Bot. Bull. 22: 8. *t. 9.* 1920. Type: *Fraser,* July, 1919, Queensland, Atherton District.

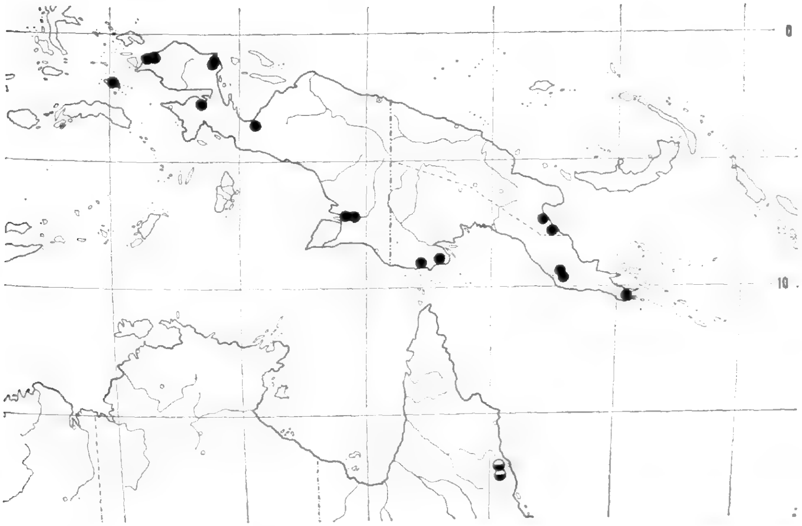
KEY TO THE VARIETIES

1. Leaves 12–30 cm. long; leaflets 2–4 pairs; filaments glabrous; capsule 2.9–4 cm. long; exocarp with smooth, slightly elevated, mound-like excrescences. . . . . 2a. var. *laevicarpa.*
1. Leaves usually less than 12 cm. long (occasional leaves to 28 cm. long); leaflets 1–2(–3) pairs; filaments sparsely to densely pubescent; capsule 3–5.2 cm. long; exocarp as above or grading to bluntly short-muricate with excrescences to 0.8 mm. long. 2b. var. *heterophylla.*

2a. **Flindersia laevicarpa** White & Francis var. **laevicarpa.**

Medium trees to 21 m.; outer bark brown with pustular lenticels; inner bark cream with yellow flecks; sapwood whitish; heartwood pinkish brown; branchlets, leaves, and inflorescences glabrous to puberulent or short-pubescent with simple trichomes. Leaves opposite, paripinnate, 12–30 cm. long; rachis glabrous; petiolules 3–13 mm. long; leaflets 2–4 pairs, subcoriaceous to coriaceous, rather densely pellucid-dotted, glabrous or sparsely puberulent below, glabrous above, elliptic-lanceolate to broadly elliptic, usually quite unequal-sided, 7.9–10.7 cm. long, 1.9–3.5 cm. wide, base acute to cuneate, main veins about 15 on each side of the midrib, apex gradually tapering to acuminate. Inflorescence terminal or upper-axillary and terminal, to 30 cm. long, about one-half as wide as long, youngest branches and axils of older branches puberulent. Flowers bisexual, about 3 mm. long; pedicels about 0.2 mm. long; sepals sparsely puberulent, broadly ovate, about 1 mm. long; petals drying maroon, appressed-pubescent abaxially, short-pubescent adaxially, elliptic, 2.5 mm. long; stamens inflexed apically, about 1.5 mm. long, filaments glabrous, about 1 mm. long, anthers basifixed, mucronulate, about 0.5 mm. long; staminodes about 0.5 mm. long; disc about 0.5 mm. high; gynoecium about 0.7 mm. high and about 1 mm. wide, ovules 1 or 2 on each side of the placentae (where two, one is smaller and apparently aborts). Capsule separating (or easily separable) into 5 distinct valves at maturity, narrowly elliptic, 2.9–4 cm. long; exocarp drying medium to dark reddish brown, glabrous, almost smooth at maturity, the excrescences represented by slightly elevated mounds; endocarp pale brown. Seeds 1 on each side of the dissepiments, winged at both ends, 2.5–3.2 cm. long; hypocotyl terminal.

Illustrations. White, C. T., & W. D. Francis, *ibid.* Francis, W. D., Australian Rain-forest Trees 427, 431. 1951.



Map 1. Distributions of *Flindersia laevicarpa* White & Francis var. *laevicarpa* (half-filled circles) and *F. laevicarpa* var. *heterophylla* (Merr. & Perry) Hartley (dots).

DISTRIBUTION. Danbulla to Gadgarra, Cook District, Queensland; rain forests at about 700 meters. See MAP 1.

Queensland. COOK DISTRICT: Danbulla, *Jones 1116* (BRI, CANB), *Tracey 2192* (CANB), *Webb 5129* (CANB); Tinaroo Range between Mt. Edith and Danbulla, *Smith & Webb 3369* (BRI); Atherton Tableland, *Tardent X232* (A, BRI), *Tardent s.n.* (MEL); Atherton District, *Fraser*, July 1919 (BRI-holotype of *Flindersia laevicarpa* White & Francis), *Webb 2503* (CANB), *5059* (CANB); Gadgarra, *Dreghorn*, January 9, 1934 (BRI).

2b. **Flindersia laevicarpa** White & Francis var. **heterophylla** (Merr. & Perry) Hartley, stat. nov.

Flindersia heterophylla Merr. & Perry, Jour. Arnold Arb. **20:** 331. 1939. Type: *Brass 8495*, Papua, Wassi Kussa River.

Medium to large trees to 45 m.; outer bark mottled, brown or gray, smooth or shallowly fissured; inner bark whitish, yellow-brown, pink, or red, often flecked with orange or red; sapwood white to yellow-brown; heartwood brown to pink, often scented. Leaves 6–12(–28) cm. long; petiolules 2–8 mm. long; leaflets 1–2(–3) pairs (occasional leaves unifoliolate due to early abscission of one leaflet of a single pair), chartaceous to coriaceous, narrowly to broadly elliptic to elliptic-ovate, equal- or slightly unequal-sided, 4–15 cm. long, 1.5–6.5 cm. wide, main veins 10–12 on each side of the midrib. Inflorescence 12–22 cm. long, about as wide as long. Flowers 2–3 mm. long; pedicels 0.5–1.7 mm. long; sepals sparsely to rather densely appressed-pubescent, 0.5–0.9 mm. long; petals cream to yellowish, red, or purple, densely appressed-pubescent abaxially, densely tomentose adaxially, 2–2.5 mm. long; stamens 1–1.2 mm. long, filaments sparsely to densely pubescent with stiff, ascending trichomes, anthers obtuse; ovules 1 on each side of the placentae. Capsule 3–5.2 cm. long; exocarp at maturity almost smooth (as in var. *laevicarpa*) to bluntly short-muricate with excrescences to 0.8 mm. long; endocarp pale brown and often flecked with orange. Seeds 2.5–4.5 cm. long. Otherwise as in var. *laevicarpa*.

DISTRIBUTION. New Guinea, from Misool Island to Milne Bay; well-drained rain forests and monsoon forests; sea level to about 1000 meters. See MAP 1.

West New Guinea (West Irian) and neighboring islands. MISOOL ISLAND: Salafen, *Malessij NIFS bb 14381* (BO). VOGELKOP DIVISION: Sorong, *NIFS bb 15459* (BO); Mlasoen Hills E of Sorong, *van Royen 3399* (BO, K, L, LAE); Waren, 60 miles S of Manokwari, *Kanehira & Hatusima 13017* (A, BO); Ransiki Onderafd, Meos Waar, Wandoswaar, *Kalkman BW 3566* (BO, K, L, LAE); Babo, *NIFS bb 22301* (A, L). GEELVINK BAY DIVISION: Boemi, 30 km. inland from Nabire, *Kanehira & Hatusima 12738* (A, BO). SOUTHERN DIVISION: Bovess Digoel, *Tetelepta NIFS bb 14523* (BO); near Omba along Digoel River, *Versteegh BW 4876* (CANB, L, LAE). **Territory of New Guinea.** MOROBE DISTRICT: Kui, *Ridsdale NGF 31636* (LAE); Mageri, *Webb 5322* (CANB). **Papua.** WESTERN DISTRICT: Tarara, Wassi Kussa River, *Brass 8495* (A-holotype of *Flindersia heterophylla* Merr. & Perry; BRI, L, LAE-isotypes), *8542* (A, BRI, L, LAE); Oriomo

River, *McDonald NGF 13012* (BM, K, L, LAE, NSW 99636), *White*, May 1960 (K, L, LAE), *White & Gray NGF 10397* (mixed coll. — fruits of *Flindersia ifflaiana*) (A, BRI, CANB, K, L, LAE), *NGF 10398* (A, BO, BRI, L, LAE). CENTRAL DISTRICT: Jogeri Subdistrict, Iarowari, *Havel NGF 17384* (BO, K, L, LAE, NSW 99635); tributary of the Laloki River 2 miles E of Rouna, *Hartley 10705* (A, L, LAE); Sogeri Road, *Eddowes NGF 13086* (LAE); Budanumu, near Sogeri, *Womersley & Barrett NGF 4184* (BO, BRI, L, LAE); Sogeri-Rouna Divide 2 miles W of Sogeri, *Schodde 2862* (BO, K, L, LAE, NSW 99633). MILNE BAY DISTRICT: Modewa Bay, Modewa, *Brass 28881* (A, CANB, K, L, LAE, US), *28906* (A, K, L, LAE, US); top of main divide above Mapo, *Smith NGF 1392* (L, LAE, NSW 99634).

Apparently the only character that does not overlap in these two varieties is the pubescence of the filaments. This, however, is a variable character in several other species of the genus.

It is only rarely that short-muricate capsules occur in var. *heterophylla,* and those seemed a little immature. Otherwise, in that variety, the exocarp may be equally as smooth as it is in var. *laevicarpa.*

Flindersia laevicarpa is apparently more closely related to *F. brayleyana* than to *F. fournieri*, both having opposite or subopposite leaves and a tendency toward blunt rather than muricate excrescences on the exocarp. They differ rather strongly, however, in the size of leaves, length of petiolules and the size of fruit. That they are genetically quite dissimilar may also be indicated by the fact that their ranges are sympatric on the Atherton Tableland in northeast Queensland and they apparently occupy the same habitat.

3. **Flindersia brayleyana** F. Muell. Frag. Phytogr. Austral. **5**: 143. 1866. Type: *Dallachy*, Queensland, Herbert's River.

Flindersia chatawaiana F. M. Bailey, Queensl. Agr. Jour. **5**: *387. t. 138.* 1899. Syntypes: *J. F. Bailey*, June 1899, Queensland, Martintown and July 1899, Queensland, Middle Tully River.

Medium to large trees to 35 m.; outer bark gray, flaky, with shallow longitudinal fissures; inner bark reddish or pinkish; wood generally pinkish; branchlets and inflorescences glabrous to puberulent or short-pubescent with simple trichomes. Leaves opposite or subopposite, paripinnate, 27–45(–75) cm. long; rachis glabrous; petiolules 10–25 mm. long; leaflets 3–5 pairs, subcoriaceous, densely pellucid-dotted, glabrous, broadly elliptic to ovate-elliptic, mostly unequal-sided and occasionally subfalcate, 8–18.5(–22) cm. long, 3.3–7.5(–9) cm. wide, base acute to cuneate, often oblique, main veins 8–12 on each side of the midrib, apex obtuse to acuminate. Inflorescence upper-axillary and terminal, to 23 cm. long, usually a little wider than long, youngest branches puberulent. Flowers bisexual, 3–4 mm. long; pedicels 1.5–2 mm. long; sepals sparsely puberulent, ciliolate, ovate-triangular, about 0.5 mm. long; petals creamy white, puberulent in the basal three-fourths abaxially, tomentulose in the basal one-half adaxially, oblong-elliptic to elliptic, 2.5–3.5 mm. long; stamens declinate, 2–2.2 mm.

long, filaments villous subapically, anthers subdorsifixed, bluntly mucronate, 0.75–1 mm. long; staminodes 0.75 mm. long; disc about 0.75 mm. high; gynoecium 1–1.4 mm. high, about 1 mm. wide, ovules 1 on each side of the placentae. Capsule separating (or easily separable) into 5 distinct valves at maturity, oblong-elliptic, 6–10 cm. long; exocarp drying medium brown, glabrous, almost smooth at maturity, the excrescences represented by slightly elevated mounds; endocarp cream to reddish brown. Seeds 1 on each side of the dissepiments, winged at both ends, 4.5–6 cm. long; hypocotyl terminal.

ILLUSTRATIONS. BAILEY, F. M., *ibid.* FRANCIS, W. D. Australian Rainforest Trees 424, 426. 1951.

DISTRIBUTION. Northeast Queensland, vicinity of Cairns south to Rockingham Bay; upland rain forests.

Queensland. COOK DISTRICT: Daintree River, *Pentracke*, 1889 (MEL); Kamerunga, *Cowley*, February 1905 (BRI); Bonjee, *Doggrell A35* (A, BRI), *Jones 2094* (CANB); Danbulla, *Webb 5130* (CANB); Atherton Tableland, *Wyat 13* (BRI); Martintown, *Bailey*, June 1899 (BRI-syntype of *Flindersia chatawaiana* F. M. Bailey); Gadgarra, *Dreghorn 13* (BRI), *14* (BRI), *Kajewski* (NY); Wongabel Forestry Nursery ca. 5 miles SSE of Atherton, *Smith*, August 19, 1948 (BRI); the Crater, ca. 11 miles S of Atherton, *Smith 3824* (BRI); Forestry Reserve 99, Great Dividing Range several miles SW of Atherton, *Smith*, August 1948 (BRI); Glenallan, Malanda, *Hayes* (BRI); Parish of Ramleh, Country of Coadwell, *Webb SN 5403* (CANB); Middle Tully River, *Bailey*, July 1899 (BRI, K-syntype of *Flindersia chatawaiana* F. M. Bailey). NORTH KENNEDY DISTRICT: Koolmoon Creek Area ca. 11 miles SSE of Ravenshoe, *Smith 5285* (BRI); Cardwell, *Anonymous* (BRI, NSW 99678); Rockingham Bay, *Anonymous* (BO, BM, BRI, GH, MEL, P, US), *Dallachy* (MEL); Herbert's River, *Dallachy* (MEL-holotype of *Flindersia brayleyana* F. Muell.; K-isotype). SOUTH KENNEDY DISTRICT: Mackay Coast (native?), *Anonymous* (NSW 99679). WIDE BAY DISTRICT: Imbil (native?), *Clemens 43373* (A, US, NY), *Wallin*, September 21, 1948 (LAE). Without definite locality: *Wood Technology Dept. Queensland Forestry Service 54* (A, NY). Cultivated. **Queensland.** Wide Bay District, Forestry Station, Imbil, *Clemens 43213* (A, NY, US), December 22, 1943 (BRI). **New South Wales.** West Pennant Hills, *Anonymous*, March 3, 1966 (NSW 99680).

Flindersia chatawaiana was previously placed in synonymy of *F. brayleyana* by C. T. White (1921).

4. **Flindersia pimenteliana** F. Muell. Frag. Phytogr. Austral. **9**: 132. 1875. Lectotype: *Dallachy*, Queensland, Rockingham Bay.

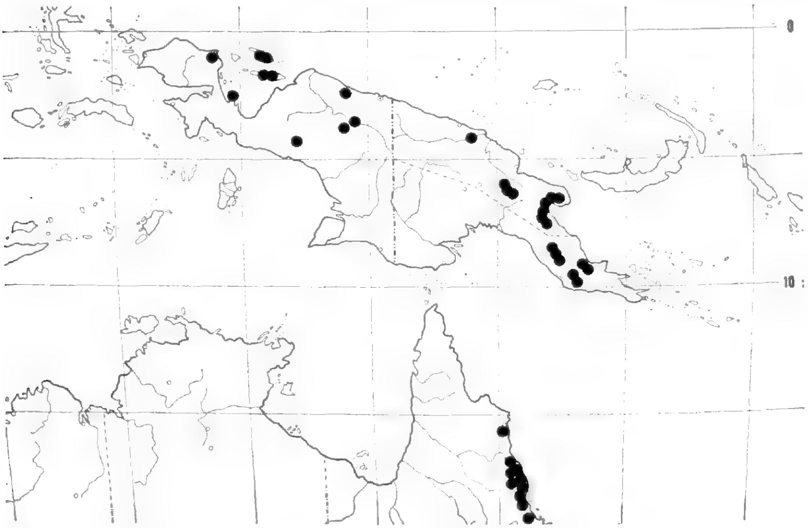
Flindersia mazlini F. M. Bailey, Queensl. Agr. Jour. **5**: 388. *t. 138.* 1899. Type: *J. F. Bailey*, July 8, 1899, Queensland, Evelyn.
Flindersia chrysantha Merr. & Perry, Jour. Arnold Arb. **22**: 59. 1941. Type: *Brass & Versteegh 11128*, West New Guinea, Bele River.

Large trees to 40 m.; outer bark brown to gray, smooth or slightly roughened with pustular lenticels or shallow longitudinal fissures; inner bark pink or reddish brown grading to white or yellowish toward the cambium; sapwood white or yellowish white to pale pink, lustrous; heartwood pink to reddish brown, lustrous; branchlets and inflorescences glabrous to puberulent or short-pubescent with simple trichomes. Leaves opposite to strongly subopposite, imparipinnate or (occasional leaves) paripinnate, 8–34 cm. long; rachis glabrous; petiolules of lateral leaflets 3.5–11 mm. long, terminal leaflet on an extension of the rachis 1.2–4 cm. long; leaflets 1–3(–5) pairs, chartaceous to subcoriaceous, with or without scattered pellucid dots, glabrous, elliptic to elliptic-oblong, often unequal-sided and occasionally subfalcate, 3.5–16 cm. long, 1.3–6.5 cm. wide, base obtuse to cuneate, usually oblique, main veins 9–14 on each side of the midrib, apex gradually tapering to acuminate. Inflorescence terminal or upper-axillary and terminal, to 30 cm. long, usually about as wide as long, axes and branches puberulent to short-pubescent. Flowers bisexual, functionally unisexual or functionally neutral, 2.5–4.2 mm. long; pedicels 1–1.5 mm. long; sepals sparsely puberulent, ciliate or ciliolate, broadly ovate, 0.8–1.2 mm. long; petals white to cream, yellow, or red, glabrous or sparsely puberulent abaxially, glabrous or with scattered papillae adaxially, elliptic-oblong, 2.5–4 mm. long; stamens declinate, about equally developed in bisexual, functionally staminate, functionally carpellate and functionally neutral flowers except lacking pollen in the latter two, 2–2.5 mm. long, filaments pilose subapically or occasionally glabrous, anthers subdorsifixed, acute to mucronulate, about 0.5 mm. long; staminodes 1–2 mm. long; disc in bisexual and functionally carpellate flowers thin, 0.7–1 mm. high; disc in functionally staminate and functionally neutral flowers comparatively thick, about 0.5 mm. high; gynoecium in bisexual and functionally carpellate flowers about 2 mm. high and about 1 mm. wide, ovules 2 on each side of the placentae; gynoecium in functionally staminate and functionally neutral flowers poorly differentiated, narrowly conical, about 1 mm. high, without ovules. Capsule separating (or easily separable) into 5 distinct valves at maturity, elliptic-oblong to oblong, 5.5–11.5 cm. long; exocarp drying reddish brown, glabrous, muricate, the excrescences densely crowded, unequal in length, to 4 mm. long; endocarp yellow-brown or cream and reddish-brown maculate, or not maculate and brown to reddish-brown. Seeds 2 on each side of the dissepiments, winged at both ends, 4–6 cm. long; hypocotyl lateral, ascending.

ILLUSTRATIONS. BAILEY, F. M., *ibid.* FRANCIS, W. D., Australian Rainforest Trees 425, 426. 1951.

DISTRIBUTION. New Guinea, from the Vogelkop Peninsula to southeastern Papua, and northeastern Queensland, between Cooktown and Townsville; upland rain forests, 100–2700 meters. See MAP 2.

West New Guinea (West Irian) and neighboring islands. BIAK ISLAND: Mansforbo, *Moll BW 9552* (L, LAE), *BW 9571* (L, LAE), *BW 9657* (L, LAE); near Parieri, *Moll BW 9745* (L, LAE); Saribi, *van Petersen BW 2419* (L, LAE). JAPEN ISLAND: Aisao, *Schram BW 10517* (L, LAE); Seroei, *NIFS bb 30466* (L), *NIFS* *bb 30526* (A, L). Vogelkop Division: Mt. Krabo, South Manokwari, *Koster BW 10786* (L, LAE). Geelvink Bay Division: Wandammen Peninsula, Wondiwoi Mts., *Koster BW 13797* (LAE). Hollandia Division: Bodem River, 60 km. SE of Sarmi, *Iwanggin BW 5889* (CANB, L, LAE), *Koster BW 8064* (CANB, L, LAE), *BW 1874* (CANB, L, LAE); Bele River, 18 km. NE of Lake Habbema, *Brass & Versteegh 11128* (A-holotype of *Flindersia chrysantha* Merr. & Perry; BRI, L, LAE-isotypes); Idenburg River, 6 km. SW of Bernhard Camp, *Brass & Versteegh 12535* (A, L). Central Division: Nassau Mountains, *Docters van Leeuwen 10478* (A, BO, BRI, K, L), *10618* (A, K, L), *10682* (A, BO, K, L). **Territory of New Guinea.** Sepik District: without definite locality, *Ledermann 9825* (L). Eastern Highlands District: Collins' Sawmill, Goroka, *Collins W966* (LAE); Leahey's logging area above Goroka, *Womersley & Floyd NGF 6132* (A, BO, BRI, K, L, LAE); ¾ mile SW of Daulo, *Saunders 894* (CANB, L, LAE); Aiyura, *Smith NGF 1075* (LAE), *Womersley NGF 3391* (BRI, CANB, LAE); Sassaura, *Hartley 12018* (A, L, LAE), *12018A* (LAE). Morobe District: Ogerammang, *Clemens 4739* (A), *5086* (A); Sambanga, *Clemens 6825* (A); hillside above Busu River, *Henty NGF 14833* (BO, K, L, LAE, NSW 99652); Yalu, *Womersley NGF 3192* (A, BRI, K, LAE); Oomsis Creek, 18 miles W of Lae, *Hartley 10493* (A, L, LAE); Bulolo, *Brass 29153* (A, K, L, LAE, NY, US), *Floyd NGF 7472* (A, BRI, L, LAE, NSW 99653), *NGF 7527* (A, BRI, K, L, LAE, NSW 99659), *Floyd & Morwood NGF 6204* (A, BO, BRI, K, L, LAE, NSW 99656, US), *McAdam 291* (LAE), *Ross NGF W1001* (A, BO, BRI, L, LAE, NSW 99660), *Womersley & Brass NGF 11025* (A, BRI, K, L, LAE); W of Bulolo near Bulolo-Watut Divide, *Frodin & Hill NGF 26355* (K, L, LAE, NSW 99658), Upper Long Island Creek, near Bulolo, *Havel & Henry NGF 17024* (A, BO, BRI, CANB, K, L, LAE), Upper Nauwata-Banda logging area, near Bulolo, *Havel & Kairo NGF 11140* (BRI, K, L, LAE), *NGF 11142* (BO, K, L, LAE); near Dengalu Village, *Womersley NGF 19063* (K, L, LAE, NSW 99668); Wau, *White NGF 2529* (L, LAE, NSW 99655); Edie Creek,



Map 2. Distribution of *Flindersia pimenteliana* F. Muell.

Streimann NGF 17476 (K, LAE); Kauli Creek, 5 miles S of Wau, Hartley *11513* (A, LAE), *Henty NGF 14726* (K, L, LAE, NSW 99654), *Millar NGF 14516* (K, L, LAE, NSW 99657), *van Royen NGF 16302* (BO, L). **Papua.** CENTRAL DISTRICT: Lala River, *Carr 15805* (CANB, L), *15989* (K, L); Isuarava, *Carr 15475* (L), *15569* (L), *15969* (K, L); Mafulu, *Brass 5339* (A, NY, US); Boridi, *Carr 13152* (A, K, L, NY), *14408* (A, K, L, NY), *14808* (L), *14910* (A, K, L, NY); Mt. Obree to Laruni Spur, *Lane-Poole 382* (BRI). NORTHERN DISTRICT: Managalase area, S side of Hydrographers Range near Siarane, *Pullen 6263* (CANB); Bariji-Managalase area, N side of Sibium Range, S of Toma, *Pullen 6358* (CANB, LAE), *6387* (CANB, LAE). **Queensland.** COOK DISTRICT: Cape York Peninsula, Mt. Finnegan, *Brass 20322* (A); Great Dividing Range ca. 6 miles S of Mossman and near "Devil Devil Creek", *Smith 3953* (BRI); Mt. Spurgeon, *White 10596* (A, K); Danbulla, *Jones 1117* (CANB); Atherton Tableland, Juara Creek area, near Danbulla, *Smith 3780* (BRI); Atherton Tableland, Lake Barrine, *Kajewski 1114* (A, BRI, NY, P); Atherton, *Mocatta*, February 1913 (BRI); Atherton Area, *Webb 2504* (CANB); Atherton, Herberton Road, East Barron, *Webb 747* (CANB); Yungaburra, *Dreghorn*, December 1935 (A, BRI, K); Gadgarra, *Dreghorn 22E* (BRI), January 9, 1934 (A, BRI, NY), *White 1566* (A, BRI); Glenallan, Malanda, *Hayes* (BRI); Paronella Park, on Mena Creek, ca. 14 miles S of Innisfail, *Smith,* August 5, 1948 (BRI). NORTH KENNEDY DISTRICT: Koolmoon Creek, ca. 11 miles SSE of Ravenshoe, *Smith 4588X* (BRI); Evelyn, *Bailey*, July 8, 1899 (BRI-holotype of *Flindersia mazlini* F. M. Bailey; K-isotype); Coast Range, *Anonymous*, February 1866 (BRI); Rockingham Bay, *Dallachy* (MEL-lectotype of *Flindersia pimenteliana F. Muell.*; BM, BO, K, NSW 99651), *Anonymous* (BRI, MEL); Mt. Macalister, *Dallachy,* April 11, 1869 (MEL); Mt. Fox, *Clemens,* September-December 1949 (GH, MICH).

C. T. White (1921) has previously placed *Flindersia mazlini* in the synonymy of *F. pimenteliana.*

The type collection of *Flindersia chrysantha* was made at 2300 m. in West New Guinea and is typical of a number of collections from mountain rain forests in New Guinea. The leaflets of these collections tend to be of thicker texture and have more prominent veins and less tapering bases and apices than typical *F. pimenteliana.* These are not sharply defined differences, however, and probably are only environmental modifications. Merrill and Perry noted in their original description of *F. chrysantha* that the petals differed from those of *F. pimenteliana* in color (yellow *vs.* red) and pubescence (glabrous *vs.* pubescent abaxially). With the larger number of collections that are now available it can be seen that both of these characters are quite variable in typical *F. pimenteliana* from lower elevations in New Guinea. Flower color ranges from red to pink, cream or white, and the petals range from pubescent to glabrous abaxially.

Flower sex and the distribution of sexes is extremely variable in this species. In some collections, such as *Moll BW 9745* and *Dreghorn,* December 1935, all of the flowers appear to be perfect. In others, such as *Dreghorn,* January 9, 1934, some appear to be perfect and many appear to be functionally staminate. A condition where all of the flowers on a specimen appear to be functionally staminate is found in a number of collections from New Guinea including *Brass 29153* and *Carr 14910.* Still other collections, such as *Brass 11128* and *Hartley 12018* have a majority of functionally carpellate flowers mixed with flowers that appear to be functionally neutral.

Insect galls are often formed from the flowers in New Guinea. These have the appearance of young fruits and were occasionally mistaken for them by collectors.

Other than *Flindersia unifoliolata*, which seems to be very closely related, *F. pimenteliana* does not appear to have any very close relatives. As is indicated above in the outline of species relationships, I think its having exclusively simple trichomes would place it closer to those species which share that character than to any of the others, but the leaf difference and especially the difference in hypocotyl position makes any very close relationship seem unlikely.

5. **Flindersia unifoliolata** Hartley sp. nov.

Arbor usque 15 m. alta; ramulis, rhachidibus et laminis subtus glabris vel minute et sparse puberulis, pilis simplicibus. Folia opposita vel subopposita, unifoliolata vel interdum imparipinnata et unijuga, 3–9 cm. longa; petiolulis foliolorum lateralium 1–4 mm. longis, rhachidi ad apicem extensa usque 1 cm. longa foliolum terminale ferente; petiolis foliorum unifoliolatorum usque 1.8 cm. longis; laminis subcoriaceis, consperse pellucido-punctatis, ellipticis, equilateris vel parum inaequilateris, 3–8 cm. longis, 1.4–3.2 cm. latis, basi acuta usque cuneata plerumque aequilatera, venis primariis utrinque 8–16, apice obtuse acuminata. Capsula secedens in valvas distinctas maturite, elliptica, 7.8 cm. longa; exocarpio in sicco atro-rufescente, glabro, muricato, processibus inaequilongis, usque 2 mm. longis; endocarpio brunnescente et leviter ferrugineo-maculato. Semina 2 inquoque latere dissepimentorum, utrinque alata, 3.5–4 cm. longa; hypocotylo laterali parum adscendente. Flores non visi. Holotypus: *Sayer 136* (MEL).

Queensland. COOK DISTRICT: Mt. Bellenden Ker, alt. 5200 ft., *Sayer 136* (MEL-holotype); Mt. Bartle Frere, in low scrub, 4000–5000 ft., *Martin & Hyland 1881* (BRI).

The localities of the above collections are about 15 miles apart about 40 miles south of Cairns, Queensland. The holotype is a fruiting branch while the *Martin & Hyland* specimen is sterile.

Closely related to *Flindersia pimenteliana* which appears to be restricted to lower elevations in this part of Queensland. The fruits and seeds of the two species appear roughly identical.

6. **Flindersia amboinensis** Poir. in Lam. Encycl. Suppl. **4**: 650. 1816. Neotype: *DeVriese & Teysmann*, Moluccas, Ceram.

Arbor radulifera Poir. in Lam. Encycl. **6**: 58. 1804 (provisional name, based on plate and description by Rumphius, Herb. Amboin. **3**: 201. *t. 129*. 1743).
Flindersia radulifera Spreng. Geschicht. Bot. **2**: 76. 1818 (*nomen illegit.*).

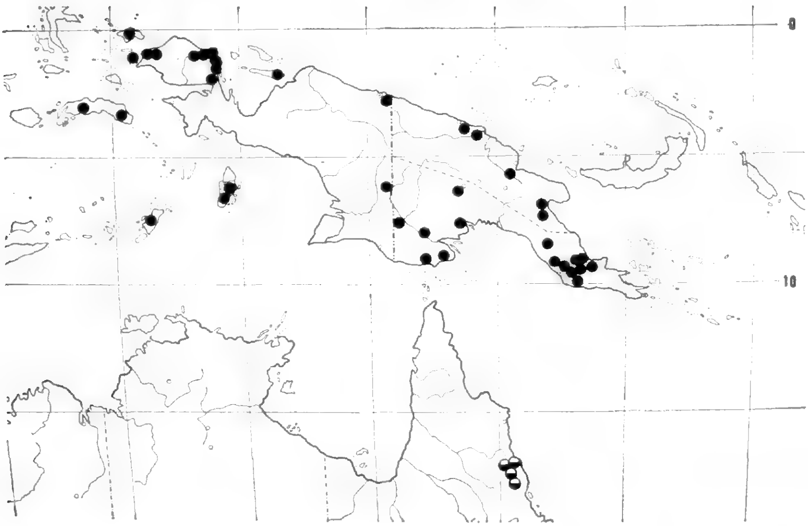
Flindersia macrocarpa Lane-Poole ex White & Francis, Proc. Roy. Soc. Queensl. **38:** *232. t. 3.* 1927. Type: *Lane-Poole 362*, Papua, Owen Stanley Range.

Large trees to 45 m.; outer bark gray to brown, smooth or slightly roughened; inner bark usually yellow grading to white or yellow-brown toward the cambium; sapwood white, cream, or yellow; heartwood yellow-brown; branchlets, leaves and inflorescences glabrous to pubescent with mostly minute, predominantly stellate trichomes. Leaves alternate, imparipinnate or (occasional leaves) paripinnate, 18–57 cm. long; rachis glabrate to appressed- or soft-pubescent; petiolules of lateral leaflets 2–8 mm. long, terminal leaflet on an extension of the rachis 1–4.3 cm. long; leaflets 2–4(–5) pairs, chartaceous to subcoriaceous, with or without scattered pellucid dots, glabrous to appressed- or soft-pubescent below, glabrous or occasionally finely pubescent along the midrib above, elliptic to elliptic-lanceolate, usually strongly unequal-sided and occasionally falcate, 8–20 cm. long, 3–9.5 cm. wide, base acute to broadly rounded, usually oblique, main veins 10–20 on each side of the midrib, apex obtuse to acuminate. Inflorescence terminal, 18–30 cm. long, usually about as wide as long, axes and branches densely appressed- to soft-pubescent. Flowers bisexual, 3.5–5 mm. long; pedicels obsolete to 1.7 mm. long; sepals densely appressed-pubescent, ciliolate, broadly ovate to suborbicular, 0.7–1 mm. long; petals yellow-brown, cream, or red, glabrous to densely appressed-pubescent abaxially, glabrous to subvillous at about the middle adaxially, elliptic-oblong, 3–4.5 mm. long; stamens declinate, 2.2–3.6 mm. long, filaments pilose subapically or (rarely) glabrate, anthers dorsifixed, obtuse, 0.7–1 mm. long; staminodes 0.7–1.8 mm. long; disc 0.7–1.3 mm. high; gynoecium about 2 mm. high and about 1.5 mm. wide, ovules 3 on each side of the placentae. Capsule separating (or easily separable) into 5 distinct valves at maturity, elliptic to elliptic-oblong, 9–21 cm. long; exocarp drying light to dark brown, densely and minutely pubescent to glabrate, muricate, the excrescences thin and flattened laterally or thick and conical, 5–8 mm. long; endocarp reddish brown or cream. Seeds 3 on each side of the dissepiments, winged at both ends, 5–8.5 cm. long; hypocotyl lateral, horizontal.

ILLUSTRATION. RUMPHIUS, G. E., *ibid.*

DISTRIBUTION. Ceram and Tanimbar Islands in the Moluccas eastward throughout New Guinea; rain forests from sea level to 1700 meters. See MAP 3.

Moluccas. CERAM: without definite locality, *DeVriese & Teysmann*, 1859–1860 (L-neotype of *Flindersia amboinensis* Poir.), *NIFS bb 25869* (L). TANIMBAR ISLANDS: Otimmer, *NIFS bb 24346* (L). **West New Guinea (West Irian) and neighboring islands.** AROE ISLANDS: Watoebaker Island, Dosimanalaoe, *NIFS bb 25298* (L), *NIFS bb 25322* (L); Trangan Island, Ngaibor, *NIFS bb 25443* (L). WAIGEO ISLAND: E bank of Majalibit Bay 8 km. NE of Waifor, *van Royen 5165* (CANB, L). SALAWATI ISLAND: Kaloal, *Koster BW 1495* (L). JAPEN ISLAND: Seroei Aisaoe, Sebosiari, *Iwanggin BW 10054* (L); Seroei,



MAP 3. Distributions of *Flindersia amboinensis* Poir. (dots) and *F. acuminata* C. T. White (half-filled circles).

Mariattoe, *NIFS bb 30424* (L). VOGELKOP DIVISION: Sorong, *van Royen 3505* (A, BRI, K, L, LAE); Warsamson Valley, E of Sorong, *Iwanggin BW 5643* (L), *Moll BW 11623* (L, LAE); Kebar Valley, *Koster BW 7116* (L), *Schram BW 7805* (L); Sidei, *Iwanggin BW 5780* (L, LAE), *Koster BW 4433* (BO, CANB, L, LAE), *BW 4470* (CANB, L, LAE), *BW 4474* (L), *BW 4497* (CANB, L, LAE), *BW 7062* (CANB, L, LAE); Wariki, ca. 50 km. W of Manokwari, *Schram BW 7615* (L); Masni Plain, *Koster BW 11059* (L, LAE), *Schram BW 1813* (CANB, L), *Versteegh BW 10444* (L); 8 km. NW of Manokwari, *Koster BW 4350* (CANB, L, LAE); Lower Pami River, ca. 5 km. N of Manokwari, *Koster BW 4359* (BO, CANB, L, LAE), *BW 4388* (CANB, L), *BW 4395* (L); Oesaibi, near Andai, SW of Manokwari, *Koster BW 11890* (L, LAE); Momi, *Kostermans 321* (L), *337* (L), *348* (L); Wariap, *Kostermans 481* (L); Inanwatan, Moetoeri (Steenkool), *NIFS bb 32680* (L). HOLLANDIA DIVISION: Hollandia, *Schram BW 1678* (CANB, L). SOUTHERN DIVISION: Opka, ca. 10 km. NE of Ninati, Subdivision Moejoe, *Kalkman BW 6454* (CANB, L, LAE). **Territory of New Guinea.** SEPIK DISTRICT: Wewak-Angoram Area, ca. 3 miles E of Urimo, *Saunders 975* (CANB, LAE); 3 miles N of Angoram, *Pullen 1882* (A, L, LAE); without definite locality, *Ledermann 10406* (L). MADANG DISTRICT: Usino, *Henty NGF 27500* (K, LAE), *Hoogland 5035* (A, BM, BRI, K, L, LAE, US). MOROBE DISTRICT: Oomsis Creek, ca. 18 miles W of Lae, *Hartley 10516* (A, LAE), *Smith & Mair NGF 1253* (LAE); Bulolo, *McViegh & Ridgwell NGF 7337* (A, BO, BRI, L, LAE, NSW 99666); Lower Taun Creek, near Bulolo, *Havel & Henry NGF 17026* (K, L, LAE, NSW 99664), *Havel & Kairo NGF 15441* (LAE); Crooked Creek, near Bulolo, *Dobson & Havel NGF 9116* (LAE). **Papua.** WESTERN DISTRICT: Lake Daviumbu, Middle Fly River, *Brass 7517* (A, BRI, L, LAE); Lower Fly River, E bank opposite Sturt Island, *Brass 8032* (A); Upper Wassi Kussa River, *Brass 8634* (A, BRI, L, LAE); Oriomo River, *Hart NGF 5018* (BO, CANB, L, LAE, NSW 99661), *White & Gray NGF 10366* (A, BO, BRI, K, L, LAE, NSW 99662).

SOUTHERN HIGHLANDS DISTRICT: Lake Kutubu Patrol Post, *Saunders 1079* (CANB, L, LAE). GULF DISTRICT: Kikori Subdistrict, Seribi River, near Middletown, *Gray & Floyd NGF 8068* (BRI, LAE). CENTRAL DISTRICT: between Okaka and Mafula, *White*, August 1918 (BRI); Kubuna, *Brass 5565* (A, NY); Brown River, *Allan & Jones NGF 2751* (BRI, CANB, L, LAE); near Karema, Brown River, *Schodde 2496* (A, K, L, LAE); Brown River Forest Reserve, Omari Creek, *McDonald NGF 8226* (BO, BRI, K, L, LAE, NSW 99665); Sogeri, *Forbes 421* (BM), *Heather NGF 2828* (BRI, L, LAE); near Rigo, *Schodde 2806* (A, BO, K, L, LAE, NSW 99663); Owen Stanley Range, *Lane-Poole 362* (BRI-holotype of *Flindersia macrocarpa* Lane-Poole ex White & Francis; K-isotype). NORTHERN DISTRICT: Yodda River, *Carr 13913* (A); Dobodura Area, *NGF 2063* (LAE); ca. 1 km. W of Popondetta, *Hoogland 3737A* (CANB, LAE); Managalase Area, S side of Hydrographers Range near Siurane, *Pullen 5584* (CANB). Cultivated. **Java.** Botanic Gardens, Bogor, *Anonymous*, January 1890 (BO, L).

Not, as the specific epithet implies, known from Ambon Island. In the original description in *Herbarium Amboinense* Rumphius gave Ceram as the locality.

As delimited here, this is probably the most variable species in the genus. Among the variable features are:

1. Petals glabrous to densely appressed-pubescent abaxially.
2. Petals glabrous to subvillous adaxially.
3. Stamens 2.2–3.6 mm. long.
4. Filaments glabrate to pilose subapically.
5. Capsules 9–21 cm. long.
6. Exocarp of capsule glabrate to minutely pubescent.
7. Excrescences of exocarp flattened laterally or thick-conical.
8. Endocarp reddish brown or cream colored.

I have not been able to find sufficient correlations among these characters to recognize more than a single taxon. The color of the endocarp, for example, does not always correlate with the pubescence of the exocarp and neither of these characters consistently correlate with the shape of the excrescences or the size of the capsule. In the flowers, the only tendency toward correlation is between petal pubescence and stamen length. Perhaps some definite correlations could be made if flowering and fruiting material could be studied for each variant. Where I have been able to do this, however, studying flowering and fruiting collections that were obviously the same morphologic type, it has seemed unlikely. Finally, it should be noted that each of the variable features of this species was found to be variable in one or more of the other species of the genus as well.

Flindersia macrocarpa, originally described as having larger capsules than had previously been attributed to any other species of the genus, now grades into typical *F. amboinensis*.

Obviously very closely related to *Flindersia acuminata*, which differs mainly in having smaller leaves, narrower, more acuminate leaflets, and shorter stamens. Neither of these species appears to be very closely related to any of the other species of the genus.

Flowers that were apparently insect-stung were noted in several collections. They are atypical in having enlarged, almost cartilaginous petals, filaments, staminodes, and ovaries. Remains of insect larvae were found in the ovaries of some of the affected flowers.

7. **Flindersia acuminata** C. T. White, Queensl. Dept. Agr. Bot. Bull. **21**: 5. *t. 2.* 1919. Type: *Mocatta*, July 3, 1915, Queensland, Atherton.

Small to rather large trees to 33 m.; outer bark brownish, with shallow longitudinal fissures; inner bark brownish grading to yellowish brown or cream toward the cambium; sapwood whitish; heartwood yellowish; branchlets, leaves, and inflorescences glabrous to pubescent with mostly minute, predominantly stellate trichomes. Leaves alternate, imparipinnate or (occasional leaves) paripinnate, 12.5–35 cm. long; rachis glabrous to finely pubescent; petiolules of lateral leaflets 4–10 mm. long; terminal leaflet on an extension of the rachis 1–3.1 cm. long; leaflets 3–5 pairs, chartaceous to subcoriaceous, sparsely to densely pellucid-dotted, glabrous to loosely pubescent below, glabrous or short-pubescent along the midrib above, elliptic to elliptic-lanceolate, usually unequal-sided and often subfalcate, 5–15 cm. long, 1.3–4.8 cm. wide, base acute to rounded, often oblique, main veins 10–17 on each side of the midrib, apex narrowly long-tapering to short and bluntly acuminate. Inflorescence terminal, 7–14 cm. long, usually about as wide as long, axes and branches short-pubescent. Flowers bisexual, 3–4 mm. long; pedicels 0.7–1 mm. long; sepals sparsely appressed-pubescent, ciliolate, suborbicular, 1–1.2 mm. long; petals creamy yellow, sparsely appressed-pubescent abaxially, glabrous or with a few papillae adaxially, elliptic-oblong, 3–3.2 mm. long; stamens inflexed apically, 1.5–2 mm. long, filaments glabrous, anthers basifixed, broadly rounded apically, about 0.5 mm. long; staminodes about 1 mm. long; disc about 1 mm. high; gynoecium about 1.5 mm. high and about 1 mm. wide, ovules 3 on each side of the placentae. Capsule separating (or easily separable) into 5 distinct valves at maturity, elliptic-oblong, 9–12 cm. long; exocarp drying light to dark brown, densely and minutely pubescent to glabrate, muricate, the excrescences thick and conical, to 5 mm. long; endocarp very pale brown flecked with medium brown. Seeds 3 on each side of the dissepiments, winged at both ends, 5 cm. long; hypocotyl lateral, horizontal.

ILLUSTRATIONS. WHITE, C. T., *ibid.* FRANCIS, W. D., Australian Rainforest Trees 427. 1951.

DISTRIBUTION. Cook District, Queensland; well-drained rain forests. See MAP 3.

Queensland. COOK DISTRICT: Kuranda, *Crothers*, January 1926 (BRI); Forestry Reserve 607 ca. 10 miles W of Cairns, *Smith 10121* (BRI), *Draper* (BRI); Tinaroo Range ca. 15 miles NE of Atherton, *Smith & Webb 3372* (BRI);

Atherton, *Mocatta*, July 3, 1915 (BRI-holotype; MEL-isotype), *Mocatta* (BRI, MEL), *Jones 1284* (CANB); Gadgarra, *Barnard 31* (CANB), *Dreghorn 11* (BRI), *20E* (BRI), *Smith 10144* (BRI), *10155* (BRI), *10424* (BRI), *Volk 1411* (BRI), *Webb 1661* (CANB), *White 1567* (BRI); Innisfail, *Michael 403* (A, BRI); head of Johnstone River, *White*, January 1918 (BRI). Without definite locality: *Wood Technology Dept. Queensland Forestry Service 56* (NY).

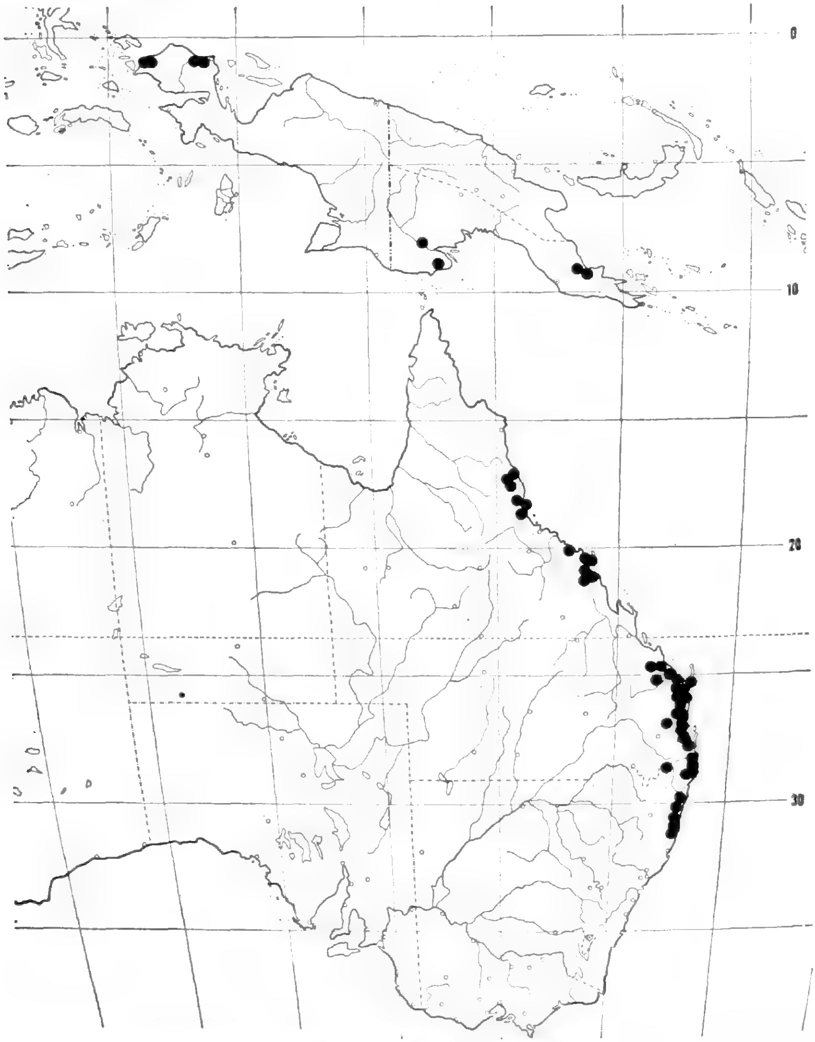
8. **Flindersia schottiana** F. Muell. Frag. Phytogr. Austral. **3**: 25. 1862. Lectotype: *Bidwill 95*, Queensland, Wide Bay.

Flindersia schottiana F. Muell. var. *pubescens* F. Muell. Frag. Phytogr. Austral. **5**: 143. 1866. Type: *Anonymous*, Queensland, Rockingham Bay.
Flindersia pubescens F. M. Bailey, Queensl. Agr. Jour. **3**: 353. 1898. Type: *F. M. Bailey*, October 23, 1883, Queensland, Brisbane (cultivated).

Large trees to 50 m.; outer bark pale brown or gray, generally quite smooth; inner bark white grading to light brown or yellow-brown toward the cambium; sapwood pale yellow; heartwood light brown; branchlets, leaves, and inflorescences glabrous to pubescent with predominantly stellate, usually rust-colored trichomes. Leaves opposite, imparipinnate or (occasional leaves) paripinnate, 19–54 cm. long (the leaves of immature trees generally much larger); rachis glabrate to appressed- or soft-pubescent; petiolules of lateral leaflets usually obsolete, occasionally to 2.5 mm. long, terminal leaflet on an extension of the rachis 1.1–2.7 cm. long; leaflets (4–)5–8 pairs, chartaceous to subcoriaceous, densely pellucid-dotted, glabrate to appressed- or soft-pubescent below, glabrous or short-pubescent along the midrib above, narrowly elliptic to oblong, usually unequal-sided and often falcate, 8–22 cm. long, 1.6–6.3 cm. wide, bases of lateral leaflets narrowly to broadly rounded to cordate oblique, base of terminal leaflet acute to cuneate, main veins 15–22 on each side of the midrib, apex gradually tapering to subacuminate. Inflorescence terminal, to 40 cm. long, generally much wider than long, axes and branches appressed- to soft-pubescent. Flowers bisexual, 4–6 mm. long; pedicels obsolete to 1 mm. long; sepals minutely appressed-pubescent, ciliolate, broadly ovate to suborbicular, 1–1.5 mm. long; petals white, sparsely appressed-pubescent abaxially, villous in the basal one-third to one-half adaxially, elliptic-oblong, 4–6 mm. long; stamens declinate, about 3 mm. long, filaments pilose subapically or (rarely) glabrous, anthers basifixed, bluntly mucronulate, about 1 mm. long; staminodes 1–1.7 mm. long; disc about 1.5 mm. high; gynoecium 2–2.8 mm. high, about 1.5 mm. wide, ovules 3 on each side of the placentae. Capsule separating (or easily separable) into 5 distinct valves at maturity, elliptic to elliptic-oblong, 8–13 cm. long; exocarp drying brown, glabrate to minutely and densely pubescent, muricate, the excrescences rather thick and conical, to 5 mm. long; endocarp reddish brown to light brown. Seeds 3 on each side of the dissepiments, winged at both ends, 5–6 cm. long; hypocotyl lateral, horizontal.

ILLUSTRATIONS. BAILEY, F. M., Comprehensive Cat. Queensl. Pl. *Pl.*

IV. 1913 (as *Flindersia pubescens*). FRANCIS, W. D., Australian Rain-forest Trees 161, 162, 163. 1929; 179, 180, 181, 427 (as *F. pubescens*), 430 (as *F. pubescens*). 1951. MAIDEN, J. H., Forest Fl. New S. Wales 2: *t. 69* & *70*. 1905.



MAP 4. Distribution of *Flindersia schottiana* F. Muell.

DISTRIBUTION. New Guinea and eastern Australia south to the Hastings River, New South Wales; rain forests to 700 meters. See MAP 4.

West New Guinea (West Irian). VOGELKOP DIVISION: Sorong, Rmoe, *Pleyte 703* (L); Sorong, near Kp. Baroe, *Pleyte 737* (BO, L); Mlasoen Hill E of Sorong, *van Royen 3406* (A, L, LAE); Warsamson Valley E of Sorong, *Schram BW 12354* (L, LAE); Kebar Valley, *Koster BW 7121* (L), *Moll BW 9531* (L, LAE), *Schram BW 7921* (L); Sidai, *Schram BW 1752* (CANB, L), *BW 1756* (L), *BW 7607* (L). **Papua.** Western District: Lower Fly River, E bank opposite Sturt Island, *Brass 7991* (A, BRI, L, LAE); Oriomo Creek, mouth of Yakup Creek, 40 miles from sea, *Womersley NGF 17729* (A, BO, K, L, LAE, NSW 99681). Northern District: Bariji-Managalase Area, N side of Sibium Range S of Toma Village, *Pullen 6383* (CANB, L, LAE); 2 miles from Mafo along Ibinamo River toward Mt. Suckling, *Darbyshire 1164* (A, L, LAE, NSW 99603). **Queensland.** Cook District: Cairns, *Bailey* (NSW 99606), *Betche*, August 1901 (NSW 99609, MEL); Trinity Bay, *Hill*, 1876 (BRI, MEL); Rocky Creek, Atherton District, *Bailey*, June 29, 1899 (BRI); Martintown, *Bailey*, June-July 1899 (BRI, MEL); Forest Reserve 185, Juara Creek, near Danbulla, *Fraser 19* (BRI), *Smith 3781* (BRI); Danbulla, *Jones & Pedley 669* (CANB); Kairi, *White*, January 24, 1918 (BRI); Atherton District, *Mocatta* (BRI, MEL); Forestry Reserve 191, Barron, Wongabel, *Forestry Department 1* (BRI), *2* (BRI), *3* (BRI, K). North Kennedy District: Rockingham Bay, *Anonymous* (MEL-holotype of *Flindersia schottiana* F. Muell. var. *pubescens* F. Muell.; BO, BRI, GH-isotypes); Pioneer Creek, *Griffiths* (MEL, NSW 99608); Hinchinbrook Island, *Anonymous* (BRI, MEL); Port Denison, *Fitzalan* (BRI, MEL), *Anonymous* (MEL). South Kennedy District: Cumberland Islands, *Anonymous* (BRI, MEL); Mount Dryander, *Kilner & Fitzalan* (BM, MEL); Dalrymple Heights and vicinity, *Clemens*, June-November 1947 (A, BRI), September-November 1947 (GH, MEL, MICH), November 1947 (GH, MICH); Eungella Range, via Mackay, *Francis*, October 3–12, 1922 (BRI); Cape Hillsborough, ca. 15 miles NW of Mackay, *Bardsley*, November 8, 1967 (BRI). Port Curtis District: Kalpower, *Floyd*, September 5, 1949 (LAE); Baffle Creek District, *White*, April 1920 (BRI). Burnett District: Mt. Perry, *Forestry Department*, October 1921 (BRI). Wide Bay District: near the Hummock, a few miles E of Bundaberg, *Smith 4100* (BRI), *4101* (BRI); Bingera, ca. 10 miles WSW of Bundaberg, *Smith 4125* (BRI); Dundowran, at Saw Mill Scrub, *Tryon*, July, 1928 (BRI); Maryborough District, near Granville Bridge, *Clemens*, November 9, 1948 (BRI, GH, MICH); Wide Bay, *Bidwill 95* (K-lectotype of *Flindersia schottiana* F. Muell.); Fraser Island, *Petrie 31* (BRI); Bauple, *Clemens*, June 13, 1945 (GH), June 10–20, 1945 (MICH); Amamoor, *Moore* in *Swain 337* (BRI); Kin Kin, *Francis*, May 1919 (BRI); Imbil, *Epps*, August 1914 (BRI), *Webb 5019* (CANB); Brooloo, *Webb SN 5339* (CANB), *1635* (CANB). Moreton District: Parish of Monsidale, *Webb SN 5422d* (CANB); Eumundi, 5 miles S of Cooroy, *Bailey & Simmonds*, November 1894 (BRI); Blackall Range, *Twine*, February 1918 (BRI), *White*, April 1918 (BRI); Sawpid Range, *White*, April 1918 (BRI); Norman Creek, Brisbane River, *Cunningham*, 1828–1829 (K); Enoggera Creek, *Bailey 10* (NSW 99611); Three-mile Scrub, near Brisbane, *Shirley* (BRI); Ithaca Creek, Simpson's Scrub Road, *White*, January 1918 (BRI); Brisbane, *Bailey* (NSW 99610); Moreton Bay, *Oldfield* (K); Burleigh Hts., *White*, December 1917 (BRI). Without definite locality: *Wood Technology Dept. Queensland Forest Service 78* (NY), *87* (NY). **New South Wales.** Acacia Creek, via Killarney, Queensland, *Dunn*, June 1905 (NSW 99598); Murwillumbah, *Campbell*, January 1904 (NSW 99600); 5 miles S of Brunswick Heads, *Gray & Gray 3915* (CANB); Potts Point, *Robbins 2612* (CANB); Byron Bay Lighthouse Road, *Constable 6505* (NSW 83976); Richmond River, *Henderson*, November 1886 (MEL, NSW 99597); Clarence and Richmond (rivers), *Northern Woods New South Wales 24* (K, MEL); Whian Whian, *Jones 469* (CANB), *939* (CANB); Casino, *District Forester*, December 1, 1905 (BRI, NSW 99594), *McAuliffe 8338/12* (NSW 99593, US); Tintenbar, *Baeuerlen 633* (BM, MICH, NSW 99602); Clarence River, *Anonymous* (MEL), *Moore 137* (MEL), *Northern Woods New South Wales 61* (K, MEL), *Selwyn* (MEL); Clarence River, Grafton, *Northern Woods New South Wales 63* (NSW 99604), *Squire*, November 1937 (NSW 99595); Mt. Yarrahappini, *Briggs 70.05F* (NSW 99601), *Smith 2* (NSW 99592); lower slopes of Dorrigo Range, *Wheen*, August 29, 1945 (NSW 99596); Taylor's Arm, *Wilshire*, June 2, 1905 (NSW 99605); Bellinger and McLeay Rivers, *Anonymous* (K); McLeay River, *MacDonald 183* (MEL), *Woolls* (MEL); Kempsey, *MacDonald 212* (MEL), *Rudder*, May 17, 1891 (NSW 99591); Hastings River, *Tozer* (*Thozet*?) (NSW 99599). Cultivated. **Java.** Bogor Botanic Gardens, *Anonymous*, 1903 (US). **Queensland.** COOK DISTRICT: Forestry Reserve 310, Gadgarra, *Smith 10824* (BRI). BURKE DISTRICT: Mt. Isa, *Pedley 1060* (BRI). PORT CURTIS DISTRICT: Rockhampton Botanic Gardens, *Simmons 4* (BRI). MORETON DISTRICT: Brisbane Botanic Gardens, *Bailey* (BRI), *Blake 2688* (BRI), *White* (BRI); Kangaroo Point, Brisbane, *Francis* (BO), *White*, November 1912 (BRI); Wickham Reserve, Brisbane, *Bailey*, October 23, 1883 (BRI-holotype of *Flindersia pubescens* F. M. Bailey). **New South Wales.** Sydney Botanic Gardens, *Boorman*, December 1908 (P).

Flindersia pubescens is apparently recognized as a distinct species by many Australian botanists. It is considered to have a rather limited distribution centering on the Cairns area in northeast Queensland whereas *F. schottiana, sensu stricto*, is considered to be wider ranging, extending from New Guinea and north Queensland south to the Hastings River in New South Wales. The morphologic differences between the two are given in the following key from White (1921):

Leaflets on flowering shoots subcoriaceous, somewhat falcate, 6.5–13 cm. long, 2–3.3 cm. broad, quite glabrous on the rachis and under surface clothed with very close and dense stellate, velvety tomentum, veins and veinlets not prominent and often scarcely discernible. ..... *F. schottiana*

Leaflets on the flowering branches chartaceous, 12.5–23 cm. long, 4.5–6.5 cm. broad, rachis densely clothed with comparatively long golden-brown stellate hairs, under surface clothed with numerous but more or less scattered stellate hairs, the veins and veinlets prominent .... *F. pubescens*

After studying a large number of collections from both Australia and New Guinea I am convinced that the differences between these two taxa all break down to a greater or lesser degree and that they represent environmental adaptations of sub-taxonomic significance. Their geographic distributions tend to substantiate this, I think, since both forms occur at widely disjunct localities in New Guinea. For example, *Brass 7991*, from the Fly River and *Pleyte 737*, from the Vogelkop Peninsula, are good matches for typical *F. schottiana*, whereas *Darbyshire 1164*, from the Northern District of Papua, and *Schram BW 12354*, from the Vogelkop Peninsula, are typical of *F. pubescens*.

As indicated above, in the outline to species relationships, *Flindersia schottiana*, *F. bourjotiana*, and *F. xanthoxyla* appear to be more closely related to one another than to any of the other species of the genus. Beyond this, however, the three are mutually quite distinct.

9. **Flindersia bourjotiana** F. Muell. Frag. Phytogr. Austral. **9:** 133. 1875. Type: *Dallachy*, Queensland, Rockingham Bay.

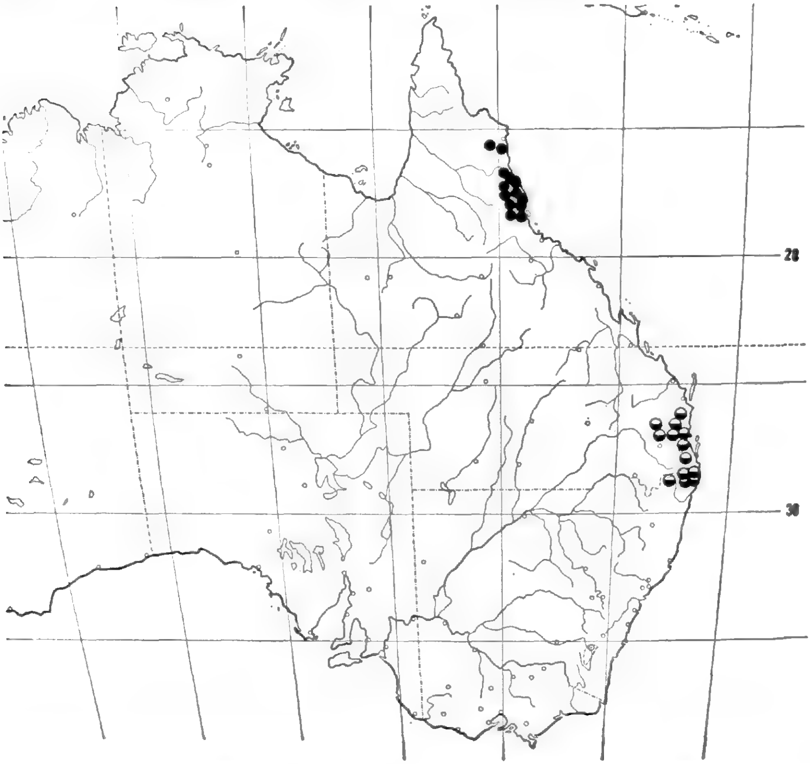
Flindersia tysoni C. DC. Bull. Herb. Boiss. ser. 2. **6:** 986. 1906. Type: *Tryon*, August 1901, Queensland, Mossman River.

Large trees to 35 m.; outer bark gray or brown, rather smooth; inner bark pale yellow-brown; sapwood whitish; heartwood pale yellow-brown; branchlets, leaves, and inflorescences glabrous to pubescent with mostly minute, predominantly stellate trichomes. Leaves opposite, imparipinnate or (occasional leaves) paripinnate, 9–33 cm. long; rachis glabrate to appressed- or velvety-pubescent; petiolules of lateral leaflets 1.5–4 mm. long, terminal leaflet on an extension of the rachis 1–2 cm. long; leaflets (1–)2–4 pairs, chartaceous to subcoriaceous, densely pellucid-dotted, glabrous to rather densely short-pubescent below, glabrous to sparsely appressed-pubescent above, elliptic to lanceolate, equal- or only slightly unequal-sided, 5.5–17 cm. long, 1.5–4.8 cm. wide, base acute to obtuse, main veins 12–17 on each side of the midrib, apex obtuse to acute or occasionally bluntly acuminate. Inflorescence terminal, to 20 cm. long, generally much wider than long, axes and branches sparsely to rather densely short-pubescent. Flowers bisexual or (a few to many flowers in an inflorescence) functionally staminate, 6–10 mm. long; pedicels obsolete to 1 mm. long; sepals glabrate to sparsely appressed-pubescent, ciliolate, broadly ovate to suborbicular, 1–2 mm. long; petals white or greenish white, sparsely appressed-pubescent abaxially, glabrous adaxially, elliptic, 5–9.5 mm. long; stamens declinate, 4–5.7 mm. long, filaments sparsely to rather densely pilose subapically, anthers dorsifixed, mucronate, 1–1.2 mm. long; staminodes 1–2 mm. long; disc thin in bisexual flowers and comparatively thick in functionally staminate flowers, 1–1.5 mm. high; gynoecium in bisexual flowers 2–3 mm. high, about 1.5 mm. wide, ovules 3 on each side of the placentae; gynoecium in functionally staminate flowers poorly differentiated, narrowly conical, about 1 mm. high, without ovules. Capsule separating (or easily separable) into 5 distinct valves at maturity, elliptic, 7–15 cm. long; exocarp drying blackish-reddish brown, glabrous, muricate, excrescences slender, often recurved, to 4 mm. long; endocarp light brown. Seeds 3 on each side of the dissepiments, winged at both ends, about 5.5 cm. long; hypocotyl lateral, ascending.

ILLUSTRATION. FRANCIS, W. D., Australian Rain-forest Trees 426. 1951.

DISTRIBUTION. Northeast Queensland, Cook and North Kennedy Districts; rain forests to 900 meters. See MAP 5.

Queensland. COOK DISTRICT: Mossman River, *Tryon*, August 1901 (BRI, NSW-isotypes of *Flindersia tysoni* C. DC.); near Ayton, *Gittons 575* (BRI 35658); Bailey's Creek Area, *Smith 11556* (BRI); Mt. Lewis, ca. 10 miles N of Mt. Malloy, *Schodde 3326* (CANB); Kuranda, *DuRietz*, August 1927 (BRI); Atherton, *Curry 5* (NY), *Jones 1289A* (CANB), *1289B* (CANB), *Mitchell*, August 1911 (NSW 99683), *Tardent X230* (BRI), *Webb 2502* (CANB); Atherton Table-



MAP 5. Distributions of *Flindersia bourjotiana* F. Muell. (dots) and *F. xanthoxyla* (A. Cunn. ex Hook.) Domin (half-filled circles).

land, *Tardent* (A, BRI); Danbulla, *Fraser 22* (BRI), *Webb 5131* (CANB); Gadgarra, *Dreghorn 12* (BRI), *Kajewski 1140* (A, BM, BRI, NY, US), *Trist 33* (NY); Lake Barrine, *Barnard*, June 15, 1941 (CANB); Glenallan, Malanda, *Tardent 188* (BRI); Ravenshoe, *Manuell 31* (K); Russel River, *Anonymous* (MEL); Innisfail, *Michael 132* (GH), *Petrie* (A); Johnstone River, *Bancroft*, 1885–1886 (BRI, MEL), *Michael*, May 1916 (BRI); Bingil Bay Road, *Gittons 575* (BRI 35542); Etty Bay, *Webb 905* (CANB). NORTH KENNEDY DISTRICT: Herberton, *Mocatta*, February 1917 (BRI); Kirrama Range W of Kennedy, between Society Flat and Yuccabine Creek, *Smith 3205* (BRI); Murray River, *Anonymous*, December 12, 1861 (MEL); Rockingham Bay, *Dallachy* (MEL-holotype of *Flindersia bourjotiana* F. Muell.; BO, MEL-isotypes).

Flindersia tysoni was previously placed in the synonymy of *F. bourjotiana* by White (1921).

10. **Flindersia xanthoxyla** (A. Cunn. ex Hook.) Domin, Bibliot. Bot. 22 (89): 298. 1927.

Oxleya xanthoxyla A. Cunn. ex Hook. in Hooker's Bot. Misc. 1: 246. *t. 54.* 1830. Type: *Cunningham 117*, Queensland, Brisbane River.

Flindersia oxleyana F. Muell. Frag. Phytogr. Austral. 1: 65. 1859 (*nomen illegit.*, based on *Oxleya xanthoxyla* A. Cunn. ex Hook.).

Medium to large trees to 40 m.; outer bark gray or gray-brown, fairly smooth; wood yellow; branchlets, leaves, and inflorescences glabrous to pubescent with mostly minute, predominantly stellate trichomes. Leaves opposite, imparipinnate, 15–32 cm. long; rachis glabrous to appressed- or short-pubescent; petiolules of lateral leaflets obsolete to 6 mm. long, terminal leaflet on an extension of the rachis 0.8–2.8 cm. long; leaflets (2–)3–5 pairs, membranaceous to chartaceous, very brittle when dry, with or without scattered pellucid dots, glabrous to appressed- or soft-pubescent below, glabrous to sparsely appressed-pubescent above, elliptic to lanceolate, usually unequal-sided and often falcate, (2.2–)4–13 cm. long, (0.6–) 1.3–3.2 cm. wide, base obtuse to cuneate, often oblique in lateral leaflets, main veins 11–15 on each side of the midrib, apex long-tapering, acute. Inflorescence terminal, to 25 cm. long, usually much wider than long, axes and branches appressed- to short-pubescent. Flowers bisexual, 4–5 mm. long; pedicels obsolete to 2 mm. long; sepals glabrous to sparsely appressed-pubescent basally, ciliate, broadly ovate, about 1 mm. long; petals pale yellow, glabrous, elliptic-oblong, about 4.3 mm. long; stamens declinate (becoming straight after anthesis), about 3 mm. long, filaments sparsely pilose subapically, anthers dorsifixed, obtuse apically, about 1 mm. long; staminodes about 1.3 mm. long; disc 0.7–1.2 mm. high; gynoecium 1.5 mm. high, about 1 mm. wide, ovules 3 on each side of the placentae. Capsule separating (or easily separable) into 5 distinct valves at maturity, elliptic-oblong, 6.5–11 cm. long; exocarp drying dark brown to pale gray-brown, densely and minutely pubescent, muricate, excrescences rather narrowly conical, unequal in length, to 4 mm. long; endocarp yellow-brown. Seeds (2–)3 on each side of the dissepiments, winged at both ends, 3.3–5 cm. long; hypocotyl lateral, horizontal.

ILLUSTRATIONS. CUNNINGHAM, A., *ibid.* FRANCIS, W. D., Australian Rain-forest Trees 164, 165. 1929 (as *Flindersia oxleyana*); 184, 185. 1951. MAIDEN, J. H., Forest Fl. New S. Wales 2: *t. 73* & *74.* 1906 (as *F. oxleyana*).

DISTRIBUTION. Southeast Queensland and adjacent New South Wales; rain forests to 500 meters. See MAP 5.

Queensland. BURNETT DISTRICT: Edenvale Hill, near Kingaroy, *Michael 3106* (BRI). WIDE BAY DISTRICT: Mary River Scrub, Gympie, *Kenny* (BRI); Imbil, *McAdam 83* (BRI, NY), *85* (A, BRI), *87* (BRI, NY), *Weatherhead*, July 1917 (BRI). MORETON DISTRICT: Parish of Monsidale, *Webb SN 5422c* (CANB); Yarraman, *Clemens*, August 4–15, 1944 (A, NY), *Floyd*, August 29, 1949 (LAE), *Webb 5143* (CANB), *SN 5337* (CANB); South Pine River near Samford, *Hubbard 5941* (A, BRI, K); South Pine River near Bald Hills, *White 7155* (A, BO, NY); Samford Range, *Shirley & White*, April 1918 (BRI); Samford, *Tracey* in *Webb & Tracey 3392* (CANB); Petrie, *Blake 3079* (BRI); Enoggera, *Bailey* (NSW 99643); Three-mile Scrub, Enoggera Creek, *Bancroft* (BRI); Brisbane River below Breakfast Creek Bridge, *Bailey* (BRI, NSW 96644); Brisbane River, *Cunningham 109* (GH), *117* (BM-holotype of *Oxleya xanthoxyla* A. Cunn. ex Hook.; K-isotype), *Hill* (MEL); Sherwood, Brisbane River, *Hubbard 5942* (K), *Anonymous*, December 18, 1930 (BRI); Tamborine Mountain, *Longman & White*, February 1917 (BRI). Without definite locality: *Wood Technology Dept. Queensland Forest Service 80* (NY). **New South Wales.** Acacia Creek via Killarney, Queensland, *Boorman*, February 1905 (NSW 99639), *Dunn*, November 1905 (NSW 99642), *Dunn 252* (NSW 99640); Tweed River, *Anonymous 59* (MEL), *Moore 14125* (BM); Murwillumbah, *Charles*, January 9, 1905 (NSW 96649); Whian Whian, *Jones 943* (CANB), *Webb 2457* (CANB), *5241* (CANB), *White 12769* (BRI); Wollongbar Experimental Farm, Lismore, *Johnson & Constable*, June 11, 1957 (NSW 96650); Tintenbar, *Baeuerlen*, March 1892 (A); Richmond River, *Fawcett* (MEL), *Henderson* (MEL), *Watts*, 1902 (NSW 99641); Richmond River to the Tweed River, *Moore* (BM, GH, K); Hastings River, *Boorman*, August 1907 (P); Sandiland Ranges, *Boorman*, November 1904 (NSW 96646). Without definite locality, *Leichhardt* (K, NSW 99638). Cultivated. **Queensland.** WIDE BAY DISTRICT: Gympie, Wickham and Channon Streets, *Kenny*, January 17, 1907 (BRI). **New South Wales.** Sydney Botanic Gardens, *Boorman*, February 1907 (NSW 96647), *Camfield*, January 1894 (NSW 96648), December 1896 (NY), January 1898 (MEL, US).

11. **Flindersia bennettiana** F. Muell. ex Benth. Fl. Austral. **1**: 389. 1863. Lectotype: *Bidwill*, Queensland, Wide Bay.

Flindersia leichhardtii C. DC. Monogr. Phanerog. **1**: 731. 1878. Type: *Leichhardt*, 1845, Queensland, Moreton Bay.

Small to large trees to 43 m.; outer bark pale gray, to reddish brown, quite smooth; inner bark whitish; branchlets, leaves, and inflorescences glabrous to minutely pubescent with stellate trichomes. Leaves opposite, imparipinnate, 8.5–36(–45) cm. long; rachis glabrous to appressed- or rarely short-pubescent; petiolules of lateral leaflets 1–6 mm. long, terminal leaflet on an extension of the rachis 0.9–3.5 cm. long; leaflets 1–3(–4) pairs, subcoriaceous to coriaceous, densely pellucid-dotted, glabrous or sparsely appressed-pubescent below, glabrous above, ovate to elliptic to elliptic-oblong, equal- or occasionally unequal-sided and subfalcate, 6–18.5 cm. long, 1.7–6.7 cm. wide, base obtuse to subacute, often slightly oblique, veins prominent above, main veins 10–30 on each side of the midrib, apex obtuse or occasionally acute. Inflorescence terminal or occasionally terminal and upper-axillary, to 25 cm. long, as wide or nearly as wide as long, axes and branches appressed- to short-pubescent. Flowers bisexual or (a few to many flowers in an inflorescence) functionally staminate, 3–6 mm. long; pedicels 0.3–3.5 mm. long; sepals sparsely to densely short-pubescent, ciliolate, ovate, 1–1.5 mm. long; petals white, sparsely appressed-pubescent abaxially, glabrous adaxially, elliptic-oblong, 2.5–5 mm. long; stamens declinate, 2.5–4 mm. long, filaments glabrous, anthers dorsifixed, bluntly mucronulate, about 0.9 mm. long; staminodes 1–1.7 mm. long; disc about 1 mm. high; gynoecium in bisexual flowers 2–2.8 mm. high, about 2 mm. wide, ovules 2 on each side of the placentae; gynoecium in functionally staminate flowers poorly differentiated, conical, about 1 mm.

high, without ovules. Capsule separating (or easily separable) into 5 distinct valves at maturity, elliptic to elliptic-oblong, 4–7 cm. long; exocarp drying medium to very dark reddish brown, glabrous, muricate, excrescences narrowly conical, unequal in length to 4 mm. long; endocarp reddish brown. Seeds 2 on each side of the dissepiments, winged at both ends, 3–4.3 cm. long; hypocotyl lateral, horizontal.

Illustrations. Francis, W. D., Australian Rain-forest Trees 168, 169. 1929; 186, 187. 1951. Maiden, J. H., Forest Fl. New S. Wales **3**: *t. 77* & *78*. 1906.

Distribution. Southeast Queensland and northeast New South Wales; rain forests to 300 meters.

Queensland. Wide Bay District: Fraser Island, *Epps 30* (NY), *Forestry Dept. 131* (BRI), *132* (BRI), *133* (BRI), *Hubbard 4403* (K), *Petrie 30* (BRI), *Trist 6* (NY); Dundowran via Gympie, *Tryon*, July 1928 (BRI); Maryborough District, *Young*, September 1916 (BRI), Mt. Bauple, *Kajewski*, September 1922 (A, BRI); Wide Bay, *Bidwill* (K-lectotype of *Flindersia bennettiana* F. Muell. ex Benth.; GH, NY); Gympie, *Hamilton-Kenny 145.05* (NSW 99582); Kin Kin, *Francis* (BRI, NSW 99586); Forest Survey Camp, Amamoor, *Anonymous*, April 22, 1919 (BRI); Imbil, *Floyd*, September 18, 1949 (LAE), *McAdam 90* (A, BRI, NY), *Weatherhead* in *Swain 346* (BRI), *Webb 5013* (CANB). Moreton District: Eumundi, *Bailey*, June 1893 (BRI, NSW 99588), *Simmonds*, June 1895 (A); Candle Mountain, *White*, May 5, 1918 (BRI); Moreton Bay, *Cunningham* (BM), *Hill* (K, MEL), *Leichhardt*, 1845 (P-holotype of *Flindersia leichhardtii* C. DC.); Brisbane, *Boorman*, April 1899 (MEL, NSW 99585), *White*, June 3, 1926 (A, BO, BRI); Mount Cotton, *Scortechini* (BRI, MEL); Tamborine Mountain, *Clemens*, March 1947 (BRI); Beech Mountain, *White 1907* (A, BRI, NSW 99584); Southport, *Simmonds*, June 1913 (A, NY); Meyer's Ferry, Nerang River, *White*, October 20, 1917 (BRI, NSW 99583). Without definite locality: *Bennett* (NSW 99587). **New South Wales.** Tweed River, *Anonymous*, November 1897 (MEL); Tweed River District, *Grime*, July 1900 (NSW 99576); Cudgen, Murwillumbah District, *McKee 9547* (BRI, CANB, NSW 99589); Hastings Point, *Trapnell*, June 7, 1960 (BRI); east foothills of Nightcap Range ca. 2–3 miles SW of Goonengerry, *Schodde & Hayes 3561* (CANB, NSW 99572); Three Mile Scrub, near Byron Bay, *Forsyth*, November 1898 (NSW 99575); Whian Whian State Forest, *Jones 937* (CANB), *Webb 5242* (CANB); Richmond River, *Baeuerlen 244* (MEL), *Boorman*, February 1899 (P), *Fawcett* (MEL), *Henderson 22* (MEL), (BM, BO, MEL, NSW 99573), *Mrs. Hodgk* (MEL); Dalwood, Richmond River, *Graham* in *Watts 37* (MEL, NSW 99579); Richmond and Clarence Districts, *Bennett* (MEL); Minyon Falls, N of Lismore, *de Beuzeville*, July 16, 1936 (NSW 99566); Dorroughby, 14 miles NE of Lismore, *Byrnes*, September 1953 (NSW 99580); Wollongbar Experimental Farm, *Anonymous*, November 1897 (NSW 99570), *Manager Experimental Farm, Wollongbar 6* (NSW 99577); Lismore, *Forest Guard*, March 1909 (NSW 99568), *Baeuerlen 350* (A, NSW 99574), *698* (NSW 99581); Ballina, *Baeuerlen 836* (MEL); 8 miles N of Woodburn, *Williams J43* (NSW 99571); Clarence River, *Beckler* (MEL), *Wilcox*, 1875 (MEL); Iluka, *Cameron 93* (NSW 99567). Cultivated. **New South Wales.** Sydney Botanic Gardens, *Boorman*, September 1919 (BRI, NSW 99578, US), *Camfield*, September 1896 (NY), February 1899 (NSW 99569, US), *Mueller* (NSW

99590); Sydney, Paddington, *Vernon*, March 11, 1879 (MEL). **Victoria.** Melbourne Botanic Gardens, *Anonymous*, October 23, 1934 (MEL).

There is apparently no authentic material of *Flindersia leichhardtii* in the Australian herbaria and it has not previously been placed in the synonymy of *F. bennettiana.*

As is indicated above, *Flindersia bennettiana*, *F. collina*, *F. dissosperma*, and *F. maculosa* comprise a group of related species. They appear to be related to one another in a linear sequence, beginning with a rain-forest species, *F. bennettiana*, and ending with a xerophyte, *F. maculosa.* The following outline shows the apparent relationships of these species as indicated by various morphologic features.

Trichomes stellate; leaves imparipinnate, 8.5–36(45) cm. long, the rachis not winged. .... 11. *F. bennettiana.*

Trichomes stellate and lepidote; leaves imparipinnate or trifoliolate, 5–14 cm. long, the rachis winged. .... 12. *F. collina.*

Trichomes predominantly lepidote; leaves predominantly trifoliolate, 1.5–6.3 cm. long, the rachis winged. .... 13. *F. dissosperma.*

Trichomes predominantly lepidote; leaves 1–9 cm. long, simple. .... 14. *F. maculosa.*

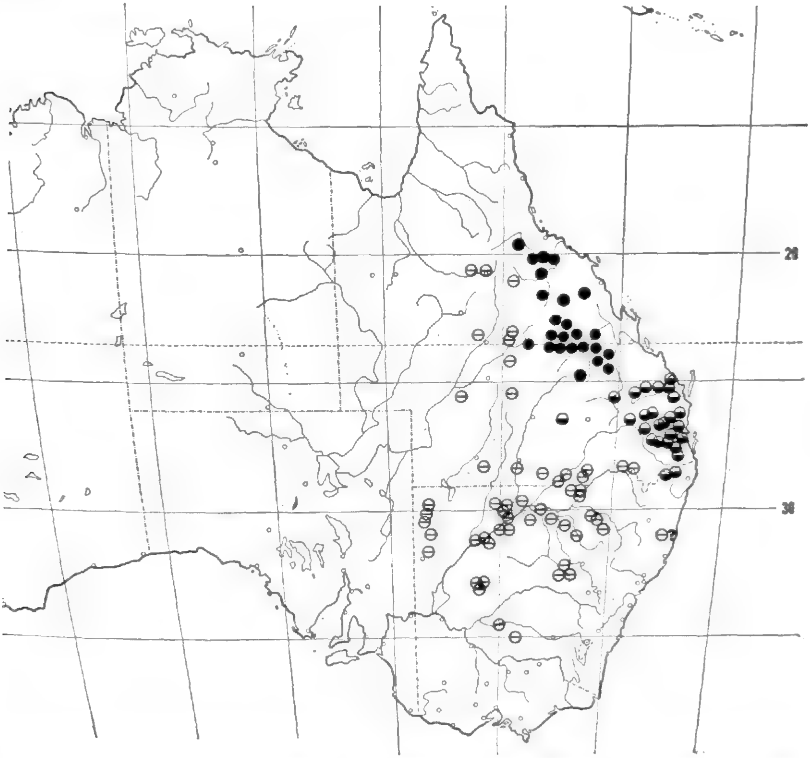
12. **Flindersia collina** F. M. Bailey, Queensl. Agr. Jour. 3: 354. 1898 (based on *Flindersia strzeleckiana* F. Muell. var. *latifolia* F. M. Bailey). Lectotype: *Bailey*, Queensland, Moreton District, Main Range.

Flindersia strzeleckiana F. Muell. var. *latifolia* F. M. Bailey, Synop. Queensl. Fl. 1st suppl. 12. 1886.

Medium to large trees to 40 m.; outer bark mottled, green and brown, exfoliating in thin roundish flakes leaving shallow depressions; inner bark reddish grading to cream toward the cambium; sapwood yellow to yellow-brown; heartwood yellow to pale brown; branchlets, leaves, and inflorescences glabrous to lepidote or minutely pubescent with predominantly scale-like and stellate trichomes. Leaves opposite or subopposite, imparipinnate or trifoliolate, 5–14 cm. long; rachis glabrous to lepidote or appressed-pubescent below, glabrous or short-pubescent above, narrowly to broadly winged laterally, the wings extending 0.3–2.4(–4) mm. on each side; leaflets sessile, 1–2(–3) pairs, chartaceous to coriaceous, with scattered pellucid dots, glabrous or sparsely lepidote or appressed-pubescent below, glabrous above, elliptic to obovate to broadly spatulate, 2–9 cm. long, 1–4.7 cm. wide, base obtuse or (in some terminal leaflets) attenuate, veins prominent above, main veins (10–)12–16 on each side of the midrib, apex obtuse to rounded, usually retuse or emarginate. Inflorescence terminal or terminal and axillary, to 17 cm. long, generally about as wide as long, axes and branches glabrate to short-pubescent. Flowers bisexual or (a few to many flowers in an inflorescence) functionally staminate, 4.7–5.3

mm. long; pedicels 0.5–4.5 mm. long; sepals appressed-pubescent, ciliate, broadly ovate, about 1 mm. long; petals white, glabrate to appressed-pubescent abaxially, short-pubescent in the basal half adaxially, elliptic, 4–5 mm. long; stamens declinate, 3.5–4 mm. long, filaments glabrous, anthers subdorsifixed, subacute apically, about 1 mm. long; staminodes about 2 mm. long; disc about 0.75 mm. high; gynoecium in bisexual flowers about 1.75 mm. high, 1.25 mm. wide, ovules 2 on each side of the placentae; gynoecium in functionally staminate flowers poorly differentiated, conical, about 1 mm. high, without ovules. Capsule separating (or easily separable) at maturity into 5 distinct valves, elliptic to elliptic-oblong, 2.8–5 cm. long; exocarp drying dark brown, glabrous or glabrate, muricate, excrescences 1–2 mm. long; endocarp rather dark brown. Seeds 2 on each side of the dissepiments, winged at both ends, 1.5–2.5 cm. long; hypocotyl lateral, horizontal.

ILLUSTRATIONS. FRANCIS, W. D., Australian Rain-forest Trees 170, 171. 1929; 188, 189. 1951. MAIDEN, J. H., Forest Fl. New S. Wales 3: *t. 81* & *82*. 1907.



MAP 6. Distributions of *Flindersia collina* F. M. Bailey (half-filled circles), *F. dissosperma* (F. Muell.) Domin (dots), and *F. maculosa* (Lindl.) Benth. (open circles with diameter line).

DISTRIBUTION. Southeast Queensland and adjacent New South Wales; rain forests and rather dry scrubs to 700 meters. See MAP 6.

Queensland. LEICHHARDT DISTRICT: Taroom, *Mobsby*, October 1912 (BRI). BURNETT DISTRICT: Eidsvold, *Bancroft*, April 1911 (BRI), April 1923 (A), April 1928 (NSW 99671); Goodnight Scrub, ca. 40 miles SW of Bundaberg, *Smith 9882* (BRI); West Wooroolin, NW of Kingaroy, *Everist*, March 23, 1961 (BRI); Kingaroy, *Smith 3115* (BRI, NY); Nanango, *Grove 131* (BRI); Cooyar and Charlestown, Gympie Forest District, *Swain*, March 1917 (BRI); without definite locality (probably Mt. Perry *fide* L. S. Smith), *Keys(?) 800* (BRI). WIDE BAY DISTRICT: Bundaberg, *Boorman*, July 1912 (NSW 96676); Kepnock, about 2 miles E of Bundaberg, *Smith 4163* (BRI); Childers, *Helms*, January 3, 1899 (BRI), *Anonymous* (NSW 99670); Bauple, *Clemens*, June 10–20, 1945 (GH, MICH); near Imbil, *Smith & Webb 3129* (BRI, CANB). MARANOA DISTRICT: about 20 miles W of Mitchell, *Everist*, March 7, 1950 (BRI). DARLING DOWNS DISTRICT: Chinchilla, *Beasley 52* (BRI); Bunga Mts., *White*, October 1919 (BRI); Rangemore School Area, Cooyar-Bunya Mountains Road, *Smith 10260* (A, BRI, K, NSW 96677); Toowoomba, *Longman*, October 1910 (K, NSW 99675). MORETON DISTRICT: Parish of Monsidale, *Webb SN 5422b* (CANB); Yarraman, *Clemens*, August 1944 (A, BRI, NY, US), *Floyd*, August 28, 1949 (LAE), *Webb SN 5338* (CANB); Kilcoy, *English*, October 1919 (A, BRI); Jimna, near Kilcoy, *Webb 5248* (CANB); Crow's Nest, *Clemens 43641* (A); Main Range, *Bailey* (BRI-lectotype of *Flindersia collina* F. M. Bailey), *Pentecost 29* (BRI, NSW 99669); Flagstone Creek, ca. 8 miles SE of Toowoomba, 7 miles SW of Helidon, *Smith*, October 13, 1965 (BRI); Helidon, *White 8765* (A); Fernvale, ca. 13 miles NW of Ipswich, *Bevington*, 1909 (BRI); Rosewood, *Anonymous*, October 1908 (BRI); Brisbane River, *Cunningham 164* (BM), October 1828 (K, MEL); Moreton Bay, *Cunningham 18* (BM, GH, NY), *Fraser* (K); Kelvin Grove, Brisbane, *White & Francis*, September 1920 (BRI); Marburg Range, western slopes, *Smith & Webb 3700* (BRI); 1 mile N of Boonah on Kalbar Road, *Everist & Webb 1413* (BRI). Without definite locality: *Bowman* (MEL), *Trist 19* (NY). **New South Wales.** Acacia Creek, near Killarney, Queensland, *Boorman 15* (NSW 99673), February 1905 (K), *Dunn*, September 1905 (MEL, NSW 99672), October 1905 (K), February 1906 (NSW 99674); Unumgar, *Jones 2371* (CANB). Without definite locality. *Hill 53* (MEL).

13. **Flindersia dissosperma** (F. Muell.) Domin, Bibliot. Bot. 22 (89): 298. 1927.

Strzeleckya dissosperma F. Muell. in Hooker's Jour. Bot. & Kew Gard. Misc. **9**: 308. 1857. Type. *Mueller*, Queensland, Burdiken River.

Flindersia strzeleckiana F. Muell. Frag. Phytogr. Austral. **1**: 65. 1859 (*nomen illegit.*, based on *Strzeleckya dissosperma* F. Muell.).

Small trees to 10 m., developing from a divaricately branched shrub stage; outer bark mottled, dark gray and white, cream or salmon, rough-scaly on the trunk, smooth above; inner bark reddish grading to cream toward the cambium; branchlets, leaves, and inflorescences glabrous to lepidote or minutely pubescent with scale-like and stellate trichomes. Leaves opposite, imparipinnate or trifoliolate, or (rare occasional leaves) simple, (0.8–)1.5–6.3 cm. long; rachis sparsely lepidote below, winged laterally, the wings extending 0.5–1.5 mm. on each side; leaflets sessile, 1–2 pairs, chartaceous to subcoriaceous, with scattered pellucid dots, sparsely lepidote below, glabrous above, elliptic, spatulate, oblong or sublinear, 0.6–3.7 cm. long, 0.2–0.7 cm. wide, base obtuse, main veins usually indiscernible, 8–10 on each side of the midrib, apex rounded to acute, occasionally retuse. Inflorescence terminal or rarely terminal and upper-axillary, to 8 cm. long, usually nearly as wide as long, axes and branches sparsely to rather densely lepidote to appressed- or short-pubescent. Flowers bisexual or (a few to many or all of the flowers in an inflorescence) functionally staminate, 3–4 mm. long; pedicels 0.7–2 mm. long; sepals glabrous or glabrate, ciliate, suborbicular, 1–1.3 mm. long; petals white to cream, glabrous, broadly elliptic, 3–3.5 mm. long; stamens inflexed apically, about 2.5 mm. long, filaments glabrous, anthers subdorsifixed, bluntly mucronulate, about 1 mm. long; staminodes 0.5–1 mm. long; disc about 0.5 mm. high; gynoecium in bisexual flowers about 1.5 mm. high and 1 mm. wide, ovules 2 on each side of the placentae; gynoecium in functionally staminate flowers poorly differentiated, pulvinate, about 0.4 mm. high, without ovules. Capsule separating (or easily separable) into 5 distinct valves at maturity, elliptic, 2–3 cm. long; exocarp drying dark reddish brown, glabrous, muricate, the excrescences 1–2 mm. long; endocarp brown. Seeds 2 on each side of the dissepiments, winged at both ends, 1.5–1.8 cm. long; hypocotyl lateral, horizontal.

ILLUSTRATION. BAILEY, F. M., Comprehensive Cat. Queensl. Pl. *t. 73.* 1913 (as *Flindersia strzeleckiana*).

DISTRIBUTION. East central Queensland; dry scrubs to 300 meters. See MAP 6.

Queensland. NORTH KENNEDY DISTRICT: Maryvale Station, *Daintree* (MEL); W of Charters Towers, *Blake 14906* (BRI); Charters Towers, *Michael 1275* (BRI), *Stephens North Queensl. Nat. Club 10468* (NSW 99689); Millchester Hill, *Stephens North Queensl. Nat. Club 9056* (BRI); Burdiken, *Kennelly 208* (CANB), *Mueller* (MEL-holotype of *Strzeleckya dissosperma* F. Muell.; K-isotype); Herbert's Creek, *Bowman 70* (MEL); near Bogie Range, lower Burdekin River, ca. 42 miles S of Ayr, *Smith 4532* (BRI); Cape River, *Daintree* (MEL), *Fitzalan* (MEL). SOUTH KENNEDY DISTRICT: Head of Suttor River, *Sutherland* (MEL); Laglan, about 80 miles W of Clermont, *Everist*, October 12, 1960 (BRI, K); 18 miles ENE of Surbiton Station, *Adams 1317* (CANB). MITCHELL DISTRICT: Jericho, *Clemens*, March 13, 1946 (GH, MICH), May 1, 1946 (MICH), *Francis*, March 1920 (BRI). LEICHHARDT DISTRICT: Peak Downs, *Mueller* (MEL); 9 miles SW of Anakie, *Adams 1281* (CANB, MEL, NSW 99685); E of Emerald, *Webb 2251* (CANB); Emerald, *Webb SN 5296* (CANB); Blair Athol, *Massey 30* (BRI); ca. 3 miles N of Clermont on road to Charters Towers, *Smith 3160* (BRI); Clermont, *Small*, September 1912 (BRI, K, NSW 99621); Chirnside, ca. 6 miles S of Capella, *Smith & Webb 3428* (BRI); 2 miles N of Emerald, *Bisset E198* (BRI); 4 miles E of Girrah Homestead, 36 miles N of Blackwater Township, *Lazarides & Story 70* (K, NSW 99690, NY); Blackwater, *Anderson*, October 1967 (BRI); 7 miles N of Goowarra, *Anderson*, October 15, 1965 (BRI); about 3 miles E of Goowarra, *Johnson 943* (A, BRI); 3 miles E of Parkes Homestead, *Speck 1672* (CANB, NSW 99686); Dingo, *O'Shanesy 2013* (MEL); 8.5 miles SW of Duaringa, *Speck 1820* (BRI, CANB, NSW 99687); near Duaringa, *Simmons*, May 1938 (BRI); between the Barcoo and Springsure, *Bailey* (MEL). Without definite locality: *Bailey* (BRI, NSW 99688), *Fitzalan* (MEL).

14. **Flindersia maculosa** (Lindl.) Benth. Fl. Austral. **1**: 389. 1863.

Elaeodendron maculosum Lindl. in Mitchell Trop. Austral. 384. 1848. Type: *Mitchell*, November 1846, New South Wales, Balonne River.

Flindersia maculata F. Muell. Quart. Jour. Trans. Pharm. Soc. Victoria **2**: 44. 1859 (*nomen illegit.*, based on *Elaeodendron maculosum* Lindl.).

Small to medium trees to 15 m., developing from a divaricately branched shrub stage; outer bark mottled, dark gray or brown and cream or white, smooth-scaly on the trunk, smooth above; wood yellow; branchlets, leaves and inflorescences glabrous to lepidote or minutely pubescent with scale-like and stellate trichomes. Leaves opposite, simple; petioles lepidote below, short-pubescent above, 1–12 mm. long; leaf blades chartaceous to subcoriaceous, with scattered pellucid dots, minutely and sparsely lepidote and appressed-pubescent below, glabrous or short-pubescent on the midrib above, narrowly elliptic-oblong, oblanceolate or sublinear, 1–8 cm. long, 0.25–1 cm. wide, base narrowly obtuse to attenuate, main veins usually indiscernible, 12–17 on each side of the midrib, apex rounded to obtuse, occasionally retuse. Inflorescence terminal or rarely terminal and upper-axillary, to 7.5 cm. long, usually about as wide as long, axes and branches sparsely to densely lepidote to appressed- or short-pubescent. Flowers bisexual, 4–4.5 mm. long; pedicels obsolete to 2.5 mm. long; sepals glabrous, ciliate, broadly ovate to orbicular, 1–1.5 mm. long; petals white to cream, glabrous, obovate, about 4 mm. long; stamens inflexed apically, about 3 mm. long, filaments glabrous, anthers subdorsifixed, obtuse to bluntly mucronulate, 1–1.2 mm. long; staminodes about 0.5 mm. long; disc about 0.75 mm. high; gynoecium about 1.5 mm. high and 1 mm. wide, ovules 2 on each side of the placentae. Capsule separating (or easily separable) into 5 distinct valves at maturity, elliptic, 2.3–2.7 cm. long; exocarp drying dark reddish brown, glabrous, muricate, the excrescences 1–1.5 mm. long; endocarp brown. Seeds 2 on each side of the dissepiments, winged at both ends, about 1.8 cm. long; hypocotyl lateral, horizontal.

ILLUSTRATIONS. BAILEY, F. M., Comprehensive Cat. Queensl. Pl. *t. 73 bis*. 1913. MAIDEN, J. H., Forest Fl. New S. Wales **1**: 213. *t. 39*. 1904.

DISTRIBUTION. Central Queensland south to southcentral New South Wales; dry, rather open places. See MAP 6.

Queensland. BURKE DISTRICT: 57 miles W of Hughenden, *McCray*, September 21, 1967 (BRI); Hughenden, *Brass & White 63* (A, BO, BRI, K). MITCHELL DISTRICT: Tiree Station, about 68 miles S of Torrens Creek, *Ford*, September 28, 1949 (K, NSW 10258, US); Evesham, between Longreach & Winton, *Everist & White 134* (BRI); Aramac, *Paulton* (MEL); Barcaldine, *Francis*, March 1920 (BRI); between Emerald and Longreach, *Jarvis*, October 1913 (BRI); Blackall, *Bailey* (NSW 99620), *Everist 1562* (A, BRI), *White 12387* (A, K, US). Gregory South District: Thylungra, about 75 miles NW of Quilpie, *Everist 5787* (BRI). Warrego District: about 19 miles N of Thargomindah, *Smith 6346* (BRI); about 34 miles N of Charleville on Ward River Road, *Smith 841* (A, BRI, K, MEL, NY); between Cunnamulla and Wyandra, *Key*, October 1940 (CANB); near Cunnamulla, *White 11782* (BRI). Maranoa District: Maranoa, *Anonymous* (MEL); Bollon Area, *Epps*, June 26, 1953 (BRI); 10 miles N of Dirranbandi, *Key*, October 17, 1937 (CANB); Buckinbah, near St. George, *Jones 215* (BRI); St. George, *Wedd*, December 1893 (BRI); Nindigully District, *Anonymous*, November 1938 (CANB); Warrie, Nindigully, *Allen A547* (CANB), *Roe R10* (CANB), October 1937 (CANB). Darling Downs District: 36 miles W of Goondiwindi on Talwood Road, *Webb SN 5319a* (CANB), *SN 5319b* (CANB), *SN 5319c* (CANB), *SN 5319d* (CANB); Goondiwindi District, *Jones C50* (CANB), *Webb 1611* (CANB), *2498* (CANB). **New South Wales.** Yantara Lake, *Anonymous 385* (MEL); E of Broken Hill, *Pidgeon & Vickery*, August 1939 (NSW 99617); Koonenberry Mountains, ca. 62 miles SSE of Milparinka, *Constable 4609* (NSW 64979), *V. E. Expedition* (MEL); Mount Hope Station, 3 miles N of White Cliffs, *Constable 4595* (NSW 67368); Wonominta River, *Kennedy*, January 1887 (MEL); Wilcannia, *Johnson 547/90* (NSW 5181), *Kennedy*, 1886 (MEL); about 12 miles S of Wilcannia, *Hogan*, October 1955 (MEL); between Wilcannia and Cobar, *Campbell 109* (CANB); 30 miles E of Wilcannia, *Riek & Common 322* (CANB); above Morinda (Menindee) and Mt. Murchinson (Murchiston), *Anonymous* (MEL); Menindee District, Neila-garri Station, *Constable*, November 20, 1947 (NSW 4879); Mt. Murchinson, *Anonymous* (MEL), *Dallachy* (BM, GH, K, NY), *Dallachy & Goodwin* (MEL); Darling River, *Anonymous* (MEL), *Dallachy* (BM), *Kennedy*, 1866 (MEL); about 1 mile E of Ivanhoe, *Johnson*, May 6, 1955 (NSW 99615); Mossgiel, *Bruckner*, October 1885 (MEL), *Mueller* (GH); between the Lachlan River and Darling River, *Bruckner*, 1885 (MEL), *Mueller* (P); Lachlan River, *Tucker* (MEL); Upper Lachlan River, *Curran 21* (MEL); 11 miles from Ivanhoe on Paddington Road, *Whaite 1388* (NSW 99616); between Kirriby and Lauradale, Warego River to Paroo River, *Boorman*, October 1912 (BRI, NSW 99619, US); near Morton Boolka, *Morris 766* (NSW 99618); Barringun, *Foyster*, 1884 (MEL); Bourke, *Betche*, November 1887 (NSW 99623), *McDougall*, 1901 (NSW 99613), *Wuerfel*, 1884 (MEL); Clover Creek, Bourke, *Mackay 112* (MEL); 20 miles SE of Bourke, *Riek & Common 132* (CANB); 40 miles S of Bourke, *Leigh*, ca. November 1967 (NSW 99632); Dunlop Station, ca. 8 miles S of Louth, *Etheridge 28* (NSW 99622); Cobar, 4 mile, Wilcannia Road, *Forestry Officer 24* (NSW 99629); between the Bogan and Darling Rivers, *Morton 77* (MEL); Bogan River, *Anonymous* (MEL); Bogan, *Morton*, 1880 (MEL); W of Nevertire, *Clarke*, June 14, 1944 (CANB); Castlereagh River, *Anonymous 8* (MEL); 40 to 50 miles NW of Collarenebri, *Jackson*, October 1911 (NSW 99628); Balonne River, St. George's Bridge (ca. 25 miles W of Mungindi), *Mitchell*, November 1846 (K-holotype of *Elaeodendron maculosum* Lindl.; NSW 99612-isotype); Brewarrina, *Boorman*, November 1903 (GH, NSW 99630, NY, US); Yarrawin Station, Barwon River, 30 miles SE of Brewarrina, *Froggatt 16* (NSW 99627); Carinda, ca. 40 miles SW of Walgett, *Bucknell & Lowe*, August 1965 (NSW 99631); Pilliga, *Rupp 13* (NSW 99625); Pilliga Scrub, *Anonymous*, November 1932 (MEL); between Pilliga and Wee Waa, *Bassett*, November 14, 1947 (NSW 99626); plains near Baradine, *Forsyth*, October 1899 (NSW 99624); Ellenborough Falls(?), *Boorman*, 1904 (A, P, US); Murrumbidgee River, *Bennett 3* (MEL); Cobar to Riverina Districts, *Anonymous* (MEL); Riverina, *Morton*, 1880 (MEL). Without definite locality. *Bidwill 74* (K), *Anonymous* (NSW 99614).

15. **Flindersia ifflaiana** F. Muell. Frag. Phytogr. Austral. **10**: 94. 1877. Type: *Hill*, Queensland, Trinity Bay.

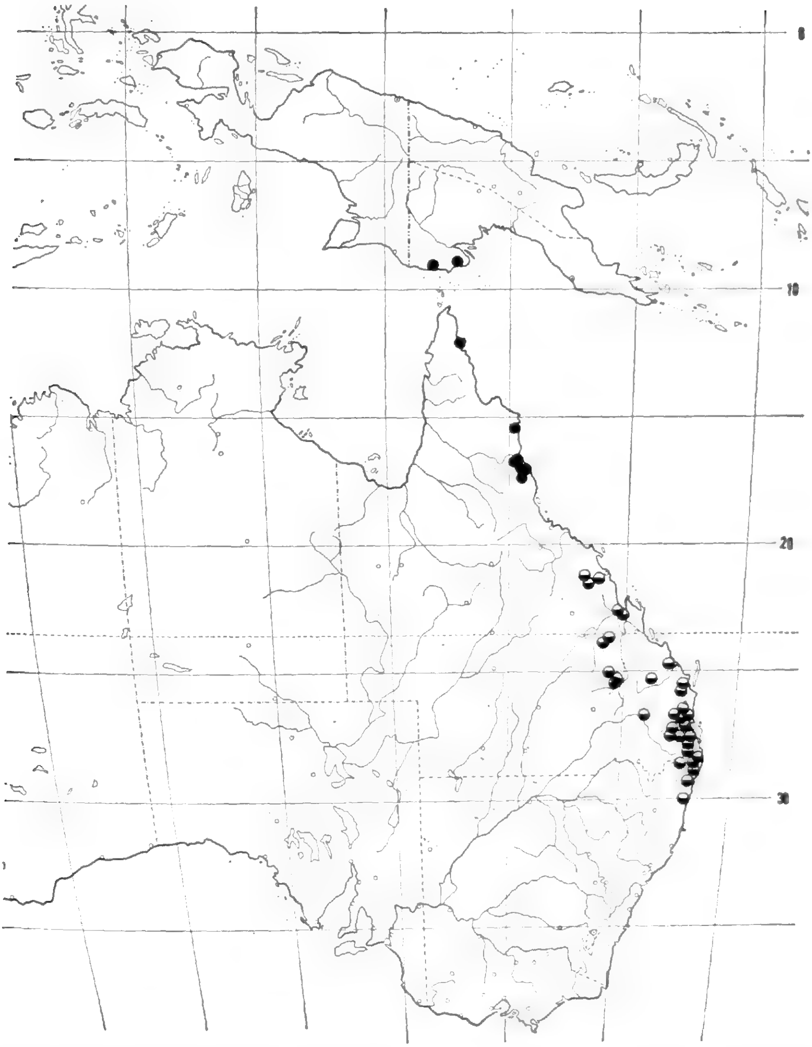
Flindersia brachycarpa Merr. & Perry, Jour. Arnold Arb. **20:** 332. 1939. Type: *Brass 8389*, Papua, Wassi Kussa River.

Medium trees to 35 m.; outer bark gray-brown, thick, deeply longitudinally fissured; inner bark red, grading to cream toward the cambium; sapwood yellow or yellow-brown; heartwood yellow-brown or brown; branchlets, inflorescences, and capsules glabrous to pubescent with mostly minute, predominantly stellate trichomes. Leaves opposite, paripinnate, 15–34 cm. long; rachis glabrous; petiolules 4–9 mm. long; leaflets 3–6 pairs, chartaceous to subcoriaceous, densely pellucid-dotted, glabrous, ovate-elliptic, elliptic, elliptic-lanceolate, or occasionally lanceolate, usually unequal-sided and often subfalcate, 6–13.5 cm. long, 2.8–5.2 cm. wide, base rounded to subcuneate, often slightly oblique, main veins 14–22 on each side of the midrib, apex rounded to narrowly obtuse, rarely subacuminate. Inflorescence terminal or terminal and upper-axillary, 14–25 cm. long, usually as wide as long or somewhat wider, axes and branches glabrate to appressed- or short-pubescent. Flowers bisexual or (a few to many flowers in an inflorescence) functionally staminate, 2.5–3 mm. long; pedicels 0.5–2.5 mm. long; sepals sparsely appressed-pubescent, ciliolate, ovate-triangular, 1–1.2 mm. long; petals white, sparsely appressed-pubescent abaxially, glabrous or with a few papillae adaxially, elliptic to elliptic-oblong, 2–2.5 mm. long; stamens inflexed apically, about 1 mm. long, filaments glabrous, anthers subdorsifixed, bluntly mucronulate, about 0.5 mm. long; staminodes 0.5 mm. long; disc about 0.7 mm. high; gynoecium in bisexual flowers about 1.5 mm. high, about 1 mm. wide, ovules 2 on each side of the placentae; gynoecium in functionally staminate flowers poorly differentiated, turbinate, about 0.5 mm. high, without ovules. Capsule comparatively woody and heavy, separating to one-half or more of the length but not completely, rounded short-cylindric, 3.2–5.5 cm. long; exocarp drying blackish brown to reddish brown, densely and minutely pubescent, often cracked with age, muricate, the excrescences rather widely spaced, to 2 mm. long; endocarp reddish brown. Seeds 2 on each side of the dissepiments, winged at the apical end only, 2.7–3.3 cm. long; hypocotyl lateral, ascending.

ILLUSTRATION. FRANCIS, W. D., Australian Rain-forest Trees 426. 1951.

DISTRIBUTION. Southern Papua south to the Atherton Tableland, Queensland; rain forests to 400 meters. See MAP 7.

Papua. WESTERN DISTRICT: Tarara, Wassi Kussa River, *Brass 8389* (A-holotype of *Flindersia brachycarpa* Merr. & Perry; BRI, L, LAE-isotypes); Oriomo Creek, mouth of Yakup Creek, 40 miles from sea, *Womersley NGF 17728* (A,



MAP 7. Distributions of *Flindersia ifflaiana* F. Muell. (dots) and *F. australis* R. Br. (half-filled circles).

BO, K, L, LAE, NSW 99667). **Queensland.** COOK DISTRICT: Cape York Peninsula, Cape Grenville, *Young 64* (BRI); Endeavour River, *Parsieh*(?) (MEL); mountains near Mossman, *Rosenstrom* (BRI); Great Dividing Range ca. 6 miles S of Mossman, *Smith 3964* (BRI); Mt. Molloy, *Crothers*, 1934 (A, BO, BRI, NY); Barron River, *Anonymous 46* (MEL); Forestry Reserve 1073, N of Kuranda, *Dansie 1995* (BRI, K), *1996* (BRI), *2008* (BRI); Timber Reserve 315, Smithfield, Kuranda, *Doggrell A36* (BRI); Black Mountain near Kuranda, *Jones 800* (CANB), *1511* (CANB), *Webb 5189* (CANB); a few miles N of Kuranda, *Smith*

5309 (BRI); Trinity Bay, *Hill* (MEL-holotype of *Flindersia ifflaiana* F. Muell.; K-isotype); Cairns, *Bailey* (NSW 99684); Freshwater Creek, *Bailey* (BRI); Kamerunga, *Cowley 43* (BRI); Edge Hill, near Cairns, *Morris North Queensl. Nat. Club 4084* (BRI); Redlynch, near Cairns, *White 12813* (A, NY); Atherton Area, *Webb 2547* (CANB), *5208* (CANB). Without definite locality: *Anonymous 10* (BRI), *Wood Technology Dept. Queensland Forest Service 91* (A, NY). Cultivated. **Queensland:** COOK DISTRICT, Cairns, on esplanade, *White*, February 1918 (BRI).

In the original description of *Flindersia brachycarpa*, Merrill and Perry stated that it strongly resembled *F. ifflaiana* but differed ". . . . . in having larger leaves with the leaflets strongly oblique at the base and more acute at the apex, and a little larger fruits." These have proven to be quite variable characters in many species of *Flindersia* and now, with additional collections available, it is evident that they do not serve to distinguish *F. brachycarpa* from *F. ifflaiana.*

As is pointed out above, *Flindersia ifflaiana* is apparently more closely related to *F. australis* than to any of the other species of the genus. The two do not appear to be particularly closely related, however. The leaves of *F. ifflaiana* are opposite and paripinnate whereas those of *F. australis* are usually alternate and basically imparipinnate. Additional differences are given in the key to species.

16. **Flindersia australis** R. Br. in Flinders' Voyage 2: 595. *t. 1.* 1814.
Type: *Brown*, September, 1802, Queensland, Broad Sound.

Medium trees to 25 m.; outer bark gray to brown, smooth or with shallow longitudinal fissures, often exfoliating in flakes; inner bark reddish; branchlets, leaves, inflorescences, and capsules glabrous to pubescent with mostly minute, predominantly stellate trichomes. Leaves alternate, subopposite or opposite, in mature growth closely crowded at the branchlet apices, imparipinnate or (occasional leaves) paripinnate, (5.5–)9–34 cm. long; rachis glabrous to densely appressed-pubescent, near the base often narrowly crisped-winged laterally; petiolules of lateral leaflets obsolete to 3(–5) mm. long, terminal leaflet sessile or on an extension of the rachis to 3.2 cm. long; leaflets 2–4(–6) pairs, chartaceous to subcoriaceous, with scattered pellucid dots, glabrous to densely appressed-pubescent below, glabrous or sparsely short-pubescent on the midrib above, broadly to narrowly elliptic to occasionally lanceolate, equal- or slightly unequal-sided, (2.4–)3–12 cm. long, (0.8–)1.5–4.3 cm. wide, bases of lateral leaflets obtuse to cuneate, base of terminal leaflet obtuse to attenuate, main veins 8–18 on each side of the midrib, apex obtuse to acute or subacuminate, occasionally rounded. Inflorescence terminal or terminal and upper-axillary, often on leafless branchlets, to 15 cm. long, about as wide as long, axes and branches rather sparsely to densely pubescent. Flowers bisexual or (a few to many flowers in an inflorescence) functionally staminate, 6.5–7.5 mm. long; pedicels 0.2–1 mm. long; sepals densely appressed-pubescent, irregularly ciliate, ovate-triangular, 2.2–2.5 mm. long; petals white to cream, densely appressed-pubescent (except for the margins) abaxially, sparsely short-pubescent in the basal one-half to two-thirds adaxially, elliptic-oblong, 6–7 mm. long; stamens declinate, 3.5–4.5 mm. long, filaments glabrous or with a few papillae and/or crisped trichomes subapically, anthers subdorsifixed, mucronate, 1–1.3 mm. long; staminodes 1.5 mm. long; disc in bisexual flowers rather thin, about 1.5 mm. high; disc in functionally staminate flowers comparatively thick, about 1 mm. high; gynoecium in bisexual flowers about 3 mm. high, and 1.4 mm. wide, ovules 2 on each side of the placentae; gynoecium in functionally staminate flowers poorly differentiated, conical, about 0.6 mm. high, without ovules. Capsule comparatively woody and heavy, separating to one-half or more of its length but not completely, rounded short-cylindric, 4.6–9 cm. long; surface of exocarp drying blackish, reddish brown, or pale brown, densely and minutely pubescent, muricate, the excrescences rather densely crowded, often recurved, to 10 mm. long; inner part of exocarp very rough where exposed by dehiscence; endocarp cream, yellowish, or pale brown. Seeds 2 on each side of the dissepiments, winged at the apical end only, 3.4–5 cm. long; hypocotyl lateral, horizontal.

ILLUSTRATIONS. BROWN, R., *ibid.* FRANCIS, W. D., Australian Rainforest Trees 158, 159. 1929; 176, 177. 1951. MAIDEN, J. H., Forest Fl. New S. Wales **2**: *t. 67* & *68.* 1905.

DISTRIBUTION. Eastcentral Queensland south to northeastern New South Wales; rain forests and rather dry thickets. See MAP 7.

Queensland. SOUTH KENNEDY DISTRICT: Pinevale via Mackay, *Webb & Tracey 3319* (BRI). LEICHHARDT DISTRICT: Lake Elphinstone, *Dietrich* (MEL); Morambah Homestead, 43 miles SW of Nebo Township, *Story & Yapp 121* (BRI, K, MEL); 4.6 miles SW of Duaringa, *Speck 1670* (CANB); Coomooboolaroo, *Berney* 1919 (BRI); Expedition Range, *Byerly* (MEL); 36 miles WSW of Theodore Township, *Lazarides 6928* (BRI, K); 18 miles N of Taroom, *Speck 1861* (BRI, CANB, K). PORT CURTIS DISTRICT: Broad Sound, *Brown*, September 1802 (K-holotype; BM, MEL, P-isotypes); near Ogmore, ca. 75 miles NW of Rockhampton, *Smith*, October 18, 1951 (BRI); Rockhampton, *Thozet* (MEL). BURNETT DISTRICT: Eidsvold, *Bancroft*, April 1912 (BRI). WIDE BAY DISTRICT: Kolan River, Smith's Crossing, ca. 14 miles WNW of Bundaberg, *Smith 4159* (BRI); Maryborough, *Clemens*, October 27, 1948 (BRI, GH, MICH); Mt. Bauple, *Clemens*, June 10–20, 1945 (MICH); Imbil, *McAdam 84* (A, BRI); Cooroy, *Douglas*, November 2, 1962 (BRI). DARLING DOWNS DISTRICT: Chinchilla, *Beasley 51* (BRI). MORETON DISTRICT: Yarraman, *Floyd*, August 29, 1949 (LAE); Coal Creek, *Shirley* (BRI); Parish of Monsidale, *Webb SN 5422a* (CANB); Jimna via Kilcoy, *Webb 5247* (CANB); Main Range, *Pentecost 26* (BRI); Rosewood, *Marquis* (BRI); North Pine River, at Draper's Crossing, *White 8696* (A, BRI); Samford, *Meebold 7999* (NY); Brisbane River, *Cunningham 60* (K), *Mueller*, July, 1855 (MEL), *White*, November 1917 (BRI, NSW 99565); Cedar Creek, near Brisbane, *White 1942* (A); near Brisbane, *Bailey* (NSW 99561); Albert River, W of Mt. Stapylton, ca. 21 miles SE of Brisbane, *Smith 5151* (BRI); Logan River at Mt. Stapylton, *Wilson 635* (BRI, US); Mt. Tamborine, *Clemens*, March 1947 (GH). Without definite locality: *Hill 12* (K). **New South Wales.** New England, *Law* (MEL); Unumgar, *Jones 2367* (CANB); Murwillumbah, *Charles 458.04* (NSW 99562); Whian Whian State Forest, *Webb & Tracey 378* (CANB), 1953–1958 (BRI); Rous, near Lismore, *Cheel*, September 1926 (NSW 99560); Richmond River, *Cameron* (MEL), *Fawcett* (MEL), *Henderson* (MEL), *Hodgkington* (MEL); Clarence River, *Moore* (MEL), *Beckler* (MEL); Kempsey, *MacDonald*, October 3, 1895 (MEL). Cultivated. **Queensland:** Brisbane Botanic Gardens, *Bailey*, November 11, 1884 (BRI), *Blake 2797* (BRI), *Hubbard 4745* (K), *White 2442* (K). **New South Wales:** Sydney Botanic Gardens, *Boorman*, October 1920 (NY, US), November 1920 (NSW 99563).

EXCLUDED NAMES

FLINDERSIA GREAVESII C. Moore, Cat. Nat. Industr. Prod. New S. Wales 53. 1861.

This name appeared in the "indigenous woods" section of a catalogue that accompanied an exhibit. Several other timber species were listed, each represented, apparently, by a wood sample. The description follows:

> A magnificent tree, the monarch of the northern forests, attaining a height of 150 feet, 3 to 6 feet in diameter, distinguishable from every other species of the genus by its dark brown and rough scaly bark, as well as by other characters; timber used for house building purposes. Mountain brushes on the Clarence [River, New South Wales].

The wood sample has apparently been lost, but an herbarium specimen at Sydney (NSW 99604), labelled *Flindersia greavesii* by Moore and bearing the number *63*, which corresponds to the number of that species in the catalogue, could be designated as the type collection.

The only really diagnostic statement in Moore's description is that pertaining to the bark, which would almost certainly apply to *Flindersia australis*. The specimen mentioned above, however, clearly matches *F. schottiana* (published a year later), a species with relatively smooth bark.

Maiden (Forest Fl. New S. Wales 2: 152. 1905) listed *Flindersia greavesii* as a synonym of *F. australis* and also designated it as a *nomen nudum*. He concluded, as I have, that the description referred to *F. australis* and that the type collection referred to *F. schottiana*. In addition, he pointed out that a tree in the Sydney Botanic Gardens, labelled by Moore as *F. greavesii*, is really *F. australis* and that Mr. W. A. B. Greaves, after whom the tree was named, gave him a fruit which he stated was that of *F. greavesii* and that it actually was *F. australis*.

Moore must have realized his error, too, since he did not mention *Flindersia greavesii* in his *Census of the plants of New South Wales* (1884) or in his *Handbook of the flora of New South Wales* (1893). *Flindersia australis* and *F. schottiana* were both mentioned in these publications.

Although I do not think *Flindersia greavesii* can be discounted as a *nomen nudum*, I think this name should be excluded since the description and the type collection clearly refer to two different species.

Flindersia papuana F. Muell. Descript. Notes Papuan Pl. 1(5): 84. 1877. Type: *D'Albertis,* Fly River, Papua (not seen).

Mueller named this species from a single immature fruit and stated that it was ". . . just a temporary name for the Papuan plant to place it on the record until foliage and flowers can be obtained." Thus it is a provisional name and is not validly published.

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The numbers in parentheses refer to the corresponding species and varieties in the text.

Iwanggin *BW 5645*, *BW 5780* (6); *BW 5889* (4); *BW 10054* (6)

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Johnson, R. W., *943* (13)
Jones, R., *215* (14)
Jones, W. T., *C50* (14); *469* (8); *800* (15); *937* (11); *939* (8); *943* (10); *1116* (2a); *1117* (4); *1284* (7); *1289A*, *1289B* (9); *1511* (15); *2094* (3); *2367* (16); *2371* (12)
Jones, W. T., & Pedley *669* (8)

Kajewski *1114* (4); *1140* (9)
Kalkman *BW 3566* (2b); *BW 6454* (6)
Kanehira & Hatusima *12738*, *13017* (2b)
Kennelly *208* (13)
Keys(?) *800* (12)
Koster *BW 1495*, *BW 4350*, *BW 4359*, *BW 4388*, *BW 4395*, *BW 4433*, *BW 4470*, *BW 4474*, *BW 4497*, *BW 7062*, *BW 7116* (6); *BW 7121* (8); *BW 8064*, *BW 8074*, *BW 10786* (4); *BW 11059*, *BW 11890* (6); *BW 13797* (4)
Kostermans *321*, *337*, *348*, *481* (6)

Lane-Poole *362* (6); *382* (4)
Lazarides *6928* (16)
Lazarides & Story *70* (13)
Ledermann *9825* (4); *10406* (6)

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Mackay *112* (14)
Malessij *NIFS bb 14381* (2b)
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Manuell *31* (9)
Martin & Hyland *1881* (5)
Massey *30* (13)
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Morris, F. R., *North Qld. Nat. Club 4084* (15)
Morton *77* (14)

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Netherlands Indies Forest Service (*NIFS*), the following by anonymous collectors: *bb 15459*, *bb 22301* (2b); *bb 24346*, *bb 25298*, *bb 25322*, *bb 25443*, *bb 25869*, *bb 30424* (6); *bb 30466*, *bb 30526* (4); *bb 32680* (6)
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ARNOLD ARBORETUM
HARVARD UNIVERSITY

A STUDY OF THE GENUS JOINVILLEA (FLAGELLARIACEAE)*

THOMAS K. NEWELL

THE SMALL FAMILY Flagellariaceae is composed of perennial herbs distributed throughout the tropics and subtropics of the Old World. The type genus of the family, *Flagellaria*, includes four species (Backer, 1951), and is easily distinguished from *Joinvillea* by its circinate leaf tip which acts as a tendril, its climbing habit, and its non-plicate leaves. The genus *Joinvillea* includes seven described species which have often been reduced to four (Backer, 1951; Christophersen, 1935).

Until recently the family was also treated as including a third genus, *Hanguana* (*Susum*), which has now been assigned to its own family, the Hanguanaceae (Airy Shaw, 1965). *Hanguana* differs from the genera of the Flagellariaceae in having pollen provided with a spinulose exine (Erdtman, 1952), and in having different structure of the guard cells, the subsidiary cells, and the subhypodermal chlorenchyma (Smithson, 1956). Macroscopically, *Hanguana* differs in being dioecious and by its petiolate leaves.

The genus *Joinvillea* is distributed from West Malaysia to Samoa and as far north as the Hawaiian Islands. It is reported to occur in the Malay Peninsula (West Malaysia), Sumatra, Borneo (Sabah and Sarawak in East Malaysia and Kalimantan), the Philippine Islands (Jolo and Palawan), the Caroline Islands (Ponape), the Solomon Islands (Santa Ysabel, Guadalcanal, and San Cristóbal), New Caledonia proper and the Île des Pins, New Hebrides (Aneityum), Fiji (Viti Levu, Vanua Levu, and Taveuni), Western Samoa (Savaii and Upolu), and the Hawaiian Islands (Kauai, Oahu, Molokai, Maui, and Hawaii). The apparently discontinuous distribution of the genus, indicated by its absence from eastern Indonesia, New Guinea, and northern Australia, may be due to inadequate collection, while future collections may show the genus occurring in one or all of these areas. The distribution map (FIG. 1) shows the ranges of the species and subspecies of *Joinvillea*, according to my definition of the genus.

Taxonomically, *Joinvillea* has been studied mainly on a local basis, previous workers having confined their interest to relatively small geographic regions. A study of the genus as a whole has not previously been undertaken. Some species descriptions do not distinguish the taxa from one another, and type specimens have not always been designated. Fortunately, information concerning collectors, collection dates, and localities has, in most cases, allowed me to select lectotypes.

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* This paper is part of a thesis submitted to the Graduate School of the University of Hawaii in partial fulfillment of the requirements for the Master's degree.

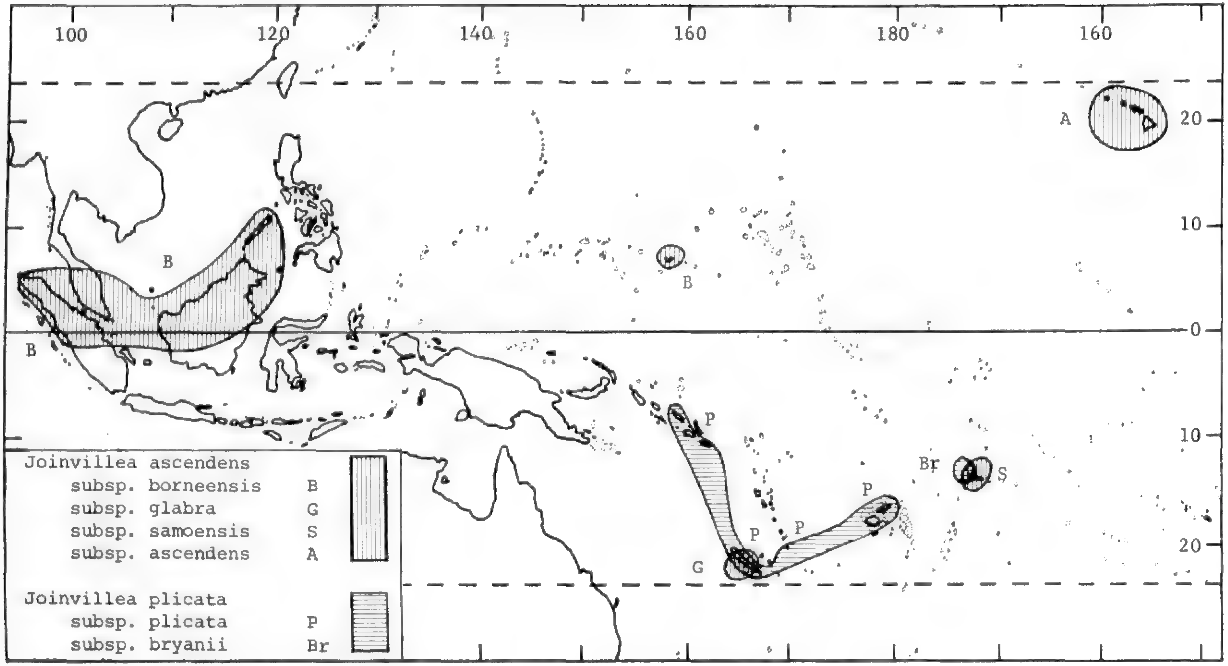

FIG. 1. Distribution of the species and subspecies of *Joinvillea*.

Previous workers have often been strongly influenced by the geographic limitations of the taxa they were studying. But if geographic distribution is ignored and abundant material is examined, it is possible to recognize two morphologically distinct groups. To me, it seems most logical to recognize these as species, and to consider further variations as subspecific. Six subspecies of the two species are here accepted as distinguishable and are treated in this paper.

TAXONOMIC LITERATURE

The generic name *Joinvillea* first appeared in the "Atlas" to the *Botany of the Voyage of the Bonite* by Gaudichaud (1841[1]). The two binomials, *J. elegans* and *J. ascendens*, published by Gaudichaud have caused confusion, since the specimens and the locality information were lost and there were no written diagnoses. *Joinvillea elegans* was typified by detailed drawings of a fertile specimen and *J. ascendens* by drawings of a sterile specimen. However, in the absence of written descriptions the genus, and therefore also the species, were invalidly published as of 1841 and should be correctly dated 1861, the publication year of "Note sur la genre *Joinvillea* de Gaudichaud et sur la famille des Flagellariées" by Brongniart and Gris (Newell & Stone, 1967).

In the work of Brongniart and Gris, along with the generic description, are formal descriptions of Gaudichaud's two species, *Joinvillea elegans* and *J. ascendens*, and a new species *J. gaudichaudiana* from the Hawaiian Islands.

Hooker (1855) described a plant from the Île des Pins (New Caledonia) which he named *Flagellaria plicata.* He did not feel that it was sufficiently different from *Flagellaria* to place it in a separate genus, and apparently he was unaware of Gaudichaud's work, since he made no mention of it. This plant, which is a *Joinvillea* in the present concept of that genus, has since been considered a synonym of *J. elegans*, and the combination *J. plicata* was only recently made by Newell and Stone (1967). If the two taxa are the same, the epithet *plicata* should be applied, and *J. elegans* reduced to synonymy for reasons explained by Newell and Stone (1967).

Seemann (1868) made the combination *Flagellaria elegans* and considered *F. plicata* Hook. f. and *J. elegans* Gaud. as synonyms. Wawra (1875), however, disagreed and considered the establishment of the genus *Joinvillea* justified.

Hillebrand (1888) considered *Joinvillea adscendens* Gaud. (orthographic variant of *J. ascendens* Gaud.) as the name to be applied to the Hawaiian material and considered *J. gaudichaudiana* to be a synonym. He also pointed out that Wawra's description (Wawra, 1875) concurred with his belief that the Hawaiian material comprised only a single species. If these species are combined, as in the present treatment, Hillebrand's

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[1] Publication date from Johnston (1944).

choice of *J. ascendens* must be followed according to Article 57, *International Code of Botanical Nomenclature* (Lanjouw, 1966).

Beccari (1902) described a new species, *Joinvillea borneensis*, from a specimen he collected at Gunong Wa, Sarawak, on the island of Borneo. Ridley (1905), apparently unaware of Beccari's paper, described a species, *J. malayana*, from West Malaysia, noting that it was found in Sarawak. Merrill (1921) and later workers have considered *J. malayana* a synonym of *J. borneensis*.

Engler (1930) recognized three species of *Joinvillea*: *J. elegans*, which he considered to occur in Fiji, Samoa, and New Caledonia; and *J. ascendens* and *J. gaudichaudiana*, both of which he credited to the Hawaiian Islands. He pointed out that the latter two species are not very different from each other.

Christophersen (1931) presented evidence for the reduction of *Joinvillea ascendens* to the synonymy of *J. gaudichaudiana*. However, the choice of Hillebrand, the first person to combine the species, must be followed. Christophersen also stated that *J. gaudichaudiana* differs from *J. elegans* mainly in shape and relative size of the tepals.

Christophersen (1935), described a new species, *Joinvillea bryanii*, from Savaii, Western Samoa. According to him, "It differs from *J. elegans* in the subequal perianth segments and from *J. gaudichaudiana* in the narrower, lanceolate segments." He indicated that *J. gaudichaudiana* also occurs in Western Samoa, both on Upolu and, with *J. bryanii*, on Savaii.

Backer (1951) recognized three species of *Joinvillea* but considered only the Malayan one, *J. borneensis*, in his paper. He considered *J. malayana* to be a synonym of *J. borneensis*.

It will be seen, then, that various authors have presented diverse interpretations of identities and limitations within the genus *Joinvillea*. My taxonomic conclusions will be indicated in the final portion of this treatment, after a consideration of morphological and other pertinent criteria.

MORPHOLOGICAL AND ANATOMICAL LITERATURE

Little anatomical or morphological work was published on *Joinvillea* prior to Smithson's paper in 1956. Arber (1925), in a morphological study of the monocotyledons, considered the leaf development of *J. elegans*. Solereder and Meyer (1929) briefly discussed the anatomy of the family.

Studies of pollen morphology such as those of Erdtman (1944, 1952) and Selling (1947), who indicated that pollen of *Joinvillea* is similar to that of grasses, inferred that, in this case, its study is more useful at the family or genus level than at that of the species.

Smithson (1956) carried out the most complete anatomical study of the Flagellariaceae, indicating several characters of possible taxonomic value. Among these is her report finding two different arrangements of the vascular bundles in the leaf sheaths of *J. gaudichaudiana* and *J. borneensis*. In the latter species she found large and small bundles alternating in one layer near the surface, while in *J. gaudichaudiana* she reported four to five layers of bundles irregularly arranged and increasing in size toward the adaxial surface. She described the abaxial bundles of *J. gaudichaudiana* as embedded in a common sclerenchymatous sheath, while toward the adaxial surface each bundle had its own sheath. These appear to be marked differences which might be applied to the taxonomy of the entire genus.

The different types of trichomes found on the lamina of the two species by Smithson may provide another character of possible taxonomic value. She reported that *Joinvillea borneensis* has thick-walled trichomes especially prevalent opposite the rows of bulliform cells, and present on both surfaces; and that *J. gaudichaudiana* has similar thick-walled trichomes and also multicellular branching trichomes with thin-walled terminal cells.

Of the characters detailed by Smithson, these seem most striking for use as taxonomic criteria; but in reality they have only limited value, and one of them is based upon a misinterpretation, to be discussed later.

ACKNOWLEDGMENTS

The following abbreviations pertain to herbarium field series numbers used by some collectors: *BSIP* (British Solomon Island Plants); *SAN* (Forestry Department, Sandakan); *SAR* (Sarawak Forestry Service); and *SF* (Singapore Field Series).

In the course of this study herbarium material was examined from the institutions here cited with the indicated abbreviations: Arnold Arboretum of Harvard University (A); Bernice P. Bishop Museum (BISH); Herbarium Universitatis Florentinae (FI); Royal Botanic Gardens, Kew (K); Rijksherbarium, Leiden (L); New York Botanical Garden (NY); Muséum National d'Histoire Naturelle, Paris (P); and U.S. National Museum (US). I am indebted to the administrators of these herbaria for the loan of valuable specimens. I am equally indebted to the numerous institutions and persons in southeast Asia and the Pacific area without whose aid my field collections and study would have been impossible.

Acknowledgment is also extended to the Lyon Arboretum and the Department of Botany, University of Hawaii, for use of facilities; to Dr. George W. Gillett for suggesting the problem and for initial direction; to Dr. Charles H. Lamoureux and Dr. Yoneo Sagawa for serving as members of my thesis committee; to Dr. Albert C. Smith for serving as thesis committee chairman and for advisory comments; to the Center for Cultural and Technical Interchange between East and West (East-West Center) for field study expenses; and to my wife, Carol, for her patience and help with typing.

FIELD STUDIES

Between August and November, 1966, observations and field collections were made throughout the range of the genus, and specifically at the following localities: West Malaysia at Gunong Hijau above Taiping, at Cameron Highlands, and at Fraser's Hill; Sabah, East Malaysia, between the town of Tamparuli and the Sabah National Park (SNP), and in the vicinity of the SNP; the British Solomon Islands Protectorate (BSIP), on northwestern Guadalcanal on the ridge above Hidden Valley; New Caledonia on the Plateau de Dogny and in the mountains southwest of the Plateau, on Mont Koghi, Route de l'Hermitage, along the road from the mouth of the Lembi Rivière to the Monts Kouanenoa, and on the Île des Pins; Fiji Islands on Viti Levu in Mba Province at Nandarivatu, in Serua Province along the road north of Ngaloa, and in Naitasiri Province along the Sawani-Serea Road; Western Samoa on Savaii southwest of Matavanu Crater and in the mountains above Samataitai, and on Upolu by Lake Lanutoo; and the Hawaiian Islands on the islands of Oahu, Molokai, Maui, and Hawaii.

To expedite reference to my own collections, they are designated by my field numbers preceded by the letter "*N*". These collections were supplemented by those of other collectors from the same areas and from several additional localities. The first set of my collections is deposited at the Bernice P. Bishop Museum, Honolulu, and duplicates have been distributed to other herbaria.

VEGETATIVE CRITERIA

The shoots of *Joinvillea* vary in height and thickness. Height seems to be related to shading from surrounding vegetation; and plants of a given subspecies tend to be noticeably taller in shaded localities. The unbranched shoots of all taxa of *Joinvillea* grow erect from the root crown like clump-forming bamboo. Height and thickness of the shoots are of minor value in distinguishing the different taxa.

The glabrous stem and leaf sheath of *Joinvillea* typically have terete cross sections, but some New Caledonian specimens, of both *J. ascendens* subsp. *glabra*, and *J. plicata* subsp. *plicata*, were found with these parts appearing laterally compressed. Compressed shoots (leaf sheaths and stems) were found only in material from New Caledonia and appear to be correlated with shortened internodes (FIG. 2). This condition seems typical of subspecies *glabra*, although I found one plant of this subspecies with an intermediate shoot and one with an essentially terete shoot. It appears to be a genetically controlled trait rather than the result of ecological differences. Three collections of subspecies *glabra*, *N199*, *N200*, and *N201*, growing within 5 meters of each other, had terete, intermediate, and compressed shoot cross sections, respectively. Seedlings grown in Honolulu showed further evidence of this. These seedlings, grown under identical greenhouse conditions from seed of a terete specimen of subspecies *plicata* (*N190*) and from a compressed specimen of subspecies *glabra* (*N201*), showed the characteristics of their respective parents. The *N190* seedlings had terete shoots and long internodes, while the *N201* seedlings had compressed shoots and shorter internodes (Fig. 2).

Since some specimens of subspecies *glabra* have terete shoots, the usual condition of compressed shoots cannot be used as an absolute criterion to separate it from the other subspecies of *Joinvillea ascendens.* In *J. plicata* subsp. *plicata* most specimens from New Caledonia have terete cross sections, but some laterally compressed specimens and some intermediates were also found. Therefore, the latter subspecies cannot be distinguished from *J. ascendens* subsp. *glabra* on this basis.

Smithson (1956) reported that the species *Joinvillea gaudichaudiana* (= *J. ascendens*) and *J. borneensis* differed in the vascular bundle arrangement of the leaf sheath. This difference was not substantiated by my study, in which leaf sheath cross sections were cut from two specimens of each of these subspecies. The sections were taken from four points along the leaf sheath and at each point all four specimens showed close similarity. The sections from the midpoints of both subspecies (Fig. 3A and B) were comparable to those which Smithson reported from the leaf sheath of subspecies *borneensis*, and none resembled those reported by her as representative of subspecies *ascendens.* However, sections were obtained similar to her cross sections of subspecies *ascendens.* These occurred, however, in the stems of both subspecies, not in the leaf sheaths (Fig. 3C and D).

Apparently the wide variation in leaf sheath anatomy indicated by Smithson was actually a difference between leaf sheath and stem. Numbers of vascular bundles and amounts of fibrous tissue varied somewhat in leaf sheaths and stems of the specimens which I studied, but the variation appeared closely related to the age and vigor of the material, and was not considered of diagnostic value.

Several specimens from each of the other subspecies were also sectioned. Each showed close similarity to the leaf sheath and stem sections of the previous material. Specimens with compressed shoots were also basically similar, except for a displacement of the vascular bundles corresponding to the shape of the shoot.

Another vegetative criterion investigated was the length of the leaf auricle. Christophersen (1931) pointed out the variability of auricle length in material he examined. This variability is due, in part, to the breakage of the auricle as it becomes dry and brittle in age. However, the maximum length attained in some subspecies is limited, and it is possible to exclude such taxa from consideration if long auricles are present.

The lamina of *Joinvillea* typically is linear-lanceolate, plicate, abaxially concave, acute to attenuate at the tip, constricted at the base, and scabrous along the margins. Although most of these characters are fairly uniform

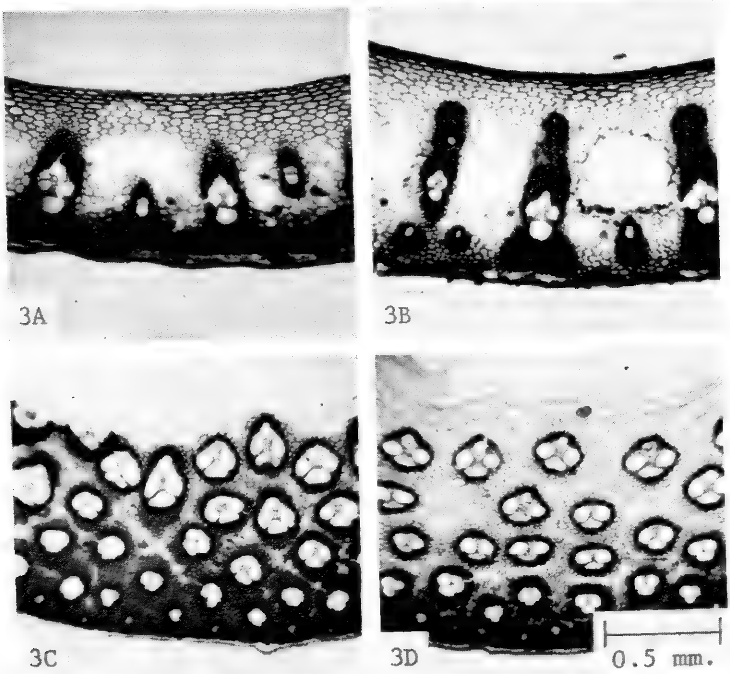

FIG. 2. Seedlings showing terete and compressed shoots. Two pots at left, *J. plicata* subsp. *plicata* (*N190*), showing terete shoots and long internodes. Two pots at right, *J. ascendens* subsp. *glabra* (*N201*), showing compressed shoots and short internodes; the planes of compression of these two plants oriented at right angles to each other.

and of little diagnostic value, the types and frequencies of the trichomes occurring on the lamina are of some taxonomic significance.

Most trichomes on the lamina of *Joinvillea* leaves are found on the abaxial surface. Those found on the adaxial surface are of a particular type and will be discussed later. One part of the study concerns those trichomes distributed over the abaxial surface of the lamina, excluding the multicellular trichomes associated with major veins. These trichomes on the abaxial surface vary in type and frequency of occurrence. Unicellular trichomes and branched and unbranched multicellular trichomes occur in the genus. Sampling several leaves of each collection number showed that types and relative frequencies of trichomes are generally uniform on a given plant. On some plants trichomes are restricted to leaf areas bordering rows of bulliform cells. In FIGURE 4 such rows of cells (totaling about 0.15–0.25 mm. wide) pass vertically between the most widely spaced veins in each drawing. The midpoint of the lamina was chosen as the site for comparison and several samples were taken from each of my collections. Scoring was relative, and the terms rare, infrequent, frequent, and abundant were used to designate observed differences. Frequency and distribution of trichomes on the leaf surface was verified by examination of corresponding dried specimens. These detailed observations on my collections were supplemented by observations on loan material from various herbaria.

Trichome type and frequency vary greatly in some subspecies, but are fairly uniform in others. This character can be used to distinguish sterile Western Samoan material, since the only two subspecies found there differ greatly. The first of the two, *Joinvillea plicata* subsp. *bryanii*, is very uniform in the type and frequency of its trichomes, having abundant trichomes of the type indicated in FIGURE 4I. The other, *J. ascendens* subsp. *samoensis*, has rare trichomes as shown in FIGURE 4C. The greatest variation in trichomes is found in *J. plicata* subsp. *plicata*. In New Caledonia alone, trichomes of this subspecies range from rare to abundant and include the types illustrated in FIGURE 4E–I. This variation does not appear directly correlated with other characters or with type of habitat. *Joinvillea ascendens* subsp. *ascendens* from Hawaii, is also variable in trichome frequency, ranging from rare to abundant, but most material is in the frequent to abundant range. FIGURE 4D represents the usual type found in this subspecies.

A separate comparison was made of the branched and unbranched multicellular trichomes associated with the major abaxial laminar veins. Some data pertaining to these trichomes are given in descriptions to taxa, but should be used with caution as the ranges often vary greatly.

FIG. 3, A–D. Leaf sheath and stem cross sections of *Joinvillea*. A, B, Leaf sheath cross sections at midpoint between auricle base and point of nodal attachment, showing vascular bundle arrangement and canals. A, *Joinvillea ascendens* subsp. *borneensis* (*N153*). B, *Joinvillea ascendens* subsp. *ascendens* (*N137*). C, D, Stem cross sections at midpoint between two nodes, showing vascular bundle arrangement and absence of canals. C, *Joinvillea ascendens* subsp. *borneensis* (*N153*). D, *Joinvillea ascendens* subsp. *ascendens* (*N137*).

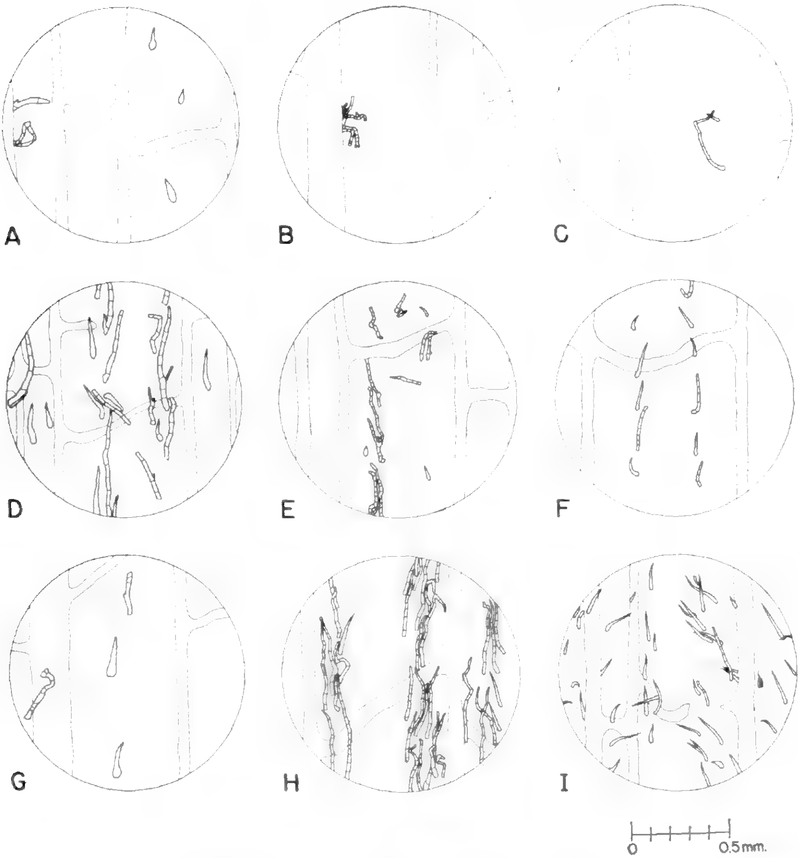

FIG. 4, A–I. Trichomes on the abaxial laminar surface of *Joinvillea.* A, Infrequent, mainly along veins and rows of bulliform cells. Trichomes predominantly unicellular. *J. ascendens* subsp. *borneensis.* B, Rare, mainly along veins. Trichomes predominantly multicellular and highly branched. *J. ascendens* subsp. *glabra.* C, Rare, mainly along rows of bulliform cells. Small unicellular and thin unbranched multicellular trichomes. *J. ascendens* subsp. *samoensis.* D, Abundant, distributed all over abaxial surface. Trichomes larger than in H and with a higher proportion of unicellular ones. *J. ascendens* subsp. *ascendens.* E, Frequent, mainly along rows of bulliform cells. Trichomes predominantly multicellular. *J. plicata* subsp. *plicata.* F, Frequent, mainly along rows of bulliform cells. Unicellular and multicellular trichomes equally apparent. *J. plicata* subsp. *plicata.* G, Infrequent, mainly along rows of bulliform cells. Unicellular trichomes larger than in A. *J. plicata* subsp. *plicata.* H, Abundant, distributed all over abaxial surface. Predominantly multicellular unbranched trichomes, but also a few unicellular ones. *J. plicata* subsp. *plicata.* I, Abundant, distributed all over abaxial surface. Trichomes predominantly thin and unicellular, but also a few thin multicellular ones. *J. plicata* subsp. *plicata* and *J. plicata* subsp. *bryanii.*

The last portion of the trichome study is a frequency evaluation of the thick stiff unicellular bristles that are mainly associated with the veins on both surfaces of the lamina. These bristles are oriented with their tips toward the leaf apex, and are easily detected by moving one's fingers over the surface from the apex toward the leaf base. For uniformity, scoring was based on the middle three-fourths of the lamina. Frequencies were scored by touch and expressed by the relative terms rare, infrequent, frequent, and abundant, which may be approximately quantified in the following manner: rare, 0–1 bristles/cm. on a few veins; infrequent, 1–2 bristles/cm. on some veins; frequent, 3–4 bristles/cm. on some veins; and abundant, 5–6 bristles/cm. on most veins. The frequency of the bristles in different subspecies was generally consistent but it was usually higher on seedlings.

This trichome study was undertaken partly because Smithson (1956) indicated that the types occurring on Hawaiian collections differed from those on the Malayan collections. She reported finding "thick-walled spines" (better referred to as bristles) on the lamina of a Malayan specimen, and these plus spiny multicellular branching hairs on a Hawaiian plant. However, after examining several specimens from each area, I have concluded that both types occur on material from both areas and on plants collected throughout the range of the genus. There is notable variation in type, frequency, and distribution of the trichomes over the lamina, but presence or absence of multicellular trichomes cannot be considered a valid criterion for distinguishing the two taxa mentioned above.

Although the leaf trichomes are variable, they are useful in delimitation of some taxa. This use is mainly at the subspecific level. However, in New Caledonia or Western Samoa, where both species occur side by side, it is possible to determine sterile specimens on the basis of trichome type, frequency, and distribution.

REPRODUCTIVE CRITERIA

The inflorescence of *Joinvillea* is a large, usually erect, three to five times branched, terminal panicle measuring 10–40 cm. long from the lowest branch to the apex, and 8–40 cm. wide. Inflorescence branch diameter is particularly useful in separating subspecies *ascendens* from all other subspecies. Its branches are usually larger in diameter and in this respect overlap only slightly with the other subspecies. Diameter measurements were made in two places: on a primary branch of the inflorescence midway between the rachis and the branch tip, and about 0.5 cm. from the tip of the ultimate branchlets. Data are presented in the key and descriptions.

The flowers which are sessile in the axils of fragile lanceolate bracts have six equal stamens and three fused carpels and do not seem to vary in the two species.

The size and especially the shape of the tepals are diagnostic, the shape of the outer tepals being the primary character of value for species

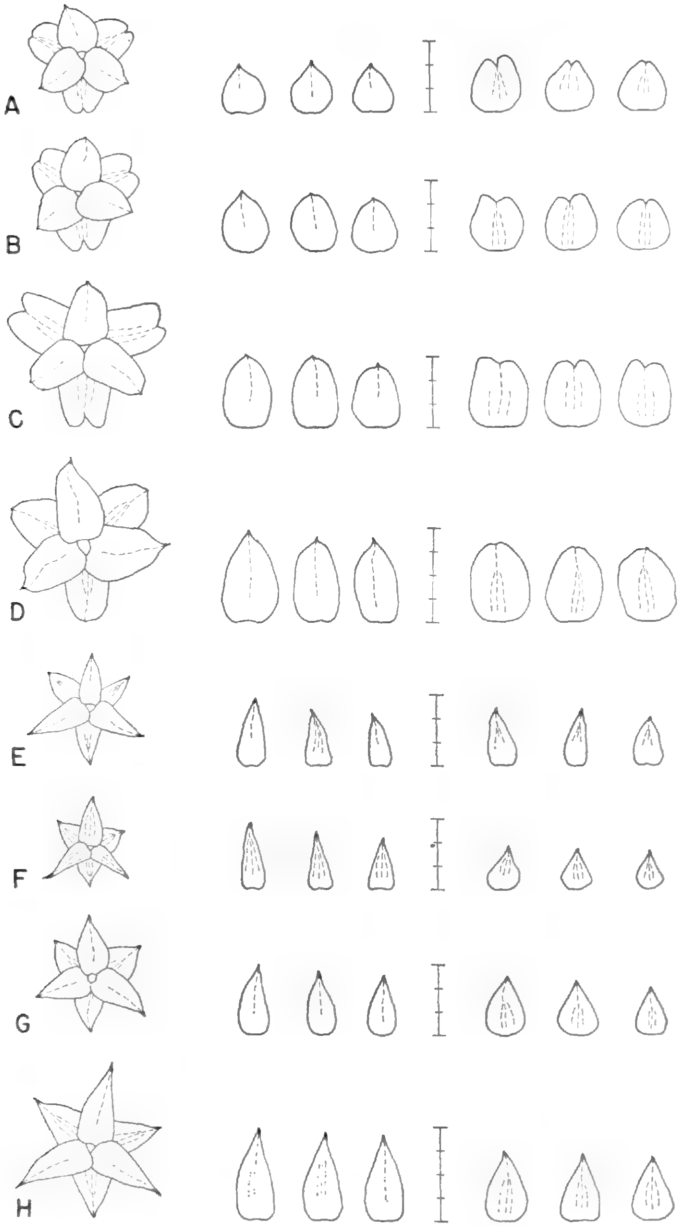

FIG. 5, A–H. Tepal shapes of *Joinvillea*. Drawings on left show abaxial view of flattened perianth. Left of scale, outer tepals; right of scale, inner tepals. Dashed lines are visible veins. *Joinvillea ascendens*, A–D. A, Subsp. *borneensis* (*N143*), from Sabah, East Malaysia; B, Subsp. *glabra* (*N193*), from Plateau de Dogny, New Caledonia; C, Subsp. *samoensis* (*N239*), from Upolu, determination. Camera lucida drawings in FIGURE 5 illustrate representative tepals of the species and subspecies recognized in this treatment. The basic difference in shape is obvious, *Joinvillea ascendens* having ovate to orbicular-ovate outer tepals and orbicular-ovate inner tepals, while *J. plicata* has deltoid-lanceolate outer tepals and deltoid-lanceolate to ovate inner tepals. The membranaceous tepal edges of both species commonly shatter in age. Tepals of both species are adaxially concave (and abaxially convex), especially in the flowering stage, becoming spread and somewhat flattened as the fruit develops distally.

The bases of the tepals are thickened in both species, but the amount of thickening is difficult to assess in dried material. This basal tissue is thicker in the outer than in the inner tepals of a given specimen. The veins are usually obscured in the basal portions of the tepals, and therefore only the visible portions of the veins are represented by the dashed lines in FIGURE 5. Clearing and staining is usually necessary to show the continuation of the veins into the base of each tepal.

Venation in the outer tepals of *Joinvillea ascendens* (FIG. 5A–D) typically consists of one central vein, although sometimes one or two weakly expressed additional traces were present. The central vein extends from the tepal base to the apex and into the tip; however, the tip is often lost as the tepals become brittle and shatter in age. Before shattering occurs, the outer tepal tips of subspecies *borneensis* and *glabra* are usually mucronulate or sometimes mucronate. Reflexed mucronate tips were also observed on some tepals of these subspecies, but they are not as pronounced as in subspecies *ascendens*, where a strongly reflexed mucronate tip is normally present. Subspecies *samoensis* also bears a reflexed mucronate tip, but it is not usually as prominent as in subspecies *ascendens*. The outer tepals of *J. ascendens* occasionally split in age.

In *Joinvillea plicata* subsp. *plicata* the outer tepals often have one or two lateral veins, and in some specimens these laterals are as prominent as the midvein. Gradation from one to three prominent veins is often found in a given population and sometimes on a single plant. Therefore, it does not seem appropriate to recognize another subspecies on the basis of this variation. Subspecies *bryanii* normally has only a single midvein in the outer tepals, although one or two weakly expressed lateral veins are occasionally present. The outer tepals of both subspecies of *J. plicata* have acute to acuminate, not mucronate, tips, although the central vein does extend to the apex.

The inner tepals of *Joinvillea ascendens* normally have three veins, a central one and two weaker laterals. The latter sometimes unite with the central vein near the apex (FIG. 5A–D). The central vein of the

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Western Samoa; D, Subsp. *ascendens* (*N261*), from Molokai, Hawaii. *Joinvillea plicata*, E–H. E, Subsp. *plicata* (*N176*), from Guadalcanal, BSIP; F, Subsp. *plicata* (*N189*), from Mont Koghi, New Caledonia; G, Subsp. *plicata* (*N227*) from Serua Province, Viti Levu, Fiji; H, Subsp. *bryanii* (*N251*), from Savaii, Western Samoa.

Each scale division = 1 mm.

inner tepals extends to the apex but does not form a noticeable projection, since the tepals usually split, forming a retuse or emarginate tip. Splitting of the inner tepals which is most prevalent in subspecies *ascendens* may be related to the flattening of the tepals by the fruit, since when mature the fruit of this subspecies is dorsiventrally flattened and larger than that of the others. The inner tepals of *J. plicata* have three veins which unite below the acute apex of the tepal. In both subspecies the midvein extends to the normally entire apex but does not form a mucro.

Tepal shape was also evaluated by expressing shape as a ratio of length to width. Results obtained are presented as ranges of ratios in the descriptions and key. The ratios indicate greater variation in *Joinvillea plicata* and reinforce the species delimitations, since little overlap occurs between species. Within *J. plicata* there is a tendency for subspecies *bryanii* to have higher inner tepal ratios than subspecies *plicata*; however, there is considerable overlap. Within *J. ascendens* there is a tendency for subspecies *ascendens* to have higher ratios for both inner and outer tepals than does subspecies *samoensis*. Christophersen (1935) considered the Hawaiian material (subspecies *ascendens*) and the Western Samoan material (subspecies *samoensis*) to be the same. However, the tendency for higher ratios in the Hawaiian material, when considered with other characters, suggests that material from these two areas should be recognized as distinct subspecies.

Within their respective species, subspecies *ascendens* and subspecies *bryanii* have the longest tepals, and therefore the upper limits of their ranges of length can be used with some confidence for determination.

Fruit morphology indicates tendencies of difference between some of the taxa. Fruit diameter ranges were obtained using a dissecting microscope equipped with an ocular micrometer. Only fruits containing two or three seeds were measured. Fruits normally have three seeds, but when two of these are aborted the fruits are greatly reduced in size. Fruits measured were either fresh, preserved in FAA (formalin-acetic acid-alcohol), or boiled in water until they approximated the fresh condition. Much overlap occurs among taxa, but the extremes in diameter are sometimes useful.

Fruit shape was expressed as a ratio of diameter to height, exclusive of the perianth and style. The ratios indicate the degree of dorsiventral flattening, high values indicating a flattened fruit and low values a more globose fruit. These values also overlap greatly, but are sometimes useful.

As the fruit matures the feathery stigmas normally break off and are lost, leaving short styles. This occurs in all taxa except *Joinvillea ascendens* subsp. *ascendens*, where the styles appear to be absent in the fruiting stage or at least do not protrude above the fruit. This character is helpful in distinguishing this subspecies from subspecies *samoensis*, which usually has noticeably protruding styles.

Tepal shape is most useful as a diagnostic character at the specific level. The other criteria are more useful at the subspecific level.

CYTOLOGICAL CRITERIA

Chromosome counts were obtained from material collected in each of the geographic areas I visited. Results were obtained mainly from microsporocytes. These were fixed in the field in a 3:1 mixture of absolute ethanol and glacial acetic acid, and later prepared by the aceto-orcein squash technique. One somatic count was obtained from root tips of seedlings grown in Honolulu, from New Caledonian seed. In each case the count was verified in several cells, and in all material counted, the haploid number was 18 and the diploid number 36. Counts were obtained from the collections indicated in Table 1. Among the meiotic configurations studied, no significant differences were observed; Figure 6 illustrates a representative chromosome complement. A count has not yet been obtained for *J. ascendens* subsp. *samoensis*.

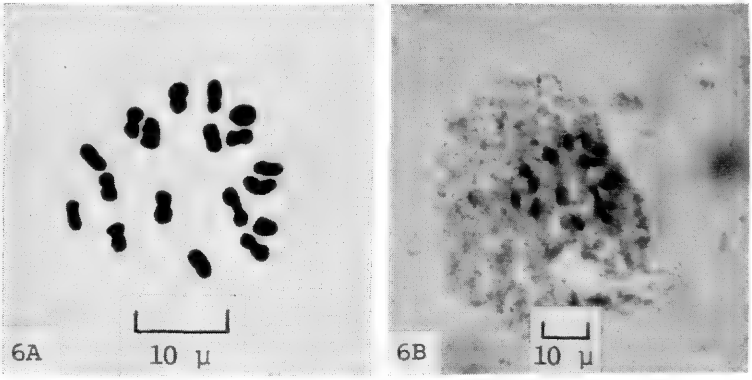

Fig. 6, A and B. Haploid chromosome complement of *Joinvillea*. A, Camera lucida drawing of the haploid chromosome complement (n = 18) from a microsporocyte of *J. plicata* subsp. *plicata* (*N232*); specimen collected north of Ngaloa, Serua Province, Viti Levu, Fiji. B, Photograph of the actual cell drawn in Fig. 6A.

In the related genus *Flagellaria*, Shetty and Subramanyam (1964) reported a haploid number of 19 and a diploid number of 38 in *F. indica* L. The presence of the additional chromosome pair in *Flagellaria* supports its consideration as a genus distinct from *Joinvillea*. Separation of taxa on the basis of chromosome number cannot be made within the latter genus. The constancy of chromosome number within *Joinvillea* may be considered evidence of close relationships within the genus.

In summarizing this discussion of the various criteria studied, the approximate order of their usefulness in delimiting the taxa may be mentioned: shape of outer tepals, type and frequency of trichomes, size of tepals, diameter of inflorescence branches, size of style on mature fruit, size of fruit, and size of inflorescence. The combined use of these characters and others of lesser value permits recognition of taxa that seem to possess stability.

DISCUSSION AND CONCLUSIONS

Several field observations were made on the possible means of pollination and dispersal for *Joinvillea*. Bees or wind, or both, may play a role as pollinators. Bees were the only insects observed on the flowers of *Joinvillea*. The observation was made on plants of *J. plicata* subsp. *plicata* in the Monts Kouanenoa area, New Caledonia. Ants were seen on the leaves of plants from various areas, but not on the flowers. Ants were commonly observed on flowers and stems of the related genus *Flagellaria* and may play a role in its pollination.

Self or cross pollination in *Joinvillea* might also be accomplished by wind. The filaments extend the mature anthers above the tepals to about the same height as the feathery stigmas, and since the stigmas and filaments are somewhat lax, the anthers and the stigmatic surfaces may easily contact each other as they move in the wind. The extruded anthers and stigmas also would provide ample opportunity for cross pollination by wind.

Dispersal is probably accomplished by birds, as suggested by Ridley (1930). The inflorescence is high on the plant and the fleshy, brightly colored fruits are readily visible to passing birds. However, I have never observed birds on the plants, nor do I know of any record of such an observation. The only tenable alternative to dispersal by birds is dispersal by high velocity storm winds. The fruits have no particular adaptation to wind dispersal, but they are light enough so that this may be a possibility.

Dispersal by man or sea is not probable for *Joinvillea*. Man can be logically excluded because no native uses for *Joinvillea* have been recorded. The stem of the related genus *Flagellaria* is sometimes used in Samoa for house construction as a stick to which thatch is tied (Christophersen, 1935), and in southeast Asia for basketwork, and for making hair-wash and medicinal applications (Backer, 1951). The application of the same native name to both genera has caused some confusion. Sea dispersal can be ruled out for two reasons. First, both fresh and dry seeds sink immediately, or shortly after placement in salt water, and second, the genus is found almost exclusively as a highland or inland plant, except in New Caledonia, where it sometimes occurs at quite low elevations, but not on the beach.

The seeds of all subspecies germinate readily even after being kept for as long as six weeks in an air dry condition. This would allow ample time for dispersal despite the large distances involved. From my experience in germinating seed and growing these plants, the main problem appears to be survival of the seedling stage.

There is some evidence for suggesting that interspecific crossing may be occurring in New Caledonia. Plants with compressed shoots are known to occur only on that island. My observations of adjacent plants, one with terete and one with compressed shoots, and observations of seeds from each developing into the parental type (FIG. 2), suggest that the trait is genetically controlled. Since compressed and terete shoots occur in both species, the trait either originated by mutation in one species and was introduced to the other by interbreeding, or originated separately in both species. The probability of the former occurring certainly exceeds that of the latter. If interspecific crossing is occurring in these plants, it has not noticeably affected tepal shape, the two basic shapes being clearly separable in all material so far examined. The conspicuous success of *Joinvillea* in New Caledonia may be due to heterosis, but as yet there is no conclusive evidence of this. Experimental hybridization would be necessary to test this hypothesis.

SYSTEMATIC TREATMENT

Joinvillea Gaud. ex Brongn. & Gris, Bull. Soc. Bot. France **8**: 268. 1861.

Flagellaria subgenus *Chortodes* Hook. f., Hook. Jour. Bot. Kew Gard. Misc. 7: 200. *tab. VI.* 1855. Type species *Flagellaria plicata* Hook. f.

Erect rhizomatous perennial herbs with few to numerous shoots, 1.5–5.5 m. high. Stem simple, terete or bilaterally compressed, hollow except at nodes, smooth, hard, glabrous, 4–14 mm. in greatest diameter at distal nodes, the distal internodes 2–14 cm. long (the distance between consecutive auricles), increasing in length toward base. Leaf sheath covering internode, open, terete or bilaterally compressed, smooth, firm, with vesture on upper part, glabrous in age, faintly and closely nerved and striated, nerves converging at base of lamina, margins scarious; ligule diminutive; auricles 2, thinner than sheath, appressed against shoot, oblong with rounded to acute apex to subulate, smooth, faintly and closely nerved and striated, scarious at margin, 2–90+ mm. long, often withering and breaking in age, then sometimes 1 mm. or less in length. Lamina linear-lanceolate, constricted at base, abaxially concave, somewhat stiff, usually with abaxial vesture and with bristles on both surfaces, margins scabrous, veins prominent on both surfaces, apex acute to attenuate but often withering in age, 7–15 longitudinal plications on each side of midrib, 48–100 cm. long and 4.5–20 cm. broad when flattened. Inflorescence a terminal panicle, erect, sometimes drooping in fruit, pyramidal, 3–5 times branched, 10–40 cm. long from proximal branch to apex and 8–40 cm. broad; rachis and branches with vesture, branches (especially thinner ones) sinuous, primary branches (in dried condition) 0.7–2 mm. in diameter at midpoint, ultimate branchlets 0.3–0.9 mm. in diameter 5 mm. from tips; peduncle bract triangular to linear, membranous, early withering and caducous, sometimes to ca. 25 cm. long; bracts subtending branches triangular, membranous, early withering and caducous, mostly 0.5–3 cm. long; bracteoles subtending flowers triangular to subulate, membranous, early withering and caducous, mostly 1–4 mm. long. Flowers bisporangiate, actinomorphic, sessile on thickenings of the branchlets. Tepals 6, alternate in 2 series, hypogynous, persistent, free or slightly adnate at base, imbricate, spreading in fruit, adaxially concave, scarious or chartaceous, base (especially of outer tepals) thickened, apex sometimes splitting in age, margins sometimes minutely ciliate; outer tepal (flattened) ovate to orbicular-ovate with a mucronulate to mucronate sometimes reflexed tip, or deltoid-lanceolate with an acute to acuminate apex, with 1 central vein and sometimes 1 or 2 laterals, 1.1–3.1 times longer than broad, 1.7–4.1 mm. long and 0.8–2.2 mm. broad; inner tepal orbicular-ovate with ± truncate apex, often becoming retuse or emarginate in age, or deltoid lanceolate to ovate with an acute to acuminate apex, with 1 central vein and usually 2 laterals which sometimes unite with the central one below the apex, 0.8–2 times longer than broad, 1.5–3.5 mm. long and 0.8–2.6 mm. broad. Stamens 6, free, hypogynous or slightly adnate to tepal bases; filament filiform, ca. 2–4 mm. long at anthesis; anther oblong, sagittate at base, retuse at apex, basifixed with a narrow connective, bilocular and exserted at anthesis, opening laterally by 2 longitudinal slits, ca. 2 mm. long. Ovary superior, conoidal, with 3 fused carpels; locules 3; ovule solitary in each locule, orthotropous, pendulous from central axis, not basally attached; styles 3, free or slightly connate at base, linear, tapering distally, becoming obscured by developing stigmas; stigmas 3, linear when immature, becoming exserted, feathery, and papillate, somewhat persistent on fruit. Fruit indehiscent, drupaceous, glabrous, globose to somewhat dorsiventrally flattened when fresh, triquetrous (especially when dry), at first green, becoming red, red-orange, or brown-black at maturity, 1–1.7 times broader than high (to base of style and exclusive of perianth), 3.3–6 mm. in diameter (2- or 3-seeded and fresh); exocarp thin, sometimes becoming crustaceous; mesocarp fleshy; endocarp hard and bony. Seeds 3 or fewer by abortion, globose, rugulose, 1.5–2 mm. in diameter; endosperm copious; embryo minute, lenticular.

TYPE SPECIES: In Newell and Stone (1967) the type species of the genus *Joinvillea* was indicated as *Flagellaria plicata* Hook. f. Upon reconsideration, however, this seems incorrect. Although the epithet *plicata* dates from 1855 and is, therefore, the oldest validly published epithet now referable to *Joinvillea,* it was not considered by Brongniart and Gris (1861) in the first valid publication of the generic name. The type species of *Joinvillea* must be chosen from among the three species validly published by Brongniart and Gris in their 1861 treatment. Since Brongniart and Gris ascribed the genus to Gaudichaud (1841), it seems logical to select one of Gaudichaud's species as the type. The more fully illustrated *J. elegans* is herewith indicated as the appropriate lectotype for the genus *Joinvillea.* As pointed out in Newell and Stone, the plates published by Gaudichaud cannot serve as a valid generic description because no description is supplied or referred to, and a plate with analytic illustrations serves only to validate a new monotypic genus. Since the genus was invalidly published by Gaudichaud (1841), the two species, *J. ascendens* and *J. elegans,* illustrated in his plates are also invalidly published as of 1841.

DISTRIBUTION. The genus *Joinvillea* is distributed from West Malaysia to Western Samoa and north to the Hawaiian Islands (FIG. 1); apparently a discontinuous distribution since there are no records from eastern Indonesia, New Guinea, or northern Australia. It occurs at elevations from near sea level to 1,920 meters, usually at the forest edge or in other partially open localities with ample light but some protection by other vegetation. The plants seem to be associated with moist, well-drained soils, and are often found on banks above streams or on slopes in areas of heavy rainfall.

When a wide selection of *Joinvillea* specimens is examined, basic tepal shape, particularly the shape of the outer tepals, appears to be the only clearly discontinuous character. Because this character seems stable, I think it forms an adequate basis for distinction of species. It can be used confidently without locality or other field data. Frequency of bristles on the adaxial laminar surface generally is correlated with tepal shape but is less precise as it must be expressed in relative terms. Further variation in these and in other characters is more appropriately applied at the subspecific level.

KEY TO THE SPECIES AND SUBSPECIES

1. Tepals usually splitting in age; outer tepals ovate to orbicular-ovate with a mucronulate to mucronate sometimes reflexed tip, 1.1–2 times longer than broad; bristles on the adaxial laminar surface usually rare to frequent. .... 1. *J. ascendens.*
    2. Fruit 4.1–5.8 mm. in diameter; inflorescence mostly villous; outer tepals usually mucronate, often reflexed; inner tepals 1.9–3.5 mm. long.
        3. Stem 5–9 mm. in diameter at distal nodes; auricles to ca. 31 mm. long; ultimate inflorescence branchlets 0.4–0.9 mm. in diameter, 5 mm. from tips; outer tepals 2.7–4 mm. long; inner tepals 2.6–3.5 mm. long; styles not evident on fruit; Hawaiian Islands. .... 1a. subsp. *ascendens.*
        3. Stem 4–6 mm. in diameter at distal nodes; auricles to 6 mm. long; ultimate inflorescence branchlets 0.3–0.5 mm. in diameter, 5 mm. from tips; outer tepals 2.1–3 mm. long; inner tepals 1.9–3 mm. long; styles persistent on fruit; Samoa. .... 1b. subsp. *samoensis.*
    2. Fruit 3.3–4.8 mm. in diameter; inflorescence mostly with erecto-patent short stiff trichomes; outer tepals usually mucronulate, rarely reflexed; inner tepals 1.8–2.6 mm. long.
        4. Stem and sheath terete, the distal internodes 5–11.5 cm. long; auricles mostly oblong with rounded apex; lamina 5–14 cm. broad, with 9–13 plications on each side of midrib, the bristles infrequent to frequent on both surfaces; southeast Asia and Ponape. .... 1c. subsp. *borneensis.*
        4. Stem and sheath bilaterally compressed, rarely terete, the distal internodes 3–6 cm. long; auricles mostly subulate; lamina 4.5–7 cm. broad, with 7–9 plications on each side of midrib, the bristles rare on both surfaces; New Caledonia. .... 1d. subsp. *glabra.*
1. Tepals usually not splitting in age; outer tepals deltoid-lanceolate with an acute to acuminate tip, 1.7–3.1 times longer than broad; bristles on the adaxial laminar surface usually frequent to abundant. .... 2. *J. plicata.*

5. Stem and sheath terete to bilaterally compressed; auricles oblong, rounded at apex, sometimes subulate, mostly straight; lamina with acute to attenuate apex; outer tepals 1.7–3.6 mm. long; inner tepals 1.1–3.1 mm. long; Solomon Islands, New Caledonia, New Hebrides, and Fiji. . . . . 2a. subsp. *plicata.*
5. Stem and sheath terete; auricles somewhat oblong, rounded to acute at apex, the apex mostly curving away from ligule; lamina with attenuate apex; outer tepals 2.9–4.1 mm. long; inner tepals 2.5–3.3 mm. long; Samoa. . . . . 2b. subsp. *bryanii.*

1. **Joinvillea ascendens** Brongn. & Gris, Bull. Soc. Bot. France **8:** 269. 1861.

Erect herb, 1.5–5 m. high; auricles to ca. 40 mm. long; lamina with variable trichome types on abaxial surface, bristles on adaxial surface rare to sometimes frequent, 7–13 plications on each side of midrib, 48–79 cm. long and 4.5–16 cm. broad when flattened. Tepal apex usually splitting in age; outer tepals ovate to orbicular-ovate with a mucronulate to mucronate sometimes reflexed tip, with 1 central vein and very rarely 1 or 2 weakly expressed lateral veins, 1.1–2 times longer than broad, 1.7–4 mm. long and 1.4–2.2 mm. broad; inner tepals orbicular-ovate with the apex somewhat truncate and often becoming retuse or emarginate in age, 0.8–1.7 times longer than broad, 1.8–3.5 mm. long and 1.6–2.6 mm. broad. Styles sometimes not evident on fruit; fruit 3.3–5.8 mm. in diam.

The species *Joinvillea ascendens* is here recognized as being composed of four subspecies. Because tendencies of morphological differences among these subspecies are correlated with geography, it seems logical to consider them at this rank rather than at varietal level. The latter rank is better ascribed to variation within a single geographic area.

1a. **Joinvillea ascendens** subsp. **ascendens** FIG. 4D; FIG. 5D.

Joinvillea ascendens Gaud. Atlas, Voy. Bonite, *pl. 39 & 40, fig. 1–6.* 1841, ***nomen nudum***; Brongn. & Gris, Bull. Soc. Bot. France **8:** 269. 1861; Wawra, Flora **58:** 248. 1875; Hillebrand (as *J. adscendens*), Fl. Hawaiian Isl. 447. 1888.

Joinvillea gaudichaudiana Brongn. & Gris, Bull. Soc. Bot. France **8:** 269. 1861; Christophersen, Bishop Mus. Occ. Pap. **9**(12): 5. 1931, Bishop Mus. Bull. **128:** 46, p.p. 1935.

Erect herb, 3.5–5 m. high; stem terete, 5–9 mm. in greatest diam. at distal nodes, the distal internodes 5–13 cm. long; sheath terete; auricles to ca. 31 mm. long (mostly 20 mm. or less), oblong, rounded to slightly acute at apex; lamina with 9–13 plications on each side of midrib, 8–16 cm. broad; unicellular and multicellular trichomes on abaxial laminal surface rare to abundant (mostly frequent); bristles rare to infrequent on both surfaces. Inflorescence villous with a few erecto-patent short stiff trichomes, primary branches 1–2 mm. in diam. at midpoint, ultimate branchlets 0.4–0.9 mm. in diam. 5 mm. from tips; outer tepals 2.7–4 mm. long, with a mucronate usually reflexed tip; inner tepals 2.6–3.5 mm. long. Styles not evident on fruit; fruit 4.6–5.8 mm. in diam.

TYPE: Kauai or Niihau, Hawaiian Islands, *Remy 156 A* (P lectotype) 1851–1855. Gaudichaud's figures (Gaudichaud, 1841) of *Joinvillea ascendens* are of incomplete material and accordingly could not have been the only basis for the description of this taxon by Brongniart and Gris (1861). Therefore it seems best to choose as lectotype the specimen cited by Brongniart and Gris, *Remy 156 A*. The specimen selected is in mature fruit. Although its label bears the locality "Kauai au Nihau" (Niihau), Kauai is probably correct as I know of no other record of *Joinvillea* from Niihau.

LOCAL NAME. Called "ohe" in Hawaiian, a name also applied to several other native plants and to bamboo.

DISTRIBUTION. Endemic to the Hawaiian Islands, occurring on Kauai, Oahu, Molokai, Maui, and Hawaii from 300 to 1,250 meters elevation. Plants rare, usually occurring as widely separated individuals on ridges, in forests, and along intermittent streams. Seedlings rarely observed.

Hawaiian Islands. KAUAI: Kokee, Halemanu, *Degener 30212* (BISH); Waipao Valley and Ridge, *Forbes & Dole 42 K* (BISH); Kilauea, Ka Loko Reservoir, *Forbes 564 K* (BISH); Hii Mts., *Forbes 623 K* (BISH); Lehue, *Mann & Brigham 330* (A, BISH, NY, US). KAUAI OR NIIHAU: *Remy 156 A* (P lectotype). OAHU. Waianae Mts.: Mt. Kaala, *Macrae s.n.* (A); Puu Hapapa, *St. John 10414* (BISH); below ridge e. of Puu Hapapa, *Christophersen 1286* (BISH); valley e. of Puu Hapapa, *N137* (*Newell 137*); Schofield side of Puu Kanehoa, *Beardsley s.n.* (BISH). Koolau Mts.: Laie, *Guppy s.n.* (K); Kawailoa Trail, middle forest, *N257*; Paalaa-Kawailoa divide, Puu Peahinaia, near crest of wooded ridge, *St. John 11124* (BISH); Paalaa Ridge, *Caum s.n.* (BISH); Paalaa, forested ridge s. of Opaeula Gulch, *Fosberg 10302* (BISH); South Opaeula Gulch, below crest of s. ridge, *St. John 12103* (BISH); South Opaeula Ridge, middle forest, *Suehiro s.n.* (BISH); Kaluanui, *St. John 10109* (BISH); between Punaluu and Kaipapau, *Forbes s.n.* (BISH); Punaluu, open hillside, *Hume 103* (BISH); Punaluu, *Degener 9785* (US); Punaluu-Wahiawa ridge, *Judd s.n.* (BISH); Poamoho Trail, *Oliveira 52* (US); Wahiawa gulches, *Forbes 1711 O* (BISH); Wahiawa, Kahana Trail, *Forbes 2205 O* (BISH); Kahana Valley Ditch Trail, *Fosberg 10402* (BISH); Waikane-Schofield Trail, near top of divide, *St. John 10177* (BISH); Waikane-Schofield Trail, *St. John 12123* (BISH); Waipio, Kipapa Gulch, *Fosberg 9548* (BISH); s. ridge of Kipapa Gulch, *Hosaka 1014* (BISH), *Yamaguchi 1237* (BISH); Halawa Valley Ridge Trail, *Cowan 556* (BISH), *N293*; Honolulu, *U.S. Expl. Exped.* (US *690602*); Palolo Valley, *Skottsberg 910* (BISH); Palolo-Waialae ridge, *Fosberg 13133* (BISH). Koolau Mts. (without definite locality): *Forbes s.n.* (BISH). Oahu (without definite locality): *Remy 156* (P), *Macrae s.n.* (K). MOLOKAI: Waikolu Valley, *Krajina s.n.* (BISH, US *1991819*); along trail to Pepeopae Bog, *N261*; Wailau pali, *Rock s.n.* (A, BISH); Wailau-Mapulehu divide, edge of cliff, *Fosberg 13509* (BISH); ridge e. of Mapulehu Valley, *St. John & Fosberg 12874* (BISH); Puniuohua, *Munro 697* (BISH), *531* (BISH); Halawa, *Hillebrand* (Herb. Lugd. Bat. *903.248 54*) (L). Molokai (without definite locality): *Forbes 285 Mo* (BISH). MAUI. West Maui: Kalaeokaea, *Forbes 2550 M* (BISH, US); Honokohau drainage basin, *Forbes 499 M* (BISH). East Maui: Kailua, *Lyon s.n.* (BISH), *Rock s.n.* (BISH); Waikamoi area, wet forest at rim of gulch, *N258*; Keanae Trail, *Rock s.n.* (A, BISH); ditch trail s. of Keanae, *Munro 487* (BISH), *664* (BISH); Nahiku, *Forbes 245 M* (BISH); ridge on left side of Kipahulu, *Forbes 1641 M* (BISH); w. part of Kipahulu Valley, *Lamoureux & DeWreede 3860* (BISH); near Hana, Puu Ki, *St. John & Catto 17879* (BISH). Maui (without definite locality): Upper ditch trail, *Lyon s.n.* (BISH); Mahikee, *Faurie 1161* (P). HAWAII: Honomu, canyon bottom in hills above Akaka Falls, *Fosberg 10475* (BISH); Hilo, *Hillebrand & Lydgate s.n.* (BISH); Kulani Road, ne. of Kulani Honor Camp, *N138, 139, 140*; Kulani Road, Upper Waiakea Forest Reserve, *Hatheway 440* (BISH); between Glenwood and Volcano House, *Degener 30213* (BISH). Hawaiian Islands (without definite locality): *U.S. Expl. Exped.* (US *809272*), *Remy 156* (A).

1b. **Joinvillea ascendens** subsp. **samoensis** T. K. Newell, subsp. nov.

FIG. 4C; FIG. 5C.

Joinvillea gaudichaudiana sensu Christophersen, Bishop Mus. Bull. **128:** 46, p.p. 1935.

Herba erecta 2–4 m. alta, caule tereti, nodis distalibus 4–6 mm. diametro, internodiis distalibus 6–14 cm. longis; vagina tereti; auriculis ad 6 mm. longis oblongis apice rotundatis vel paulo acutis; foliorum laminis 6.5–13 cm. latis utroque costae 9–12-plicatis; supra trichomatibus raris uni- et multicellularibus etiam setis raris vel infrequentibus; subtus setis raris vel frequentibus. Inflorescentia villosa etiam trichomatibus erecto-patentibus brevibus rigidis aliquam ornata, ramulis primariis medium versus 0.9–1.3 mm. diametro, ramulis ultimis apicem versus 0.3–0.5 mm. diametro; tepalis exterioribus 2.1–3 mm. longis apice mucronulatis vel mucronatis et interdum reflexis, tepalis interioribus 1.9–3 mm. longis. Stylis persistentibus; fructibus 4.1–5.6 mm. diametro.

TYPE: North rim of Lake Lanutoo Crater, Upolu, Western Samoa, at 700 meters elevation, *Newell 239* (BISH holotype) 26 October, 1966.

DISTRIBUTION. Endemic and so far recorded only from Western Samoa, from elevations of 700 to 1,600 meters, in wet forests and often in shaded localities.

Western Samoa. SAVAII: Forest ne. of Samataitai, *N247, 248, 249*; ne. of Salailua, *Christophersen 2562* (BISH); crater rim above Matavanu Crater, *Christophersen & Hume 2206* (BISH, NY, US); forest above Matavanu Crater, *Christophersen & Hume 2030* (BISH, US); forest sw. of Matavanu Crater, *N245*. Savaii (without definite locality): *Whitmee 245* (K); *U.S. Expl. Exped.* (US *690600*). UPOLU: Lake Lanutoo, *Christophersen 122* (BISH, NY), *372* (BISH), *Hochreutiner 3269* (L); n. rim of Lake Lanutoo Crater, *N235, 237, 238, 239* (BISH holotype), *240, 241, 242, 243, 244*. Upolu (without definite locality): *Reinecke 305* (BISH). SAMOA (without definite locality): *Whitmee 23* (K), *s.n.* (A, K).

1c. **Joinvillea ascendens** subsp. **borneensis** (Beccari) T. K. Newell, comb. nov. FIG. 4A; FIG. 5A.

Joinvillea borneensis Beccari, Nelle Foreste di Borneo, 198. 1902; Merrill, Enum. Philip. Fl. Pl. **1**: 190. 1923; Backer, Fl. Males. I. **4**: 245. 1951.
Joinvillea malayana Ridley, Jour. Straits Branch Roy. Asiatic Soc. **44**: 199. 1905; Fl. Malay Pen. **4**: 368. 1924.

Erect herb, 2–5.5 m. high; stem terete, 4–9 mm. in greatest diam. at distal nodes, the distal internodes 5–11.5 cm. long; sheath terete; auricles to 14 mm. long, oblong, rounded at apex; lamina with 9–13 plications on each side of midrib, 5–14 cm. broad; unicellular and multicellular trichomes on abaxial laminal surface rare to infrequent; bristles infrequent to frequent on both surfaces. Inflorescence with erecto-patent short stiff trichomes, primary branches 0.7–1.2 mm. in diam. at midpoint, ultimate branchlets 0.3–0.5 mm. in diam. 5 mm. from tips; outer tepals 1.7–2.8 mm. long, with a mucronulate, rarely reflexed, tip; inner tepals 1.8–2.6 mm. long. Styles persistent on fruit; fruit 3.4–4.8 mm. in diam.

TYPE: Since neither Beccari nor subsequent workers indicated a type I am choosing *Beccari 2816* (FI) as lectotype. This specimen is from Gunong Wa, Sarawak, East Malaysia, the type locality, and may have been part of Beccari's original collection. He reported finding the new species on 19 November, 1866 (Beccari, 1902); the label of *Beccari 2816* bears the date November, 1866. The specimen chosen is in mature fruit with the perianths in good condition.

LOCAL NAMES. In West Malaysia known as "rotan bini" (Backer, 1951), a name apparently shared with *Flagellaria indica* L. (Ridley, 1924). The name "si marboeloe-boeloe" on the label of *Rahmat si Boeea 5921* (L), a specimen collected on Sumatra. In the Philippines called "odyung" in Tagbanua (Backer, 1951).

DISTRIBUTION. Malay Peninsula (West Malaysia), Sumatra, Borneo (Sabah and Sarawak in East Malaysia and Kalimantan), the Philippine Islands (Jolo and Palawan), and the Caroline Islands (Ponape), from about 50 to 1,920 meters elevation. Growing along roadsides, forest edges, and other partially open, wet but well drained sites; common as a pioneer plant in open roadcuts near the Sabah National Park (SNP) Headquarters.

Malaysia. WEST MALAYSIA. Perak: Taiping Hills, *Ridley 11916* (K); Maxwell's Hill, mile 8, *N164*; G. Hijau, near summit, *N161, 162, 163*; G. Batu Puteh, *Wray 253* (K). PAHANG. Cameron Highlands: *Md. Nur SF 32579* (A); n. of Brinchang, along trail to G. Batu Brinchang, *N165*; along road to G. Batu Brinchang, *N166, 167, 168, 169*; along road ne. of Brinchang, *N170, 171*; along road between Brinchang and Tanah Rata, *N172*. SELANGOR (at border): Fraser's Hill, *Burkill & Holttum SF 8649* (K), *N173, 174, 175*; Fraser's Hill, gap road, *Purseglove 4124* (L); Semangkok Pass, *Ridley s.n.* (K). EAST MALAYSIA. Sabah: near Jesselton, Hulu Inanam, *Otik SAN 4165* (K); along Tamparuli-Ranau road, mile 14, *N157*; mile 18, *N156*; mile 19, *N155*; mile 20, *N153*, *154*; mile 21, *N152*; vicinity of SNP Headquarters, *N144, 149, 150, 151;* along Tamparuli-Ranau road, mile 35.5, *N145, 146, 147, 148*; mile 37, *N143*; Mt. Kinabalu, Bungal Trail, *J. & M. S. Clemens 26015* (A, K, L, NY); Mt. Kinabalu, Gurulau Spur, *M. S. Clemens 10799* (A); Mt. Kinabalu, Pinosuk Plateau, *Chew, Corner & Stainton 1809* (K). Sarawak: G. Wa, *Beccari 2816* (FI, 2 specimens, including lectotype, in fruit; K). Sarawak (without definite locality): *native collector SAR 1707* (A, K, US).

Indonesia. SUMATRA: Atjeh, Gajolanden, *van Steenis 8784* (A, L); trail from Medan road to top of Sibajak Volcano, *W.N. & C.M. Bangham 1025* (A, NY); Sibajak, *Lörzing 13893* (K, L), *Stomps* (Herb. Lugd. Bat. *948.59 441*) (L); Tapianoeli, *Rahmat si Boeea 5921* (L); Air Putih, e. of Pajokumbuh, *Alston 14375* (L). Sumatra (without definite locality): *Alston 14787* (L), *Bunnemeyer 8695* (L), collector unknown (Herb. Lugd. Bat. *925.206 829*) (L). KALIMANTAN: Central East Borneo, West Koetai, *Endert 4502* (A, K, L).

Philippine Islands. PALAWAN: Mt. Capoas, *Merrill 9515* (BISH, K, L, NY, US); Brooke's Point, Mt. Mantaliñgahan, *Edaño 119* (L), *1050* (A). Palawan (without definite locality): *Foxworthy 42135* (US).

Caroline Islands. PONAPE: Kuporujo (Mt. Kuprish), *Takamatsu 667* (BISH).

1d. **Joinvillea ascendens** subsp. **glabra** T. K. Newell, subsp. nov.

FIG. 4B; FIG. 5B.

Herba erecta 1.5–2.5 m. alta, caule lateraliter compresso raro tereti, nodis distalibus 5–11 mm. diametro, internodiis distalibus 3.6 cm. longis; vagina lateraliter compressa raro tereti; auriculis ad 40 mm. longis subulatis raro oblongis; foliorum laminis 4.5–7 cm. latis utroque costae 7–9-plicatis; supra trichomatibus raris plerumque multicellularibus et ramulosis; utrinque setis raris. Inflorescentia trichomatibus erecto-patentibus brevibus rigidis ornata etiam interdum parce villosa, ramulis primariis medium versus 0.9–1.3 mm. diametro, ramulis ultimis apicem versus 0.3–0.5 mm. diametro; tepalis exterioribus 1.9–3 mm. longis apice mucronulatis raro reflexis, tepalis interioribus 1.9–2.6 mm. longis. Stylis persistentibus; fructibus 3.3–4.6 mm. diametro.

TYPE: Plateau de Dogny, New Caledonia, edge of gallery forest at 950 meters elevation, *Newell 196* (BISH holotype) 1 October, 1966.

DISTRIBUTION. Endemic to New Caledonia, and so far known only from the vicinity of the Plateau de Dogny, from elevations of 720 to 980 meters. Growing mainly at the forest edges in wet but generally well-drained areas.

New Caledonia. Plateau de Dogny, at edges of forested areas on the Plateau, *N196* (BISH holotype), *198, 199, 200, 201, 202*; somewhat open forest on slopes sw. of the Plateau, *N192, 193, 194*.

2. **Joinvillea plicata** (Hook. f.) T. K. Newell & B. C. Stone, Taxon **16**: 193. 1967.

Flagellaria plicata Hook. f., Hook. Jour. Bot. Kew Gard. Misc. **7**: 200. *pl. VIII*. 1855.

Erect herb, 1.5–5.5 m. high; auricles to ca. 90 mm. long; lamina with variable trichomes on the abaxial surface, bristles on adaxial surface frequent to abundant, 8–15 plications on each side of midrib, 50–100 cm. long and 5–20 cm. broad when flattened. Tepal apex usually not splitting in age; outer tepals deltoid-lanceolate with an acute to acuminate tip, with 1 central vein and sometimes 1 or 2 lateral veins, 1.7–3.1 times longer than broad, 1.7–4.1 mm. long and 0.8–1.9 mm. broad; inner tepals deltoid-lanceolate to ovate with an acute to acuminate apex, 1–2 times longer than broad, 1.1–3.3 mm. long and 0.8–2.1 mm. broad. Styles usually persistent on fruit; fruit 4–6 mm. in diam.

2a. **Joinvillea plicata** subsp. **plicata.** FIG. 4E–I; FIG. 5E–G.

Flagellaria plicata Hook. f., Hook. Jour. Bot. Kew Gard. Misc. **7**: 200. *pl. VIII.* 1855.
Joinvillea elegans Gaud. Atlas, Voy. Bonite. *pl. 39 & 40, fig. 7–26.* 1841, *nomen nudum*; Brongn. & Gris, Bull. Soc. Bot. France **8**: 268. 1861.
Flagellaria elegans Seem. Fl. Vit. 315. 1868.

Erect herb 1.5–5.5 m. high; stem terete to bilaterally compressed, 5–14 mm. in greatest diam. at distal nodes, distal internodes 2–11 cm. long. Leaf sheath terete to bilaterally compressed; auricles to ca. 90 mm. long (mostly 15 mm. or less), oblong, rounded at apex, sometimes subulate, mostly straight. Lamina 50–100 cm. long and 5–20 cm. broad, apex acute to attenuate; variable trichome types on abaxial surface infrequent to abundant; multicellular trichomes on abaxial veins rare to abundant (mostly infrequent to frequent). Inflorescence 3–5 times branched, 10–40 cm. long and 9–40 cm. broad; outer tepals 1.7–3.6 mm. long and 0.8–1.9 mm. broad, sometimes with 2 lateral veins; inner tepals 1–2 times longer than broad, 1.1–3.1 mm. long and 0.8–1.9 mm. broad; fruit globose to somewhat dorsiventrally flattened, 1.1–1.7 times broader than high, 4–6 mm. in diam.

TYPE: Île des Pins, New Caledonia, *Macgillivray 770* (K lectotype). Hooker (1855) cites two specimens, *M'Gillivray* (*Macgillivray*) and *Milne*, October 1853 (young fruit). I have examined them and found both in good condition with young fruit; *Macgillivray 770* is here selected, because the herbarium sheet also bears drawings of fertile structures appearing in the plate accompanying Hooker's description.

LOCAL NAME. Called "wahedali" on the label of *Brass 3254* (BISH) from Santa Ysabel. BSIP.

DISTRIBUTION. Solomon Islands (Santa Ysabel, Guadalcanal, and San Cristóbal), New Caledonia proper and Île des Pins, New Hebrides (Aneityum), and Fiji (Viti Levu, Vanua Levu, and Taveuni), from near sea level to 1,195 meters elevation. Frequently found in the Solomon Islands and Fiji, and forming a conspicuous part of the New Caledonian flora. *Joinvillea elegans* Gaud., as illustrated in Gaudichaud (1841), clearly belongs here, and most closely resembles New Caledonian specimens. Gaudichaud's specimen was lost and its collection locality is unknown. Since the Bonite did not stop at any of the islands where this taxon is known to occur, a specimen was probably sent to Gaudichaud. However, he may have collected it on a previous visit to the New Caledonia area.

Subspecies *plicata* is quite variable, but the New Caledonian plants overlap so strongly with those of the Solomon Islands and Fiji, that I find no good basis for recognition of additional subspecies. Although several varieties of subspecies *plicata* might be distinguished in New Caledonia, it seems inadvisable to suggest these without additional material and more detailed field investigation.

British Solomon Islands Protectorate. SANTA YSABEL: Kakatio, *Brass 3254* (A, BISH). GUADALCANAL: Nw. end of island on ridge above Hidden Valley, *N176, 177, 178, 179, 180, 181*; Gold Ridge, up from bungalow, *Whitmore BSIP 646* (L). SAN CRISTÓBAL: Hinuahaoro, *Brass 2908* (A, BISH, L).

New Caledonia. Wagap, *Vieillard 1396* (A, FI, K, L, NY); at edge of forested area on Plateau de Dogny, *N197*; open forest just below sw. edge of Plateau de Dogny, *N195*; forested slopes sw. of Plateau de Dogny, *N190, 191, 203*; Pirogue, *MacDavids & Barrau 2449* (P); auf den bergen bei Paita, *Schlechter 14870* (L); La Dumbéa, *Franc 27* (US); Mt. Koghi, Route de l'Hermitage, *N184, 186, 187, 188, 189*; Kae (Caferie), *Chabert s.n.* (FI); ne. of Conception, *Balansa 944* (P); Nouméa, *Cribes 897* (A, NY); along road from mouth of Lembi R. to Mts. Kouanenoa, *N215, 216, 217, 218, 219, 221, 222, 223, 224, 225*; base of Mt. Dore, *Buchholz 1009* (US); Prony, *M. et Mme. Le Rat 1599* (P, US); Baie de Prony, *Godefroy* (Herb. Lugd. Bat. *951.74 740*) (L); Isle of Pines, bank of stream, *Milne 172* (K), by stream in a wood, *Macgillivray 770* (K lectotype), on bank above small stream about 2 km. nw. of Pic Nga, *N205, 206, 207, 208, 209, 210, 211, 212, 213, 214*. New Caledonia (without definite locality): *Baumann-Bodenheim 5016* (A), *Deplanche 358* (P), *Franc 27* (NY), *Le Rat 2467* (A), *Germain* (US *1506846*), *s.n.* (A, K), *Pancher s.n.* (K, NY).

Fiji. VITI LEVU. Mba: Mt. Evans Range, Mt. Koroyanitu, *Smith 4182* (BISH, L, US); w. of Nandarivatu, Mt. Ndelaiyoö, *Smith 5080* (A, BISH, L, US); along road in vicinity of Nandarivatu, *N234*; inland from Navai, *Reay 862* (A); Navai, Vuninatambua, *Degener 14876* (A, NY). Mba or Naitasiri: Between Nandarivatu and Nasonggo, *Reay 34* (A). Serua: Between Ngaloa and Korovou, *Smith 9247* (US); along road n. of Ngaloa, *N227, 228, 229, 230, 231, 232, 233*; vicinity of Ngaloa, *Degener 15139* (A, BISH, L, NY, US); e. of Navua R., *Smith 9121* (US). Namosi: Hills between Navua R. and Suva, *Greenwood 1008* (A, BISH). Naitasiri: Rairaimatuku Plateau, *Smith 6113* (A, US); along Sawani-Serea road, *N226*. Viti Levu (without definite locality): *Seemann 645* (A, K). VANUA LEVU. Mbua: Navotuvotu, Mt. Seatura summit, *Smith 1642* (BISH, NY, P, US). Mathuata: Ndreketi, *Parham et al.* (Fiji Dept. Agric. *13456*) (K). Thakaundrove: Eastern drainage of Yanawai R., *Degener & Ordonez 14063* (A, BISH, NY, US); Mt. Mbatini, crest of range, *Smith 655* (BISH, NY, US). Taveuni: Trail from Somosomo, *Gillespie 4820* (BISH). Fiji (without definite locality): *Yeoward 27* (K).

2b. **Joinvillea plicata** subsp. **bryanii** (E. Christophersen) T. K. Newell, comb. nov. FIG. 4I; FIG. 5H.

Joinvillea bryanii Christophersen, Bishop Mus. Bull. **128:** 44. 1935.

Erect herb, 3–5.5 m. high; stem terete, 4–8 mm. in greatest diam. at distal nodes, distal internodes 6–7 cm. long. Leaf sheath terete; auricles to 12 mm. long (mostly 6 mm. or less), somewhat oblong, rounded to acute at apex, apex mostly curving away from ligule. Lamina 52–74 cm. long and 6–15 cm. broad, apex attenuate; trichomes on abaxial surface unicellular and some multicellular, mostly abundant; multicellular trichomes on abaxial veins frequent to abundant. Inflorescence 3–4 times branched, 11–22 cm. long and 10–25 cm. broad; outer tepals 2.9–4.1 mm. long and 1.2–1.8 mm. broad, usually without lateral veins; inner tepals 1.3–2 times longer than broad, 2.5–3.3 mm. long and 1.5–2.1 mm. broad; fruit globose, 1.2–1.3 times broader than high, 4.3–5.4 mm. in diam.

TYPE: Forest above Aopo, Savaii, Western Samoa, at 900–1,000 meters elevation, *Christophersen 3457* (BISH holotype) 7 December, 1931.

LOCAL NAME. Called "ū vao" on the label of *Christophersen 2714.*

DISTRIBUTION. Endemic, and so far recorded only from Savaii, Western Samoa, from elevations of 800 to 1,500 meters, in wet forests and often in shaded localities.

Subspecies *bryanii* is a very homogeneous taxon but does not differ strongly from some Fijian and New Caledonian material. The extent of overlap, seems to justify the reduction of this taxon to the rank of subspecies. Its uniformity and the fact that it has been found only on Savaii indicate that it may be a relatively recent arrival in Western Samoa and might be considered a peripheral isolate. It probably arrived as a single introduction; lack of variation could be a result of a small gene pool.

Western Samoa. SAVAII: Forest ne. of Samataitai, *N250, 251, 252, 253, 254, 255*; forest above Aopo, *Christophersen 3457* (BISH holotype, P isotype); above Salailua, forest slopes above Papafu Crater, *Christophersen 2682* (BISH); forest just below rim of Papafu Crater, *Christophersen 2714* (BISH); forest above Salailua, *Christophersen 2747* (BISH), *3097* (BISH, US); rain-forest above Safune, *Bryan 125* (BISH, NY); forest above Matavanu Crater, *Christophersen & Hume 2040* (BISH, US), *2088* (BISH), *2283* (BISH).

TABLE 1. **Chromosome numbers in Joinvillea**

SPECIES	COLLECTION NUMBER	CHROMOSOME NUMBER	LOCALITY
J. ascendens			
subsp. *borneensis*	N170	$n = 18$	G. Brinchang, West Malaysia
subsp. *borneensis*	N146	$n = 18$	SNP, East Malaysia
subsp. *glabra*	N201	$2n = 36$	Plateau de Dogny, New Caledonia
subsp. *ascendens*	N139	$n = 18$	Hawaii, Hawaii

J. plicata			
subsp. *plicata*	N180	$n = 18$	Guadalcanal, BSIP
subsp. *plicata*	N225	$n = 18$	Monts Kouanenoa, New Caledonia
subsp. *plicata*	N208	$n = 18$	Île des Pins, New Caledonia
subsp. *plicata*	N230	$n = 18$	Serua, Viti Levu, Fiji
subsp. *plicata*	N232	$n = 18$	Serua, Viti Levu, Fiji
subsp. *bryanii*	N255	$n = 18$	Savaii, Western Samoa

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THE ECOLOGY OF AN ELFIN FOREST IN PUERTO RICO, 9. CHEMICAL STUDIES OF COLORED LEAVES

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ONE OF THE SPECTACULAR FEATURES of tropical vegetation is the frequent occurrence of brightly colored leaves. The color may be found in young foliage, produced either regularly or seasonally, or in the mature foliage of certain taxa as common in cultivation as *Codiaeum variegatum* var. *pictum* or *Acalypha wilkesiana*. Color development in the fall or with the change from dry to rainy season is less frequent. The red colors are assumed to be due to the dominance of anthocyanin pigments and may appear in young leaves before the chlorophyll develops, in mature leaves in segments of the blade or partially masked by chlorophyll, and in senescent leaves after the chlorophyll has been destroyed. Red color may also be a pathological symptom frequently associated with phosphorous deficiency. Macmillan (1952) stated "anthocyanin may appear temporarily in the young leaves, and, if abundant before the chlorophyll is largely developed, a bright red immature foliage results. This is very evident in many tropical trees, e.g. *Mesua ferrea*, a species of *Calophyllum*, *Eugenia*, *Cinnamomum* etc. The coloration is at times so vivid that from a distance such trees appear to be in flower." Anthocyanins are usually red in acid solution and may become purplish to blue as the pH is increased. A previous paper (Howard, 1969) has shown that the pH of the plant sap of the component species of the elfin forest on Pico del Oeste ranges from 2.5 to 6.5. Anthocyanins are often associated as well with the occurrence of sugars in the plant cells and, in temperate areas, with the occurrence of frost or low temperatures. Crocker (1938) stated "anthocyanins appear in many plant cells mainly in the early spring and in autumn at times of low temperatures; under these conditions soluble sugars are also abundant in plant organs. Arthur finds that low temperature favors the development of anthocyanin in the apple without a change in sugar content. He also points out that the small amount of pigment found in cells calls for relatively little sugar as a building material and concludes that temperature probably acts directly rather than through sugar accumulation." More recent work has shown an association of color due to anthocyanin with a shortened photoperiod and suggests that it may be regulated by a phytochrome system. Finally it is evident to anyone familiar with a fall season in New England that potential for the development of color is also inherent in certain plants.

The elfin forest on Pico del Oeste displays a localized brilliance in the vivid colors of young leaves and in the flush growth of many of the woody components. The development of color with age was noted only in *Miconia pachyphylla*, *Mecranium amygdalinum*, and *Calycogonium squamulosum*. Perhaps the greatest year-round color, however, is found in many plants of the bromeliad genus *Vriesea*.

We were not able to attempt tests of the ratio of red to far-red light as a factor in the leaf color we observed in the various plants of the cloud-dominated environment. We were able, however, to establish a small laboratory through the courtesy of Mr. Joseph Martinson, in which we attempted simple tests to examine the chemical bases previously proposed for the color we observed. Tests were run to determine the sugar content of young and old leaves, and of the red- and green-leaved forms of Vrieseas, and that of the water soluble phosphorus.

The epiphyte *Vriesea sintenisii* occurs throughout the forest: on the branches of isolated trees, on upper branches of trees forming the canopy, with many young plants on the horizontal branches or, occasionally, on the ground in cut-over areas. The plants that are exposed to the sky exhibit a brilliant red color. Within the forest, on shaded branches, and frequently on the ground other plants of the same species lack the red color and are pale green in appearance. Although the color difference is intense, the red plants may have the leaf bases green within the rosette but very few plants could be truly called intermediate, that is, partly green and partly red. The principal variation is in the intensity of red. The color difference is also apparent at a very young age. Seedling plants in exposed areas, with developing leaves, have red color at the tips while the protected or shaded seedlings are all green. The intensity of color does not appear to vary throughout the year or to suggest a photoperiod variation. However, the maximum variation in daylength during the year in Puerto Rico is only 2 hours and 18 minutes.

Gleason and Cook (1927) do not mention *Vriesea sintenisii* in their description of elfin forest types, and previous workers on the family or on the flora of Puerto Rico have not described the color variations or suggested any taxonomic value for them. Our initial encounter with these two color forms of *Vriesea sintenisii* suggested that two ecotypes were present.

The brilliance of the red form of *Vriesea sintenisii* suggested that the plants might make attractive ornamentals. However, when bright red plants were taken to a lower elevation within the Luquillo Mountains and placed in an area with less cloud cover, the plants died even when supplied with water daily. Red color forms which were returned to Boston and kept in the greenhouse under high humidity, without any adjustment of the natural photoperiod of the Boston area, retained their red color but failed to flourish, remaining in a vegetative state long after plants of comparable size on Pico del Oeste had flowered, shed seeds, and reproduced vegetatively. Red-colored plants taken from the exposed tree tops and placed on the forest floor in the shade gradually lost their red color and by the time of flowering were almost completely green.

The green-colored plants were also subjected to transplant experiments. These, too, failed to survive when transferred to a lower location, while those transported to the greenhouse in Boston grew well in the new location and flowered on schedule when compared with plants on Pico del Oeste. Green-colored plants within the elfin forest were also transferred from their protected positions to exposed positions by strapping branches holding these plants to upper branches of the forest canopy. These green plants died in the exposed positions. Unfortunately we were unable to attempt a gradual transfer of these plants from one position to another. Clearly the green plants were physiologically adapted to shaded location and could not survive an abrupt although seemingly slight change in exposure to greater light. The red plants became adapted to the shaded location with the apparent loss or masking of the red pigment.

A second bromeliad found in the elfin forest was *Guzmania berteroniana.* Plants of *Guzmania* occurred primarily on the trunks of *Prestoea montana* or on the ground in protected areas on the lee slopes of the trail. All plants of *Guzmania* were green and no red forms were seen. Transplant experiments produced results nearly comparable to those for green forms of *Vriesea.* Plants taken to lower elevations died; those taken to Boston have persisted, but the rate of maturation was slower; plants which were transferred to exposed locations in the canopy died even more quickly than did the green forms of *Vriesea.*

When initial sugar tests suggested a higher sugar level in red-leaved plants of *Vriesea,* we continued a comparative study through two years, making analyses of plants in various stages of development.

In each test an average of eight plants was collected in the Pico del Oeste forest and taken to the laboratory. The leaves were all separated and washed thoroughly in running water and hand dried with towels. Roots and rhizomes were discarded. After the fresh weight of the leaves was obtained for each plant they were oven dried at 70°–75° for two days. When the dry weight was obtained the leaves were finely cut, and after a thorough mixing of the fragments of the individual plants, 1 gm. of dry leaves was placed in an Erlenmeyer flask; 100 cc. of distilled water was added; and the mixture was simmered for 30 minutes. When cooled to air temperature, distilled water was added to regain the original volume of 100 cc. The solution was allowed to mix for about two hours, then the sugar content was estimated quantitatively, following the colorimetrical method of Folin and Wu (1920). In a second Folin-Wu tube 0.1 cc. of 1:10 diluted HCl was added and the tube submerged for 5 minutes in a boiling water bath to hydrolize the higher sugars to a hexose before a second colorimetric sugar determination was made. The results are expressed in the following tables as percentages of sugar per gram of dry weight of the plant, and are the average of the eight plants of each sample category. There was no significant variation between the eight samples.

Soluble phosphorus determinations were made from 2 grams of the dried material which was diluted with 100 cc. of distilled water and simmered at 90°C. for 30 minutes; this was cooled to air temperature and distilled water was added to regain the original weight. The soluble phosphorus was determined according to the procedure of Benedict and Theis (1924): 10 cc. of the extract and 10 cc. of a standard were mixed with 1 cc. of a 5% hypochlorate solution to decolorize the brownish mixture; after 24 hours the solution was filtered and 5 cc. of the standard and the unknown were measured in test tubes; the results are expressed as mg.% of dried plant material.

1966 Red-colored Vriesea

Column no.	1	2	3	4	5	Mean
Water	83%	83%	83%	81%	80%	82%
Hexose	1.92%	1.88%	1.88%	1.44%	1.51%	1.73%
Total sugar	2.27%	1.96%	2.05%	1.72%	1.96%	1.99%

1966 Green-colored Vriesea

Water	86%	85%	86%	85%	82%	84.8%
Hexose	1.27%	1.32%	1.29%	1.09%	1.36%	1.26%
Total sugar	1.56%	1.82%	2.36%	1.15%	2.06%	1.79%

Columns: 1. Young plants in vegetative rosettes. 2. Inflorescence present, basal flowers open. 3. Inflorescence mature, basal flower in young fruit stage. 4. Fruit forming, seeds turning black. 5. Fruiting stage, seeds mature.

1967 Red-colored Vriesea

Column no.	1	2	3	Mean
Water	80%	85%	80%	82%
Hexose	1.5%	1.9%	1.8%	1.7%
Total sugar	1.8%	2.1%	2.0%	2.0%
Soluble phosphorus	23mg%	30mg%	21mg%	24mg%

1967 Green-colored Vriesea

Water	83%	86%	83%	84%
Hexose	1.2%	1.5%	1.4%	1.4%
Total sugar	1.4%	1.7%	1.6%	1.6%
Soluble phosphorus	26mg%	24mg%	25mg%	25mg%

Columns: 1. Young plants. 2. Inflorescence mature. 3. Fruit mature.

Guzmania berteroniana

Column no.	1	2	3	4	Mean
Water	86%	85%	87%	88%	86%
Hexose	1.0%	1.1%	2.0%	1.2%	1.3%
Total sugar	1.3%	1.3%	2.2%	1.2%	1.5%
Soluble phosphorus	24mg%	25mg%	25mg%	n.e.	25mg%

Columns: 1. Young vegetative rosettes. 2. Mature vegetative plants. 3. Inflorescence mature. 4. Fruits mature.

The water content of the leaf tissue of the components of the elfin forest has been given in a previous paper (Howard, 1969). Tissues tested contained from 93 percent water to 44 percent water. *Vriesea* ranked in the lower portion of the upper third of all the plants tested in water content. All the plants tested which revealed a higher water content were understory plants. The red color-form of *Vriesea*, being primarily a canopy epiphyte had a slightly lower water content than did the green-colored *Vriesea* which occurred in protected locations. The water content of the plant tended to diminish as the plant matured and was lowest when the plant was in fruiting condition. The total sugar in the green-colored form increased to the flowering period, decreased during the development of the fruit, but increased as the fruit matured.

Hexose and total sugar content proved to average higher in red-colored *Vriesea* and the total sugar content was approximately 40 percent higher in the red than in the green forms during the growing season.

In *Guzmania* the water content averaged higher than in *Vriesea*, increasing slightly in the life cycle to the fruiting stage. Hexose and total sugars increased in *Guzmania* during the development of the inflorescence and was 100 percent higher in the flowering cycle, exceeding the red form of *Vriesea*.

The amount of soluble phosphorus averaged about the same in the red and green Vrieseas. However, it seemed to increase in the red *Vriesea* during the flowering period and decrease in the green forms during the same period.

The amount of soluble phosphorus is evidently not a limiting factor in the coloration found in the red form of *Vriesea sintenisii*.

In *Guzmania*, soluble phosphorus levels remain fairly constant through the life cycle and were approximately the same as those of *Vriesea*. Since both bromeliads would receive inorganic materials as wind-blown debris collected in the leaf bases directly, it appears the supply or utilization of phosphorus is equally available to the plants no matter what their position in the forest structure.

The distinctive coloration of young developing leaves in tropical forests is mentioned in many previous studies. An earlier study (Howard, 1969) indicated red, orange, pink, yellow, and bronze tones in the young leaves of specific plants within the elfin forest of Pico del Oeste. Many taxa which did not produce colored leaves when young did show a lighter green or a yellow-green color to the young foliage. Tests for hexose sugars and for total sugars were made on selected leaves from individual taxa. One to four brightly colored leaves were taken, as available, from a flush of growth and tests on these were compared with material from older leaves of the same branch. The following results were obtained:

TAXON	Color of young leaf	Percent water		Percent hexose sugar		Percent all sugars	
		yg lf	old lf	yg lf	old lf	yg lf	old lf
Calycogonium squamulosum	pale red	75	74	4.3	2.6	—	—
Calyptranthes krugii	yellow-green	61	48	5.7	4.45	7.85	4.40

Cleyera albopunctata	yellow	70	57	8.35	8.75	8.35	8.90
Eugenia borinquensis	deep red	70	55	5.62	5.80	5.70	8.05
Gonocalyx portoricensis	pink	89	75	2.8	2.3	—	—
Hillia parasitica	light green	83	81	2.86	4.45	3.57	5.00
Hornemannia racemosa	orange-pink	67	55	4.96	8.50	6.08	8.88
Ilex sintenisii	yellow-green	70	63	7.05	7.30	9.55	8.00
Mecranium amygdalinum	yellow-green	69	70	coagulates copper reagent			
Marcgravia sintenisii							
juvenile leaves	red	82	78	7.6	5.7	—	—
		86	81	7.20	8.84	7.90	8.86
adult leaves	red	84	69	3.4	3.8	—	—
		89	69	7.10	10.00	7.35	10.10
Miconia pachyphylla	red-purple	62	56	coagulates copper reagent			
Miconia foveolata	red-pink	71	68	7.31	5.73	7.82	7.55
Miconia pycnoneura	red-purple	60	53	coagulates copper-reagent			
Ocotea spathulata	bronze-red	62	68	7.7	6.7	—	—
Tabebuia rigida	red-purple	83	70	6.4	3.7	—	—
Torralbasia cuneifolia	yellow-green	71	63	8.80	9.55	8.84	10.89
Wallenia yunquensis	wine-red	75	63	9.80	7.85	10.00	8.90

With the exception of one plant of *Marcgravia sintenisii* and those of *Eugenia* and *Hornemania*, all taxa tested which had red or orange, brightly colored leaves had a higher hexose sugar content in juvenile foliage than in mature foliage of the same plant. In the taxa which produced yellow or pale green juvenile foliage, the hexose sugar content was lower in juvenile leaves than in mature leaves, with the exception of *Calyptranthes* *krugii.* For total sugars in yellow-green juvenile leaves, the same exception occurs, with the addition of *Ilex sintenisii.*

It is of interest to record that the plant extracts obtained during the month of April from four taxa of the Melastomataceae all contain some chemical substances which form a gelatinous coagulate in the Folin and Wu copper reagent. One sample of *Calycogonium squamulosum*, of the same family, formed the coagulate in March but a second test in April from the same plant did not. A similar reaction was experienced for *Miconia foveolata.*

The contrast between the higher hexose and total sugar content in the brightly colored juvenile leaves and that of the mature green foliage in the woody plants is similar to that condition found in *Vriesea sintenisii* when the anthocyanin-dominant plants were compared with the green color-form.

VARIATIONS IN pH OF CELL SAP

The pH of liquid expressed from leaf tissues was mentioned in relation to vulnerability to insect damage in an earlier paper in this series (Howard, 1969). Where possible liquid was obtained from fully expanded leaves and leaves normally green but which had not completely hardened. The leaves were pressed between clean microscope slides, a drop or two of expressed fluid collected, and the pH checked with a Beckman pH meter. The amount of liquid and the ease with which it could be obtained varied considerably between the plants of the elfin forest of Pico del Oeste, and also varied with the time of year for individual plants. The liquids varied in their color and consistency, and in the rate of color changes upon exposure to air. The results of this survey are presented in the following table:

Variations in the liquid extract of crushed leaves and in the pH of plant sap

	Color or consistency of sap	Feb.	July	Nov.
CYATHEACEAE				
Cyathea pubescens	clear	—	4.6	—
PALMAE				
Prestoea montana	yellow-green	5.1	6.2	5.4
ARACAE				
Anthurium dominicense	clear	5.0	5.5	5.8
BROMELIACEAE				
Guzmania berteroniana	rusty	—	4.0	—
Vriesea sintenisii	clear	—	5.1	—
DIOSCOREACEAE				
Rajania cordata	—	—	—	4.9

Zingiberaceae				
Renealmia antillarum	—	5.2	5.3	4.8
Piperaceae				
Peperomia emarginella	—	5.0	5.0	5.5
Peperomia hernandiifolia	—	5.0	4.6	5.1
Chloranthaceae				
Hedyosmum arborescens	orange-brown	4.5	5.3	5.6
Moraceae				
Cecropia peltata	—	5.1	5.1	5.1
Urticaceae				
Pilea krugii	lilac	5.3	5.1	6.0
Pilea yunquensis	—	5.5	5.9	6.4
Lauraceae				
Ocotea spathulata	gelatinous	5.1	4.9	4.9
Meliaceae				
Trichilia pallida	dirty green	5.6	5.2	5.4
Aquifoliaceae				
Ilex sintenisii	—	5.3	5.2	5.1
Celastraceae				
Torralbasia cuneifolia	—	5.0	4.8	4.7
Ochnaceae				
Sauvagesia erecta	yellow-green	4.9	4.9	5.6
Marcgraviaceae				
Marcgravia sintenisii	—	4.6	5.4	4.8
Theaceae				
Cleyera albopunctata	—	3.8	4.1	4.2
Guttiferae				
Clusia grisebachiana	yellow-orange	3.9	3.9	4.3
Begoniaceae				
Begonia decandra	cherry-red	2.5	2.5	2.9
Myrtaceae				
Calyptranthes krugii	—	—	4.0	5.1
Eugenia borinquensis	dirty brown	4.8	4.8	4.8
Melastomataceae				
Calycogonium squamulosum	lavender	3.4	3.3	3.7
Mecranium amygdalinum	rose-purple	3.2	3.8	3.7
Miconia foveolata	red-purple	3.9	3.9	4.0
Miconia pachyphylla	rose	3.7	4.0	4.3
Miconia pycnoneura	rose	3.3	3.4	3.8
Ericaceae				
Gonocalyx portoricensis	—	3.3	3.3	3.5
Hornemannia racemosa	—	3.9	4.2	5.3

MYRSINACEAE				
Ardisia luquillensis	dirty lavender	4.4	4.4	4.4
Grammadenia sintenisii [1]	—	4.1	4.5	4.1
Wallenia yunquensis	—	4.2	4.1	3.5
SAPOTACEAE				
Micropholis garciniaefolia	straw color	4.2	4.1	4.8
SYMPLOCACEAE				
Symplocos micrantha	blue-purple	4.0	4.2	4.8
OLEACEAE				
Haenianthus salicifolius var. *obovatus*	—	5.1	5.2	5.1
CONVOLVULACEAE				
Ipomoea repanda	—	4.5	6.2	5.9
BIGNONIACEAE				
Tabebuia rigida	—	5.0	5.5	5.3
GESNERIACEAE				
Alloplectus ambiguus	—	5.1	4.6	5.5
Gesneria sintenisii	rust-brown	5.3	5.7	5.6
ACANTHACEAE				
Justicia martinsoniana	slimy	5.5	4.1	6.5
RUBIACEAE				
Hillia parasitica	lime-green	4.9	4.7	4.9
Psychotria berteriana	—	5.0	5.7	5.7
Psychotria guadalupensis	brick-red	4.9	5.0	4.9
CAMPANULACEAE				
Lobelia portoricensis	lime-green	5.0	4.8	4.7
COMPOSITAE				
Mikania pachyphylla	—	5.1	5.9	5.8

The leaves from which the liquid was expressed to obtain the records in the preceding table were a normal green color. Where the color is not indicated the liquid was pale green. Accessory pigments, however, were present in several plants and were usually seen in the petiole; yet there was no consistent correlation with the color of the plant liquid obtained. The petioles and lower leaf surface of *Peperomia hernandiifolia*, *Wallenia yunquensis*, and *Tabebuia rigida* were red-purple in appearance. *Miconia foveolata* had red pubescence and *Miconia pachyphylla* appeared to have an underlying tone of red-purple to the leaf blade. The veins of *Begonia decandra* appeared bright red in fresh condition, and the cherry red color of the expressed liquid suggests this pigmentation was released in crushing. *Psychotria guadalupensis* exhibited a red pig-

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[1] In a recent paper Lundell has established a new genus based on this taxon and has made the combination *Cybianthopsis sintenisii* (Urb.) Lundell, Wrightia **4**: 68. 1968.

ment in the petioles and inflorescence axis but not in the leaf blade. The brick red color of the liquid extracted was darker than the pigmentation observed in the whole plant.

It was not possible to extract liquid by the hand pressure method used, from any member of the Gramineae, Cyperaceae, or Orchidaceae.

The pH of the extracted liquid ranged from 2.5 in *Begonia decandra* to 6.5 in *Justicia martinsoniana*. In three taxa tested in February, July, and November, the pH was identical. For 12 taxa two identical readings were obtained in the three unit test. The pH was highest in November for 20 taxa, with high readings in July in 10 taxa, and in February for 6. In 16 taxa the lowest pH reading was obtained in February, in 9 taxa during July, and for 4 taxa in November. In all cases except the herbaceous species the material examined was taken from a single marked plant for the tests. In a general observation the greatest number of plants would be in flower in July, in fruit in November, and in dormant condition during February.

The average pH of the expressed fluid of 11 taxa, in which the juvenile leaves are predominantly red, is 4.6 in a range of 3.4 to 5.2. The comparable pH of 6 taxa, in which the young leaves are yellow or yellow-green, is 4.7 with a range of 3.5 to 5.2. The average pH of the remaining 23 taxa of dicotyledonous plants tested, in which the young leaves are not noticeably different in color from the mature foliage, is 4.9 in a range of 2.7 to 6.0. The color of the young leaves and the associated pH appears to be characteristic of the individual species, with no direct correlation evident between the color of the leaf or of the expressed pigment, the pH, or the sugar content.

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THE GENERA OF PORTULACACEAE AND BASELLACEAE IN THE SOUTHEASTERN UNITED STATES [1]

A. LINN BOGLE

PORTULACACEAE A. L. de Jussieu, Gen. Pl. 312. 1789, "Portulaceae," nom. cons. (PURSLANE FAMILY)

Fleshy or succulent herbs or subshrubs [shrubs or rarely small trees], with erect to procumbent branches, reproducing vegetatively by means of rhizomes, stolons, or axillary bulblets. Roots fleshy, basal or adventitious, fibrous, tuberous, cormose, or plant with a simple to branched taproot. Leaves alternate, opposite, or in basal rosettes, the blades entire, cylindrical (or nearly so) to flat; stipules scarious, fimbriate, of tufted hairs, or absent. Inflorescence terminal or lateral, basically cymose but often appearing racemose or paniculiform, or flowers solitary in the axils. Flowers perfect, regular, inconspicuous or often showy, erect, spreading or nodding. Perianth biseriate (or uniseriate). Sepals (involucral bracts?) 2 [4–8], imbricate, ± equal, free or basally connate, deciduous or persistent. Petals (tepals?) 4–6 (sometimes 2 or 3), free or basally connate, hypogynous or perigynous, often ephemeral. Stamens few to many, alternate with and/or opposite the petals, free or inserted on the corolla base; filaments filiform; anthers 2-loculate, dehiscing longitudinally and introrsely. Gynoecium 2–9-carpellate, syncarpous; styles as many as the carpels, ± united, rarely simple, with linear to capitate stigmas; ovary superior to half-inferior, or inferior, unilocular; ovules many to few [–1], sometimes on long, ascending funiculi, anatropous or amphitropous; placentation free-central or basal, the placenta 2–9-parted or 1. Fruit a pyxis or capsule [rarely an achene], dehiscence

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circumscissile, or by 3 longitudinal valves. Seeds one to many, ± round-reniform, flattened. Seed coat often crustaceous, sometimes arillate, smooth or variously sculptured (rugulate, granulate, muricate, tuberculate). Embryo curved to annular, enclosing the abundant mealy endosperm; cotyledons (1–)2 [rarely 4]. TYPE GENUS: *Portulaca* L.

A small family of 15 to 31 genera with centers of distribution in western North America, southern South America, and South Africa, but extending to eastern Siberia, Australia, New Zealand, and Madagascar. Many of the genera are small or monotypic and restricted in distribution. Only a few have more than about a dozen species (*Anacampseros, Calandrinia, Claytonia, Montia* sensu lato, *Portulaca, Talinum*). Interesting patterns of distribution are evident in several genera: *Portulaca* and *Talinum* have attained wide distributions in the tropics and subtropics of both hemispheres; *Calandrinia* has centers of development in western North America, South America (Chile), and Australia; and *Montia*, which is principally boreal in range, is represented in far flung areas of the Southern Hemisphere.

De Candolle and Bentham & Hooker viewed the family in a narrow sense, essentially as it is regarded today, including 12–15 genera but no subfamilial categories, while Fenzl (followed by Endlicher) took a much broader view of the family, recognizing seven tribes and including many genera now placed in such related families as Basellaceae, Aizoaceae, and Molluginaceae. Similarly Baillon established three series within his Portulacaceae: Portulaceae, Aizoideae, and Mollugineae.

The system of the family established by Franz, which was based on a wide range of morphological and anatomical characteristics, has been followed with modification by Pax & Hoffman and by Eckardt. The genera of Basellaceae originally included by Franz were removed, as were some of doubtful affinity (*Hectorella* Hook. f., and *Lyallia* Hook. f. which have recently been established as a family Hectorellaceae). Of the two subfamilies now recognized in the Portulacaceae, the smaller Montioideae Franz includes only *Montia* L., *Claytonia* L., and the monotypic Chilean *Wangerinia* Franz. Rydberg and, more recently, Nilsson have split eight segregate genera out of the *Claytonia-Montia* complex, but these are not universally recognized. The large subfamily Portulacoideae consists of about 13 genera arranged in two tribes, each with two subtribes. Of primary interest in our area are tribe Portulaceae, subtribe Portulacinae, containing only *Portulaca* L., and tribe Calandrinieae, subtribe Calandriniinae, containing *Talinum* Juss. and four related genera.

The Portulacaceae share several features with other Centrospermae, including the presence of betacyanins (betalains) in place of anthocyanins, curved to annular peripheral embryos, and basal placentation in a compound ovary. The family is considered closely related and possibly ancestral to the Basellaceae through such features as intraxylary phloem (weakly developed in some Montioideae), uniovulate ovaries in advanced genera, a tendency toward unisexual flowers, and similar floral plans. Relationships to the Caryophyllaceae, Chenopodiaceae, and Amaranthaceae are seen in the morphology and anatomy of the seeds, and to the Aizoaceae (through *Sesuvium*), from which the Portulacaceae differ principally in characteristics of floral organization and the lack of well-developed anomalous secondary growth. A relationship to the Primulaceae, advanced particularly on embryological evidence (Guignard, cf. *Talinum*), has found little support.

Embryological studies in a few of the better known genera reveal anatropous to amphitropous, crassinucellar ovules in which the inner of the two integuments forms the micropyle. A Polygonum-type embryo sac is formed from the chalazal cell of a linear tetrad. Endosperm formation is initially nuclear, later becoming entirely cellular (or only partially so in *Portulaca oleracea*). Both solanad (in *Portulaca*) and caryophyllad (in *Claytonia*) types of embryo development occur in the family, and polyembryony is reported in *Portulaca oleracea*. Anthers are tetrasporangiate, and pollen grains are generally three celled (rarely two celled) when shed. Embryos with only one cotyledon are reported in *Claytonia virginica* L., while four cotyledons have been found in *Anacampseros lanceolata* (Haw.) Sweet.

The pollen morphology of the family is diverse, ranging from tricolpate to rugate (with several to many colpi distributed evenly over the surface), to forate (with many evenly distributed round pores). The surfaces of the grains usually bear small spines (Erdtman, Franz).

On the basis of studies of floral development and anatomy the perianth and androecium in the family have been variously interpreted as biseriate or uniseriate, while the pentamerous floral plan evident in many genera has been considered as either basic, or derived from a basically trimerous (Payer, Eichler) or bimerous (Sharma) pattern. Thus the two (to several) sepals are considered by some as involucral bracts, and the petals as tepals (cf. Pax & Hoffman, 237, 238). In the light of conflicting interpretations, as well as for taxonomic convenience, the traditional terms sepal (calyx) and petal (corolla) are used here.

The ovary has been shown in several genera (*Anacampseros*, *Calandrinia*, *Montia*, *Portulaca*) to be septate early in ontogeny. The septa are lost as the ovary develops, resulting in free-central or basal placentation, with the ovules arranged in one to several groups, each group presumably representing a lost locule. Anatomical data for the family are fragmentary and not particularly distinctive. The intraxylary phloem reported to occur in *Montia* and its allies is not always well defined. A petiolar vascular supply of a single bundle has been reported in species of *Portulaca* and illustrated in the monotypic genera *Mona* O. Nilss. and *Neopaxia* O. Nilss.

Chromosome counts available for some of the better known genera (*Calandrinia*, *Claytonia*, *Lewisia*, *Montia*, *Oreobroma*, *Portulaca*, *Talinum*) show diploid numbers ranging from $2n = 8$ to ca. 191, in either dysploid or euploid series, suggesting a rather complex evolution through the development of polyploidy followed by the formation of aneuploids.

The family is of only minor economic importance. Species of *Anacampseros, Calandrinia, Lewisia, Montia, Portulaca,* and *Talinum* are grown as ornamentals. A few species are used as vegetable or salad "greens" or in folk medicine for various internal complaints. Species of *Portulaca* and *Calandrinia* have proven poisonous to livestock in the southwestern United States and Australia due to high concentrations of oxalic acid.

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KEY TO THE GENERA OF PORTULACACEAE

General characters: *low, succulent to suffrutescent herbs with simple, fleshy, flat to terete, alternate, opposite, or basal leaves; stipules scarious, or of tufted hairs, or absent; stems erect to procumbent; inflorescence axillary, terminal, or scapose, diffuse to congested, basically cymose but often appearing racemose or paniculate; flowers complete, small to large, regular, hypogynous to epigynous; sepals 2; petals usually 5 (4–6); stamens 5–100, alternate or opposite the petals, free or fasciculate; ovary 2–9-carpellate, unilocular, with basal placentation; ovules few to numerous, ascending; fruit a 3- to many-seeded capsule, circumscissile or valvate.*

A. Stipules present, scarious or laciniate, or of tufts of hair; inflorescence a terminal head or congested helicoid cyme, usually surrounded by a whorl of leaves; ovary half-inferior to inferior; stamens few to many, perigynous; fruit a circumscissile capsule; ovules and seeds numerous, stalked. .... 1. *Portulaca.*

A. Stipules absent; ovary superior; fruit a 3-valved capsule.
  B. Leaves cauline or basally tufted on stems from tuberous roots or rhizomes; inflorescence a terminal peduncled cyme, or flowers axillary, solitary; stamens 5–100, alternate with or opposite the petals; ovules and seeds numerous. .... 2. *Talinum.*

B. Leaves few to many from a deep-seated corm; flowering stem scapose, bearing a single pair of opposite leaves; inflorescence a loose raceme; stamens 5, opposite the petals; ovules and seeds (3–)6. . . 3. *Claytonia.*

Subfamily PORTULACOIDEAE [Franz]

Tribe PORTULACEAE [Franz]

Subtribe **Portulacinae** [Franz]

1. **Portulaca** Linnaeus, Sp. Pl. 1: 445. 1753; Gen. Pl. ed. 5. 204. 1754.

Low, annual or perennial herbs with erect, ascending or procumbent, fleshy or suffrutescent, sometimes reddish stems from fleshy or fibrous roots. Leaves alternate to subopposite, terete, subterete, or flat, entire, often congested in an involucre about the flowers. Stipules scarious or reduced to tufts of hairs, rarely absent. Flowers erect, sessile to subsessile, solitary and axillary or few in terminal heads or compact helicoid cymes. Sepals 2, opposite, the abaxial larger than the adaxial, united below. Petals 4–6, free or basally connate, gelatinous-deliquescent after flowering. Stamens 6–40 [4–100], inserted perigynously; filaments usually pubescent below; pollen polyrugate. Carpels as many as the style branches; styles short, 2–9-parted [rarely simple]; ovary semi-inferior to inferior, globose to obovate, plurilocular below to unilocular above; ovules numerous, amphitropous, on a simple or branched free-central placenta. Capsule membranaceous, chartaceous, circumscissile. Seeds numerous, reniform to cochleate; seed coat smooth or variously sculptured, in ours granular to stellate-tubercular or -echinate, brown to black or gray. Embryo peripheral, annular, surrounding the endosperm. (Including *Portulacca* Haw.). LECTOTYPE SPECIES: *P. oleracea* L.; see Britton & Brown, Illus. Fl. No. U.S. ed. 2. 2: 39. 1913. (Name probably derived from Latin, *portula*, a small gate or door, in reference to the calyptra of the capsule.) — PURSLANE.

A genus of about 100–125 species widely distributed in tropical, subtropical, and temperate regions of the world. Eight to ten species occur in our area.

In the early literature the North American species were generally grouped in two or three subgeneric categories of undesignated rank, based on either leaf shape (flat or cylindrical) or the presence or absence of pubescence. Wilson (N. Am. Fl.) recognized 23 species, but no subgeneric groupings. In Poellnitz's provisional monograph of the genus (1934), 104 species were disposed in two subgenera, one with two sections and eight subsections. For lack of comparable material, Poellnitz could not key all of the species to their appropriate subsections, but each is described and discussed in detail. The American species have since been monographed by Legrand, who recognized six subgenera, of which three, containing about 62 species, occur in the Western Hemisphere. All

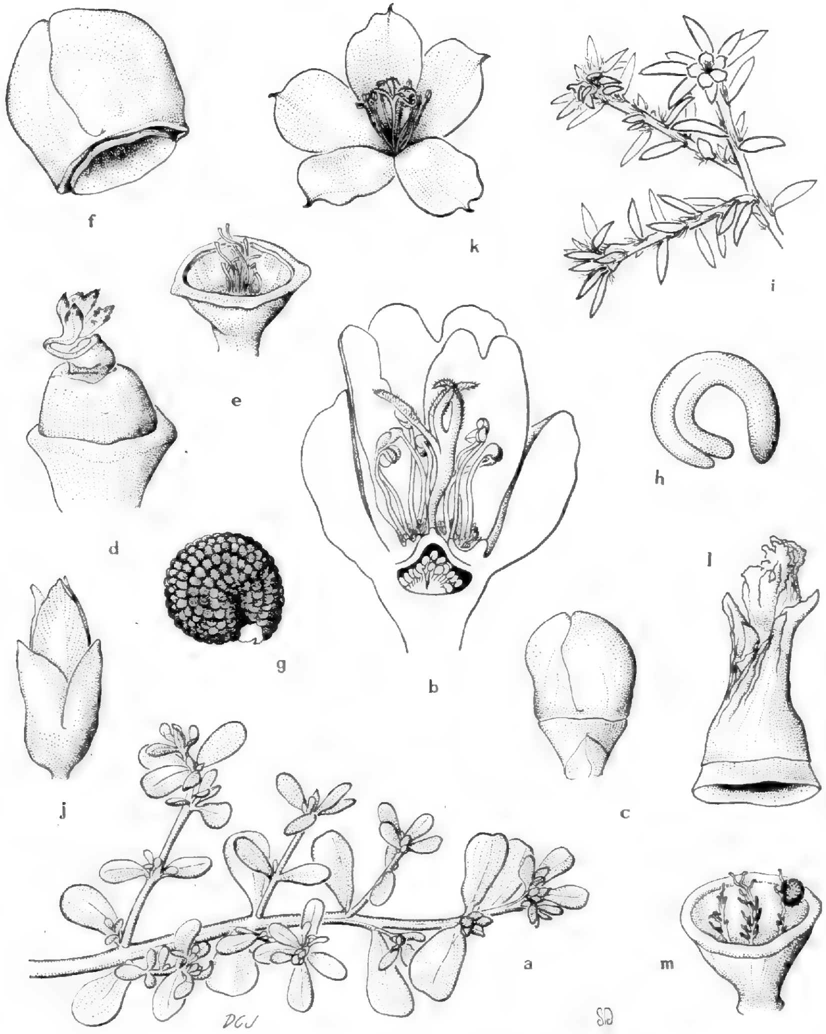

FIG. 1. **Portulaca.** a–h, *P. oleracea*: a, flowering and fruiting branch, × 1/2; b, flower in semidiagrammatic vertical section to show perigynous floral organs and basal placentation, × 6; c, nearly mature fruit inclosed above by accrescent sepals — note bracteole at base of ovary, × 3; d, same, with perianth removed to show top of ovary with constricted apex and persistent style, × 5; e, base of circumscissile fruit after dehiscence, with persistent funicles from basal placenta, × 5; f, upper part of fruit after dehiscence, with mature accrescent sepals, included remains of gelatinous-deliquescent petals and stamens (not visible), and top of pericarp, × 5; g, seed, × 25; h, embryo, oriented as in seed, × 25. i–m, *P. pilosa*: 1, branches with terminal flower and fruit, × 1/3; j, flower bud just before anthesis to show sepals connate at base, × 8; k, flower with forward petals depressed to show stamens and style, × 4; l, withered perianth (sepals and petals, stamens not visible) adhering to upper part of circumscissile pericarp, × 10; m, base of fruit after dehiscence, showing four ascending basal placentae, one bearing a seed, × 10.

of our species belong in subgenus PORTULACA. Several species of the southern United States (*P. coronata*, *P. neglecta*, *P. parvula*, *P. phaeosperma*, *P. retusa*) fall into synonymy through the expansion of species limits and ranges. Our species are discussed here under their older, more familiar names, followed by their disposition in Legrand's system.

Four flat-leaved species, with carinate to subcarinate sepals, and usually with yellow flowers, have been described in our area. *Portulaca olèracea* L. (pusley, pursley, purslane, pigweed), $2n = 18, 45, 52$, and 54, is a common procumbent weed of waste places, fields, and cultivated areas, with almost world-wide distribution. Its flat, fleshy, obovate-cuneate to spatulate leaves; strongly keeled sepals; yellowish, apically notched petals; and black, granulate seeds are characteristic. Birds have been observed to eat the seeds and may have played a role in the widespread distribution, but its origins are lost in antiquity (see discussion in De Candolle). West of the Mississippi River in Arkansas, Kansas, and Missouri, the place of *P. oleracea* may be taken by *P. neglecta* Mack. & Bush, which differs in its upright ascending habit; larger size; larger, broader, and thinner leaves; more numerous stamens; muricate seeds; and different flowering time. Where the two occur together, *P. oleracea* flowers open at about 9:30 A.M., while those of *P. neglecta* open at about 7:40 A.M. Poellnitz suggested that *P. neglecta* may be only a variety of *P. oleracea*. The closely related *P. retusa* Engelm., ranging from Arkansas and Missouri to Arizona and Utah, is similar to *P. oleracea* in its procumbent habit, but differs from both of the above in its thinner, retuse leaves; more slender habit; smaller flowers; and echinate-tuberculate seeds. All three species were recognized by Poellnitz, but Legrand reduced *P. neglecta* and *P. retusa* to synonymy under *P. oleracea*.

The fourth flat-leaved species, *Portulaca coronata* Small (including *P. lanceolata* Engelm.,[2] not Haw.), inhabits granite outcrops and sandy soils in South Carolina (very rare), Georgia, and Mississippi. In the southwestern United States it ranges from the granitic region of western Texas to lower California. The species is especially marked by the flaring, corona-like rim surrounding the ovary just below the line of dehiscence, as well as by its subcarinate sepals, lanceolate leaves, yellow (to orange or red-tinged) petals with acute tips, and gray seeds. According to McVaugh it is often found growing with *P. Smallii* on the granitic flat-rocks of the Southeast, but in slightly more shaded conditions. In Legrand's system, *P. coronata* becomes a synonym of *P. umbraticola* HBK., which ranges to Cuba, Central America, and much of South America.

The six remaining species of the area have more or less cylindrical leaves, dorsally rounded sepals, and, for the most part, characteristic pubescence of the leaf axils and inflorescences. *Portulaca pilosa* L., $2n =$

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[2] According to Fosberg, *P. coronata* Small is the only name available for *P. lanceolata* Engelm., since *P. lanceolata* Haw. (1803), antedating Engelmann's name by 47 years, was validly published for a species now referred to *Anacampseros*. In his original description of *P. coronata* (1896) Small compared it with *P. lanceolata* Engelm. Wilson (1932) considered *P. coronata* a synonym of *P. lanceolata*, but Poellnitz (1934) treated the two as different species with very different seeds.

16, has conspicuous stipules of tufted whitish hair in its leaf axils, and whitish to brownish hairs around the flowers. Its small, obovate, notched petals are usually purplish pink, with a small mucronate tip at the base of the notch. It is reported on sandhills and in dry, sandy soils of woods, roadsides, and cultivated grounds from the Carolinas to Florida, and westward to Texas, as well as in the West Indies, Mexico, and Central and South America.

Portulaca Smallii P. Wils., $2n = 16$, has only slightly tufted axils and pale brown hairs in the inflorescence surrounding inconspicuous flowers with deep lavender to pure white petals. The species is abundant in the shallow soils of surface depressions and particularly of the marginal ecotone of granite flat-rocks in North Carolina and in Georgia to DeKalb and Pike counties (but not in South Carolina or Alabama). This species is very closely related to, and possibly derived from, *P. pilosa*, the two being distinguished chiefly by the endemism of the former and the greater overall size and larger number of stamens in the latter (Cotter & Platt). *Portulaca suffrutescens* Engelm. is a linear-cylindric-leaved suffrutescent perennial with copper or yellow-brown (buff), notched petals, and black, rounded-tuberculate seeds. It ranges from Arkansas to Arizona and Mexico. *Portulaca grandiflora* Hook. (rose-moss, moss-rose), $2n = 18$, 36, a native of South America, has escaped cultivation and become widely naturalized in North America and Europe. Its flowers, 2–5 cm. in diameter, are larger than those of any of the native species and have 40 or more stamens. Flower color ranges from white to pink, red, orange, salmon, or yellow. Its cylindric leaves also have hair-tufted axils.

Portulaca parvula Gray, with ascending branches, copiously hairy nodes, nearly cylindrical leaves, yellow, orange, or copper petals (red, according to Wilson and Poellnitz), and stipitate capsules, occurs from western Missouri and Arkansas westward to Colorado, California, and southward into Mexico. This species was redefined by Johnston, who segregated the purple-flowered plants included in it by Gray as *P. mundula* I. M. Johnston (Mexico to Oklahoma, Kansas, and Missouri). Such plants have also been included under *P. pilosa* L., but Johnston considered that species attributable to specimens from Curaçao, and not conspecific with the plants of Mexico and the southwestern United States. Legrand, however, reduced *P. mundula* to varietal status under *P. pilosa* and the remainder of *P. parvula* to synonymy under *P. halimoides* L.

Portulaca phaeosperma Urb. has small yellow flowers surrounded by brownish to whitish hairs and nearly cylindrical leaves with inconspicuously tufted axils. It is found in sand-dunes, scrub, and shell-mounds of southern peninsular Florida and the Keys, southward throughout the West Indies to Yucatán and Curaçao. According to Legrand, *P. phaeosperma* is synonymous with *P. rubricaulis* HBK.

Chromosome counts indicate that basic numbers in *Portulaca* may be $x = 4$, 5, 8, and 9. At least two chromosome series are present, with $2n = 8$, 16, and 48 in one, and $2n = 18$, 36, 45, 54, and 108 in the other. The Japanese 'Jewel' strain of *P. grandiflora* is reported to have

$2n = 10$, while *P. quadrifida* L. has $2n = 50$ (Bouharmont). These data indicate that chromosomal duplications or deletions, concurrent with polyploidy, have played an important part in the evolution of the genus. There are no records of natural interspecific hybridization, and attempted reciprocal crosses (involving *P. grandiflora* and *P. marginata* HBK. in one case, *P. grandiflora* and *P. grandiflora* 'Jewel' in the other) have failed. Bouharmont reports very irregular meiosis in an artificial hybrid between the African *P. centrali-africana* R. E. Fries, $2n = 108$, and *P. Kermesiana* N. E. Br., $2n = 108$. He also found chromosomes to be much larger in *P. foliosa* and *P. grandiflora* than in other species.

Ikeno's efforts to explain color variation in *Portulaca grandiflora* in terms of simple Mendelian principles was only partially successful. Blakeslee attributed various changes and reversions in habit and in petal coloration (sectorial and periclinal chimeras, stripes and spots) to spontaneous vegetative mutations. Other cytological peculiarities include the presence of polyploid cells ($2n = 36, 72$) in adventitious roots of *P. grandiflora* and *P. foliosa* (Bouharmont) and the formation of up to 12 secondary cells of varying size within the primary epidermal cells of *P. grandiflora* (Czeika). The presence of betacyanins has been confirmed in *P. grandiflora*, *P. oleracea*, and *P. pilosa* (Wohlpart & Mabry).

The opening and closing of flowers in response to light intensity and temperature have been studied by several workers. Iwanami *et al.* concluded that temperature controls flowering time in *Portulaca grandiflora*, while Cotter & Platt suggest that light is the controlling factor in *P. Smallii*. Lebrun found that three vegetative races of *P. quadrifida* from different sources show a divergence of behavior under the same conditions appreciably corresponding to the difference in local times of their places of origin. Similarly, offspring of an artificial hybrid between *P. centrali-africana* and *P. Kermesiana* were intermediate in their behavior to those of the two parents.

On the basis of floral vascular anatomy Sharma suggests that the pentamerous floral condition in *Portulaca* is derived from a basically bimerous plan, with a biseriate (rather than uniseriate) perianth, and a modified androecium consisting basically of two cycles. The ovary in *Portulaca* is generally considered to be semi-inferior to inferior, but Soetiarto & Ball have demonstrated that in *P. grandiflora* all the floral organs arise on the flanks of the floral apex as in a hypogynous flower, and that all except the carpels are then lifted on the lip of the floral cup. They conclude that perigyny is an ontogenetically late development in *P. grandiflora* and may be interpreted as a derived condition.

The anthers of *Portulaca tuberosa* and *P. grandiflora* have binucleate tapetal cells and binucleate pollen grains at anthesis, but *P. oleracea* has multinucleate tapetal cells and trinucleate grains. Seed coat morphology may be an important specific character, but is not necessarily consistent in all species. Kowal states that in both *P. oleracea* and *P. sativa* L. seeds occur with sculpturing of two forms and that a particular specimen may produce seeds of one or both types.

Several species of the genus are grown as garden ornamentals. *Por-*

tulaca oleracea is reported in Jamaican folk-lore to be of value in the treatment of cardiovascular diseases (possibly due to the presence of (–)-noradrenaline in relatively high amounts in the fresh plant tissues), as a diuretic, and as an antiscorbutic. It is also widely cultivated and used as a vegetable or salad-green, or as fodder for pigs. *Portulaca pilosa* is sometimes used as a diuretic, an emmenagogue, and as a stomach tonic. High oxalate or nitrate content in plants of *P. oleracea* and other species may prove toxic to livestock.

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Tribe CALANDRINIEAE Fenzl

Subtribe **Calandriniinae** [Franz]

2. **Talinum** A. L. de Jussieu, Gen. Pl. 312. 1789, nom. cons. prop.

Annual or perennial, glabrous, succulent herbs, subshrubs [or shrubs], with simple or branched, short to elongate stems with fleshy, tuberous roots or rhizomes. Stems frequently terminating in wiry, short or long peduncles. Leaves alternate to subopposite or basally tufted, exstipulate, cylindrical or flattened, entire, fleshy. Inflorescence a terminal or axillary, wiry-peduncled cyme, or flowers sometimes solitary on short pedicels in the leaf axils. Sepals 2, deciduous or persistent. Petals 5, rarely more, free or connate at the base, often showy, purplish to red, pink, yellow, or white, ephemeral. Stamens 5–100, alternate with or opposite the petals or in fascicles opposite and basally affixed to the petals; filaments slender, sometimes colored. Style elongate, deeply 3-parted to subcapitately lobed or capitate, equaling or exceeding the stamens; ovary superior, unilocular (at least above); ovules numerous, amphitropous, placentation free central. Fruit a unilocular many-seeded, chartaceous capsule, dehiscing loculicidally from the apex to the base by 3 valves. Seeds compressed, round-reniform, dull gray or shiny brown to black, smooth, striate, or tuberculate, distinctly to indistinctly arillate. Embryo peripheral, incompletely annular; endosperm starchy. (*Talinum Adans.,* 1763, nom. superfl.; *Helianthemoides* Medic., *Phemeranthus* Raf., *Litanum* Nieuwl.) LECTOTYPE SPECIES: *T. patens* A. L. Juss., nom. illegit. = *T. paniculatum* (Jacq.) Gaertn., typ. cons. prop.; see J. E. Dandy, Taxon **18:** 465. 1969. (Origin of name obscure, said to be derived from the aboriginal name of an African species.) — FAME FLOWER.

A genus of about 50 species distributed in the tropical, subtropical, and temperate regions of both hemispheres, but best developed in North America (30–35 species), and particularly in Mexico (Rose & Standley).

The genus was last monographed by Poellnitz (1934) who recognized 47 species but found no basis for maintaining the three sections established by De Candolle (§ *Phemeranthus* Raf., with cylindrical leaves; § *Talinastrum* DC., with flat leaves; and § *Talinellum* DC., since transferred to *Calandrinia* HBK.).

Eight species are now recognized in our area, six wholly or partially east of, and two mostly west of the Mississippi River. Two flat-leaved species frequent the lowlands, forming erect, suffrutescent plants ranging

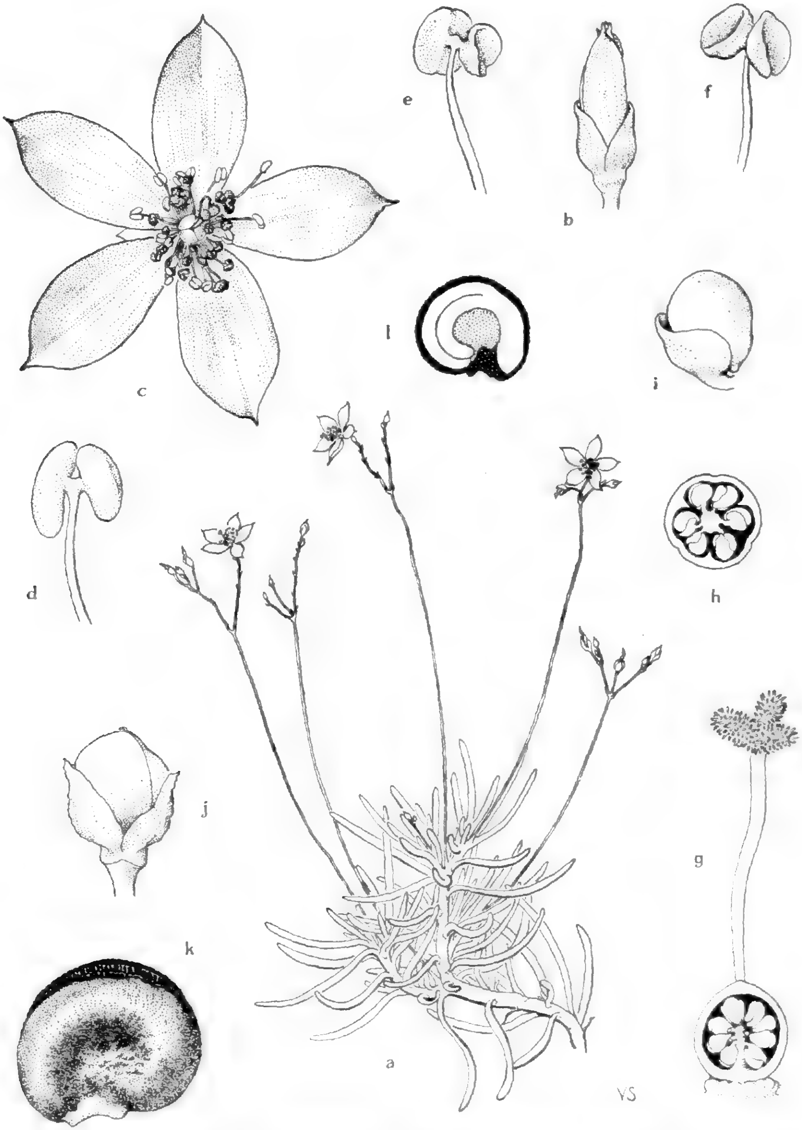

FIG. 2. **Talinum.** a–l, *T. calcaricum*: a. flowering plant, × 1/2; b, flower bud, shortly before anthesis to show sepals, × 3; c, flower, × 3; d, stamen before anthesis, × 20; e, f, two views of stamen after anthesis, × 20; g, gynoecium with one side of ovary removed to show free-central placentation, × 10; h, cross section of ovary showing placentation and remnants of septa, × 10; i, lateral view of ovule at time of anthesis showing aril beginning to grow from funiculus, × 40; j, fruit just before dehiscence, × 5; k, seed with thin, tightly investing aril imperfectly developed (the two sides not meeting at midline of seed), × 25; l, seed in section, the curved embryo surrounding endosperm (black stipples), diagrammatic, × 15.

in height from about 6 dm. to more than 1 m. *Talinum paniculatum* (Jacq.) Gaertn. (including "*T. patens* Willd." and *T. reflexum* Cav.), $2n = 24$, is sparingly branched with terminal, paniculate inflorescences, terete peduncles, and red or pink to yellowish flowers with about 15–20 stamens. The species occurs in both the New and Old Worlds, ranging in North America from Florida to Arizona, southward through the West Indies and Mexico to Central and South America. It favors sandy and cultivated soils, and is seen only rarely in waste places in the Carolinas as an escape from cultivation (Radford *et al.*). Several authors recognize var. *sarmentosum* (Engelm.) Poell., with procumbent branches, in Texas. In contrast with *T. paniculatum, T. triangulare* (Jacq.) Willd. is much branched and bears corymbiform, racemose or cymose inflorescences with three-angled peduncles and purplish to pink or yellow flowers with about 30 stamens. It occurs from southern peninsular Florida and the Keys, where it inhabits hammocks, pinelands, and waste places, to the West Indies, Mexico, and Central and South America.

The cylindric-leaved species of the southeastern United States are herbaceous "rock plants," particularly in the Appalachian highlands, favoring exposed, arid sites in the shallow soil or debris on the margins or surfaces of granite, limestone, or serpentine outcrops. They are distinguished primarily by floral characteristics, including the number of stamens, length of style relative to stamens, persistence of sepals, and seed color. (See Ware for a key to these species in the Southeast.)

The best-known and most widespread *Talinum* of our area is *T. teretifolium* Pursh, $2n = 24, 48$, which ranges from the serpentine barrens of southeastern Pennsylvania, southward in acid soils to the granite outcrops of the Piedmont of the Carolinas and Georgia, and to the Altamaha Grit region of Georgia. Its pink flowers have 15–20 stamens, a three-lobed style as long as the stamens, small deciduous sepals, and small, shiny, black seeds. Three species with more restricted distributions have been segregated from *T. teretifolium*. *Talinum calcaricum* Ware, confined to shallow soil at the margins of limestone exposures in the cedar glades of middle Tennessee and northern Alabama, has purple-pink petals, persistent sepals, 25–45 stamens shorter than the three-lobed style, and large, shiny, dark-brown seeds marked by longitudinal rows of low, broad, raised cells. *Talinum Mengesii* Wolf, $2n = 24$, occurring on sandstone or granite in Alabama, Georgia, and Tennessee, has deciduous-sepaled pink flowers with 50–80 (40–100) stamens shorter than the subcapitate style, and small, shiny, black seeds. Wright finds that "*T. teretifolium* is replacing *T. Mengesii* on granite outcrops in central Georgia where their distribution ranges overlap, and where their niche requirement appears to be very similar." *Talinum appalachianum* Wolf, $2n = 24$, is confined to granite outcrops along the Coosa River in two counties of Alabama. Its flowers have five stamens which alternate with the petals, and there are sometimes one or two extra stamens opposite the petals. The three-lobed style is longer than the stamens, and the seeds at maturity are smooth and brown.

West of the Mississippi two more or less cylindric-leaved species enter our area in Arkansas. *Talinum calycinum* Engelm., $2n = 24$, with red petals and 30–45 stamens, occurs in southernmost Illinois and from Missouri and Arkansas to Montana, Nebraska, Kansas, Oklahoma, Texas, New Mexico, and Mexico (Poellnitz). *Talinum parviflorum* Nutt., $2n = 48$, with white to rose-colored petals and 4–8 stamens, also occurs in southern Illinois and ranges northward from Arkansas to Minnesota and North Dakota, westward to Colorado, Texas, Arizona, and possibly Mexico. *Talinum rugospermum* Holz. may approach our area to the northwest, for it occurs from northwestern Indiana through Illinois to northeastern Iowa, Wisconsin, and eastern Minnesota. It is distinguished by its deeply trifid style, 12–25 stamens with subglobose anthers, and strongly wrinkled seeds.

The flowers of all the species are very delicate and ephemeral. Several authors have pointed out the need for studying living plants, in either the field or cultivation, since critical characters, such as the color, size, shape, and persistence of the floral organs, are damaged or lost in pressing and drying. The flowers usually open for only a short period in full sunshine, the time and duration of daily flowering differing among the species, or even among different populations of the same species, but appearing to be more or less characteristic in a given geographical area. Wolf observed the usual flowering time in *T. Mengesii* to extend from about 11 A.M. to 5 P.M., while in *T. appalachianum* the flowers open between 3 and 4 P.M. and close between 5 and 6 P.M. Ware reports for *T. calcaricum* flowering times of 1 to 6 P.M. in Tennessee, but 3:30 to 6:00 P.M. in Franklin County, Alabama. It is not known, however, whether anthesis is controlled by temperature, light intensity, or both. The significance of flowering times and of the relative lengths of styles and stamens in the genus has not been investigated. Harshberger, the only reporter of pollinators, observed two species of the hymenopteran *Calliopis* on flowers of *T. teretifolium*.

Ecological studies by Ware have shown that *Talinum calcaricum* and *T. Mengesii* are restricted to their narrow ecological niches through inability to compete with other species in more favorable sites. Adaptations of species of *Talinum* which favor survival under the conditions of extreme drought which often prevail in their habitat include succulence of leaf and stem, cylindrical leaves with low surface-to-volume ratio, few sunken stomata, pronounced cuticle, profusely branched root system, and the ability to flower even when a water deficit exists in the leaves (Guptill, Harshberger, Ware).

Steiner found no record of interspecific hybridization in *Talinum*, and his attempts to cross *T. teretifolium* with *T. parviflorum* and *T. parviflorum* with *T. aurantiacum* Engelm., $2n = 48$, of the southwestern United States were unsuccessful. Both his chromosome counts (eight species) and those of others indicate a polyploid series with $2n = 24$, 48, and 72. He also reported polyploid cortical cells with $2n = 96$ in the root tips of *T. parviflorum*. Ware tried the crosses *T. calcaricum* ×

calycinum, *T. calcaricum* × *Mengesii*, and *T. Mengesii* × *calcaricum*, but the resulting low seed yields led him to conclude that partial genetic barriers exist between these morphologically similar taxa.

On the basis of seed morphology and anatomy, Kowal proposed that "*Talinum patens* Willd." and *T. reflexum* Cav., which have been treated as conspecific with *T. paniculatum* since early in this century, are distinct species. In our specimens the development of the aril varies considerably in different species. At maturity the seeds of *T. calcaricum*, *T. Mengesii*, and *T. teretifolium* are enclosed in a fragile, membranaceous, although tightly investing, aril, and all appear dull gray. Disintegration or removal of the aril reveals a shiny dark brown seed in *T. calcaricum*, and shiny black seeds in the other two species.

Guignard found the embryology of *T. paniculatum* to be the same as that of *Portulaca oleracea* and some species of *Calandrinia* (i.e., Polygonum-type embryo sac, solanad-type embryogeny). Anatomical details of the genus include the presence of unicellular epidermal papillae and drusiform calcium-oxalate crystals in the leaves. Incomplete septa have frequently been described in the unilocular ovary. The pollen of *T. teretifolium* is 12-forate (i.e., with ± circular apertures distributed evenly over the surface of the grain), with three of the fora larger than the rest (Franz, Erdtman), while that of *T. triangulare* var. *crassifolium* Hort. are about 18-rugate (i.e., with elongate apertures distributed evenly over the surface), with a thin, psilate exine (Huang). Sharma describes the floral vascular anatomy of *T. paniculatum* and interprets the androecium as consisting of two alternate cycles of stamens. Saponins are reported in the leaves of *T. paniculatum*.

The genus is of little economic importance. *Talinum paniculatum* (Jewels of Opar) and *T. triangulare*, as well as several western American species are grown as border or rock-garden plants for their foliage, and red, white, or yellowish flowers. The roots of *T. aurantiacum* Engelm. are cooked and eaten by Indians of the southwestern United States, while the leaves of *T. portulacifolium* (Forsk.) Aschers., of Africa and of *T. triangulare* in the Americas, are sometimes cultivated as a leafy vegetable. *Talinum cuneifolium* (Vahl) Willd. is used in Tanganyika as an aphrodisiac.

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Subfamily MONTIOIDEAE Franz

3. **Claytonia** Linnaeus, Sp. Pl. 1: 204. 1753; Gen. Pl. ed. 5. 96. 1754.

Small perennial [or annual] unbranched herbs from deep-seated corms, [branched or unbranched tap-roots, rhizomes or stolons], producing 1 to many succulent, scapose flowering stems. Leaves basal, 1 to many in a rosette, petiolate [or sessile], ± fleshy, glabrous, exstipulate, narrowly linear to lanceolate, oblanceolate, elliptic, spatulate, narrowly ovate, or oblong. Flowering stems bearing 2 opposite, sessile to petiolate leaves, ± similar to the basal leaves, a small herbaceous bract at the base of the lowest pedicel, and one or more reduced bracts above. Inflorescence a loose, terminal, racemose scorpioid cyme bearing up to 19 showy pedicellate flowers, the pedicels often spreading or recurving in fruit. Sepals 2, free, ovate, rounded, obtuse or acute at apex, persistent. Petals 5 [or fewer] slightly united basally, broadly oblong to obovate, exceeding the sepals (or exceeded by the stamens and sepals in *C. virginica* f. *micropetala* Fern.), apex rounded to truncate or slightly emarginate, pink to white, with pink veining, rarely yellow; convolute in the bud, drying in place. Stamens 5, opposite the petals; filament adnate to the petal claw; anthers pink; pollen mostly 3-colpate. Gynoecium 3-carpellate; style 1, with 3-cleft stigma; ovary superior, often 3-angled, unilocular usually with 6 (3–6) ovules on a basal placenta. Fruit a membranaceous, ovoid capsule dehiscing by 3 valves, the valves often inrolling after dehiscence. Seeds shiny, brown to black, smooth to alveolate, orbicular to lenticular. Embryo with 1 or 2 cotyledons, peripheral, curved around the endosperm. LECTOTYPE SPECIES: *C. virginica* L.; see Britton & Brown, Illus. Fl. No. U.S. ed. 2. 2: 37. 1913. (Named for John Clayton, 1686(?)–1773, English doctor and botanist, resident of eastern Virginia from 1705, who contributed material to Gronovius for the *Flora Virginica.*) — SPRING BEAUTY.

A distinctly North American genus of about 32 species, when considered in the broad sense of Gray or Poellnitz, or of about 20 species when interpreted in the narrower sense of Greene, Robinson, Rydberg, Pax & Hoffman, Swanson, and Nilsson. Two complex species (*C. virginica* L. and *C. caroliniana* Michx.) of sect. CLAYTONIA occur in eastern North America. The remaining species, including *C. lanceolata* Pursh, *C. tuberosa* Pallas ex Willd., and *C. umbellata* S. Wats., closely related to ours, are distributed from the Rocky Mountains, westward to the Pacific Ocean, northward to Alaska, and westward to eastern Siberia and the Kamchatka Peninsula.

Both species of our area are cormose perennials inhabiting shady woodlands, grassy banks, wet meadows, and bog habitats or in association with bald granite exposures (in South Carolina, plants of this habitat are more robust than those of adjacent habitats). The two differ mainly in leaf shape and size. *Claytonia virginica* (spring beauty, rose elf, grass flower), with two varieties and two forms, has linear to linear-oblanceolate leaf blades more than eight times longer than broad (Davis, Voss) and gradually narrowed to the petiole. It occurs from Nova Scotia and New Brunswick, westward across southern Quebec and Ontario to Minnesota, and southward to Texas and Georgia (Davis). The more northern *C. caroliniana* is generally smaller than *C. virginica*, with possibly darker flowers, and has spatulate leaves less than eight times longer than broad, with the blade narrowed abruptly to the petiole. It ranges from southwestern Newfoundland, westward through southern Quebec and Ontario and the northern parts of the border states to eastern Minnesota, southward through Nova Scotia to New England and along the Appalachians to western North Carolina and northern Georgia, and westward through Kentucky and Tennessee to northwestern Arkansas. Davis says that the two "seldom grow in the same immediate area, but when they do *C. virginica* blooms earlier." Voss, however, describes sites in central Michigan in which populations of the two species are thoroughly intermixed. Here their flowering periods overlap, but *C. caroliniana* reaches its peak of flowering slightly earlier than *C. virginica*. No obvious evidence of hybridization was seen, however. Uttal reports a hybrid swarm between the two species at a location in Virginia where highly disturbed conditions have broken down the ecological barriers usually separating them there.

Narrow-leaved and broad-leaved taxa are recognized within *Claytonia virginica* by Davis, Fernald, Gleason & Cronquist, and Lewis *et al.* This variation is apparently correlated with chromosome numbers. At least 45 different chromosomal races are known in *C. virginica*, with numbers ranging from $2n = 12$ to about 191. Rothwell, and Lewis *et al.*, have worked out the chromosomal evolution of *C. virginica* throughout its range. Lewis proposes that "*C. virginica* has evolved from an ancestral narrow-leafed race having $n = 6$ from which the widespread $n = 12 \pm$ and southern $n = 7$ races arose. From the latter was derived an $n = 14$ race also common in the south. These races and at least some of their higher polyploid derivatives make up the narrow-leafed var. *acutiflora* (= var. *Simsii* of Davis). From continuing autoaneuploidy at the diploid level evolved the $n = 8$ race where, we believe, particular chromosomal redundancies with certain genetic combinations or duplications lead to the expression of broad leaves. Such plants became widespread in the north as did the morphologically similar $n = 16 \pm$ race. These races and their derivatives, largely aneutetraploids, represent the more recently evolved broad-leafed var. *virginica*. We agree with Davis . . . that no other gross morphological features correlate with leaf width."

Similar lines of evolution in chromosome number, although less extensive, are also known in *Claytonia caroliniana* L., in which reported chromosome numbers range from $2n = 16$ to 38, and in the western *C. lanceolata*, $2n = 16$ to 72.

The generic and subgeneric classification of *Claytonia* is chaotic. Two to ten infrageneric categories, designated or incorrectly cited as subgenera and sections, have been recognized. The nomenclature is confusingly intertwined with that of the closely related *Montia* L. and various segregate genera. The boundary between the two is indistinct, prompting numerous transfers of species and sections. The *Claytonia-Montia* complex has been interpreted in three divergent ways, all of which have found some support in recent literature.

Claytonia has been distinguished from *Montia* either on meristic grounds (e.g., by Linnaeus, Gray, Poellnitz) or on the basis of habit (e.g., by Greene, Swanson). In the former case *Claytonia* is said to have 5 more or less equal petals slightly connate basally, usually 5 stamens, and capsules with several seeds (up to 6), while *Montia* is distinguished by distinctly unequal basally connate petals, 3 stamens, and 2 or 3 ovules and seeds per capsule. In this "broad" sense Gray (1887) recognized twenty species of *Claytonia*, but only one of *Montia* (*M. fontana* L.).

Torrey & Gray (1838) recognized four sections in *Claytonia* (*Claytonia, Limnia* (Haw.) Torr. & Gray, *Alsinastrum* Torr. & Gray, *Naiocrene* Torr. & Gray). Much later (1887) Gray divided the species of the genus among two subgenera or sections (it is not clear which) and 7 subgroups based on habit ("section" *Euclaytonia* with subgroups *Cormosae, Caudicosae,* and *Rhizomatosae*; "section" *Limnia* (Haw.) Torr. & Gray, with subgroups *Limnia, Alsinastrum* Torr. & Gray, *Naiocrene* Torr. & Gray, and *Montiastrum* Gray).

In the subsequent literature these subgroups are referred to as sections, although Gray apparently did not designate them as such. More recently, Poellnitz placed 32 species of *Claytonia* in 10 sections and recognized only five species of *Montia*. This restricted view of *Montia* finds support in recent papers by Moore and by Walters who recognize only *M. fontana* L., with four subspecies, distinguished by characters of the seed coat, in Europe, North America, and Australia.

A second approach to the complex is to transfer certain sections of *Claytonia* to *Montia*. Swanson, in pointing out transitional floral types in both genera, notes that all Montioideae are basically pentamerous and draws generic and sectional lines primarily on plant habit (as did Greene and others before him), rather than on a meristic basis. In Swanson's narrower circumscription *Claytonia*, with about 20 species in four sections (*Caudicosae* (Gray) Poell., *Rhizomatosae* (Gray) Poell., *Claytonia*, and *Limnia* (Haw.) Torr. & Gray), becomes limited to those perennial and annual species forming an unbranched basal rosette from a tuber, taproot, or rhizome, and producing upright, axillary, scapose flowering branches bearing a single pair of opposite leaves subtending the generally simple inflorescence ("section" *Euclaytonia* and "section" *Limnia-Limnia* of Gray). The remaining species (subgroups *Naiocrene, Alsinastrum,* and *Montiastrum* of Gray) are transferred to *Montia*, which is then characterized by plants of varying habit which are branched above the base, with cauline leaves and axillary or terminal inflorescence. Swanson recognizes eight species of *Montia*, in four sections (*Montia, Limnalsine*

(Rydb.) Pax. & Hoffm., *Naiocrene* (Torr. & Gray) Pax & Hoffm., *Montiastrum* (Gray) Pax & Hoffm.), in North America.

The third approach to the complex is that of Rydberg (followed by Pax & Hoffmann) who also restricted *Claytonia*, recognizing only two subgenera (*Euclaytonia* and *Belia* (Steller) Rydb., treated as sections by Pax & Hoffmann). In contrast to previous workers, however, Rydberg established segregate genera for the sections or species excluded from *Claytonia* (*Crunocallis* Rydb., *Limnalsine* Rydb., *Limnia* L., *Montiastrum* (Gray) Rydb., and *Naiocrene* (Torr. & Gray) Rydb.). Such splitting has been supported and furthered by Nilsson, who segregated three new monotypic genera primarily on the basis of pollen morphology (*Maxia* Ö. Nils., *Mona* Ö. Nils., *Neopaxia* Ö. Nils.), raising the number of genera in the complex to ten.

Swanson considers the members of sect. CAUDICOSAE, with heavy taproots, to be primitive within the genus. The RHIZOMATOSAE and the cormose CLAYTONIA species are considered to be progressively more advanced, and the taprooted annuals of sect. LIMNIA are thought to be most advanced. Lewis and Suda find that trends in chromosomal morphology (decreasing size, increasing asymmetry, increase in satellite number) support Swanson's sequence. Their data suggest at least two lines of evolution in *Claytonia*, "from sect. *Caudicosae* through sect. *Rhizomatosae* to sect. *Claytonia*, and from a taxon similar to *C. sibirica* ($2n = 12, 24, 36, 48$; in sect. Caudicosae) to sect. Limnia."

Flower color in our species ranges from white to dark pink, with pink to rose veining. In *Claytonia virginica* a yellowish blotch often occurs above the claw of the petal. Orange-yellow-flowered variants are reported in *C. virginica* (f. *lutea* R. J. Davis) from Maryland and Pennsylvania, as well as in the western *C. lanceolata* from Idaho and Washington. Flowering occurs in the spring for two to three weeks, beginning in late March in Kentucky, with a new flower opening every day and lasting for 2–3 days. Anthesis is apparently controlled by temperature, with not more than two flowers open at the same time on an inflorescence (Wood). The plants are apparently outbreeding, adapted to insect pollination by Dipterans and Hymenopterans (Lovell), but self-pollination occurs if the flowers fail to open due to poor weather conditions. Flowers of *C. virginica* are proterandrous, being functionally staminate the first day, pistillate the second and third days. The life cycle of *Andrena erigeniae* (Hymenoptera), a common short-tongued bee pollinator that appears and disappears with the flowers of *C. virginica*, may be keyed to that of the plant species. Seed dispersal through forcible ejection has been observed in *C. alsinoides* Sims and *C. sibirica* L., with the seeds shooting out 1–1.5 meters.

Pollen of *Claytonia* (sensu Greene and Swanson) is mostly tricolpate, with some grains 6-rugate, as opposed to polyrugate or dodecacolpate in those former species of *Claytonia* which are now placed in *Montia* or the various segregate genera. Pollen-grain size in *C. virginica* has been found to be slightly larger in tetraploids than in diploids.

Anatomical and developmental aspects of the embryo sac, embryo, seed, and young sporophyte of *Claytonia virginica* are reported in detail by several workers. This species differs from other members of the genus in usually having only one developed cotyledon in the embryo. In the seedling, formation of the corm begins in the first year through abnormal development of pericyclic cells of the primary root. The corm soon becomes covered with a protective layer of cork.

The genus is of no particular economic significance. In parts of West Virginia *Claytonia caroliniana* is known as "tangle-gut." The leaves are eaten as "spring-greens" after being steeped in hot grease. Leaves of *C. perfoliata* Donn ex Willd. ($2n = 12, 24, 36$) are eaten like spinach. A tea was made for use as a diuretic from leaves of *C. sibirica* L. The starchy tubers or taproots of *C. virginica*, *C. caroliniana*, and *C. acutifolia* Pallas are edible.

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BASELLACEAE Moquin-Tandon, Chenopod. Monogr. Enum. x. 1840, nom. cons.

(MADEIRA-VINE FAMILY)

A small family of herbaceous, somewhat succulent, glabrous, (?dextrorsely) twining vines, lax herbs [or subshrubs?] producing annual shoots from perennial, fleshy rhizomes or tubers; leaves fleshy, alternate, exstipulate, sessile or petioled; inflorescence an axillary or terminal raceme, spike, or panicle of numerous small flowers, each subtended by a small bract; bracts of the pedicel 2, small, opposite, membranaceous or fleshy, caducous or persistent; flowers regular, bisexual [or unisexual]; sepals (involucral bracts?) 2, free or basally connate; petals (tepals?) 5, membranaceous or slightly fleshy, basally connate to form a shallow floral cup, aestivation quincuncial or imbricate; stamens 5, inserted on lip of floral cup or on bases of the petals; filaments [erect or] recurved in bud; anthers 4-locular, insertion of filament basal or versatile; gynoecium of 3 united carpels; ovary superior, unilocular; ovule 1, basal, campylotropous to anacampylotropous; styles 3, basally united, stigmas slender, ± bifid [or capitate to clavate, or style 1 with capitate stigma entire to 3-lobed]; fruit a utricle [or berry], included in the perianth; seed 1, with copious endosperm; embryo annular [or spirally twisted]. TYPE GENUS: *Basella* L.

A family of four or five genera containing 15–20 species, most native to the New World tropics or the Andean regions of South America. *Basella,* including about five species and thought to have originated in the tropics of the Old World, has probably achieved its present pantropic distribution through cultivation. Of the New World genera, *Tournonia* Moq. and *Ullucus* Loz. are monotypic, *Anredera* Juss. (*sensu stricto*) is generally considered to be monotypic, and *Boussingaultia* HBK. consists of 10–15 species. *Anredera* and *Boussingaultia* were united by Baillon, and more recently by van Steenis, under *Anredera.* The family is represented in the southeastern United States only by a single species of *Anredera* (*A. leptostachys*), of the tribe Boussingaultieae Benth. & Hook.

The genera of Basellaceae fall into two natural groups: those with spirally twisted embryos and stamen filaments erect in the bud (*Basella, Tournonia, Ullucus*) and those with annular embryos and filaments outwardly reflexed in the bud (*Anredera, Boussingaultia*). These two groups have consistently been given systematic recognition as tribes, subtribes, or series, when included in the Chenopodiaceae (Endlicher, Bentham & Hooker, Baillon), or as subfamilies or tribes of the Basellaceae (Moquin-Tandon, Engler, Ulbrich, Eckardt). Franz treated the Baselleae as a tribe of subfam. Montioideae in the Portulacaceae and included the five genera of Basellaceae and the transitional genus *Portulacaria* Jacq.

Anatomically the Basellaceae differ from Chenopodiaceae in the absence of anomalous secondary growth and in the presence of bicollateral stelar bundles resulting from the tardy development of internal phloem. Bicollateral bundles, and similar features of floral ontogeny and morphology, are shared with some Montioideae (Portulacaceae).

Observations on *Basella rubra* L. and *Anredera vesicaria* (Lam.) Gaertn. f. indicate that the Basellaceae share with other Centrospermae possession of betacyanin pigments (here basellain-r, basellain-v) in place of anthocyanins. Saponins have been found in the seeds of this species, while calcium oxalate occurs in the form of druses and single crystals. Slime cells occur in parenchymatous tissues of the various taxa, and stomata of the rubiaceous type occur on both surfaces of the leaves.

As in the Portulacaceae, the perianth is interpreted as either biseriate, with two sepals and five petals, or uniseriate, with a single cycle of five sepals (or tepals) subtended by two large involucral bracts. The position of the five stamens in opposition to the five "sepals" suggests the loss of either the corolla or an intervening cycle of stamens, most probably the latter. According to Payer, and Eichler, the floral plan in *Basella rubra* is basically trimerous, the present pentamerous cycles each arising as successive whorls of three, one member of the outer perianth and androecial cycles aborting. Sharma considers the basal placentation of *B. rubra* to represent an extreme reduction from an originally axile placentation.

Embryological characteristics of the family include bitegmic ovules in which the inner integument forms the micropyle. Within a bulky nucellus the chalazal megaspore of a linear tetrad develops into Polygonum-type embryo sac. The endosperm is initially nuclear, later becoming cellular. Anthers of the family are tetrasporangiate and produce a glandular tapetum of multinucleate cells. Pollen grains are three celled when shed.

The pollen of the family is polymorphic. Grains are spheroidal in all genera except *Basella*, in which elaboration of the exine in the interapertural areas has produced a cubical shape. Aperture configuration varies from a basic pattern of six furrows arranged as on the sides of a cube (*Basella*, some species of *Boussingaultia*), through reduction in size and increase in number of apertures (as in "*Boussingaultia leptostachys*," *Ullucus tuberosus*), to many pores distributed evenly over the surface of the grain (*Anredera vesicaria*). Similar patterns occur in Portulacaceae and other families of Centrospermae.

Knuth states that pollination in *Basella rubra* is largely cleistogamous, with a few chasmogamous flowers pollinated by small, short-tongued insects. Observations on the floral biology of American taxa are lacking. Structures resembling berry-like fruits found in an inflorescence of *Anredera leptostachys* from southern Texas were originally mistaken for fruits, but proved on dissection to be the much enlarged, fleshy petals enclosing an insect larva. The insect attack apparently stimulates this aberration of growth in the host flower.

Chromosome counts from species of three genera suggest that the base number of the family is 12, with $2n = 24$, 48, and 60 in *Basella*, 24 and 28 in *Boussingaultia*, and 24 or 36 in *Ullucus*.

The family is of economic importance in that several species are cultivated for their fleshy leaves, which are used as a substitute for spinach (*Basella rubra*), or for their fleshy, starchy rhizomes or tubers (*Ullucus, Anredera vesicaria*, species of *Boussingaultia*). The tubers of *Ullucus tuberosus* are an ancient and important food crop in Bolivia, Chile, Colombia, Peru. *Basella rubra* and some species of *Anredera* and *Boussingaultia* which are cultivated as ornamentals have become naturalized in many places. The reddish pigments of *Basella rubra* fruits are used in Asia as food coloring and may serve as a substitute dye for carmine.

The dextrorsely twining habit often cited in descriptions of the Basellaceae is open to question. Nevling notes that this characteristic is seldom constant among climbers, and Sloane's illustration of *Anredera vesicaria* shows leftward twining stems.

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1. **Anredera** A. L. de Jussieu, Gen. Pl. 84. 1789.[3]

Twining or scrambling, herbaceous vines with slender, much branched, somewhat fleshy, glabrous and sometimes reddish stems produced annually from fleshy rhizomes or tubers. Leaves alternate, exstipulate, petioled [or sessile], slightly fleshy, entire margined, blades suborbicular to elliptic, ovate [or cordate], with apex acute to acuminate [or obtuse], and base gradually or abruptly narrowed [to truncate or cordate]. Inflorescence axillary or terminal, a simple nodding raceme, racemose spike, or panicle, with numerous small, sessile or pedicellate flowers in axils of small bracts. Bracts of the pedicel 2, small, opposite, free or deciduous [or basally connate and persistent at level of pedicel articulation]. Flow-

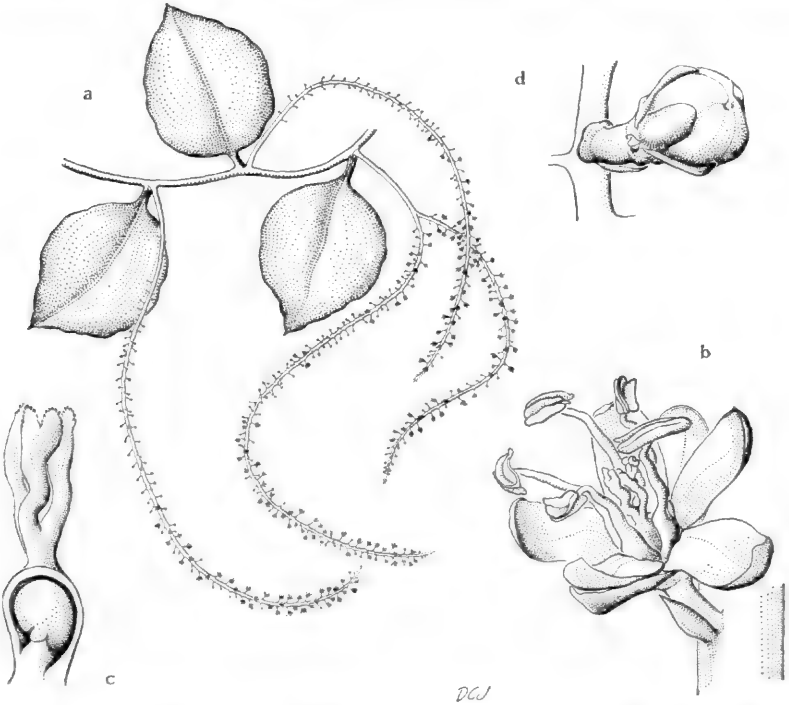

FIG. 3. **Anredera.** a–d, *A. leptostachys*: a, part of stem with inflorescences, × 1/2; b, flower, × 12; c, partial vertical section of gynoecium to show ovule, × 24; d, teratological flower, the tepals accrescent from insect attack — note thickened pedicel, × 6.

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[3] According to Rickett (1960), the investigation of a proposal to conserve the name *Anredera* Juss. (1789) over *Fallopia* Adans. (1763) has shown that "the actual type of *Anredera* (Sloane's specimen in BM) . . . is not *Polygonum scandens* L. as stated in the proposal. The genus is therefore not identical with *Fallopia*, the names are not even taxonomic synonyms. *Anredera* therefore stands without conservation, so far as *Fallopia* is concerned."

ers fragrant, perfect [or imperfect]. Sepals 2, ± adnate to the floral cup, nearly flat to boat-shaped [keeled or narrowly to broadly winged along the back]; slightly shorter than [to slightly exceeding] the petals at anthesis. Petals 5, small, white or greenish [turning purple at maturity in some species] thin or somewhat fleshy, united basally to form a short floral tube, more or less spreading at maturity. Stamens 5, opposite and inserted on the petal bases. Filament filiform or subulate, recurved in the bud. Anthers oblong [to ovate], versatile, pollen rugate or polyforate. Ovary small, superior, ovoid [or slightly compressed] 1-locular. Styles 3, free, with bifid, papillose stigmas [or styles variously fused below, with capitate to clavate stigmas, or style 1, with capitate, 3-lobed stigma]. Ovule 1, basal, subsessile [or sessile]. Fruit a utricle with fleshy or parchment-like pericarp, enclosed by the perianth. Seed erect, lenticular, with crustaceous [or coriaceous] seed-coat. Embryo semiannular [to annular]. Cotyledons plano-convex [or subclavate]. TYPE SPECIES: *Anredera spicata* J. F. Gmel. = *Anredera vesicaria* (Lam.) Gaertn. f.; see Gmel. Linn. Syst. Nat. 2: 454. 1791, and P. Wilson, N. Am. Fl. 21: 337. 1932. (Derivation of generic name unknown.) — MADEIRA-VINE.

A New World genus of 10–15 species, inhabiting tropical regions from southern Florida and southernmost Texas, through Central America (about three species), to northern South America (about 13 species); represented in our area only by *Anredera leptostachys* (Moq.) Steenis in southern Florida, and in southern Texas by both *A. leptostachys* and *A. vesicaria* (Lam.) Gaertn. *Anredera leptostachys* is distinguished by its three bifid styles and wingless sepals, while *A. vesicaria*, better but erroneously known as *A. scandens* (L.) Moq., has broadly winged sepals and three undivided styles. Both species belong to sect. ANREDERA (see below) and may be most closely related to the South American *A. cordifolia* (Tenore) Steenis and *Boussingaultia floribunda* Moq.

The distribution of *Anredera leptostachys* in our area is not well defined, but it is known from Dade, Monroe, and Collier counties, Florida. The best known location appears to be Key West, where the species has been collected in hammocks and where it is said to occur in vacant lots and fence rows.

In his original circumscription of the Basellaceae Moquin-Tandon (1840) recognized two genera in his subfamily Anredereae Endl.: *Anredera* Juss., characterized by winged sepals ("perigone") and *Boussingaultia* HBK. with wingless sepals. He later (1849) segregated a third genus, *Tandonia* Moq., to accommodate those species of *Boussingaultia* distinguished primarily by ovaries bearing a single style with capitate stigma. Bentham and Hooker, however, reunited the two genera, and *Tandonia* has since been accorded only sectional rank.

Volkens divided *Boussingaultia* into two sections: TANDONIA (Moq.) Volk., containing the single-styled species, and EUBOUSSINGAULTIEAE Volk., containing the three-styled species. In the latter section Volkens included the type of the genus, *B. baselloides* HBK. Hauman, however, in the only recent revision of *Boussingaultia*, pointed out that the original description of *B. baselloides* mentions a single style, with a capitate, three-lobed stigma, and that the flower erroneously figured by Volkens for the type species is one of *B. leptostachys* Moq., with three bifid styles. The type species thus belongs to Volkens's section TANDONIA. Hauman replaced the name EUBOUSSINGAULTIEAE with sect. MOQUINELLA Haum. He further clarified some areas of confusion in identification and nomenclature, and provided a "provisional" enumeration of specimens and a key to thirteen species but did not give detailed descriptions for them. Ulbrich accepted Hauman's treatment of the genus.

Baillon, and more recently van Steenis, reduced *Boussingaultia* to synonymy under the older *Anredera*. Van Steenis states that winged sepals occur in some species of *Boussingaultia* and that the difference between the two genera is only a matter of degree in the development of the wings. In his expanded genus *Anredera* van Steenis recognizes two sections (*Tandonia* (Moq.) Volk. and *Anredera*) based on the bracts ("lower bracteoles") of the pedicel rather than on the stylar characteristics formerly used. Section TANDONIA, with bracts basally connate and persistent on the pedicel, is not changed in composition. Section ANREDERA, with bracts free and caducous, is formed by the addition of *Anredera vesicaria* (as *A. scandens*) to the former sect. MOQUINELLA Haum. of *Boussingaultia*. The systematics of the genus is currently in a state of flux, since van Steenis transferred only a few species of *Boussingaultia* to *Anredera*. The remaining species must be cited under *Boussingaultia* until formally transferred. Soukup attempted to transfer several South American species, but his combinations are invalid for lack of proper basionym citation. The genus is badly in need of critical study and revision.

A tendency toward imperfect or functionally imperfect flowers may exist within the genus. Van Steenis concluded that the flowers of the type specimens of *Boussingaultia baselloides* HBK. "appear . . . female with small barren anthers." He also states that fruits of *Anredera cordifolia* have never been found and that *A. scandens* (= *A. vesicaria*) does not produce seed in Malaysia. Furthermore, Hauman describes sexually dimorphic flowers of *Boussingaultia ramosa* (Moq.) Hemsley, and Heimmerl describes a collection of "*B. gracilis*" from southern Brazil in which "all flowers are female." The presence and extent of dioecism among the species of *Anredera* should be investigated.

Beille described the floral vascular anatomy of "*Boussingaultia baselloides*" (cultivated). He found five vascular bundles in the pedicellar stele, each bundle supplying a single trace to a "sepal" and its opposing stamen, and three of the bundles each supplying a single trace to one of the three carpels. There are no vestigial vascular traces in the intervals between the "sepals," from which he concluded that the abortion of the "corolla" is complete.

Chromosome counts for the genus indicate that both diploid and tetraploid species exist: $n = 12$ for *Anredera cordifolia*, and $n = 24$ in *Boussingaultia diffusa* (Moq.) Volk.

Anredera leptostachys, *A. cordifolia*, and *A. vesicaria* are widely grown as ornamental vines for their foliage and fragrant flowers. They can be propagated vegetatively from their fleshy rhizomes or tubers, or in *A. cordifolia* from small tubercles which form in the leaf axils. Webb reports that plants of "*Boussingaultia baselloides*," naturalized in New South Wales, Australia, are suspected of causing death of cows (symptoms of irritant poisoning). Hot-water extracts of these plants proved fatal to experimental rabbits.

A tangle of misidentification has developed around plants of *Boussingaultia* collected in South America and those cultivated and naturalized in various areas. Many of these have been identified as *B. baselloides* HBK., but they are specimens of *Anredera cordifolia* (including *B. gracilis* Miers, *B. gracilis* f. *pseudo-baselloides* Haum., and *B. baselloides* sensu Hook. Bot. Mag. *pl. 3620*). Hauman states that very few of the many specimens labeled *B. baselloides* which he examined were correctly identified and that most were attributable to *B. gracilis*. The latter was introduced into horticulture during the 18th century and has become widespread. For this reason references in the literature to *B. baselloides* HBK., such as those of Webb, are especially subject to question.

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THE ARNOLD ARBORETUM
OF
HARVARD UNIVERSITY

STUDIES IN THE NORTH AMERICAN GENUS FOTHERGILLA (HAMAMELIDACEAE)

RICHARD E. WEAVER, JR.[1]

FOTHERGILLA is a small genus of spring-blooming shrubs in the Hamamelidaceae endemic to the southeastern United States. The first specimens of the genus were collected by Dr. Alexander Garden of Charleston, South Carolina, and the material was sent by him to Linnaeus. The genus was named in honor of Dr. John Fothergill, a London physician and patron of early American botanists. As they usually occur in very localized clumps, none of the species of *Fothergilla* is abundant. Hence the genus is relatively poorly represented in most herbaria.

The genus *Fothergilla* is one of a considerable number of plant genera (e.g. *Bartonia, Hudsonia, Leiophyllum, Cleistes, Clethra*) which show a disjunct distributional pattern in the southeastern United States, i.e., the genus is well represented by one or more species in both the Atlantic Coastal Plain and the Appalachian Mountains but is absent or very rare in the intervening Piedmont. The coastal plain and montane populations of *Fothergilla* have long been recognized as being taxonomically distinct; however, the morphological variation in the genus is great, and as a result as many as four taxa, two in the mountains and two in the coastal plain, have been recognized by the various authors.

HISTORY OF THE GENUS

As indicated by the very short list of "excluded names" at the end of this paper, the generic limits of *Fothergilla* appear to be fairly well marked.

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However, *Parrotiopsis jacquemontiana* (Decne.) Rehder, a plant native to Kashmir and Afghanistan, has been referred to *Fothergilla* by several authors. Falconer (Proc. Linn. Soc. London 1: 18. 1839) originally reported the plant, unaccompanied by a description, as *Fothergilla involucrata.* Niedenzu (1891) treated the plant as the sole member of his subgenus *Parrotiopsis* of *Fothergilla,* but remarked that perhaps it should be treated as a separate monotypic genus. Decaisne (in Jacquemont, Voyage dans l'Inde **6**: 73. 1844), Clarke (in Hooker f., Fl. Brit. India **2**: 426. 1879), and Hooker (Bot. Mag. **122**: *f. 7501.* 1896) considered the plant in question to be a species of *Parrotia.* According to Rehder (Jour. Arnold Arb. **1**: 256. 1920) *Parrotiopsis* differs from *Fothergilla* in its capitate rather than spicate inflorescence, subtended at the base by large bracts, and in its less numerous stamens with linear rather than clavate filaments. The genus *Parrotiopsis* was proposed by Schneider (Ill. Handb. Laubholzk. **1**: 429. 1905), and, to my knowledge, has been accepted by all subsequent authors.

The number of taxa meriting specific rank in the genus *Fothergilla* has been the subject of considerable debate for nearly 70 years. During much of this period four species have been variously recognized as occurring in the southeastern United States: (1) *F. major* Lodd., ranging along the mountains and inner Piedmont from North Carolina to Alabama; (2) *F. monticola* Ashe, occupying the same range as the preceding species; (3) *F. gardenii* Murr., occurring along the Atlantic and Gulf Coastal Plains from North Carolina to Alabama; and (4) *F. parvifolia* Kearney, occupying approximately the same range as *F. gardenii.* It can be seen, therefore, that, although the range of the montane element does not overlap that of the coastal plain element, the ranges of the commonly accepted montane taxa are entirely sympatric as are those of the supposed coastal plain taxa.

To my knowledge all investigators during the last 100 years, with the exception of Sargent (Garden and Forest **8**: 446. 1895) have agreed that the mountain and coastal plain elements of *Fothergilla* are so distinct that the recognition of at least two taxa of specific rank is required.

However, the morphological features distinguishing *Fothergilla monticola* from *F. major* are less than convincing, and as a result a number of investigators have questioned the status of *F. monticola* as a taxon specifically, or even varietally, distinct from *F. major.* The primary morphological character used to distinguish the two is the presence or absence of a waxy bloom on the undersides of the leaves, *F. major* being glaucous and *F. monticola* nonglaucous. Differences in habit, dentition, and pubescence of the leaves, and color of the inside of the capsule have been reported by the various authors. More recently, reports of differing chromosome numbers (Anderson & Sax, 1935; Thomas, in Ernst, 1963) have added a new dimension to the problem.

Britton (1905) treated *F. monticola* as a synonym of *F. major.* Small (1903, 1913, 1933) and Radford *et al.* (1964) made no mention of *F. monticola,* and since the plant has been reported as occurring in the Southeast, including the Carolinas, it is assumed that they also rejected it. Investigators who have accepted *F. monticola* as a distinct species include Hesse (1909), Rehder (1910), Bailey (1949), Harms (1930), Anderson and Sax (1935) and Ernst (1963). However, Anderson and Sax (1935) and Rehder (1910) pointed out that *F. monticola* might better be treated as a variety of *F. major* rather than as a species distinct from it. Ernst (1963) noted that the two are sympatric and are nearly indistinguishable, and that the relationship between them is in need of study. It is perhaps of significance that Ashe (1897), in describing *F. monticola,* considered it to be the only species of *Fothergilla* in the southern Appalachians. Indeed he states "the only published name that could possibly apply to this species [*F. monticola*] is *F. major* Lodd." It was Ashe's opinion, however, that *F. major* Lodd. was merely a robust specimen of the coastal plain species.

The status of *Fothergilla parvifolia* as a taxon distinct from *F. gardenii* is also open to question. The supposed coastal plain taxa reportedly differ in the shape and dentition of the leaves and in the length of the capsules.

Authors who have accepted *Fothergilla parvifolia* as a distinct species include Small (1903, 1913, 1933), Britton (1905), and Harms (1930). More recent authors, including Ernst (1963) and Radford *et al.* (1964) have treated *F. parvifolia* as a synonym of *F. gardenii.*

The present paper is an attempt to evaluate, both morphologically and cytologically, the taxonomy of the genus *Fothergilla.*

PHENOLOGY

The flowering period of the populations of *Fothergilla* in the coastal plain begins in late March in northern Florida and southern Alabama and continues until mid-May in North Carolina. The peak of flowering in North Carolina is during the second and third weeks of April. *F. alnifolia* (= *F. gardenii*) δ *serotina,* originally described by Sims (1810) and taken up by DeCandolle (1830) and Harms (1930) reportedly blooms in August. I have found no evidence, either from herbarium specimens or from field observations, of a *Fothergilla* blooming in August. *F. alnifolia* δ *serotina* was based on a cultivated plant, and its blooming in August was probably an abnormal occurrence.

The flowering period of the montane Fothergillas is affected by altitude as well as latitude but generally extends from late March until mid-May in various parts of their range.

The appearance of the flowers in relation to that of the leaves has been used by several authors (Small, 1903, 1913, 1933; Britton, 1905) as a key character for distinguishing the species of *Fothergilla.* It has been reported that the flowers of the coastal plants appear before the leaves, while the flowers of *F. major* appear as the leaves are unfolding. Observation of the plants in the field, as well as examination of herbarium specimens, indicates that this is generally true. Although exceptions have been noted, the distinction remains a fairly usable diagnostic character.

Van Dersal (U.S.D.A. Miscell. Publ. #303, pp. 128, 129. 1938) found that the seeds do not germinate until the second year, evidently requiring a period of low temperatures to break the dormancy of the embryo.

Flowers are initiated during the summer growing season and complete inflorescences are formed before the leaf drop in the fall. Meiosis, however, does not take place until the following spring.

MORPHOLOGY

Habit. Plants of the genus *Fothergilla*, generally low shrubs with erect or strongly ascending aërial stems, spread profusely by means of woody underground stems, frequently forming dense clumps. The aërial stems are typically unbranched for one-half to one-third their height, and in the case of the coastal plain populations may be completely unbranched. The coastal plain plants are seldom more than one meter tall, although exceptional specimens up to 2.6 meters in height have been seen; flowering specimens of the montane plants are generally between one and three meters in height, but in extreme cases may be nearly 6.5 meters tall.

Hesse (1909), Rehder (1910), and Bailey (1949) have used supposed differences in habit to distinguish *F. major* from *F. monticola*. The glaucous *F. major* is reportedly an erect, pyramidal shrub, while the nonglaucous *F. monticola* is less tall and more spreading. Examination of several populations of *Fothergilla*, consisting of both glaucous and nonglaucous plants, in the mountains of western North Carolina has given no indication of such a difference in habit. Most plants of both types are rather low, spreading shrubs. Occasionally, especially when growing in moister situations, the plants of both types become taller and more erect. The tallest and most nearly erect plant examined was nonglaucous.

On the other hand, examination of *Fothergilla* plants cultivated at the Arnold Arboretum of Harvard University has shown that several of the shrubs in the collection are indeed erect with a more or less pyramidal shape, totally different from any of the numerous plants which were studied in the field. Other plants at the Arboretum, more typical of the wild type, are low and spreading. While all of the erect plants are glaucous, the spreading plants are of both types. The significance of this difference in habit is unknown, but since it is not consistently correlated with the presence or absence of a waxy bloom on the undersides of the leaves, it should be ruled out as a character substantiating the existence of two taxa of *Fothergilla* in the mountains of the southeastern United States.

Vestiture. The undersides of the leaves of both the montane and coastal plain forms of *Fothergilla* are occasionally covered with a fine, waxy bloom. As mentioned earlier, the presence or absence of this bloom has been used as the primary morphological character for distinguishing *F. major* from *F. monticola*.

Since the waxy bloom generally disappears when specimens are heat dried, and since most collectors regrettably have failed to mention whether or not the plants were glaucous, herbarium specimens are useless for the study of this character. Therefore field studies were necessary. Populations were studied in the following localities:

PIEDMONT

1. Near Hillsborough, Orange County, North Carolina.
2. Hanging Rock State Park, Stokes County, North Carolina.

MOUNTAINS

3. Gorge of the Thompson River, Transylvania County, North Carolina.
4. Gorge of the Horsepasture River, Transylvania County, North Carolina.

The Piedmont populations are composed entirely of nonglaucous individuals; the mountain populations are composed of approximately equal numbers of glaucous and nonglaucous individuals. There appears to be little variation in the amount of bloom among those plants which are glaucous at all; the bloom when present is very striking and in all probability is genetically controlled. Aside from the presence or absence of a waxy bloom the plants are indistinguishable as far as leaf, capsule, and habital characters are concerned. In view of this fact and since glaucous and nonglaucous individuals grow side by side in the same population, this single character seems to offer insufficient grounds for the recognition of two taxa of any rank.

A single population of *Fothergilla* in the coastal plain of North Carolina (Scotland County) was found to consist of glaucous and nonglaucous individuals. As in the case of the montane populations both types grow side by side and are identical in other respects.

The aërial organs of *Fothergilla*, both floral and vegetative, with the exception of the styles and stamens, are clothed to varying degrees with a soft, downy pubescence. The individual trichomes are stellate in form, composed of six to ten unicellular segments radiating from a single modified epidermal cell. The color of the trichomes varies from dark brown on the stipules and floral bracts to a pale yellow on the remaining parts. Interspersed among the stellate trichomes on the apex of the ovary and persisting on the mature fruit are stiff, yellow, simple trichomes which are apparently the only simple ones to be found on the plant.

In general the coastal plain plants are pubescent to a greater degree than are the montane plants; however, in both groups the amount of pubescence varies among the respective organs, as well as on the same organ of different plants. The trichomes are generally dense and overlapping on the petioles, stipules, calyx, floral bracts, and peduncles. The aërial stems of the montane plants are generally pubescent on the distal portions, especially at the bases of the spikes and the leaves where the pubescence may be considerable, and on the present year's growth, but become completely glabrous in the proximal portions; those of the coastal plain plants are frequently pubescent, at least sparingly so, to the base.

The leaves are pubescent on both surfaces, but generally more densely so on the abaxial surface; the trichomes are scattered to varying degrees over the lamina but are often concentrated on the principal veins or in their axils. The lamina is frequently glabrous in the montane plants but is always pubescent to some degree in the coastal plain plants examined.

Rehder (1910) reported that the leaves of *F. major* varied from scattered to rather densely pubescent beneath, while those of *F. monticola* were pubescent chiefly on the veins, the lamina often being nearly glabrous. Ernst (1963) also noted that *F. monticola* was pubescent to a lesser degree than *F. major*. Bailey (1949) was vague on the matter, having described the leaves of *F. major* as pubescent below, at least on the veins, as opposed to scattered pubescent below in *F. monticola*.

Examination of herbarium specimens as well as observations of the plants in the field has indicated that the degree of pubescence of the leaves on an individual plant of both the glaucous and nonglaucous types is quite variable. For example, the pubescence on the undersides of the twenty-five mature leaves taken at random from plants of both the glaucous and nonglaucous types in each of two populations in Transylvania County, North Carolina, demonstrated that the range of variation in the degree of pubescence is the same for both types: in each of the plants studied the variation ranges from leaves in which the lamina is glabrous to leaves in which the lamina is covered with a nearly continuous indumentum.

In order to quantify these impressions herbarium specimens prepared from two populations of *Fothergilla* (one from Burke County and one from Transylvania County, North Carolina) were studied intensively, and the number of trichomes present on four square millimeters of laminal surface at comparable positions on the undersides of the leaves of both the glaucous and nonglaucous types was counted. The results are summarized in TABLE 1.

TABLE 1. **Variation in the Number of Trichomes on the Leaves in Two Populations of the Montane Fothergilla**

LOCALITY	COLLECTOR AND NUMBER	FORM	NUMBER OF LEAVES	RANGE OF VARIATION IN # OF HAIRS	MEAN # OF HAIRS
Burke Co.	*Wilbur 7040*	glaucous	40	0–40	5.09
Burke Co.	*Wilbur 7038*	nonglaucous	40	0–30	5.98
Transylvania Co.	*Weaver 300*	glaucous	20	7–35	16.65
Transylvania Co.	*Weaver 301*	nonglaucous	20	4–29	13.55

From the data in TABLE 1 the following conclusions may be drawn as far as the populations studied are concerned: (1) the variation in degree of pubescence of each form is great within one population as well as between different populations; (2) the variation in the degree of pubescence of each form is approximately equal in each population.

Even though the samples were small the results indicate that there is no consistent difference in the degree of pubescence between glaucous and nonglaucous individuals.

Leaves. The leaves of *Fothergilla* are simple, alternate, deciduous and somewhat coriaceous in the coastal plain populations, while they are thinner and membranaceous in the montane populations. Variation in shape and type of dentition is great; it is not at all unusual to find on a single plant leaves with (1) shape ranging from elliptic through ovate and obovate to suborbicular; (2) bases cordate, truncate, and rounded; (3) apices acute, obtuse, and emarginate; and (4) margins varying from coarsely serrate-dentate to entire. Extent of the dentition, however, is more nearly constant than the type of dentition; in general among the coastal plain populations the dentition when present is restricted to the upper half of the leaf, while among the montane populations it almost invariably extends below the middle of the leaf.

Leaf size has traditionally been used to distinguish the montane and coastal plain forms of *Fothergilla*, and it remains a usable diagnostic character. The leaves of the coastal plain plants are typically and usually conspicuously smaller than those of the montane plants. Although there is a considerable overlap in absolute leaf lengths and width between the two forms, the largest leaf on any given specimen examined from the coastal plain never exceeded 5.2 cm. in width, while the largest leaf on a specimen from the mountains was never less than 5.1 cm. wide.

Fothergilla parvifolia, described by Kearney (in Small, 1903), has usually been distinguished from *F. gardenii* by the shape and dentition of the leaves. Britton (1905) and Small (1933) agreed that the leaves are different: *F. parvifolia* with leaves broadly ovate, oval, or suborbicular, toothed mainly from below the middle, and cordate at the base; and *F. gardenii* with leaves oblong, oblong-ovate, or ovate-orbicular, toothed above the middle, and narrowed at the base, according to Britton, and elliptic, elliptic-ovate, or elliptic-orbicular, toothed only near the apex, and cuneate or rounded at the base, according to Small. Earlier, however, Small (1903, 1913) had reported that the leaf margins of *F. parvifolia* were coarsely crenate above the middle, while those of *F. gardenii* were undulate or coarsely toothed near the apex.

As may be inferred from these conflicting descriptions the distinctions, at least as regards leaf shape and dentition, between *F. parvifolia* and *F. gardenii* are hazy at best. In view of the variation among the leaves of an individual plant as described above, it would seem that the delimitation of taxa of *Fothergilla* on the basis of leaf shape and dentition is unwarranted.

Flowers. The perianth of *Fothergilla* is greatly reduced, consisting of a gamosepalous calyx, the 5–7 lobes of which are reduced to minute, irregularly shaped teeth. Petals are lacking. The base of the androecium is adnate to the calyx, forming a shallowly campanulate hypanthium. The stamens vary in number from 12–32, and are arranged in a single series on the rim of the hypanthium. The coastal plain populations tend to have fewer stamens than the montane populations; in the material studied the number ranged from 12 to 24 in the coastal plain plants and from 18 to 32 in the montane plants. The filaments, easily the most conspicuous parts of the flower, vary greatly in length with no apparent pattern in a single flower. The longer ones are conspicuously thickened distally while the shorter ones tend to be nearly filiform. The pistil is made up of two carpels fused below but divergent near the apex of the ovary into separate filiform styles.

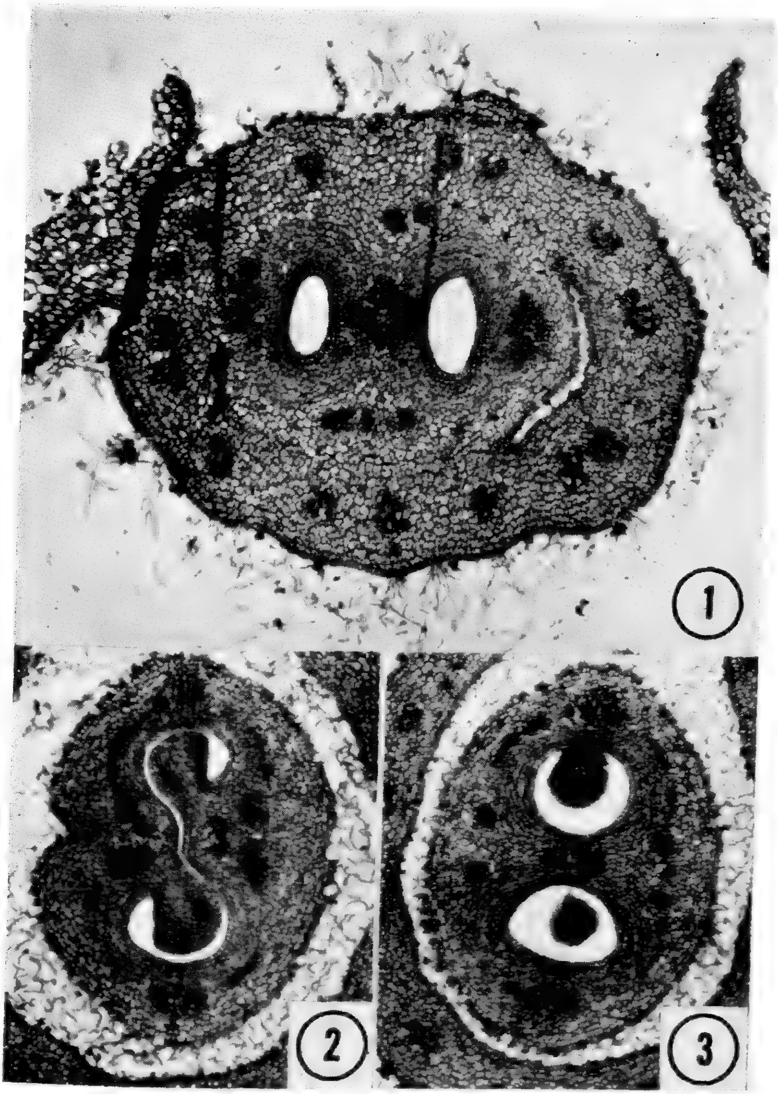
Most previous authors have considered the ovary of *Fothergilla* to be weakly perigynous; Ernst (1963) described the ovary as being "slightly recessed in the receptacle" but considered the fruit to be "partly inferior." Macroscopic examination of the ovary indicates that it is partially fused to the receptacle and is therefore semi-inferior.

In order to determine the histological relationship between the ovary and the hypanthium, flowers of *Fothergilla major* collected in Transylvania County, North Carolina, and preserved in 70% ethyl alcohol were dehydrated using the tertiary butyl alcohol series suggested by Johansen (1940), and infiltrated with paraffin. The material was sectioned on a rotary microtome at 12 microns and stained in 1% safranin in 95% ethyl alcohol and 1% fast green in 95% ethyl alcohol. The investigations have shown that the hypanthium is actually adnate to the ovary to a point slightly above the base of the ovary, i.e., at least one-third the total length of the latter (FIG. 1). Therefore the ovary is, indeed, somewhat semi-inferior.

Serial sections of the pistil have given further insight into the morphology of that organ. Macroscopically the pistil in cross section appears to be 2-locular; to my knowledge all previous authors have described the pistil accordingly.

Actually, as shown in FIGURES 2 and 3, the closure of the individual carpels is not complete from a point immediately below the attachment point of the ovules to the apex of the ovary. As a result the ovary appears to be bilocular below the attachment point of the ovules but unilocular above it. In actuality, then, the ovary is characterized by having a single deeply lobed locule. Horne (1914) reported that a similar situation, but in reverse, i.e. unilocular below and bilocular above, was found in *Rhodoleia*, a member of the subfamily Bucklandioideae of the Hamamelidaceae native of eastern Asia; he also stated, however, that the Hamamelidoideae, of which *Fothergilla* is a member, possessed septa, rendering them bilocular.

Fruits and seeds. The fruit of *Fothergilla*, a grayish or brownish loculicidal capsule, is rendered partly inferior by the fusion of the per-



FIGURES 1–3, Cross section of the flower of *Fothergilla major*, × 60. FIG. 1, Fusion of the ovary to the hypanthium. FIG. 2, Ovary at attachment point of the ovules. FIG. 3, Ovary below attachment point of the ovules.

sistent hypanthium to the ripened ovary. Each of the carpels dehisces along a median dorsal suture, and, as a result, the capsule is 4-beaked at maturity. The capsules of the montane and coastal plain forms are similar in shape, but those of the montane populations are decidedly larger in size. Although there is a considerable overlap in total capsule length in the material at hand, the fruiting hypanthium of the coastal plain form varies from 3 to 4.5 mm. in length while that of the montane form varies in length from 4 to 9.2 mm.

Small (1903, 1913, 1933) and Britton (1905) reported that the capsules of *Fothergilla parvifolia* varied from 6 to 8 mm. in length, while those of *F. gardenii* varied from 8 to 10 mm. Examination of specimens from Jesup, Georgia, the type locality of *F. parvifolia*, including a specimen identified as *F. parvifolia* by Kearney (*Kearney s.n.*, 1893 [NY]) has shown that the capsules of these plants actually vary from 7 to 10 mm. in length. In addition numerous capsules of typical *F. gardenii* measuring less than 8 mm. have been seen.

Rehder (1947) and Bailey (1949) reported that the capsules of *Fothergilla major* were light brown inside with red markings on the inner sutures, while those of *F. monticola* were darker inside without the red markings. Examination, in the field, of the capsules of the glaucous and nonglaucous forms of the montane *Fothergilla* shows that the color of the inside of the capsules often varies from light to dark brown on the same plants. The red markings reported by Rehder and Bailey are indistinct at best and are not constant even among the capsules of a single inflorescence.

The seeds of *Fothergilla*, two per capsule at maturity, are ellipsoid or narrowly ovoid with a very hard, shiny, reddish-brown seed coat. A whitish area, decurrent on opposite sides of the seed and including the sub-apical hilum, is present at the micropylar end. In the material examined, the seeds of the montane populations vary in length from 6.2 to 7.8 mm., while those of the coastal plain populations vary from 4.8 to 6.3 mm. in length.

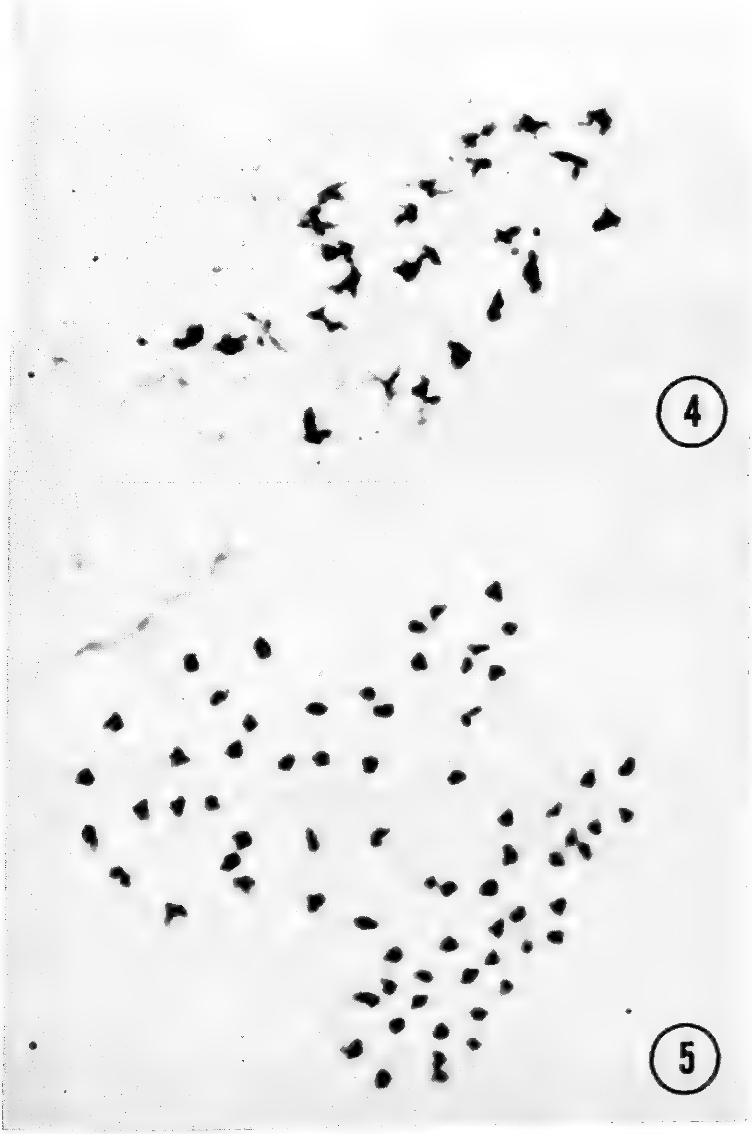
CYTOLOGY

The first account known to me of the chromosome number of any of the species of *Fothergilla* is that of Anderson and Sax (1935) in their survey of the chromosome numbers in the Hamamelidaceae. They reported the haploid number to be $n = 36$ for *F. major* and $n = 24$ for *F. monticola*. The counts were made from aceto-carmine smears of pollen mother cells from plants growing at the Arnold Arboretum of Harvard University. Anderson and Sax pointed out, however, that the "species" are so similar that it is doubtful whether *F. monticola* deserves more than varietal rank. It was their opinion, from the cytological evidence, that "*F. monticola* is merely a tetraploid variety which arose spontaneously from the hexaploid species, *F. major*."

Thomas (in Ernst, 1963) also reported the chromosome numbers of *Fothergilla*, the counts again having been made from plants growing at the Arnold Arboretum. His results were as follows:

SPECIES	ARNOLD ARBORETUM ACCESSION NUMBER	HAPLOID NUMBER
F. monticola	AA # 4163–A	$n = 24$
F. major	AA # 694–34	$n = 36$
F. gardenii	AA # 684–50	$n = 36$

In the course of this study the chromosomes of *Fothergilla* were again recounted. Inflorescence buds were originally collected during April, 1966. In addition buds of *F. gardenii* were obtained from Mrs. Anne B. McCrary, of Wilmington, N.C. All buds were fixed in modified Carnoy's Solution (3 parts absolute ethyl alcohol: 1 part glacial acetic acid) and stored under refrigeration in 70% ethyl alcohol.



FIGURES 4 and 5, Meiotic chromosomes of *Fothergilla*, × 1500. FIG. 4, *F. gardenii*, $n = 24$, Telophase I, *Weaver 350*. FIG. 5. *F. major*, $n = 36$, Metaphase II, *Weaver 1294*.

Since the waxy bloom is not yet developed on newly expanding leaves, the montane forms are indistinguishable from one another while in bud. Therefore it was necessary to mark the plants from which the buds were collected and to return later in the season to determine whether the plants were glaucous or nonglaucous. Unfortunately all buds collected in 1966 were from nonglaucous plants. Glaucous plants were located in Transylvania County, N.C., and tagged during August, 1966. These plants were relocated in April, 1967, when buds were collected.

Voucher specimens were made from plants in the immediate population from which the buds were taken. Wherever possible floral specimens were made at the time the buds were collected. In addition most of the populations were revisited later in the season and vegetative or fruiting specimens were made.

My investigations have shown that, in general, inflorescence buds contain anthers undergoing sporogenesis as long as the stamens of none of the individual flowers exceed the subtending bracts. Buds at this stage are generally less than 1 cm. long.

All counts were made from aceto-carmine squashes of pollen mother cells. The results of the study are summarized in TABLE 2.

TABLE 2. **Chromosome Numbers of Fothergilla**

COASTAL PLAIN FORMS:

COLLECTOR AND NUMBER	LOCATION	HAPLOID NUMBER	NUMBER OF COUNTS
Weaver 355 (DUKE, GH, MICH)	Scotland Co., N.C.	$n = 24$	2
McCrary (No Voucher Made)	New Hanover Co., N.C.	$n = 24$	2
Weaver 350 * (DUKE, GH, MICH)	Scotland Co., N.C.	$n = 24$	4

MONTANE FORMS:

FORM	COLLECTOR AND NUMBER	LOCATION	HAPLOID NUMBER	NUMBER OF COUNTS
Nonglaucous	*Weaver 330* (DUKE, GH, US)	Orange Co., N.C.	$n = 36$	2
Nonglaucous	*Weaver 460* (DUKE)	Stokes Co., N.C.	$n = 36$	2
Nonglaucous	*Weaver 360* (DUKE, GH)	Transylvania Co., N.C.	$n = 36$	4
Glaucous	*Weaver 370* (DUKE, GH)	Transylvania Co., N.C.	$n = 36$	1

* See FIG. 4 for a photograph of the chromosomes of this plant.

TABLE 3. **Chromosome Numbers of Fothergilla Plants at the Arnold Arboretum**

ARNOLD ARBORETUM ACCESSION NUMBER	FORM	HAPLOID NUMBER	NUMBER OF COUNTS	VOUCHER
4163–A *	Nonglaucous	$n = 36$	15	*Weaver 1294* (DUKE)
4163–C	Nonglaucous	$n = 36$	2	*Weaver 1295* (DUKE)
577	Glaucous	$n = 36$	2	*Weaver 1296* (DUKE)
326–49–A	Glaucous	$n = 36$	2	*Weaver 1297* (DUKE)
694–34–A	Glaucous	$n = 36$	2	*Weaver 1298* (DUKE)
695–34–A	Nonglaucous	$n = 36$	2	*Weaver 1299* (DUKE)
14610–A	Glaucous	$n = 36$	2	*Weaver 1300* (DUKE)
1265–62–B	Nonglaucous	$n = 36$	2	*Weaver 1301* (DUKE)

* See FIG. 5 for photograph of the chromosomes of this plant.

Since Thomas recorded the accession numbers of the plants from which his counts were made, a direct check on his work is possible. Preserved inflorescence buds from *Fothergilla* plants at the Arnold Arboretum were obtained by Dr. Carroll E. Wood, Jr., who most generously placed them at my disposal. Chromosome counts were made from aceto-carmine smears of pollen mother cells as before. The plants from which the counts were made were examined at the Arboretum and voucher specimens were made. The results of this investigation are summarized in TABLE 3.

My counts for AA 4163–A are in striking disagreement with those of Thomas. The possibility that the plant might be a mixed clump of coastal plain and montane plants has been ruled out by a personal examination of the plant at the Arnold Arboretum. Considering that pairing of the chromosomes at Metaphase I appeared normal in all the cells examined, the possibility of an aberrant meiotic division of the magnitude necessary to produce a cell containing 24 chromosomes instead of the normal 36 is very slight. There seems to be no alternative than to suggest that the previous counts were in error.

The culture AA 684–50 is no longer present among the collections at the Arnold Arboretum. However, the accession data of this plant shows that the plant was originally collected on Crowder's Mountain, Gaston County, North Carolina. This locality is in the upper Piedmont and hence is considerably outside of the range of the coastal plain species of *Fother-*

gilla. Since typical *F. major* has been collected on Crowder's Mountain (*Beadle s.n.*, 1938 [NCU]; *Biltmore Herb. 708g* [NY]), it seems very likely that AA 684–50 was misidentified. The previously reported haploid number of $n = 36$ for the coastal plain species of *Fothergilla* should be disregarded as a valid count; the specimen from which the count was derived is, in all probability, the montane *F. major*.

As Anderson and Sax neither prepared voucher specimens nor reported the accession numbers of the plants from which their counts were made (C. E. Wood, Jr., *in litt.*), a direct check on their work is impossible. However, the present study would suggest either that the count by Anderson and Sax for "*F. monticola*" was incorrect, or more probably that the plant from which the count was made was in fact a specimen of the coastal plain plant rather than *F. monticola* as reported.

On the basis of the cytological and morphological investigations carried out in this study, there seems to be no basis whatever for the recognition of separate taxa of any rank within either the coastal plain or the Appalachian Highlands populations of *Fothergilla*.

SYSTEMATIC TREATMENT

Fothergilla Murray in Linn. Syst. Veg. ed. 13. 418. 1774.

Yongsonia W. Young, Cat. Arb. Arbust. 54. 1783, *nomen illegit.* Art. 32.
Foterghilla Dumort. Anal. Fam. 35. 1829.
Fothergillia Spreng. in Linn. Gen. Pl. ed. 9. **1:** 445. 1830.

Stellate-pubescent, often clump-forming shrubs, proliferating by means of woody underground stems. Roots fibrous, adventitious from the bases of the aërial stems or from nodes on the underground stems. Aërial stems erect or strongly ascending, unbranched in the lower portions, sparsely or profusely branched in the upper portions, occasionally entirely unbranched; branches proliferating or strongly ascending. Bark smooth, reddish-brown with conspicuous whitish lenticels in younger growth, uniformly light gray in older growth. Vegetative buds naked. Leaves alternate, deciduous, simple, petiolate, membranaceous or somewhat coriaceous, pale green or glaucous beneath, typically elliptical or obovate, more rarely oblong, ovate, or suborbicular; margins coarsely crenate or serrate-dentate, occasionally undulate or even entire; apices acute or obtuse, rarely retuse; bases often unequal, typically obtuse or cordate, occasionally truncate; veins pinnate, alternate or sub-opposite, the 4 to 6 pairs often excurrent into short mucros. Stipules chaffy, narrowly lanceolate to ovate, shortly deciduous. Inflorescence a dense, erect ament-like spike, sessile or short-pedunculate, terminal but often borne on very short lateral shoots and seeming axillary, appearing with the leaves or before them. Inflorescence buds enclosed by an ovate or lanceolate, frequently tridentate scale, which is persistent on the mature inflorescence and generally subtends the lowermost flower. Flowers mostly perfect, but the lower ones frequently female-sterile due to the presence of an abortive pistil, subtended by an ovate to suborbicular, densely brownish-tomentose, soon deciduous bract. Petals lacking. Calyx gamosepalous, adnate to the androecium to form a shallowly campanulate hypanthium; lobes 5 to 7, reduced to minute, irregularly shaped teeth. Inner rim of the hypanthium encircled by a series of very minute, fleshy teeth. Stamens indefinite in number, varying from 12 to 32, apparently inserted in a single series on the rim of the hypanthium; filaments white, conspicuous, unequal in length, the longer ones conspicuously expanded distally, the shortest ones nearly filiform, all greatly exserted; anthers yellow, often becoming purple with age, cuboidal to pyramidal in shape, innate with 4 pollen sacs but becoming 2-locular at anthesis, dehiscent by 2 longitudinal flaps along an I-shaped suture; connective inserted. Pistil 2-carpellate, the carpels connate below but divergent near the apex of the ovary into 2 separate styles; ovary semi-inferior, adnate to the hypanthium for about one-third of its total length, shallowly bilobed, unilocular, the locule deeply bilobed and appearing 2-locular below the attachment of the ovules; styles exceeded by the longest stamens, persistent, subulate-filiform, slightly expanded distally, the stigmatic surfaces linear, introrsely decurrent. Ovules anatropous, 2-integumented, the micropyle facing upwards, at anthesis 2 per ovary on parietal placentae. Fruit a grayish to brownish loculicidal capsule 4-beaked at maturity with the lustrous, bony endocarp distinct from but not separating from the exocarp, semi-inferior, the ripened ovary adnate more or less to the middle with the persistent hypanthium. Seeds 2 at maturity, ellipsoid or slightly ovoid; seed coat very hard, smooth, shiny, reddish-brown; hilum subapical, surrounded by a whitish area; endosperm very hard, white. TYPE SPECIES: *F. gardenii* Murray.

KEY TO THE SPECIES OF FOTHERGILLA

1. Earliest flowers appearing with the leaves; leaves generally toothed only in upper half, rarely asymmetric at base, the largest ones never more than 5.2 cm. wide; stamens generally 12–24; hypanthium at anthesis 1.5–2.6 mm. wide and 0.9–1.5 mm. deep; fruiting hypanthium 3–4.5 mm. long; seeds 4.8–6.3 mm. long. Atlantic and Gulf Coastal Plains from North Carolina to Florida and Alabama. . . . . 1. *F. gardenii.*

1. Earliest flowers appearing with the leaves; leaves generally toothed from below the middle, conspicuously asymmetric at base, the largest ones not less than 5.2 cm. wide; stamens generally 22–32 in number; hypanthium at anthesis 2.4–3.9 mm. long and 1.5–3 mm. deep; fruiting hypanthium 4–9.2 mm. long; seeds 6.2–7.8 mm. long. Mountains and Piedmont from North Carolina to Alabama. . . . . 2. *F. major.*

1. **Fothergilla gardenii** Murray in Linn. Syst. Veg. ed. 13. 418. 1774 [as *F. Gardeni*].

Hamamelis virginiana carolina L. Mant. Pl. Alt. 333. 1771.
Fothergilla alnifolia L.f. Suppl. Pl. 52. 1781, *nomen illegit.* Art. 63.
F. alnifolia α obtusa Ait. Hort. Kew. 2: 241. 1789.
F. alnifolia β acuta Ait. *Ibid.*

F. alnifolia δ *serotina* Sims, Bot. Mag. **33:** *t. 1341.* 1810.
F. carolina (L.) Britton, Mem. Torrey Bot. Club **5:** 180. 1894.
F. parvifolia Kearney in Small, Fl. Se. U.S. 509. 1903.

Plants stellate-pubescent, the undersides of the leaves occasionally glaucous. Aërial stems solitary or in clumps, simple or sparingly to ± profusely branched in upper portions, in flowering specimens 0.3–2 cm. in diam. and 2.5–10(26) dm. tall, densely brown pubescent in distal portions, glabrous or occasionally sparingly pubescent in proximal portions. Underground stems unbranched or sparsely branched, 0.5–2 cm. in diam. Leaf blades coriaceous in texture, 0.9–6.3 (9.8) cm. long and 0.7–4.1(5.2) cm. wide, sparsely to densely yellow or rusty pubescent on both surfaces, but generally more so below, never glabrous, variable in shape, most often elliptical or oblong but not infrequently ovate, obovate, or suborbicular; margins frequently entire or undulate, but equally frequently coarsely crenate or serrate-dentate, the dentition when present generally restricted to upper half of blade, the teeth often ending in short mucros; apices generally acute or obtuse, occasionally retuse or emarginate; bases obtuse or truncate, rarely cordate or asymmetrical. Petioles densely yellow-pubescent, 1–11(14) mm. long. Stipules lanceolate or lance-ovate, 1.5–4(6.1) mm. long, moderately to densely brown-pubescent. Spikes generally appearing before the leaves begin to unfold, (1.1)2.2–4.4(5.2) cm. long and 1.6–3 cm. wide, elongating as flowering progresses, sessile or short-pedunculate, the peduncles then up to 6.2 mm. long and densely yellow-pubescent. Floral bracts ovate or suborbicular, densely brown-pubescent, the lowermost 4.1–7.9 mm. long and 2–6 mm. wide, the others 2.2–5.1 mm. long and 1.7–3.5 mm. wide. Calyx lobes 5–7, minute and inconspicuous, at anthesis less than 1 mm. long. Hypanthium at anthesis 1.5–2.6 mm. wide and 0.9–1.5 mm. deep, densely yellow-pubescent. Stamens 12–24; filaments (2.8)4.5–12(15.8) mm. long, 0.2–0.8 mm. wide; anthers 0.5–1 mm. long, 0.4–0.9 mm. wide. Styles and stigmas together 4.5–10.5 mm. long. Ovary at anthesis 1–2 mm. long, densely yellow-pubescent. Capsules 6.5–10.5(13) mm. long, the persistent hypanthium 3–4.5 mm. long and 4–7(8.8) mm. wide; beaks 3.5–6(8.7) mm. long. Seeds 4.8–6.3 mm. long and 2.3–3.2 mm. wide. $2n = 48$.

Margins of swamps in the Atlantic and Gulf Coastal Plains from Central North Carolina to eastern Alabama (FIG. 6).

REPRESENTATIVE COLLECTIONS. **North Carolina.** Beaufort Co.: *Sawyer 2475* (NCU); Bladen Co.: 1.5 mi. nw. of Bladenboro, *Ahles 23593* (NCU); Brunswick Co.: 5 mi. n. of Orton, *Bell 11546* (NCU); Carteret Co.: 14 mi. w. of Morehead City, *Wilbur 6924* (DUKE); Craven Co.: Bridgeton, *Radford 31924* (GH, NCU); Columbus Co.: 6 mi. nw. of Pireway, *Bell 11417* (NCU); Cumberland Co.: Fayetteville, *Biltmore Herbarium 7609h* (US); Duplin Co.: 3.2 mi. ese. of Kenansville, *Radford 23990* (NCU); Harnett Co.: 1.5 mi. s. of Spout Springs, *Radford 8380* (NCU); Hoke Co.: 8 mi. ne. of Dundarrach, *Ahles 29627* (NCU); Lee Co.: 1 mi. s. of Juniper Spring Church, *Stewart 451* (NCU); Montgomery Co.: 2.5 mi. e. of Norman, *Radford 19633* (NCU); Moore Co.:

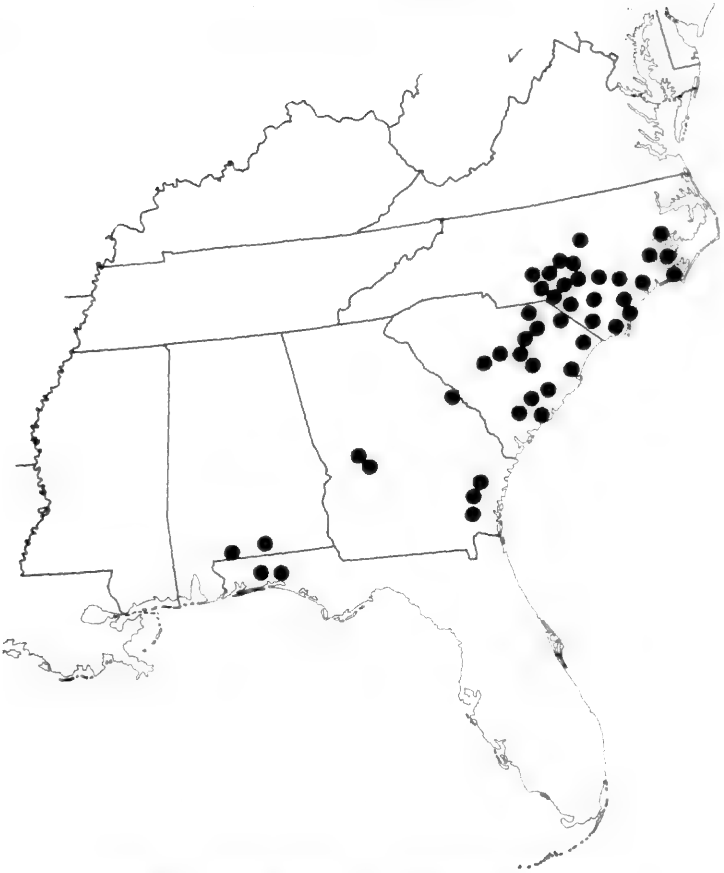


FIGURE 6, Distribution of *Fothergilla gardenii* Murr.

10 mi. s. of Aberdeen, *Coker*, 20 April 1942 (NCU); Onslow Co.: 5 mi. e. of Camp Cowhorn, *Boyce & Moreland 647* (GH, NY); Pamlico Co.: 5.2 mi. n. of Grantsboro, *Radford 42285* (NCU); Pender Co.: 2.7 mi. ne. of Hampstead, *Ahles 23440* (NCU); Richmond Co.: 3.1 mi. e. of Ellerbe, *Gupton 1286* (NCU); Robeson Co.: 2.5 mi. ssw. of Pembroke, *Terrell 3019* (NCU); Sampson Co.: 7.4 mi. n. of Delway, *Radford & Stewart 176* (NCU); Scotland Co.: just s. of bridge over Lumber Creek on US 15–501, *Weaver 355* (DUKE, GH, MICH); Wake Co.: Raleigh, *Hyanis 1898* (NY). **South Carolina.** Berkeley Co.: 16 mi. ne. of Charleston, *Duncan 5923* (GA, GH, MO); Charleston Co.: 1.5 mi. n. of Ravenel, *Duncan 5885* (GA, MO); Chesterfield Co.: just e. of Middendorf, *Oosting 340* (DUKE); Clarendon Co.: 1 mi. nw. of Turbeville, *Radford 21097* (NCU); Colleton Co.: *Bell 1862* (FSU, GA, NCU); Darlington Co.: Dovesville, *Smith 1374* (NCU); Dillon Co.: .5 mi. e. of Dillon, *Radford & Stewart 56* (NCU); Dorchester Co.: w. of Ridgeville, *Ahles 31966* (NCU); Georgetown Co.: 2 mi. w. of Georgetown, *Weatherby & Griscom 16548* (GH); Horry Co.: 10 mi. n. of Myrtle Beach, *Griscom 16547* (A, GH, NY); Lee Co.: .2 mi. n. of Lucknow, *Radford*

27396 (NCU); Lexington Co.: 3.5 mi. ne. of Gaston, *Radford 23378* (NCU); Richland Co.: Columbia, *Philson*, 20 April 1936 (GA); Sumter Co.: *Rehder 954* (A). **Georgia.** Brantley Co.: near Schlatterville, *Thorne & Norris 6284* (GH); Long Co.: 4 mi. w. of Glennville, *Duncan 2222* (GA); Macon Co.: 5 mi. s. of Reynolds, *Pyron & McVaugh 1521* (GA, US); Richmond Co.: near Augusta, *Sargent*, 24 April 1900 (A); Taylor Co.: 6 mi. sw. of Butler, *Duncan 5115* (GA); Wayne Co.: *Duncan 1986* (GA). **Florida.** Okaloosa Co.: on US 90 in Crestview, *Stone 2586* (DUKE, GH); Walton Co.: DeFuniak Springs, *Biltmore Herbarium 7609e* (US). **Alabama.** Covington Co.: about 2 mi. s. of Andalusia, *Harper 108* (GH, MO, US, NY); Escambia Co.: Atmore, *Blanton 206* (A).

Although *Fothergilla* must take its nomenclatural starting point with Murray's description (1774) of *F. gardenii*, Linnaeus apparently confused *Fothergilla* with *Hamamelis* and on two occasions prior to 1774 included a plant fitting the description of *Fothergilla* in his characterization of *Hamamelis virginiana*.

In his account of *Hamamelis virginica* (= *H. virginiana*) Linnaeus (Syst. Nat. ed. 12. 129. 1767) enumerated the characters of a plant sent to him by Dr. Garden of Charleston, South Carolina, which he considered to be very similar to *H. virginiana*. The plant in question, which Linnaeus described as being apetalous with 20 to 40 long, yellowish, filiform stamens, is definitely a *Fothergilla*. Linnaeus, however, did not propose a new name for the plant.

Later, Linnaeus (Mant. Pl. **2**: 333. 1771) described two varieties of *Hamamelis virginiana*, of which the second, *carolina*, characterized as being apetalous with many stamens and a spicate inflorescence, is again, definitely, a *Fothergilla*. Britton (Mem. Torrey Bot. Club **5**: 180. 1894), working under the American Code, took up the epithet *carolina* as the legitimate name for the plant previously known as *Fothergilla gardenii* Murr., but later (1905) evidently changed his mind and treated *F. carolina* (L.) Britton as a synonym of *F. gardenii*. Under the present International Code (Art. 60) the epithet *carolina* does not have priority except in the rank of variety and therefore should not be considered as the name for a species of *Fothergilla*.

2. **Fothergilla major** Loddiges Bot. Cab. **16**: 6. *t. 1520*. 1829.
   F. alnifolia γ *major* Sims, Bot. Mag. **33**: *t. 1341*. 1810.
   F. monticola Ashe, Bot. Gaz. **24**: 374. 1897.

Plants stellate-pubescent, the undersides of the leaves frequently glaucous. Aërial stems in clumps of 3–9, sparingly branched in upper portions, never simple, in flowering specimens 0.3–3.5 cm. in diam. and 0.8–6.2 m. tall, densely brown-pubescent at base of leaves and peduncles, more sparingly so on new growth, completely glabrous in proximal portions. Underground stems unbranched or sparingly branched, 0.3–4.3 cm. in diam. Leaf blades membranaceous, 2.5–13.2(14.4) cm. long and 1.8–11.2 (13.4) cm. wide, moderately to sparsely yellow-pubescent on both surfaces, or lamina glabrous and trichomes present only on veins, variable in shape, typically broadly elliptic or suborbicular but often ovate or obovate; margins entire or undulate to coarsely crenate or serrate-dentate, the dentition when present typically extending below the middle of the blade, rarely restricted to upper half, the teeth typically ending in short mucros; apices acute or obtuse, occasionally retuse or emarginate; bases obtuse or subcordate, conspicuously unequal. Petioles densely yellow-pubescent, 3–15(18) mm. long. Stipules lanceolate or ovate-lanceolate, 2.8–7(10.2) mm. long and 2.1–3.8 mm. wide, moderately to densely brown-pubescent. Spikes generally appearing with the leaves, rarely before them, 1–5(6.4) cm. long and 1.1–3.9 cm. wide, elongating as flowering progresses, sessile or short-pedunculate, the peduncles to 12 mm. long and densely yellow-pubescent. Floral bracts broadly ovate or suborbicular, densely brown-pubescent, the lowermost 4.1–12 mm. long and 3.5–8.8 mm. wide, the others 1.5–5.9 mm. long and 1.9–3.6 mm. wide. Calyx lobes at anthesis 0.4–1.6 mm. long. Hypanthium at anthesis 2.4–3.9 mm. wide and 1.5–3

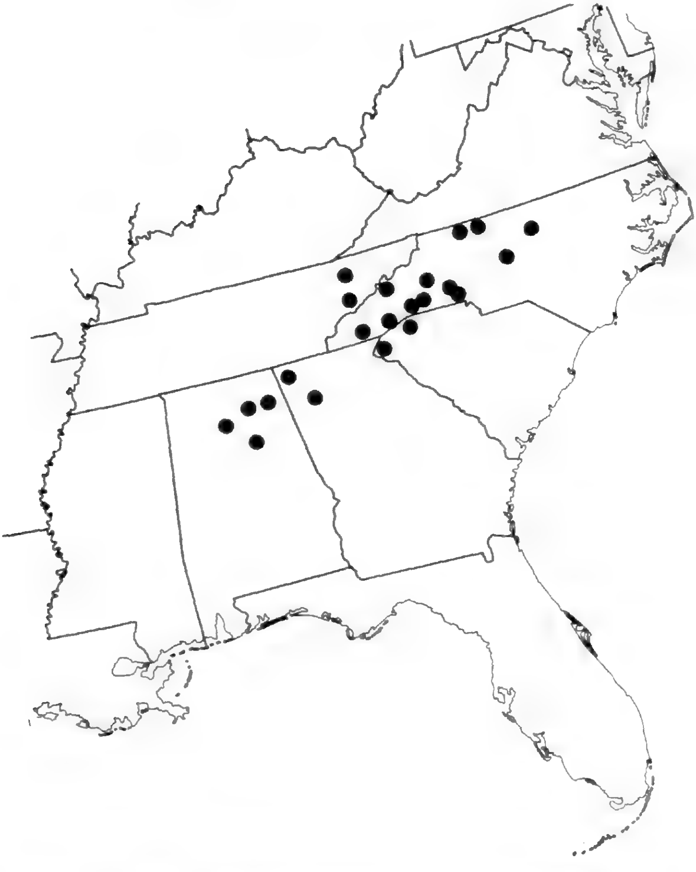


FIGURE 7, Distribution of *Fothergilla major* Lodd.

mm. deep, densely yellow-pubescent. Stamens (18)22–32; filaments 2–16 mm. long, 0.3–1.2 mm. wide. Styles and stigmas together 6.2–12 mm. long. Ovary at anthesis 1.5–2.2 mm. long, densely yellow-pubescent. Capsules 8–15.2 mm. long, the persistent hypanthium 4–9.2 mm. long, 6–8.6 mm. wide; beaks 4.9–8.3 mm. long. Seeds 6.2–7.8 mm. long, 2.7–3.5 mm. wide. $2n = 72$.

Dry rocky or sparsely wooded slopes in the Blue Ridge and upper Piedmont from northern North Carolina to central Alabama; also found in the Great Smoky Mountains of Tennessee (FIG. 7).

REPRESENTATIVE COLLECTIONS. **North Carolina.** Burke Co.: trail to "The Chimneys," Table Mountain, *Wilbur 7038* (DUKE, GH, MICH, LL, FSU, GA); Gaston Co.: near top of King's Mountain, *Coker*, 19 May 1919 (FSU, NCU); Lincoln Co.: *Heunter s.n.* (NY); Macon Co.: Highlands, *Harbison*, May 1905 (GH); Madison Co.: *Newberry*, Apr. 1891 (NY); Orange Co.: 4 mi. w. of Hillsborough Exit on Interstate 85, *Weaver 330* (DUKE, GH, US); Polk Co.: Green River Cove, *Weaver 1333* (DUKE, GH, US, NY); Randolph Co.: Carraway Mountain, *Melvin*, 22 Apr. 1958 (NCU); Rutherford Co.: Pool Creek, Lake Lure, *Bell 2118* (FSU, NCU); Stokes Co.: Sauratown Mountain, *Radford 34675* (GA, NCU, NY); Surry Co.: slopes of Pilot Mountain, *Oosting 3520* (DUKE, NCU); Transylvania Co.: Thompson River Gorge, *Weaver 360* (DUKE, GH). **South Carolina.** Greenville Co.: Caesar's Head Mountain, *Biltmore Herbarium 708* (GH, US, NY); Oconee Co.: Rich Mountain, *Radford 44707* (NCU). **Georgia.** Bartow Co.: se. of Adairsville, *Duncan & Venard 12339* (GA); Walker Co.: Lula Falls, Lookout Mountain, *Churchill 453* (MO). **Tennessee.** Grainger Co.: Lea Lakes, *Sharp & Underwood 4437* (TENN); Sevier Co.: along Walden Creek, near Cornpone, *Sharp 26818* (DUKE, FSU, GA, GH, NCU, TENN). **Alabama.** Cullman Co.: Cullman, *Mohr*, Apr. 1893 (US); Dekalb Co.: Little River Canyon, *Sherman & Shanks 005* (TENN); Marshall Co.: near Short Creek, *Biltmore Herbarium 708d* (US); St. Clair Co.: 12 mi. w. of Pell City, *McVaugh 8594* (GH).

EXCLUDED NAMES

FOTHERGILLA Aubl. Hist. Pl. Guiane Française **1:** 440. *t. 175.* 1775, *nomen illegit.* Art. 64 = **Miconia** Ruiz & Pav. Prodr. 60. 1794 (Melastomataceae).

FOTHERGILLA INVOLUCRATA Falconer, Proc. Linn. Soc. **1:** 18. 1839, *nomen nudum* = **Parrotiopsis jacquemontiana** (Decne.) Rehder, Jour. Arnold Arb. **1:** 256. 1920 (Hamamelidaceae).

FOTHERGILLA MIRABILIS Aubl. Hist. Pl. Guiane Française **1:** 440. *t. 175.* 1775 = **Miconia mirabilis** (Aubl.) L. O. Williams, Fieldiana Bot. **29:** 574. 1963 (Melastomataceae).

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DEPARTMENT OF BOTANY
DUKE UNIVERSITY
DURHAM, NORTH CAROLINA

THE TRIBE MUTISIEAE (COMPOSITAE) IN THE SOUTHEASTERN UNITED STATES [1]

BERYL SIMPSON VUILLEUMIER

MUTISIEAE Cassini, Jour. Phys. Hist. Nat. Arts **88**: 199. 1819.[2]
(MUTISIA TRIBE)

Subtribe **Gerberinae** Bentham & Hooker, Gen. Pl. 2: 168, 217. 1873, "Gerberinieae, Gerberae."

A predominantly South American subtribe of about 135 species (sensu Bentham & Hooker) characterized by multiseriate involucres of imbricate bracts, radiate capitula of monochromatic, bilabiate florets (appearing ligulate in ours due to reduction of the inner teeth), long-tailed and terminally appendaged anthers, and rounded style-branch tips.

1. **Chaptalia** Ventenat, Descr. Pl. Jard. Cels. *pl. 61.* 1802.

Perennial rosette herbs with monocephalous, more or less scapose flowering stems. Undersides of basal leaves, scapes, and outer surfaces of the bracts tomentose. Leaves lanceolate or oblanceolate [linear, lyrate, or runcinate], entire, dentate, or lobate [revolute]. Heads turbinate [campanulate], upright [or nodding]; involucres composed of several rows of linear-lanceolate bracts increasing in size toward the inside; receptacles flat, foveolate. Florets trimorphic: the outermost carpellate, lacking stamens, the corolla ligulate with the outer lip tridentate [3] [in

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[1] Prepared for a generic flora of the southeastern United States, a project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation (Grant GB-6459X, principal investigator Carroll E. Wood, Jr.). The scheme and terminology follow those outlined at the beginning of the series (Jour. Arnold Arb. **39**: 296-346. 1958). As in previous treatments, the area includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions apply primarily to the plants of this area, with supplementary information in brackets. References which the author has not seen are marked by an asterisk.

I am grateful to Dr. Wood for his multifarious help, to Olga Lakela and Robert W. Long, Jr., for living plants of the two species of *Chaptalia* illustrated, and to Donovan Correll and Marshall C. Johnston for some distributional information. The illustration was drawn by Sydney B. Devore (a-e, n) and Irene Brady (f-m).

[2] The tribes of the Compositae have been treated previously by O. T. Solbrig (Jour. Arnold Arb. **44**: 436-461. 1963). The reader should consult this work for additional information (e.g., familial and tribal descriptions, notes, and references) not included here.

[3] Despite Koch's contention that the ray corollas of *Chaptalia* and *Gerbera* which lack an inner lip are distinct from, and not derived from, bilabiate corollas, the pre-

some bilabiate with 1 or 2 minute inner teeth]; the second series of florets also carpellate, lacking stamens, but the corolla reduced to a sheath of variable length (almost absent in *C. dentata*); innermost florets perfect, or functionally staminate due to abortion of the ovule, the corolla bilabiate, or subequal, with the outer lip tripartite and the inner two-parted; corollas uniform in color, white, pale violet, or pink. Style branches of perfect florets thicker and shorter than those of carpellate florets. Pappus setose-capillary, copious, white or pinkish. Achenes fusiform, 5- to several-nerved, glabrous or sparsely villous [papillose], usually beaked (beakless in *C. tomentosa*), topped by the pappus. TYPE SPECIES: *C. tomentosa* Vent. (Named for Count Chaptal de Canteloupe, 1756–1832, a French chemist who published several works on economically important plants, including a study of the resins of *Pinus* species and methods of improving the wine grape.) — SUNBONNETS.

A genus of about 53 species grouped into seven sections (Burkart). Six species [4] representing four of the sections occur in the United States, but the majority of the species is found in the Greater Antilles, Central America, and South America (south to northern Chile and Argentina).

Although three genera of the Mutisieae occur in the United States (*Chaptalia* and two members of the subtribe Nassauviinae: *Perezia*, with 5 species, and *Trixis*, with two species), only two species occur in the Southeast. *Chaptalia tomentosa*, pineland daisy, of sect. CHAPTALIA, is endemic to the pinelands of the Coastal Plain from southeastern North Carolina to southern Florida, west to eastern Texas. *Chaptalia dentata* (L.) Cass., of sect. LIEBERKUHNA (Cass.) Burkart, is primarily West Indian in distribution,[5] but has several scattered populations in the pinelands of subtropical Florida. These two species are placed in different sections because the central florets of *C. tomentosa* are functionally staminate, while those of *C. dentata* are perfect; but the two species are more easily separated by their achenes (long beaked in *C. dentata* and beakless in *C. tomentosa*), by the length of the ligulate corollas, and by the position of the heads before and after anthesis (see illustration).

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dominance of bilabiate "ray" florets in *Gerbera*, the vestiges of an inner lip in many species of *Chaptalia*, and the tridentate ligule in corollas lacking an inner lip, all indicate that in these two genera, the ligulate ray florets are derived from bilabiate forms by loss of the inner lip.

[4] Burkart recorded only *Chaptalia alsophila* Greene, *C. dentata* (L.) Cass., *C. tomentosa*, and *C. nutans* (L.) Polak. as occurring in the United States, but Watson (Proc. Am. Acad. Arts Sci. **23**: 265. 1888) recorded *C. Seemannii* (Sch. Bip.) Hemsl. from Mexico and Arizona, and Kearney & Peebles (Ariz. Fl. ed. 2. 957. 1960) listed *C. leucocephala* Greene as occurring from Arizona to Mexico and added New Mexico to the range of *C. Seemannii.*

[5] Standley (Fieldiana Bot. **3**(3): 441. 1930) mentioned that *Chaptalia dentata* was cultivated at two localities in Yucatán. Burkart, however, referring to the original reference (Millspaugh & Chase, Fieldiana Bot. **3**(2): 148. 1904) decided that the species involved was actually the closely related *C. obovata* Wright. Burkart did cite, however, one specimen of *C. dentata* from Huasteca, Veracruz, Mexico.

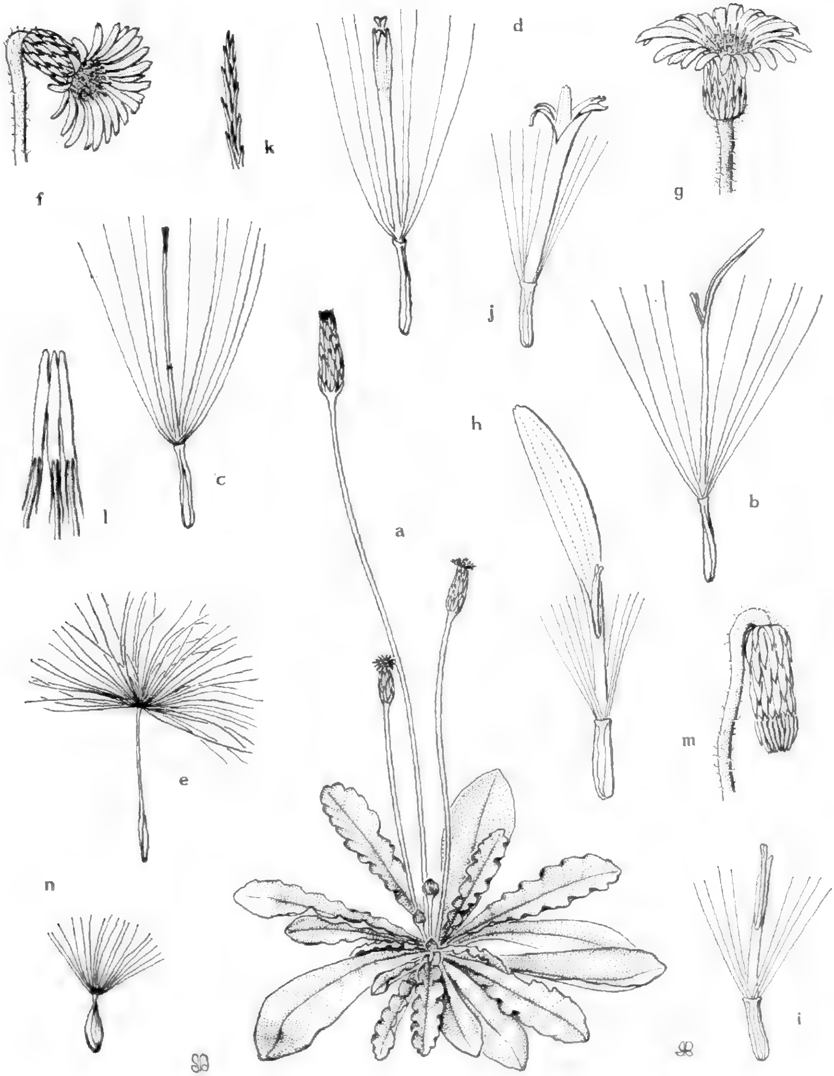

FIG. 1. **Chaptalia.** a–e, *C. dentata*: a, flowering plant, × 1/2; b, outer floret, side view, × 4; c, filiform floret of second series, × 4; d, perfect central floret, × 4; e, mature achene with pappus, × 2. f–n, *C. tomentosa*: f, flowering head on a cloudy day, × 1; g, same on a sunny day, × 1; h, outer floret, × 4; i, floret of second series, × 4 (cf. *c*); j, bilabiate central floret, × 4; k, tip of pappus bristle, × 50; l, three stamens, abaxial side, partly separated, with blunt apical appendage and "tailed" base, × 6; m, lateral view of head with developing fruit, × 1; n, mature achene with pappus, × 2. Note most pappus bristles omitted throughout with only enough included to show appropriate length and spread.

The phenomenon of trimorphic florets found in this genus is not rare in the Compositae (Uexküll-Gyllenband), but inaccurate observations on the condition in *Chaptalia* have led to misinterpretations of both the origin of the ligulate florets (see footnote 3) and the relationships of the genus.

Most workers (Cassini, Bentham & Hooker, Hoffmann, Burkart) have allied *Chaptalia* with *Gerbera* L. (Africa and southeastern Asia) and *Trichocline* Cass. (Andean with a species in Australia). All three are similar in habit, having basal rosettes, scapose flowering stems, and the same type of white tomentum. Palynologically, however, *Chaptalia* is distinct from both *Gerbera* and *Trichocline* and is similar to *Lycoseris* Cass.,[6] another genus of the Gerberinae (cf. Bentham & Hooker). Wodehouse postulated on the basis of pollen similarities a relationship between *Chaptalia* and *Lycoseris* which he supported with evidence from floral morphology, suggesting that both have outer florets without (or with reduced) inner lips and "staminate" florets with undivided styles. *Gerbera* and *Trichocline*, he maintained, have, in contrast, monomorphic perfect florets with bilabiate corollas. Examination of specimens, however, shows the styles of *Chaptalia* always to be bipartite, even in the functionally staminate central florets of certain species (presumably the "staminate" florets of Wodehouse), and the ray corollas of several species of *Chaptalia* are distinctly bilabiate. The floral morphology of *Gerbera*, like that of *Chaptalia*, appears to be much more variable than Wodehouse thought. Monomorphic bilabiate corollas are not a constant character throughout *Gerbera*, and eight or nine species (of 30 to 35 species) have heads with dimorphic florets. In addition, some individuals of *Chaptalia* lack one of the three floret types. In fact, when all the species of both *Chaptalia* and *Gerbera* are carefully examined, there is complete transition between the two genera. Baillon went so far as to combine them, and both Bentham and Burkart thought it necessary to state specifically that, despite the transitions, there are enough characters in combination to justify maintaining the two as distinct genera.

The occurrence of cleistogamous (always closed) as well as chasmogamous (open and radiate) heads in *Chaptalia* is of special interest, for cleistogamy is rare in the Compositae, although it has been known in one species of *Gerbera* since the time of Linnaeus. Burkart found that both kinds of heads occur in three Argentine species of *Chaptalia* (*C. exscapa* (Pers.) Baker, *C. piloselloides* (Vahl) Baker, and *C. runcinata* HBK., the last two in the same section as our *C. dentata*). In contrast to the species of *Gerbera* which produce both types of head simultaneously on the same plant, species of *Chaptalia* apparently produce only one type at a given time on an individual plant (e.g., on a cultivated plant of *C. runcinata* cleistogamous heads in May, chasmogamous ones in

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[6] The pollen of both *Chaptalia* and *Lycoseris* is spherical, tricolporate, and has vestiges of spines. *Gerbera* and *Trichocline* have pollen which is slightly ellipsoidal, tricolporate, almost smooth, and which has the "remarkable character" (cf. Wodehouse) of intercolpar thickenings (i.e., between the furrows).

winter (July), and cleistogamous again the next February). Burkart interpreted this seasonal variation as an adaptation to life on the Argentine pampas.

Although Solbrig mentioned the possibility of apomixis in *Chaptalia*, various experiments suggest that this does not occur. Burkart emasculated and bagged the heads of five South American species but found no indication of seed production. On the other hand, nonemasculated, bagged heads produced abundant viable seeds, showing that autogamy is probable. That self-pollination does occur in nature is suggested both by the presence of cleistogamy and by the reports that some species have involucral bracts that curl inward and force the stigmas against the pollen-producing florets. Recent experiments with *C. dentata* have shown that the plants are self-compatible. All of the full, mature achenes from a head which was not accessible to pollinators germinated. However, about 50 per cent of the achenes never matured, indicating that self-pollination is not completely effective, but, once it has occurred, there are no self-incompatibility barriers (Vuilleumier).

Artificial crosses made by Burkart between three South American species all produced F_1 hybrids which were completely, or nearly, sterile. However, natural hybrids between two other species not investigated are found in southern Brazil and northern Argentina. Chromosome numbers have been reported only for *Chaptalia piloselloides* (a species with cleistogamy, but in Burkart's experiments not apomictic), with $2n = 49–54$, 54, 51–54, 60; *C. nutans*, $2n = 48$; and *C. integerrima* (Vell.) Burkart (= *C. integrifolia* (Cass.) Baker), $2n = 48$.

The genus has no economic importance, but *Chaptalia nutans* is apparently used by Argentine Indians for infections (the leaves being applied with a little oil) and for respiratory ailments. *Chaptalia tomentosa* has been cultivated to a limited extent (cf. Bailey, Cyclop. Am. Hort. **1**: 288. 1900, and **1**: 734. 1928, as well as Roy. Hort. Soc. Dict. Gard. ed. 2. **1**: 450. 1956).

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THE ARNOLD ARBORETUM
OF
HARVARD UNIVERSITY

Present address:
THE GRAY HERBARIUM
OF
HARVARD UNIVERSITY

A NEW SPECIES OF ARENARIA FROM THE BHUTAN HIMALAYA

N. C. MAJUMDAR AND C. R. BABU

THE NEW SPECIES described in this paper was collected from Bhutan, a small mountainous country in the Eastern Himalayas, situated between 26° 40′ and 28° 0′ N. latitude and between 88° 10′ and 91° 45′ E. longitude, and lying between Tibet and India. It is composed of lofty and rugged mountains which vary in elevation from 300 meters to 7500 meters above sea level, and are separated by deep valleys. The climate of Bhutan varies according to elevation; thus, the lower southern valleys are saturated with moisture, hot and steamy; the central valleys enjoy a temperate coolness; and the extreme northern higher region has the rigors of frost and ice.

The vegetation of Bhutan, in general, is composed of tropical, subtropical, temperate, and alpine elements. Chila, the locality from which this interesting taxon has come, is a mountainous ridge situated between 3630 meters and 4120 meters in altitude, in the central tract. It is characterized by alpine vegetation which is composed of herbaceous plants such as *Ranunculus*, *Gentiana*, *Primula*, *Potentilla*, *Gaultheria*, *Arenaria*, *Cerastium*, *Stellaria*, and *Swertia*, in addition to shrubs like *Symplocos*, *Eurya*, and *Pentapanax*.

Arenaria bhutanica Majumdar & Babu spec. nov. FIG. 1.

Pertinet ad subgenus ARENARIA, affinisque nulli speciei huius generis adhuc usque notae; valde distincta habitu annuo, floribus solitariis, caule uno, pedicellis duplici linea pilorum ornatis, sepalis subacutis quam petalis brevioribus, seminibus 3–6 in una capsula.

Herba annua, gracilis, ramosa, 5–10 cm. alta; caulis quadrangularis, prostratus et glaber infra, ascendens vel suberectus et una linea longitudinali pilorum sursum; folia sessilia, opposita quidem aequalia, ad basin connata, lineari-lanceolata, carnosiuscula, integra, margine haud incrassato, ad apicem acuta, pungentia, brunneola, glabra, utrinque punctata, punctis elevatis tubercularibus circularibus, uninervia, 5–10 × 1.5–2 mm.; flores solitarii, axillares et terminales, longe pedicellati, albi, 5–8 mm. diametro; pedicello gracili, quadrangulari, fructifero paulum recurvato, linea duplici longitudinali reflexorum pilorum ornato, 1–2.5(–3) cm. longo; bracteae foliosae, saepe minores foliis inferioribus; sepala 5, usque ad basin libera, lanceolata, subacuta, marginibus late scariosis, obscure uninervia, glabra, 3.8–4 × 0.8–1(–1.2) mm.; petala alba, breviter unguiculata, oblongo-spathulata, integra, obtuso-rotundata, sepalis longiora, 5 mm. longa; stamina 10, uniseriata, 3–3.5 mm. longa; filamenta linearia,

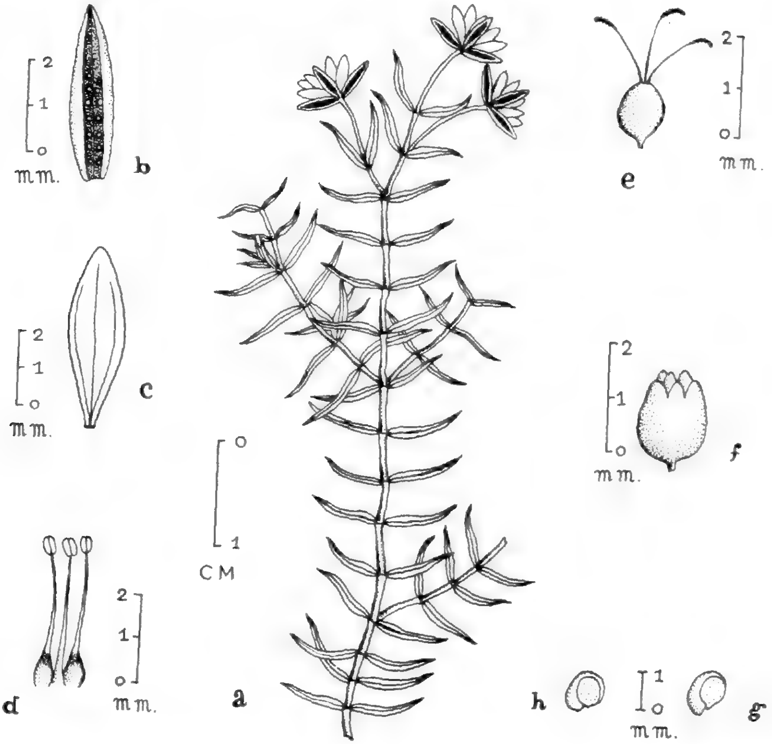

FIGURE 1. *Arenaria bhutanica,* a–h. a, habit; b, sepal; c, petal; d, stamens with and without glands at base; e, pistil; f, capsule; g and h, seeds.

ad ipsam basin connata, eorum singula alterna basi glandulifera, ovoideae brunneolae insidentia, 0.2 mm. longa; antherae minutae, ovoideae, atropurpureae, basifixae, 0.2 mm. longae; ovarium subsessile, ovoideum, glabrum, tricarpellatum, 1.1–1.3(–1.4) mm. longum; styli terni, lineares, papillosi; capsula ovoideo-subglobosa, breviter stipitata, dehiscens ad apicem in dentes 6 obtusos, 2.8–3 mm. longos; semina (immatura) 3–6(–8), subreniformia, compressa, rubro-brunnea, levia? 0.8–1 mm. lata.

Bhutan: Chila, on way to Paro, alt. 3630–4125 m., 24 August 1963, *G. Sen Gupta 721* (holotype and isotype, CAL). Small prostrate, delicate herb with white flowers; stamens blue.

The very slender annual habit, the linear one-nerved leaves, and the obscurely nerved subacute sepals which are shorter than the petals of this remarkable species may bring it under sect. OCCIDENTALES of the subgenus ARENARIA; but apart from the fact that all the eleven species included in this section by McNeill (in Notes Roy. Bot. Gard. Edinburgh **24**: 115. 1962) are either Spanish or North African in distribution, they differ from this species in having dichasial cymose inflorescences. Among the Indo-Tibetan species, this distinctive species with uncertain affinity shows superficial resemblance to *Arenaria monosperma* Williams in its slender habit, linear one-nerved sharply acute leaves, and solitary axillary and terminal flowers; but it differs in its annual growth, presence of a single line of hairs on the stems, two lines of hairs on the pedicels, petals longer than the subacute sepals, and in the 3–6-seeded capsule.

ACKNOWLEDGMENT

The authors are grateful to Rev. Dr. H. Santapau, S.J., Department of Botany, St. Xavier's College, Bombay, for kindly making a few corrections in the Latin description.

CENTRAL NATIONAL HERBARIUM
BOTANICAL SURVEY OF INDIA
CALCUTTA, INDIA

THE DIRECTOR'S REPORT

THE ARNOLD ARBORETUM DURING THE FISCAL YEAR ENDED JUNE 30, 1969

IT SEEMS AN APPROPRIATE TIME, while preparing the annual Director's Report, to reflect on the pleasures and difficulties of implementing the original purpose of the Arboretum "to grow all of the trees, shrubs, and herbaceous plants hardy in the vicinity of West Roxbury" and the concomitant goal of increasing our knowledge of these plants, their relatives, and the vegetation associated with them in their natural areas. How well this charge is being accomplished the record will show.

Again in the first months of 1969, New England suffered characteristic diversity of climate. A severe ice storm in January was localized in the suburban area, causing extensive damage on the Case Estates in Weston, but none in Jamaica Plain. Two storms in February and one in March produced accumulations of wet heavy snow that damaged plants severely, primarily in Jamaica Plain, almost equalling the destruction of past hurricanes. The weather bureau reported a record of 47.6 inches of snow in Boston for February alone (annual average is 41.7 inches), including probably the longest recorded period of uninterrupted snow fall, 78 hours. The accumulation was even greater at the Arboretum than that officially reported at the airport. The extent of damage is almost immediately apparent to visitors because of the nearly complete destruction of the *Magnolia stellata* plantings near the Administration Building as well as in the loss of some entire trees, and many branches, in the cluster of 40-year old specimens of *Prunus sargentii.* Elsewhere on the grounds the damage was equally severe, as in the species apples; the oaks, where a single large tree well over 200 years old was toppled; in the conifers; and in the *Carpinus* and *Ostrya* collections. The grounds crew used chain saws and brush chippers to handle the damaged branches in an immediate effort to clear the grounds, later returning the wood as mulch to the area. Proper pruning and repair of the damaged trees will take the rest of the year. Replacements for many specimen trees must be propagated so that clones of known lineage will be retained. There is still injury to be assessed in the shrub collection where many specimens which were bent to the ground, their branches twisted or fractured, may not live through the season. However, even though the damage of the winter of 1968–69 will long be evident, the spring season which followed was again without a late frost and the display of forsythias, lilacs, crab apples, tree peonies, and rhododendrons was superb. The spring was, in fact, one of the finest in many years.

Staff:

The President and Fellows of Harvard College approved the promotion of Associate Curators Dr. Lorin I. Nevling, Dr. Bernice G. Schubert, and Dr. Carroll E. Wood to be Curators, effective July 1, 1969.

Dr. Alfred Linn Bogle, a graduate of the University of Minnesota was appointed Assistant Curator at the beginning of this fiscal year; Dr. Thomas S. Elias, who recently received his degree from St. Louis University, was also appointed an Assistant Curator, effective July 1, 1969. Both men will work with Dr. Wood in continuing the preparation of the *Generic Flora of the Southeastern United States.*

Dr. Beryl S. Vuilleumier concluded her term of work on the *Southeastern Flora* project and has taken up research problems on her own recent South American collections.

Mr. Robert S. Hebb, a recent graduate of the Gardening program at the Royal Botanical Gardens, Kew, is serving as Assistant Horticulturist. Mrs. Winifred P. Hebb is an assistant in the herbarium and library.

The President and Fellows approved the appointment of Mrs. Ara R. Derderian as Honorary Curator of the Bonsai Collection, effective June 1, 1969.

Honors from outside the University were received by two members of the staff. Dr. Wyman was awarded the Veitch Memorial Medal, in gold, of the Royal Horticultural Society with the citation "By this Veitch Medal we today pay tribute to Dr. Wyman's contribution to the science, to the practice, and to the literature of horticulture." Since the medal is rarely awarded to persons outside of England, we are happy to record that Dr. Wyman is the third member of our staff to receive this prestigious honor.

Dr. Bernice Schubert, together with Dr. Lyman B. Smith, of the Smithsonian Institution, received the Eva Kenworthy Gray award of the American Begonia Society in recognition of their joint contribution of original material which aided members of the Society in the study of begonias. These botanists have published a series of papers on the classification and distribution of *Begonia* in Central and South America.

Dr. Wyman was elected a Vice-President of the Massachusetts Horticultural Society, and Dr. DeWolf was asked to serve on the Library Committee of the Society. Dr. Schubert was elected a member of the Council of the Society for Economic Botany.

Horticulture:

The development of the Weld-Walter Street tract of land for expansion of the living collection was begun during the winter months of the current fiscal year. This tract of 15 acres is held by Harvard University for the purposes of the Arnold Arboretum. Our own crew repaired and reconditioned the stone wall surrounding a large part of the land. After competitive bidding a contract was let to place units of 4- and 6-foot chain-link fence around the area. Two driving gates and three pedestrian gates will control access to the property. A second contract, for land

ABOVE: Development of the Weld-Walter Street tract of the Arnold Arboretum began with the cutting of a roadway.

BELOW: View from the summit of the hill showing Route 1 and the Hebrew Rehabilitation Center Buildings.

movement, has established 1,840 feet of roadway 24 feet wide which sweeps gracefully from Walter Street to the highest point, where a turn-around will be developed. The road will be surfaced with a compacting gravel and an oil seal for the present. The land was treated with lime and fertilizer in the fall, following recommendations of the Soil Conservation Service of the U.S. Department of Agriculture. Planting of species which will tolerate the dry hillside conditions will be gradual, and the area will be opened to the public in 1972.

To improve the appearance of the largest of the three ponds along the meadow road, which had become filled with aquatic weeds during recent years, it was dredged. Late fall rains and winter snow filled it, and a program of planting around the pond has begun.

Income available from the Isabella P. Shaw fund helped provide six tons of fertilizer for application to the collection of azaleas and rhododendrons in 1968 and permitted rapid replacement of storm-damaged plants of mountain laurel along the base of Hemlock Hill.

Pond along the meadow road within the Arboretum which was excavated during the summer of 1968.

The growth control chemical Casoron is proving helpful in restricting grass and weeds near special plantings. Its use has reduced mowing time required to maintain the appearance of the grounds and has nearly eliminated the problem of injury to the base of tree trunks, caused by the use of mowing machines.

The genetic dwarf conifer collection established in terraced plantings near the greenhouses in Jamaica Plain has done well in that location where it attracts much popular interest and where it has survived the winter without special protection. Limited to specimens of known origin and unquestioned identification, this collection has great reference value. A gift of 21 previously unrepresented taxa from Mr. Joel Spingarn, of Baldwin, New York, and collections of native plants from locations along the coast of Maine, made by Mr. Fordham, have increased the variety of the dwarf conifer collection.

Mrs. Ara R. Derderian has accepted responsibility for curating the Larz Anderson collection of *bonsai*, a famous and popular display which has needed competent care for several years. With the help of members of the staff she has carefully pruned and repotted most of the plants during the winter months. Many of the specimens are thought to be imperial *bonsai* because of their age and special character.

For the protection of lawns, nursery area, and roads, special steel edging is being used in the vicinity of the Dana Greenhouses, and, for more efficient work procedures, steel storage bins, shelving, and work benches have been installed in the greenhouse. A new well provided continuous water pressure and flow for irrigation in the nursery area during the dry summer months. The emergency electric generator worked well during electric power failures resulting from the February and March snow storms. Without it the oil-fueled furnaces would have been inoperative and the greenhouse plantings might not have survived two periods of more than six hours without heat.

During the year a total of 672 specimens were planted on the grounds as replacements or additions. Cuttings or grafts have been prepared for 287 taxa which may need replacement. A total of 152 additional taxa have been prepared for distribution to Cooperating Nurserymen, to other arboreta, or to the Friends of the Arnold Arboretum for testing. Staff research required propagation of 78 taxa.

During the year 11 recent staff introductions were distributed to botanical gardens and Cooperating Nurserymen. In addition, 169 shipments of plant materials representing 918 species and varieties were made to gardens and individuals in the United States and 14 other countries. Thirty-seven lots of seeds, including 182 taxa, were sent in response to specific requests from correspondents in the United States and 24 other countries. The 88 shipments of plant materials received during the year included 287 taxa, and 72 lots of seeds represented 182 taxa. Plants not needed by the Arboretum were offered to the Department of Buildings and Grounds of Harvard University and to other colleges and universities, as well as to botanic gardens.

Dr. Wyman cooperated with representatives of the U.S. Bureau of Public Roads and several Roadside Development engineers of the Massachusetts Department of Highways, Bureau of Public Works, in advising and by supplying some plant materials for programs of highway beautification. The Massachusetts Department of Highways also accepted four truck-loads of trees and shrubs for demonstration plantings along the new Blue Star Memorial Highway in eastern Massachusetts.

A collection of 36 plants was donated to Channel 2, Boston's educational television station, for "sale" at its benefit auction in early June.

As the application of electronic data-processing equipment and techniques to collection records has become of great national and international concern, our staff has collaborated with others on projects under way at other institutions. Several types of projects are in a trial period but may be able to incorporate data from our collections in the future. Dr. Howard serves as chairman of the Plant Records Center of the American Horticultural Society. The Plant Records Center, operating under a grant from the Longwood Foundation, has been devising a method for placing the records of the living and herbarium collections of the Longwood Gardens in a retrieval system. The goal of the Plant Records Center is to establish a central data bank of sources of plant materials by recording, eventually, the accession records of all botanical gardens and arboreta in the country. The Arnold Arboretum has the largest collection of woody plants and probably the best records on the origin and behavior of plant species under cultivation, and its records should be a valuable addition to those of the Plant Records Center. Other projects involving electronic data-processing systems are mentioned under the section on the herbarium.

Case Estates:

The Case Estates in Weston, Massachusetts, are the location for the nursery area for the Arnold Arboretum, as well as for special display plantings, demonstration plots for comparison of mulching materials and pruning techniques, ground covers, street trees, and perennial beds; areas of natural woodland, and various materials which cannot be accommodated in Jamaica Plain.

Additions were made to the already established wild flower garden this year and a small collection of rock garden plants was established for trial and demonstration.

The diversity and educational nature of the plantings has made the Case Estates increasingly popular with school classes, colleges, and garden clubs. All of the Weston Schools sent classes for talks or tours during the year, while guided tours were held at the request of many groups from Massachusetts and other states. To facilitate special lectures and the regular popular classes for adults of the surrounding suburban communities, one of the buildings was redesigned as a class room and was equipped with carpeting, shades for darkening the room (for showing slides), and new chairs. The building occupied by the superintendent of the grounds was also reconditioned.

After a severe ice storm in January, a special study session was offered for the Friends of the Arnold Arboretum. Forty-four people spent a cold, sunny day observing the damage and discussing methods of repair and later care for the injured plants. Afterward the trees were pruned by the staff, or where necessary, removed.

Dr. Wyman was requested to aid the town of Weston in planning a small park at the junction of Newton Street and South Avenue, for which the Arboretum donated plants. The town expressed its deep appreciation in a vote of thanks. The Arboretum also made a gift of fiery red crabapple trees of the cultivar BARBARA ANN for planting near the new fire station.

Herbarium:

The herbarium collections of the Arnold Arboretum are divided in two parts. The portion housed in Jamaica Plain is composed of cultivated plants and serves as a reference collection for the identification of and distribution studies on plants in cultivation. It now comprises over 136,000 specimens and has particularly representative collections of woody ornamental trees and shrubs, especially those which form the large part of our living collections. As a result of the special effort devoted to increasing representation in the cultivated herbarium, additions of some size came this year from Massachusetts, Pennsylvania, Florida, Puerto Rico, Mexico, Venezuela, Brazil, and South Africa.

A new collection of historical interest to us consists of herbarium specimens prepared by F. L. Olmsted who worked with Charles Sargent in planning the Arboretum plantings and who was responsible for the development of the park system in Boston and of Central Park in New York. Given by the Olmsted Associates, this unmounted collection will require much work before it is fully available. It includes specimens collected in the Arnold Arboretum in 1875, the oldest material from our collections and probably some of the first specimens taken from early Arboretum introductions, as well as material of the same period from Central Park.

The major portion of the Arboretum herbarium, housed together with that of the Gray Herbarium in the Harvard University Herbaria in Cambridge, is composed of native plants of the floras of the world. It is most representative for woody plants of the United States and temperate and tropical areas of eastern Asia. The herbarium collection is the basis for monographic and floristic studies, work in plant anatomy, morphology, and palynology, and is used for general identifications or to answer special questions.

The several research projects of the staff center on a number of geographic areas. Dr. Wood and his associates continue their studies toward a *Generic Flora of the Southeastern United States*, which actually has implications affecting a much larger area of the country. During the year Dr. Wood treated the families Betulaceae and Aristolochiaceae for this project; Dr. Vuilleumier worked on some tribes of the Compositae; Dr. Bogle, on the families of the Centrospermae; Dr. Long and Sister Victoria Hayden, as Mercer Fellows, studied the Acanthaceae and Rubiaceae, respectively; Dr. Sorensen is studying the Phytolaccaceae, and Dr. David Bates, of Cornell University, has agreed to continue the work on the Malvaceae started by the late Dr. Brizicky. Other areas in the United States were involved in Dr. Schubert's work on species of the genus *Desmodium* for the *Manual of the Flora of Texas* and Dr. Howard's descrip-

Students and staff of the 1968 Tropical Botany Seminar held at the Fairchild Tropical Garden and the University of Miami. Dr. Howard was one of the instructors.

tive treatment of the plants of the Isles of Shoals (near New Hampshire and Maine).

Dr. Nevling is conducting a cooperative program with scientists of the Universidad Nacional Autónoma de México on the environments and plant resources of the state of Veracruz. The native plants of the region are being studied by him and his associates, or by specialists on particular groups, with emphasis on the ecology and biology of the vegetation, in addition to purely floristic studies. Special data handling techniques are being employed in certain aspects of this project. Plants cultivated in the area are also being studied and will serve as a valuable addition to the cultivated collections at Jamaica Plain. The Arboretum has helped to support, in part, two collectors in Veracruz, Marino Rosas R. and Guadeloupe Martínez Calderón.

Dr. Schubert has special research interest in some species of the genus *Dioscorea* in Mexico which have very small stature but occur in various sections of the genus, not being related by their characteristic habit. She is also concerned with studies of species of *Desmodium* occurring throughout the Americas. Dr. Sorensen has a particular interest in the genus *Dahlia*, the national flower of Mexico, and his studies in that country have increased his understanding of the distribution and growth patterns of the group.

The Caribbean islands are the floristic area of intensive research by Dr. Howard and Miss Powell. Attention has been focused most recently on biological studies of elfin forests in Puerto Rico and St. Kitts. Large general collections have been studied by them from the Bahamas, Puerto Rico, Guadeloupe, Martinique, and St. Lucia.

Dr. DeWolf is preparing studies of the family Moraceae or of the genus *Ficus* for the floras of Surinam and Venezuela being published in those countries. Other staff work on South America includes that on *Begonia* in Colombia by Dr. Schubert and that on *Schoenobiblus*, of the Thymelaeaceae, by Dr. Nevling, who is also preparing a treatment of the entire family for the flora of Venezuela.

African members of the Moraceae and the genus *Ficus* are being studied by Dr. DeWolf for Uganda and for the Flora of East Tropical Africa; and African *Desmodium* is being treated by Dr. Schubert for the latter flora also.

Several of our botanists are working on aspects of the flora of Asia, which has for a long time been of much interest to the staff of the Arboretum. Dr. Hu has spent most of the past year in Hong Kong. Dr. Perry is working with our collections from Papua and New Guinea, concentrating on the family Myrtaceae. Dr. Hartley has completed the work of identifying his general collections from New Guinea, of which the duplicate series are being prepared for distribution. His special research concerns the family Rutaceae in tropical Asia and his monograph of the genus *Flindersia* is completed. Dr. S. Kazmi, a Mercer Fellow from Pakistan, is undertaking a revision of the family Boraginaceae from West Pakistan and Kashmir.

The largest herbarium project during the year was the rehousing of the fruit and seed collection. This move was necessitated by the appointment of a senior member to the Gray Herbarium staff. The collection is again available for consultation in the Cambridge building. The use of self-sealing polyethylene bags for fruit storage is in the experimental stage and, hopefully, this technique will permit significant growth without requiring additional floor space.

The importance of the herbarium as a scientific tool cannot be underestimated. The scientific needs which use of the herbarium fulfills have been partly demonstrated already. Each year, however, because of new techniques or new methods in which old techniques are employed, along with the growth of the collection, the demands on it become greater and its overall usefulness is extended. In addition to its use by the resident staff, many parts of the collection are studied by scholars from other institutions, usually through a system of inter-institutional loans. During the year just ended loans to other institutions continued at a very high level: 154 loans to 23 foreign and 39 domestic institutions, the total of specimens loaned being 19,351. On the other side of the ledger, 12,300 specimens (110 loans from 31 foreign and 27 domestic institutions) were borrowed for study by our staff.

Added to the herbarium this year were 26,985 sheets, increasing the collection to 908,925 sheets. Of the total collection 136,556 are deposited in the herbarium of cultivated plants in Jamaica Plain, the remainder in the collection in Cambridge. While herbarium growth is at a satisfactory level, the problem of adequate space to house the collection properly increases proportionately. Several areas are seriously overcrowded and some emergency measures have already had to be taken. We hope for adequate expansion space before the need becomes desperate.

The Department of Botany of the Smithsonian Institution is recording data on type collections in its herbarium. Test cards on a few selected genera have been sent to other herbaria and data from our herbarium have been supplied for this project. Through cooperation we learn the kind of information required, the time and effort needed to record it, the methods of recovery, and most important, we gain further knowledge on the accessibility of information in our own collections.

The cooperative project with the Universidad Nacional Autónoma de México is utilizing the computer facilities of that university to store and process the data acquired under the project entitled "Environments and Plant Resources of Veracruz." At present, data processing techniques are used in the preparation of herbarium labels and for the storage and recovery of the label data. Bibliographic materials for Veracruz are also being processed for retrieval by automatic means.

Library:

The use and the size of our important botanical library continued to increase during the year, necessitating some thought about the amount and kind of space needed to house the collections in the near future. Total accessions this year were nearly double the number indicated in recent reports. While the number of books purchased was up 40 percent, binding of periodicals showed a 150 percent increase. The acquisition of 859 bound volumes brought the total to 55,126, and 138 pamphlets were added to the collection, which now numbers 21,236. The growth of the library may be realized from the new total of 76,362 catalogued items.

Four reels of microfilm and 2141 microfiche cards from various herbaria were purchased jointly with the Gray Herbarium, to keep current these important tools of botanical research. A total of 9175 microfiches are now available for study.

Regular issues of the *Gray Herbarium Index of American Plants*, the *Index Nominum Genericorum*, and the *Torrey Index of Botanical Literature* were incorporated to maintain the regular sequences.

We were pleased to receive a large number of single volume gifts during the year, in addition to a special gift of volumes from the Olmsted Associates of Boston. The library of the late Harold H. Knowlton was also presented to the Arnold Arboretum. A bookplate was prepared with the Knowlton family seal and the inscription "From the library of Harold W. Knowlton, presented in loving memory by his family to the Arnold Arboretum of Harvard University." The Knowlton library is particularly strong in volumes on iris, daylilies, and other horticultural groups.

Improvements have been made in the forestry collection housed in Jamaica Plain. Additional library help has made it possible to complete

Unusual accumulations of snow marked the early months of 1969 when sections of the Arboretum could not be visited on foot.

catalogue changes for the books returned from the Harvard Forest library two years ago. This year the Arboretum accepted the transfer to Jamaica Plain of Widener Library's books on forestry which will be recatalogued later.

A major rearrangement of the periodicals in Jamaica Plain was completed during the winter to provide space for growth. The American periodicals now occupy the main library room, with the British, French, and German language periodicals each in separate alcoves. The reprint files and the collections of nursery catalogues and pamphlets dealing with botanical gardens and arboreta were also reorganized.

Systematic Plant Anatomy:

At the time that the fruit and seed collection was moved to provide additional laboratory space in the Harvard University Herbaria building, the wood collection was consolidated. This procedure offered an opportunity to re-examine the collection of dry and preserved wood specimens and slides and to begin some needed curatorial work. The collection was increased this year by 400 microscope slides of woods of North American trees, prepared in a cooperative program with the North Carolina State University at Raleigh. As usual, specimens of wood samples and slides were sent on loan as requested.

The Arboretum received as a gift the wood collection of the late Ralph F. Perry presented by his family through Mrs. Lyman C. Morrill. This collection of display woods, housed in a special cabinet and maintained in Jamaica Plain, is a valuable teaching aid which includes both polished samples and bark sections

Our collections are being used in several active research programs, including studies of the Ulmaceae by Dr. William Stern and his students at the University of Maryland, who have used wood samples supplemented by material from the living collections. Dr. Bogle is completing his study of the floral morphology and vascular anatomy of the genera of the Hamamelidaceae. With the assistance of Mrs. Roca-Garcia, Dr. Howard has begun an anatomical study of the floral nectaries of the Puerto Rican species of the genus *Marcgravia*. Work on nodal and petiolar anatomy of the families of dicotyledons continues as a major program. Special collections of preserved material from Hong Kong and Macau, supplied by Dr. Hu, have added four families and 40 new genera to the study. A special project was initiated to prepare a key to the plants of Barro Colorado Island based on the structural characteristics of the node and petiole. The material was supplied for this project by Dr. Thomas Croat, in cooperation with the staff of the Missouri Botanical Garden, as part of their study of the *Flora of Panama*.

Education:

Two formal courses in the Department of Biology were offered by members of the Arboretum staff. Dr. Howard taught an advanced one-semester course in plant systematics, Biology 209, "Phylogeny of the Flowering Plants," and Dr. Wood gave Biology 103, "The Taxonomy of Vascular Plants." Dr. Hartley taught the Harvard University Extension Course in general botany throughout the year.

The program of luncheon seminars in systematics held at the Harvard University Herbaria building was conducted by Dr. Wood during the fall semester. Several staff members presented lectures in this series through the year. Drs. Howard, Nevling, and Schubert offered "300" or research courses for graduate students during the year.

At Harvard, as at other universities throughout the world, there was student "unrest" this spring. Several senior staff members, who are members of the Faculty of Arts and Sciences, spent long hours in special meetings of the Faculty and of the Department of Biology during the crisis. They also carried on extended conversations with students as a small contribution toward better communication and improved understanding.

This year Dr. Howard served as one of three teachers in a Tropical Botany Seminar sponsored jointly by the Fairchild Tropical Garden and the University of Miami. The seminar, attended by 12 students from as many colleges, was financed by the National Science Foundation and offered at the Fairchild Tropical Garden. He also took part in symposia in New York, sponsored by the Herb Society of America, and in Geneva, Switzerland, under the auspices of the Jardin Botanique. He presented lectures on the Baldwin Wallace and Franklin Pierce campuses and was sponsored by the American Institute of Biological Sciences at St. Anselm's College. In addition, he spoke in the series of the Torrey Botanical Club lectures and that of the Worcester Horticultural Society.

Mr. Fordham prepared special lectures and demonstrations for visiting classes from the Universities of Massachusetts, Rhode Island, and Connecticut, and for groups from Tufts, Wheaton, and Pine Manor Junior College. He attended the national convention of the American Rhododendron Society at Pine Mountain, Georgia, where he gave a talk on Rhododendron Propagation. Dr. Sorensen was speaker for a seminar series at the University of New Hampshire. Dr. Nevling gave a seminar on the nature and diversity of climbing plants at the Universidad Nacional Autónoma de México. Mr. Pride talked about the Case Estates and about native plants of New England in a two-day lectures series on Nantucket, in addition to speaking for the Worcester and the Massachusetts Horticultural Societies. Dr. Wood participated in the symposium at the Virginia Polytechnic Institute on the distributional history of the biota of the Southern Appalachians. His lecture was on "Some Floristic Relationships Between the Southern Appalachians and Western North America." In addition, nearly all staff members filled one or more lecture engagements with garden clubs.

Educational displays utilizing materials from the Arboretum collections were prepared by the staff for the Fall Harvest Show of the Massachusetts Horticultural Society and an Iris exhibit for the Worcester County Horticultural Show. Mr. Fordham and Mr. Williams presented lectures in special programs held at the Spring Flower Show of the Massachusetts Horticultural Society.

The Arnold Arboretum Achievement Award for Botanical or Horticultural Excellence was established last year through a special gift for that purpose. The award is made to an outstanding student in one of the high schools in the vicinity of the Arnold Arboretum. This year the award, a choice of books and plant specimens, was made to Mr. Stephen Grace, of Jamaica Plain High School, who plans to continue his education at Salem State College.

Travel and Exploration:

Members of the staff travelled widely during the past year. Dr. Hu returned to Hong Kong where she continued her work towards a revised flora of Hong Kong and the New Territories. She again taught a class at Chung Chi College in exchange for facilities for collecting and drying herbarium specimens. Several new records of plant distribution were obtained for the islands.

Mr. Pride joined a trip to India and Nepal, conducted by Dr. Oleg Polunin, during which he visited montane areas around Darjeeling and Katmandu. On the return trip he visited Wisley; Wageningen, and the

Belmonte Arboretum in Holland; and the Floralie Internationale in Paris. He collected some herbarium specimens and obtained some seeds for trial at the Arnold Arboretum.

Dr. DeWolf, with the support of a grant from the National Science Foundation, made field studies of the species of *Ficus* in Venezuela. He was able to locate and study 97 trees, or populations of 15 taxa, to obtain ecological and morphological data from living plants. Several species which were considered rare or uncommon on the basis of herbarium records proved to be abundant in restricted locations. He was also able to make 38 collections of fig insects for the cooperative study of Mr. J. T. Wiebes, of the Rijksherbarium, Leiden. Herbarium specimens in sets of several duplicates were prepared, dried, and returned with the cooperation of the staff of the Instituto Botánico in Caracas. The aid of many people who assisted Dr. DeWolf is acknowledged with gratitude, among them, Drs. Tobias Lasser and Leandro Aristeguieta, of the Instituto Botánico; Dr. José Rafael García, of the Ministerio de Agricultura; Lic. José de Jesús San José, of the Sociedad Venezolana de Ciencias Naturales; and Dr. Argirmiro Bracemonte, of the Universidad de la Region Centro-Occidental.

Dr. Nevling made a trip to Mexico to continue his collaboration with Dr. Arturo Gómez-Pompa and the staff of the Universidad Nacional Autónoma de México and the Jardín Botánico in their investigations of the flora of the state of Veracruz.

Dr. Howard had completed the biological study of the elfin forest on Pico del Oeste in Puerto Rico as proposed in the original N.S.F. grant, when an unfortunate airplane crash opened a new area of study on a ridge less than a mile from the Pico del Oeste study site, where the elfin forest vegetation was removed for a distance of 300 yards. The exposed site was visited and marked for subsequent studies of regrowth and the development of adventitious shoots, invasion of new species, or the replacement by taxa of the present vegetation, and for erosion under the heavy rainfall conditions of the area.

Members of the staff attended professional meetings in their areas of interest, most of which have been cited in other sections of this report.

Dr. Howard was an invited speaker on the occasion of the 150th anniversary of the founding of the Jardin Botanique in Geneva, Switzerland. A brief vacation following the assembly permitted a visit to the tundra areas of Norway to obtain kodachromes useful in teaching.

Dr. DeWolf, again with the aid of a grant from the National Science Foundation, was able to visit and study at herbaria in England, Germany, and the Netherlands in connection with his research on the species of *Ficus* in Africa and *Dorstenia* in the New World.

Gifts and Grants:

By permission of the President and Fellows of Harvard University and with the aid of members of the Committee to Visit the Arnold Arboretum, invitations were sent this year to solicit membership as Friends of the

An example of snow damage to a hemlock tree. Many of the conifers lost their tops while others were stripped of lower branches.

Arnold Arboretum. The Friends are an informal group of contributors, some of whom have been supporting the general work or special collections for over twenty years. Its members have participated in the open houses and the popular classes in horticulture and botany offered by the staff and have shared in a program of plant distribution and hardiness testing. The Friends supplied active political support in opposition to a bill filed in the Massachusetts legislature to build a ski tow in the Arnold Arboretum, and again this year in opposing a swimming pool and recreational area on the grounds. Over 300 new Friends have joined to help support the Arboretum during the past year, and it is our hope that many more will participate as the Arboretum approaches its Centennial Year.

A Centennial Fund has been established by the Treasurer of the University for gifts to be used during 1972 or in anticipation of it. Part of the development of the Weld-Walter tract has been made possible by this extra financial aid. We are particularly grateful for the generous but currently anonymous gifts to be capitalized until 1972 which are to support field work, plant introduction, and work in special areas of horticulture.

Work on the Generic Flora continued with support from a grant by the National Science Foundation, as has Dr. DeWolf's work on *Ficus*.

Throughout the year the Arnold Arboretum receives many gifts of living plants, books, herbarium specimens, and articles of scientific or historical value which are acknowledged individually by the staff and by the University.

Publications:

The Arnold Arboretum publishes regularly a scientific quarterly, the *Journal of the Arnold Arboretum*, and a popular bulletin, *Arnoldia*, issued in twelve single or combined numbers. The *Journal* gives priority to technical papers by members of the staff but accepts papers from other authors when the subject matter concerns our collections or involves topics of particular relevance to the work of the Arboretum. Under the editorial direction of Dr. Bernice Schubert, 29 articles by 40 authors were published during the past fiscal year for a total of 582 pages. Subscriptions have increased substantially in the last two years, particularly since the first forty-five volumes have become available in a reprint edition. Circulation is the responsibility of Miss Dulcie Powell, who has recently completed a reorganization of the files and records.

Arnoldia was edited, and largely prepared, this year by Dr. Wyman. A total of ten numbers containing 119 pages was published. The largest single issue was an article by Dr. DeWolf entitled "Notes on making an herbarium." This is a modern presentation of the techniques of preparing specimens and contains an excellent bibliography of special articles on the subject. It will replace an article by the late Ivan M. Johnston which is long out of print. Up to now this special number has been requested by twenty-two colleges.

Two special publications were issued during the year. The booklet "Through the Arnold Arboretum," with photographs by Mary Rosenfeld, text by Stephanne Sutton, and art work by Pamela Bruns, is a popular guide to the living collections of the Arboretum. Some of Mrs. Rosenfeld's fine photographs were reproduced in the *Harvard Alumni Bulletin* of March 17, 1969, an issue devoted to Harvard's botanical collections. The Arboretum story, entitled "Harvard is Green," is available for distribution as reprints.

The second special publication, *Flowers of Star Island*, is a study of the vegetation on the Isles of Shoals, a conference center located off the coast of Portsmouth, New Hampshire. Dr. Howard prepared the text and Helen Roca-Garcia the line drawings and silhouettes.

Mercer Fellows:

A portion of the income from the bequest of Mrs. Martha Dana Mercer is used annually as "Mercer Research Fellowships." In most cases the fellowships permit the holder to live in Cambridge or Jamaica Plain while using the collections of the Arnold Arboretum for his special research studies. A few fellowships have been awarded to individuals who wished to work with members of the Arboretum staff in order to learn a particular technique or to become experienced in the operation of various units within the Arboretum. This year for the first time a fellowship was awarded to a graduate student to pursue an academic program leading to a degree, under the direction of a member of the staff. Mr. Mario Sousa-Sanchez from Mexico, who was admitted to the Graduate School of Arts and Sciences, will be engaged in studies toward a Ph.D. degree. His research interest and thesis project concern the genus *Lonchocarpus*, an arborescent member of the Leguminosae, as it occurs in tropical America.

Four scholars were appointed Mercer Research Fellows for all or part of the year. Arthur Charles Gibson, of Miami University, for work with the cultivated plants of New England; Sister Mary Victoria Hayden, of Catherine Spalding College, for work on the family Rubiaceae; Syed Mohammed Anward Kazmi, of Peshawar University, Pakistan, for work on the Boraginaceae of West Pakistan and Kashmir; and Robert William Long, University of South Florida, for work on the family Acanthaceae.

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Richard A. Howard, *Director*

The Board of Overseers of Harvard College
Committee to Visit the Arnold Arboretum

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1968–1969

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* Appointed jointly with the Gray Herbarium.

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