

MONOGRAPH OF DAPHNIPHYLLUM (1)*

by

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ABSTRACT

The identification of species of *Daphniphyllum* has been extraordinarily difficult. Access to a wealth of herbarium material, including almost all type specimens, has made it possible to present a more complete classification of the genus. Based on a study of 2600 specimens, seven species have been retained as valid from a total of 65 specific names, and two new species have been proposed within three recognized sections of the genus. The conclusion is reached that speciation in *Daphniphyllum* is undergoing a reductional modification in floral morphology which I recognize in several intermediate stages representing members of the sections *Lunata* and *Calycifera* and a final stage consisting of taxa in the section *Staminodia*.

The taxonomic position and affinity of *Daphniphyllum* have remained ambiguous. The genus has been placed in the Euphorbiales, Hamamelidales, Pittosporales, and in the monotypic order Daphniphyllales, but opinions have usually been based on fragmentary evidence. Following a comparative study of the gross morphology, wood anatomy, pollen morphology, chromosome complements, and chemical components of *Daphniphyllum* in relation to those families thought to be allied to the genus, viz., Buxaceae, Cercidiphyllaceae, Eucommiaceae, Euphorbiaceae, Hamamelidaceae, Pittosporaceae, Platanaceae, Stachyuraceae, and Trochodendraceae, I am able to confirm Hurusawa's proposal that *Daphniphyllum* be treated as an independent order, the Daphniphyllales, and also Hallier's proposal that the order be closely associated with the Hamamelidales.

I. INTRODUCTION

The genus *Daphniphyllum* consists of shrubs and trees widely distributed in eastern Asia and extending from New Guinea to India and north through central China to Japan. Sixty-five species have been described (cf. Index Kewensis, 1895-1955).

Mueller of Aargau (1869) completed the first monograph of *Daphniphyllum* and although the treatment was undoubtedly adequate for the time, it is insufficient for determining the many specimens which have been collected in the past one hundred years. He recognized 13 species on the basis of the following characteristics: calyx

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of pistillate flowers caducous versus persistent; anthers tetragonal and introrse vs. compressed and open; anthers laterally compressed vs. dorsally compressed; and drupes smooth vs. tuberculate.

The second monographic study of *Daphniphyllum* was completed by Rosenthal (1916, 1919). It, too, proves inadequate for Rosenthal was not able to examine a number of classic type collections and fifty years ago few specimens existed from several critical areas within the range of *Daphniphyllum*. However, she recognized 24 species on the basis of the following characteristics: petiole thick versus slender; leaves glaucous vs. brown; leaves papillate vs. epapillate; veins few vs. many; fruiting pedicels dilated vs. equally thickened at apex; calyx obscure vs. evolute; calyx persistent vs. caducous; calyx lobes free vs. campanulate; anthers laterally compressed vs. dorsally compressed; stamens glandulate vs. eglandulate; stigmas longer than ovary vs. shorter; stigmas persistent vs. caducous; stigmas circinate vs. revolute or recurved; drupes tuberculate vs. smooth; and staminodia on the ovary present vs. absent. In addition, several taxa recognized by Rosenthal (1916, 1919) were based on anther and inflorescence size, and anther shape. She considered all such characteristics as having equal significance in the classification of *Daphniphyllum*. Subsequently, new taxa have usually been described without an adequate knowledge of the genus as a whole and with only regional collections, and by and large taxonomists have followed without question the basis of classification outlined by Rosenthal.

For this study, 2,600 specimens from 22 major herbaria throughout the world have been examined including representatives of almost all type collections. Based on this material, I shall present a more complete treatment of *Daphniphyllum* than has been possible before and introduce a classification which in many ways is novel. Moreover, a comparative study of gross morphology, wood anatomy, chromosome complements, pollen morphology, and chemical components of the family Daphniphyllaceae in relation to the Buxaceae, Cercidiphyllaceae, Eucommiaceae, Euphorbiaceae, Eupteleaceae, Hamamelidaceae, Pittosporaceae, Stachyuraceae, and Trochodendraceae was completed in order to illucidate the taxonomic position and apparent affinities of the Daphniphyllaceae.

II. HISTORY

The genus *Daphniphyllum* was first described by Blume (1826) as a member of the Rhamnaceae, a treatment accepted by Meisner (1826) and Endlicher (1840). Wight (1852) placed *Gouphia neilgherrensis* (*Daphniphyllum neilgherrense* (Wight) Rosenth.) in the tribe Buxee of the Euphorbiaceae. Baillon (1858, 1874) removed the genus *Daphniphyllum* to the tribe Phyllanthee of the Euphorbiaceae and this association was followed subsequently by Bentham (1880), Hayata (1916), and Kanehira (1936).

Daphniphyllum has been known as *Gouphia* and *Gyrandra*. Not only was *Gyrandra* Lindl. published without a description but it also has been used in the Gentianaceae (Grisebach, 1845). *Gouphia* Wight is synonymous with *Daphniphyllum*.

Mueller (1869) first described the family Daphniphyllaceae. His treatment was neglected by most botanists until Rosenthal (1916) revived the familial classification. Mueller (1869) described the ovules of *Daphniphyllum* with external and apical microphytes which are similar to those reported for the Euphorbiaceae. The non-perigynous position of the stamens is similar to that known for the Buxaceae, and sections Caliciflorae and Illicineae of the Euphorbiaceae. However, *Daphniphyllum* differs from all genera of the Euphorbiaceae by having small apical embryos in the albumen and from the Buxaceae by having diverse microphytes. Rosenthal (1916) developed the premise that *Daphniphyllum* is closely related to the Euphorbiaceae and the Buxaceae. Since this time, most taxonomists have accepted *Daphniphyllum* as a family related to the Euphorbiaceae, but this association is questioned by many (Hallier, 1904; Croizat, 1941; Hurusawa, 1954; Hutchinson, 1959; Scholz, 1964).

The question of relationship of the Daphniphyllaceae with other families is perhaps best illustrated by the varying classification at the ordinal level. The family was placed by Diels (1936) and Scholz (1964) in the order Geraniales, which was divided into six suborders and 21 families. The suborder Tricoccae contained only two families, viz., the Daphniphyllaceae and Euphorbiaceae. Hallier (1904) placed this genus *Daphniphyllum* in the Daphniphyllaeen, a tribe of the Hamamelidaceae of the order Hamamelidales. His conclusion was based chiefly on wood anatomy, the rosette arrangements of leaves at the apex of branchlets, and the naked flowers. Hallier believed that *Daphniphyllum* represents an intermediate form between the Magnoliaceae and the Amentiferae. Croizat (1941) thought that the Daphniphyllaceae should be grouped in the Pittosporales. This idea is considered valid by Dr. R. F. Thorne (personal correspondence) who suggested that the Daphniphyllaceae might best be treated as the suborder Daphniphyllineae in the order Pittosporales. On the other hand, Hurusawa (1954) established a new order for *Daphniphyllum*, the Daphniphyllales, and in his classification he placed it near the Euphorbiales. Agreeing with Hallier (1904), Hutchinson (1959) placed the Daphniphyllaceae in the order Hamamelidales in association with the Buxaceae and the Stachyuraceae. However, Hutchinson proposed that the Daphniphyllaceae is closely allied to the Rosales rather than to the Magnoliaceae and that the family is intermediate between the Rosales and the Amentiferae.

III. MORPHOLOGY

HABIT:—*Daphniphyllum* includes small shrubs (Fig. 4, A-B) to large trees ranging from 1 to 20 m. high. The stems are more or less round, erect to decumbent or crooked, not particularly hard, and with diameters from 2 to 80 cm. in thickness.

The bark of the stem is smooth or fissured, grayish-brown, grayish-green or dark gray and frequently dotted with large, whitish spots resembling foliose lichens. The branches are terete, arising from below the middle of the stem, ascending, and branching dichotomously. The young apical parts of branchlets are usually longitudinally grooved, gray to brown, and with numerous oval to elliptic lenticels.

STEM:—The inner bark of the stem is brown, yellow or ochre. The wood is light yellow, relatively odorless or aromatic in *D. glaucescens* subsp. *sumatraense* Huang, subsp. nov.. The sap is white and bitter.

Transverse, radial, and tangential sections of stem (Fig. 1 and 2) have been studied. Permanent slides were prepared by the methods outlined by Johansen (1940) and Sass (1958).

Epidermal cells are rectangular, cutinized, and thick-walled. The cork is located subepidermally and is composed of elongate cells with thick walls. The phloem rays in the secondary phloem are uniseriate and the phloem fibers occur in distinct bundles. Clusters of crystals are distributed throughout these tissues. The wood is characterized by small vessels (tracheae), numerous solitary pores, rarely in pairs, scalariform perforation plated, and scalariform to opposite bordered intervacular pits. In cross sections of the vessels, the pores are rectangular, square to 5-7 sided, and either regular or irregular in shape. Fiber tracheids have bordered pits with paired slit-like inner apertures extending beyond the outline of the pit border. Wood parenchyma cells are apotracheal, diffuse, and very sparse, and are usually scattered among the fibers and often are in contact with the vessels. Wood rays are heterogeneous, and largely 1 to 2 or rarely 3 to 4 cells wide in a non-storied arrangement. The pith is septate, consisting of isodiametric and tubular parenchyma cells with abundantly clustered crystals. The walls of both ray and parenchyma cells have half bordered pits. Tanniniferous canals are spread throughout the parenchyma cells, fibers, and even the vessels.

The uniform characteristics observed in the wood of *Daphniphyllum* are the scalariform perforation plates, the bordered pits of the fiber tracheids having paired, long, inner apertures, the diffuse and sparse wood parenchyma cells, the heterogeneous rays, the septate and elongate pith, and the ramified tanniniferous canals with gum-like contents (chocolate color when stained with safranin) in the rays, wood parenchyma, fiber tracheids, and vessels.

Wood of representative species from each of three sections of *Daphniphyllum* (sections formulated on the basis of gross morphological data) were examined

Fig. 1. Wood of *D. gracile* Gage (A-C) and *D. himalaense* subsp. *macropodum* (Miq.) Huang (D-F) $\times 80$. **A** and **D**, radial sections showing tanniniferous canals, scalariform perforated plates, opposite bordered intervacular pits and heterogeneous rays; **B** and **E**, cross sections showing pores, diffuse, apotracheal, with prominent tanniniferous; and **C** and **F**, tangential sections, showing rays and prominent tanniniferous canals.

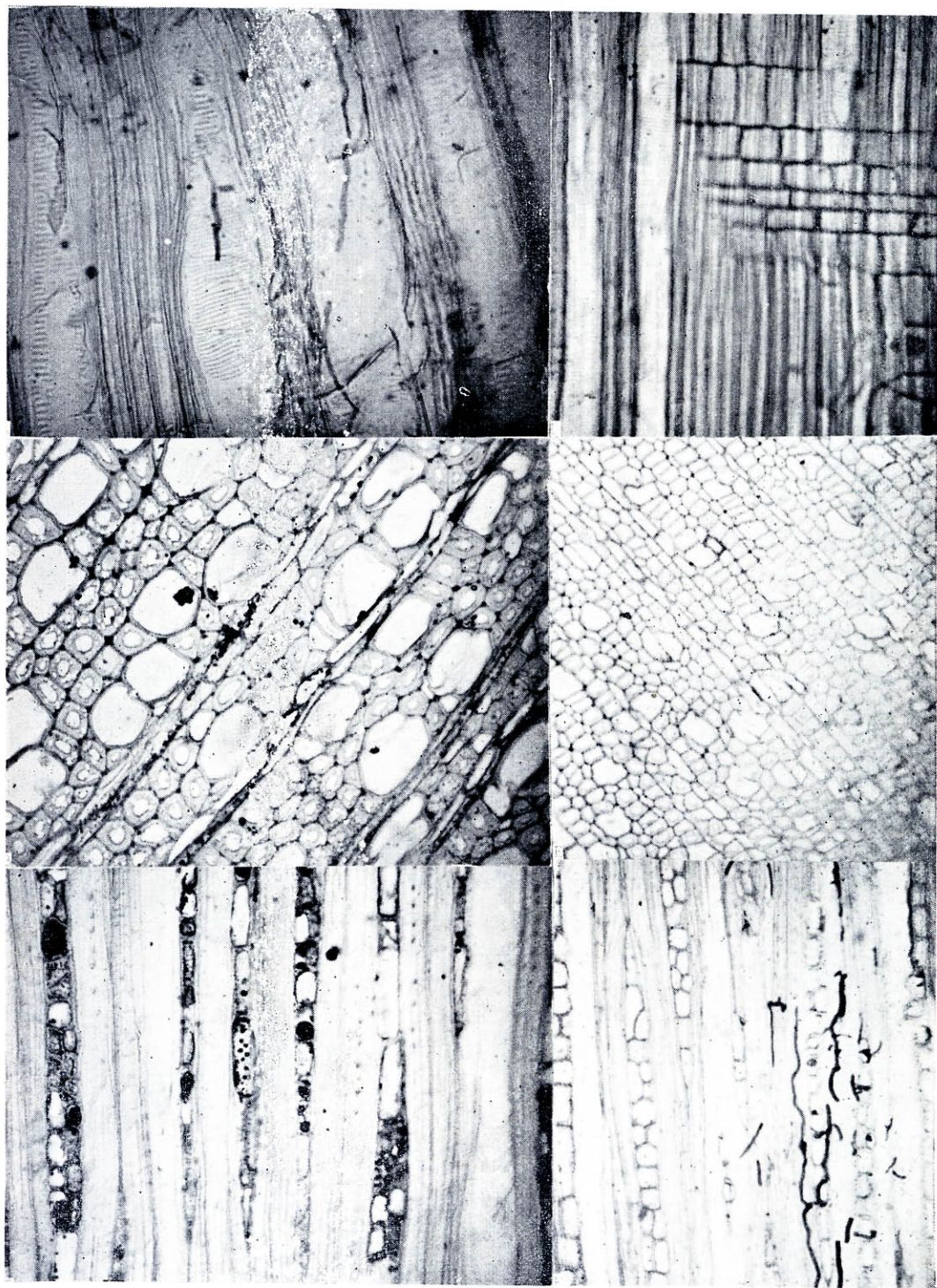


Fig. 1.

(Table 2). The wood for all species is similar, but it did separate into two groups according to ray characteristics. For members in the sections *Staminodia* and *Lunata* Huang, sect. nov., the rays, in tangential view, are characteristically long, slender, and uniseriate. Triseriate rays are rarely present. Members of the section *Calycifera* have biseriate and uniseriate rays which are shorter and thicker and the triseriate rays occur more frequently than in species of the other sections.

The wood of 10 morphologically or phylogenetically related families (Hallier, 1904; Croizat, 1941; Hutchinson, 1959), i. e., the *Buxaceae*, *Cercidiphyllaceae*, *Eucommiaceae*, *Euphorbiaceae*, *Eupteleaceae*, *Hamamelidaceae* (Fig. 2, D-F), *Pittosporaceae* (Fig. 2, G-I), *Platanaceae*, *Stachyuraceae*, and *Trochodendraceae* has also been studied either from prepared slides or by reference to Metcalfe and Chalk (1950). The results show that wood characteristics of *Daphniphyllum* species are more similar morphologically to those of the *Buxaceae* and *Hamamelidaceae* than to the other families noted by having in common scalariform perforation plates, paired bordered pits in the fiber tracheids, diffuse wood parenchyma, heterogeneous rays, clustered crystals, and tanniniferous canals. However, the wood of species of *Daphniphyllum* differs mainly from the wood of members of these two families by having scalariform piths. The wood of the other eight families is more or less clearly distinct from that of *Daphniphyllum* (Table. 1).

LEAVES:—Leaves of *Daphniphyllum* are simple. The phyllotaxy is alternate, rarely opposite, and fasciculate to subverticillate. The petioles are flat or triangular to quadrangular, frequently sulcate above, and either green or red. They are usually ascending, but rarely the petioles are reflexed in *D. himalaense* (Benth.) Muell.-Arg. var. *triangulatum* Huang, var. nov., *D. glaucescens* subsp. *teijsmannii* var. *hisautii* (Hurusawa) Huang, comb. nov.⁽¹⁾ and *D. calycinum* Benth. in part. The petiole length varies more in the section *Lunata* than in the other two sections. For example, in *D. calycinum* some petioles are markedly different in length on the same plant (0.2-2 to 2.5-6 cm. long), but usually the larger leaves have longer petioles, whereas those with short petioles have small blades giving an apparent dimorphism on the same organism. The shape of blades varies from narrowly elliptic to oblong and obovate to broadly obovate. The apex and the base vary from acuminate to acute and obtuse to mucronate or rotundate. The margins are usually entire. In addition,

(1) *D. teijsmannii* var. *hisautii* Hurusawa, Jour. Jap. Bot. 18: 265. 1942.

Fig. 2. Wood of *Daphniphyllum glaucescens* subsp. *oldhamii* (Hemsl.) Huang (A-C), *Hamamelis vernalis* Sarg. (D-F) and *Pittosporum tobira* Ait. (G-I) $\times 90$. A, D, G: radial sections showing scalariform perforation plates and bordered intervascular pits in A and D, and simple perforation plates and opposite bordered intervascular pits with tertiary thickening in G; B, E, H: cross sections; C, F, I: tangential sections showing presence of both uniseriate and biseriate rays and scalariform perforation plates in C, the presence of uniseriate rays and scalariform perforation plates in F, and the presence of both uniseriate and multiseriate rays, simple perforation plates, and tertiary thickening on intervascular walls in I.

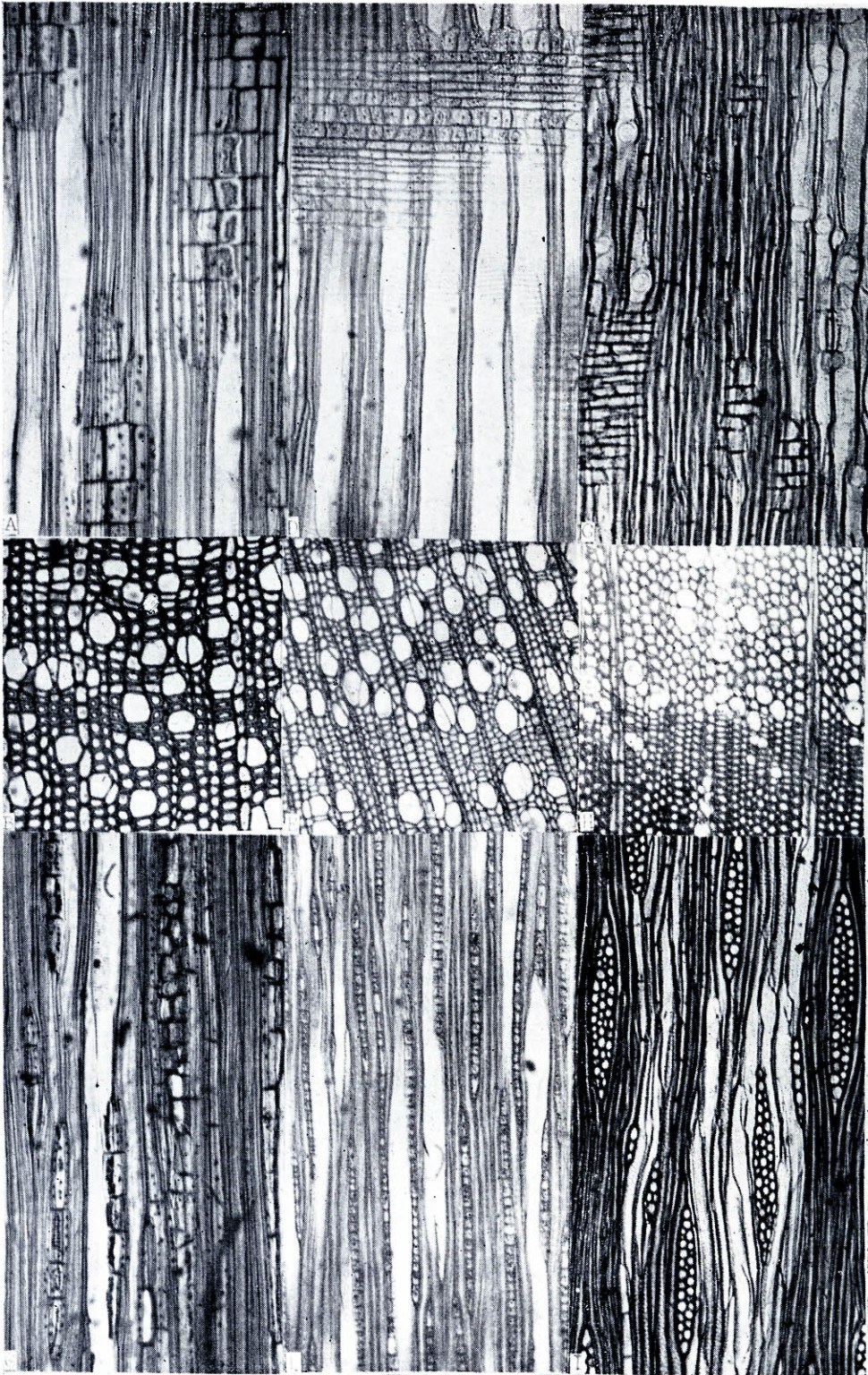


Fig. 2.

Table 1. Comparative study of the anatomical characteristics of the Daphniphyllaceae and its related 10 families. The following are the abbreviations for the respective families: B, Buxaceae; C, Cercidiphyllaceae; E, Eucommiaceae; Eh, Euphorbiaceae (cf. *Aporosa* group only); Et, Eupteleaceae; H, Hamamelidaceae; P, Pittosporaceae; Pl, Platanaceae; S, Stachyuraceae; and T, Trochodendraceae

Characteristics of the Daphniphyllaceae	Families with characteristics resembling the Daphniphyllaceae (*)	Families with characteristics differing from the Daphniphyllaceae (*)
A. Leaves		
1. papillous on the dorsal surface	C, Et	B, E, Eh, H, P, Pl, S, T
2. Stomata rubiaceous	H, P	B, C, E, Eh, Et, Pl, S, T
3. Crystals in cluster	B, C, Eh, Et, H, P, Pl, S, T	E, H, T
B. Vessels		
4. Pore solitary	B, C, E, Et, H, P, Pl, S	Eh, T
5. Perforation plates scalariform	B, C, Eh, Et, H, Pl, S	B, E, Eh, P, Pl, T
6. Intervascular pitting scalariform to opposite	B, C, Eh, Et, H, Pl, S	E, Eh, Et, P, Pl, T
7. Vessels without spiral thickening	B, Et, H, Pl	C, E, Eh, P, S, T
C. Wood parenchyma		
8. Sparse and diffuse	B, C, E, Eh, H, Pl, S, T	Eh, Et, P, Pl
9. Apotracheal	B, H, Pl, S, T	C, E, Eh, Et, P
D. Ray parenchyma		
10. 1- cell wide	B, C, H, T	B, E, Eh, Et, H, P, Pl, S, T
11. Heterogeneous	B, C, Eh, Et, H, S, T	E, P, Pl
E. Pith		
12. Scalariform	absent	10 families
F. Secretory element		
13. Tanniniferous canals	B?, Eh, Et, H, P, Pl?, T	C, E
14. Laticiferous canals absent	B, C, Et, H, P, Pl, S, T	E, Eh

* According to Metcalfe and Chalk (1950).

Table 2. Wood specimens of *Daphniphyllum*, *Pittosporum*, and *Hamamelis* examined. Wood collections (cf. Stern and Chambers, 1960): Smithsonian Institution (USw), Yale University, School of Forestry (Yw), Division of Forest Products, CSIRO (DFP) and Missouri Botanical Garden (MOw). Herbaria: Missouri Botanical Garden (MO), Harvard University, Arnold Arboretum (A) and C. S. I. R. O. Herbarium (CANB).

Taxa examined	Collector and number	Country of Origin	Wood Collection Catalog Number	Location of Vouchers
<i>D. calycinum</i>	How 71894	China	—	A
<i>D. himalaense</i> subsp. <i>macropodum</i>	Tang 0131	China	Yw 21743	—
	Kao 4203	Taiwan	MOw	MO
	Yu s. n.	Taiwan	MOw	MO
	Liao s. n.	Taiwan	MOw	MO
<i>D. gracile</i>	HGI. 5484	New Guinea	DFP	CANB
	NGF. 6781	New Guinea	DFP	CANB
<i>D. glaucescens</i> subsp. <i>oldhamii</i>	Prof. Kishima	*	DFP 17322	—
	Tang 0516	China	Yw 29843	—
	Tang 0546	China	Yw 22013	—
	Kanehira s. n.	Taiwan	Yw 6477	—
	Huang 2313	Taiwan	MOw	MO
	s. coll.	Taiwan	USw 24570	—
	Fukioka 141	Japan	Yw 29843	—
	Yamabayasi 63	Korea	Yw 16886	—
	Ex Government Forest Station	Japan	DFP 13212	—
	s. coll.	Japan	USw 24570	—
var. <i>iriomotense</i>	s. coll.	Japan	USw 14115	—
<i>D. sp.</i>	Chung sp.	China	Yw 7690	—
<i>P. Pentandrum</i>	Huang 2264	Taiwan	MOw	MO
<i>P. tobira</i>	Huang 2281	Taiwan	MOw	MO
<i>P. illicinoides</i>	Chen s. n.	Taiwan	MOw	MO
<i>H. vernalis</i>	Huang s. n.	U. S. A.	MOw	MO

* The binomial name is in question, since the origin of wood is unknown.

a few collections of *D. glaucescens* subsp. *oldhamii* (Hemsl.) Huang, stat. nov.⁽¹⁾ and subsp. *luzonense* (Elmer) Huang, stat. nov.⁽²⁾ have several lobes near the apex of

(1) *D. glaucescens* var. *oldhamii* Hemsl., Jour. Linn. Soc. 26: 429. 1894.

(2) *D. luzonense* Elmer, Leaf. Philip. Bot. 1: 309. 1908.

the blades which is a common character found in the leaves of the seedling. The texture of leaves varies from chartaceous, firmly chartaceous to coriaceous and they are glabrous and green on both surfaces or glaucous abaxially. The venation is pinnate with usually prominent secondary veinlets on both surfaces, but for a few members of the section *Staminodia*, the veins are impressed on the adaxial surface and for those in the section *Calycifera*, the veins are obviously reticulated, excepting *D. glaucescens* subsp. *scortechinii* (Hooker) Huang, stat. nov.⁽¹⁾. Leaves tend to have a certain dominant morphology according to geographical distribution, yet exceptions very often exist.

The combination of leaf morphology with either staminate flowers or with drupes frequently is of little value in determining species. However, *D. woodsonianum* Huang, sp. nov. and *D. parvifolium* Merr. can be distinguished by their petiole lengths, and leaf sizes and shapes in combination with geographical data.

Some leaves were cleared in 5% NaOH and stained with safranin. Stomata are paracytic (Fig. 3) and are confined to the abaxial surface of the blade in *D. calycinum* (McClure 147.4377), *D. himalaense* subsp. *angustifolium* (Hutch.) Huang, stat. nov.⁽²⁾ (Wilson 3552), subsp. *macropodum* (Kao 4203), subsp. *himalaense* var. *longeracemosum* (Rosenth.) Huang, stat. nov.⁽³⁾ (Henry 9657), *D. glaucescens* subsp. *oldhamii* (Huang 2401), and *D. gracile* Gage (Pullen 300). The size of subsidiary cells is variable, but in *D. gracile* (Pullen 300), they are almost the same size as the guard cells.

Blades were studied by transections of leaves from *D. himalaense* subsp. *angustifolium* (Fang 958), subsp. *macropodum* (Miq.) Huang, stat. nov.⁽⁴⁾ (Chuang 13), *D. calycinum* (Seemann 2448), *D. gracile* (Pullen 300), and *D. glaucescens* subsp. *oldhamii* (Huang 2307, 2403).

Based on a blue-green color reaction of blade sections placed in 10% aqueous ferric chloride and a small amount of Na_2CO_3 (Johansen, 1940), tanniniferous canals were abundant in all tissues of the blade being especially concentrated on the abaxial surfaces in *D. glaucescens* subsp. *oldhamii*, *D. himalaense* subsp. *angustifolium*, *D. calycinum*, and *D. gracile* (Fig. 4, D). Cluster crystals were found scattered among all cells of the blade, but these were more concentrated around cells adjacent to the vascular tissue.

The blade is typically dorsiventral. The epidermis is cutinized and consists of one layer of cells in *D. glaucescens* subsp. *oldhamii*, *D. himalaense* subsp. *macropodum*, and *D. calycinum*, and of two layers of cells in *D. gracile* and *D. himalaense* subsp. *angustifolium* on the adaxial surface and of one layer of cells for *D. himalaense* subsp. *angustifolium* and of 4-5 layers of cells for *D. gracile* on the abaxial surface. Papillose

(1) *D. scortechinii* Hooker, Fl. Brit. Ind. 5: 254. 1887.

(2) *D. angustifolium* Hutch. in Sarg., Pl. Wils. 2: 521. 1916.

(3) *D. longeracemosum* Rosenth. in Engl., Pflanzenreich 68 (IV. 147a): 14. 1919.

(4) *D. macropodum* Miq., Ann. Mus. Bot. Lugd. Bat. 3: 129. 1867.

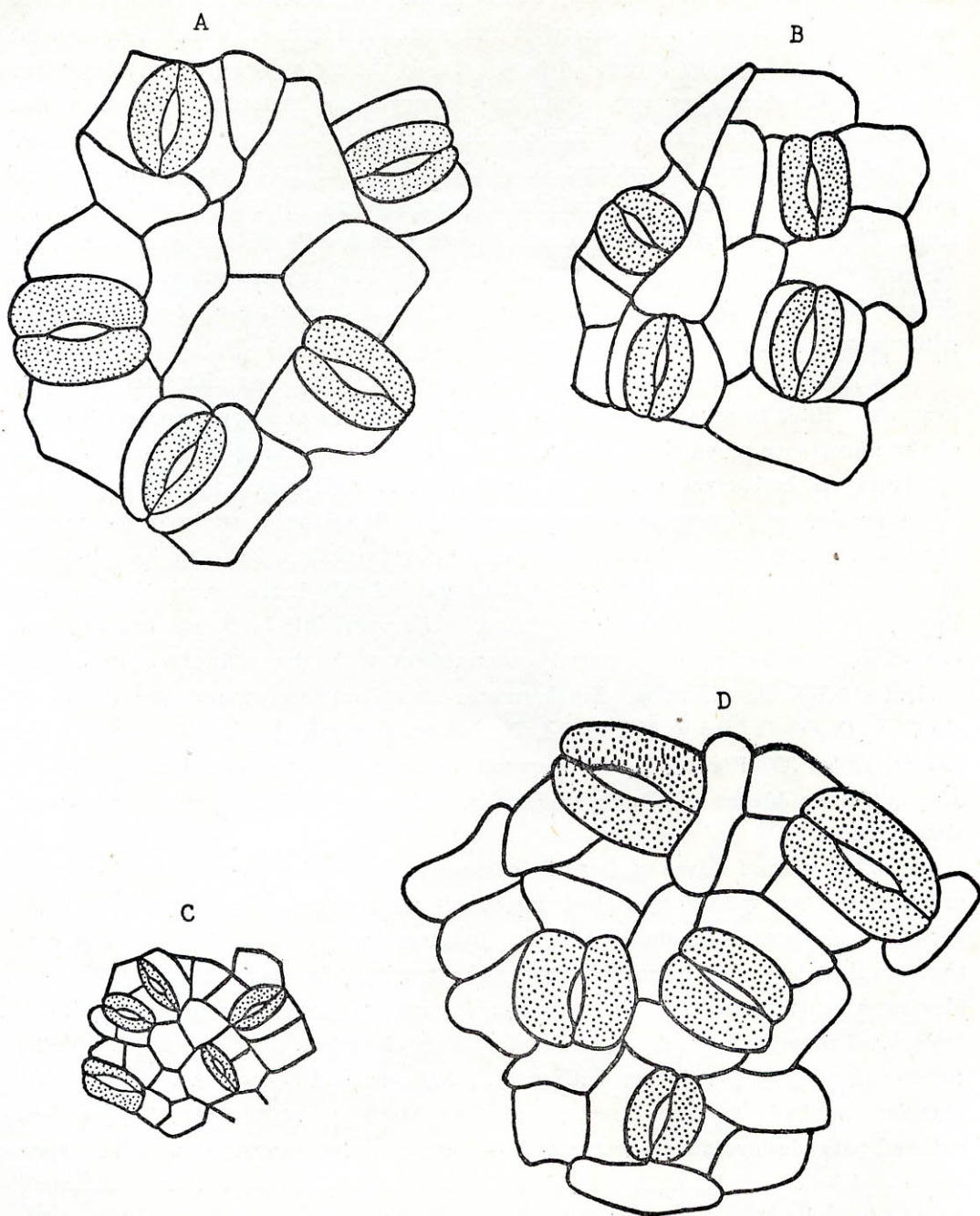


Fig. 3. Epidermal structure of leaves of *Daphniphyllum* showing the paracytic type of stomata on the adaxial face of leaves. **A:** *D. calycinum* Benth. (McClure 147, 4377); **B:** *D. glaucescens* subsp. *oldhamii* (Hemsl.) Huang (Huang 2301); **C:** *D. gracile* Gage (Pullen 300); and **D:** *D. himalaense* subsp. *macropodium* (Miq.) Huang (Kao 4203).

(called by Rosenthal, 1916) are very abundant and prominent on the lower epidermis and the mesophyll tissues are mesophytic in nature being usually well differentiated into palisade and spongy layers. An exception is the mesophyll of *D. gracile* (Pullen 300, Fig. 4, C.) which has very small and compact, isodiametric or quadrangular cells consisting of two layers of palisade tissues and several layers of poorly differentiated spongy tissue. In contrast, *D. calycinum* has one layer of poorly differentiated palisade tissue with large round cells and 3 to 4 layers of well differentiated spongy tissue. *Daphniphyllum glaucescens* subsp. *oldhamii*, *D. gracile* (Robins 425, Fig. 4, D) *D. himalaense* subsp. *macropodum* (Chuang 13), and *D. himalaense* subsp. *angustifolium* (Fig. 4, E) have well differentiated mesophyll tissues consisting of 2(-3) layers of palisade cells and 4 to 8 layers of spongy tissue.

The presence or absence of papillae on blades was the key character used by Rosenthal (1916) to separate species of *Daphniphyllum* into two large groups. Because of the importance given this character by Rosenthal and others, free-hand sections of blades and herbarium material of leaves were carefully examined.

A number of observations are noteworthy. Based on a study of herbarium specimens, young leaves of some specimens of *Daphniphyllum* lack papillae while the abaxial surface of mature leaves from the same individuals are covered by papillae. Even more striking is the fact that papillae, while not visible in *D. himalaense* subsp. *angustifolium* in herbarium material examined at 20 X magnification, are clearly evident at 160 X magnification. Furthermore, one collection of a species may possess papillae (*D. gracile*, Robins 425, Fig. 4, D). but another may be devoid of them (*D. gracile*, Pullen 300, Fig. 4, C). These results suggest that the presence or absence of papillae on blades of *Daphniphyllum* is not a worthwhile generic or specific character.

Whether mature leaves of *Daphniphyllum* are papillose or epapillose and whether or not they have well-differentiated mesophyll tissues, probably depends on their geographical distribution and/or habitat. Judging from collectors' notes it appears that papillose leaves with well-differentiated mesophyll are most abundant at low elevations in open forests and in grasslands; that epapillose leaves with well-differentiated mesophyll are most abundant at high elevations (ca. 1,000 m.) in shaded forests; that epapillose leaves with poorly differentiated spongy layers are most abundant in shady tropical forests; and that papillose leaves with poorly differentiated palisade layers often occur at low elevations on sunny, open hills. Such

Fig. 4. A-B, habit of *D. glaucescens* subsp. *oldhamii* (Hemsl.) Huang in Taiwan; C-D, transections of blades of *D. gracile* Gage showing epapillate leaves with a impressed vein, C, (Pullen 300, microtoming sections), $\times 70$ and a papillate leaf, D, (Robins 425, freehand section), $\times 160$; E, microtoming section of blade of *D. himalaense* subsp. *angustifolium* (Hutch.) Huang showing a papillate leaf, $\times 160$; F, microtoming section of *D. glaucescens* subsp. *oldhamii* (Hemsl.) Huang showing a papillate leaf (Huang 2403), $\times 70$; and G, an abaxial surface of blade of *D. gracile* (Robins 425) showing tanniferous canals.

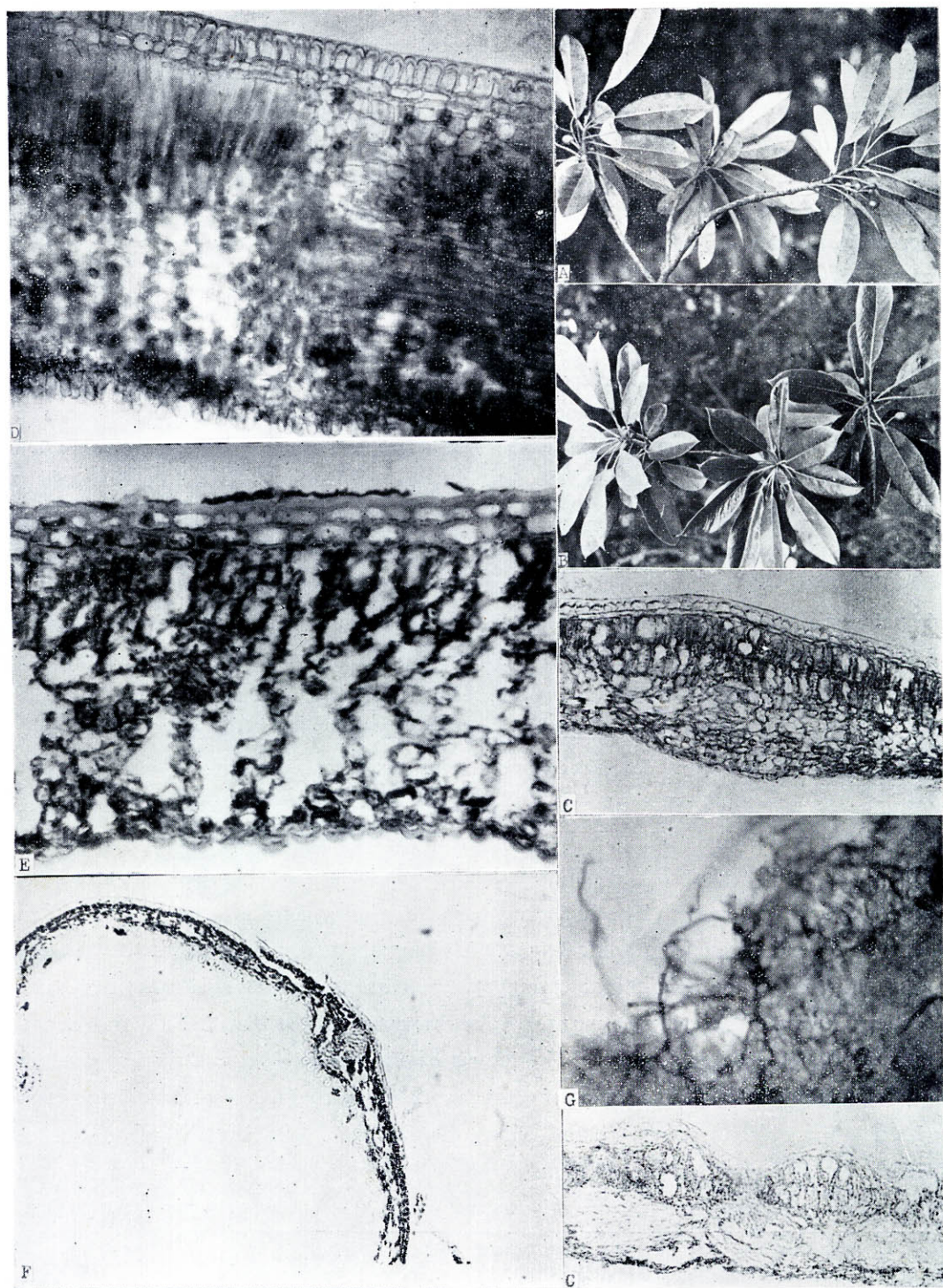


Fig. 4.

characteristics of leaves may be due to the adaptation of the plants to these various environmental conditions. Only in the section Calycifera has the character of papillose or epapillose leaves been used taxonomically and then only at the rank of subspecies and variety.

INFLORESCENCE:—The inflorescence of *Daphniphyllum* is glabrous, simple, racemiform, and axillary or subterminal in position. The upper part is usually modified into an umbel-like or aggregated corymb-like arrangement. Thus, the inflorescence of *Daphniphyllum* is not a scorpioid cyme, a condition which is frequently confused with the raceme. Several persistent, imbricate bracts in 1-3 whorls are found at the base of the inflorescence. Moreover, at the base of each pedicel, there is a caducous bract which varies in size and shape and this may be of diagnostic value. The sizes of the racemes and the pedicels vary greatly and these do not provide definite criteria for specific distinction. There is, however, a range of value in raceme and pedicel size which tends to separate infraspecific taxa in limited areas only. Rosenthal (1916) separated *D. longeracemosum* Rosenth. from *D. chartaceum* Rosenth. and *D. bengalense* Rosenth. solely on this basis, but such a separation on limited quantitative data showing no discontinuity is unsound.

FLOWER:—The flower in *Daphniphyllum* is more or less actinomorphic, unisexual; hypogynous, and pedicellate, the species are dioecious, rarely polygamodioecious. Pistillodes are frequently observed in *D. laurinum* (Benth.) Baill., *D. himalaense* subsp. *macropodum*, *D. gracile*, and *D. glaucescens* subsp. *oldhamii*. Floral parts and pedicels are glabrous. The flower is small, ranging from 1 to 5 mm. long and 1 to 4 mm. wide. Flower colors are described by collectors as white, gray-green, olive, white-orange, cream-white, yellowish-green, pink, and deep purple for staminate flowers, and green, white, and pinkish-brown for pistillate flowers. *Daphniphyllum glaucescens* subsp. *paxianum* (Rosenth.) Huang, stat. nov.⁽¹⁾ from China has been reported as having fragrant flowers. The blooming period for all species is from February to August depending on geographical location. The size of compact staminate flowers is often striking and this character may be used in interspecific delimitation in the section Lunata. The compact nature is also important for distinguishing the section Lunata from the other sections. The length of the pedicel is a useful character in distinguishing infraspecific taxa of *D. glaucescens*, namely, subsp. *subverticillatum* (Merr.) Huang, stat. nov.⁽²⁾ from subsp. *teijsmannii* (Zoll. ex Teysm. & Binn.) Huang, stat. nov.⁽³⁾ and subsp. *lancifolium* (Hook. f.) Huang, stat. nov.⁽⁴⁾ and subsp. *sumatraense* from subsp. *glaucescens*, and subsp. *sumatraense* from subsp.

(1) *D. paxianum* Rosenth. in Engl., Pflanzenreich 68 (IV. 147a): 13. 1919

(2) *D. subverticillatum* Merr., Ling. Sci. Jour. 13: 34. 1934

(3) *D. teijsmannii* Zoll. ex Teysm. & Binn., Natur. Tijdschr. Nederl. Ind. 27: 52. 1864

(4) *D. lancifolium* Hook. f., Fl. Brit. Ind. 5: 354. 1887

glaucescens, and subsp. *dichotomum* Huang, nom. & stat. nov.⁽¹⁾ from subsp. *borneense* (Stapf) Huang, stat. nov.⁽²⁾.

Calyx:—The calyx is chorisepalous consisting of 3-6 sepals or gamosepalous with (3-) 4-5(-6) lobes, imbricate and uniseriate in one whorl. The gamosepalous calyx may be disciform or campanulate depending on the degree of division and the length of the lobe. The lobes are narrowly to broadly ovate or narrowly to broadly oblong, unequal in size, and glabrous; the apex may be acute, obtuse or acuminate and the margin may be entire to serrulate, but usually serrulate just below the apex. The calyx normally arises at the insertion of the stamens, but in two subspecies, *D. glaucescens* subsp. *borneense* and subsp. *glaucescens*, it may arise from the fused base of the filaments which forms an androgonophore. The size of the calyx lobes, especially in staminate flowers, provide a useful interspecific and infraspecific character. For example, *D. glaucescens* and its infraspecific taxa can be separated from *D. gracile* by their short and persistent calyces. This character is also valuable in distinguishing taxa in the section Lunata. A separation of species solely on the serrated margin of calyx lobes is inadequate, however, for I have found different serrated margins among the lobes of a single individual for most species in the genus. This treatment was applied by Hurusawa (1942) to separate *D. teijsmanni* var. *okinawense* Hurusawa from var. *teijsmanni*.

A persistent calyx is typical of taxa in the section Lunata excepting *D. majus* var. *deciduum* Huang, var. nov.. Those in the section Calycifera usually have persistent calyx lobes in their staminate flowers, but the calyx lobes of *D. gracile* and *D. glaucescens* may also be caducous. They are frequently persistent in the pistillate flowers. I have found that the persistent or caducous nature of the calyx lobes cannot be used in distinguishing species. In *D. gracile* and often in *D. glaucescens*, the calyx scars are so prominent that they were mistaken for glands by Gage (1917); but two species found in the subsection Ucalycifera Huang subsect. nov., *D. woodsonianum* and *D. philippinense* Huang, sp. nov. lack calyces on the staminate flowers, but these are found in the pistillate flowers. Occasionally, however, *D. himalaense* subsp. *himalaense* var. *chartaceum* (Rosenth.) Huang, stat. nov.⁽³⁾ and subsp. *macro-podum* can be distinguished from *D. glaucescens* subsp. *paxianum* and subsp. *oldhamii* only by the absence of a calyx; otherwise taxa are very similar morphologically. On the basis of the above observations, I regard the sections Staminodia and Calycifera as unnatural sections, for, in my opinion, some morphologically closely related taxa have been separated by one prominent character, namely, the presence or absence of a calyx.

Stamens:—Staminate flowers consist of from 5 to 14 stamens, which most fre-

(1) *D. reticulatum* Heine, Rep. Spec. Nov. 54: 232. 1951

(2) *D. borneense* Stapf, Trans. Linn. Soc., Ser. 2. 4: 224. 1894

(3) *D. chartaceum* Rosenth. in Engl., Pflanzenreich 68 (IV. 147a): 8. 1919

quently are arranged radially. Rarely stamens are arranged on an elongated base (Fig. 30, F). The filaments are free, but one collection of *D. glaucescens* subsp. *luzonense* (Fig. 30, E) from the Philippines has coherent filaments. Length of filaments vary from 0.05 to 2.3 mm. In the section *Lunata*, the filament is always less than 0.5 mm. in length, while in the sections *Calycifera* and *Staminodia*, it is usually more than 0.5 mm. long. Shapes of anther apices vary from beaked, triangular, apiculate, obtuse to emarginate. Members of the section *Lunata* possess triangular, lunate anthers with beaked apices, while those in the section *Calycifera* and *Staminodia* possess elliptic to ovate anthers with obtuse, apiculate or emarginate apices. Triangular apices are also known in *D. himalaense* var. *himalaense*. and the var. *triangulatum*, *D. gracile* and *D. glaucescens*. The persistent or caducous nature of the apex varies with the individual and, furthermore, any taxon in the sections *Staminodia* and *Calycifera* may have a combination of anther shapes. Thus, I find that the anther is of little taxonomic value at the species level in *Daphniophyllum*. The size of anthers varies from 0.5 to 5 mm. long and 0.5 to 2 mm. wide. I find the separation of *D. bengalense* and *D. chartaceum* from *D. himalaense* by Rosenthal (1919) based mainly on the size of anthers acceptable only at the varietal level. *Staminodia* in staminate flowers occur occasionally in most taxa. Usually the stamens of *Daphniophyllum* mature as do the simplices of the *Osmundaceae*, but for some reason, some stamens develop in a manner resembling the mixtae of the *Polypodiaceae*. Such undeveloped anthers have been mistaken for glands by Hayata (1911), Rosenthal (1919), and others. Since I have observed both types of anther development in the same specimen of many taxa, *D. pentandrum* which as separated from *D. glaucescens* var. *oldhamii* on this basis is treated as a synonym of *D. glaucescens* subsp. *oldhamii*. The stamens have been reported by collectors as reddish-purple and greenish-yellow in color. Cruciform and hexagonal raphides are abundant in the anthers.

Pistil:—The pistil is 2(–3–4)–carpellate. The ovary is subglobose or ovoidal, superior, smooth, green, and glaucous, with the apex narrowing into a style. Rarely does the ovary have a short basal stalk. The ovary is one celled or with 2(–3–4) incompletely septate cells (Fig. 5). Each cell has two ovules which are usually born in the uppermost angle formed by the peripheral ovary wall and septum. Thus the placentation is parietal and subapical. The ovule is pendulous and anatropous (Fig. 5, C–Co). The number of styles is correlated with the number of carpels. Each style is generally bistigmatic, the lobes being erect, divaricate, revolute, circinate, versatile or radiate. The styles are very short in members of the section *Lunata* and in *D. himalaense* subsp. *angustifolium*. Some of these are discoid as result of the fusion of the upper style parts. Normally the styles are derived from

Fig. 5. Structure of the ovaries of *Daphniophyllum*. **A–A₀**: showing septum on the upper part of an incomplete bicarpellary ovary; **B–B₀**: showing the cross section of the incomplete bicarpellary ovary; and **C–C₀**: showing an anatropous ovule.

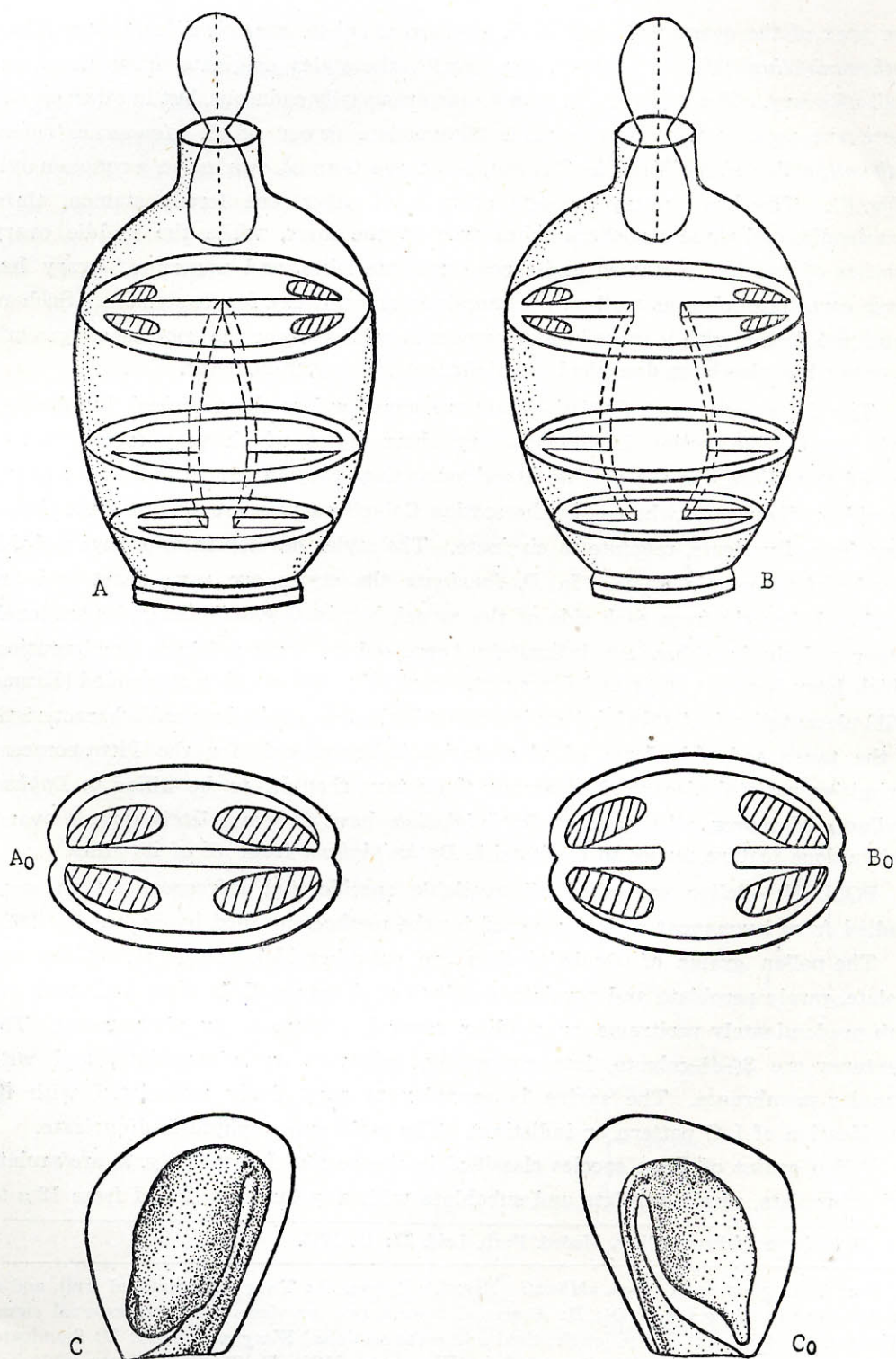


Fig. 5.

the apex of the ovary wall, but in *D. glaucescens* subsp. *scortechinii* and the subsp. *buchananiiifolium* (Hallier) Huang, stat. nov.⁽¹⁾, the styles originate from the inner wall of ovary. The styles in *D. glaucescens* are usually caducous, but in other species these are persistent. One abnormal tricarpellate flower of *D. glaucescens* subsp. *oldhamii*, collected by Wang in Taiwan, has three tiers of ovaries on a common axis (Fig. 6). The basal ovary consists of a basal calyx, one fertile stamen, three staminodia, and three carpellate lobes free at the apex, while the middle ovary consists of one fertile stamen and three carpellate lobes, and uppermost ovary has three carpellate lobes as well as one staminodium and two fertile stamens. Such an abnormal flower with a spike-like inflorescence arising from the continuous growth of ovary has also been described for *Arisaema* (Huang, 1960, 1962).

The three sections of *Daphniphyllum* are more or less characterized by distinct style types. The section *Lunata* has very short styles which vary from erect or discoid to radiate. In the section *Staminodia*, they vary in length and are radiate, discoid or divaricate, whereas in the section *Calycifera* they are long and the shapes vary from divaricate, revolute to circinate. The styles develop in two ways and this may be of taxonomic value. In *D. laurinum* the styles are very short and are developed directly from each side of the carpel, but in *D. gracile* the styles are much longer and the branches are intimately appressed to form a falcate configuration, which later becomes erect and divergent. Parietal to subapical or suspended (Eames, 1961) placentation in *Daphniphyllum* is a most distinctive (and advanced) characteristic of the taxon and this form of placentation is known only for the Pittosporaceae (primitive parietal placentation) among those taxa thought to be allied to *Daphniphyllum*. Moreover, all species of *Daphniphyllum* have an incompletely septate ovary. This unique feature serves to distinguish *Daphniphyllum* from all of its allies.

POLLEN:—Pollen grains of all available specific and infraspecific taxa were studied from permanent slides prepared by the method outlined by Erdtman (1952).

The pollen grains of *Daphniphyllum* are subspheroidal, frequently oblate and prolate, rarely peroblate and perolate, small to medium-small in size, and with an amb predominately peritreme or tending toward gonotreme or pleurotreme. The apertures are 3(–4)–colpate, less commonly, colporate or colpoidate, and with granular membranes. The sexine is granular to very finely reticulated with its stratification of L-O pattern or indistinct. The male gametophyte is dinucleate.

Pollen grains of those species classified in the section *Lunata* (Fig. 7) are prolate and subprolate, rarely perolate and suboblate with a polar axis (P) of from 12 μ to

(1) *D. buchananiiifolium* Hallier, Meded. Herb. Leid. 37: 13. 1918.

Fig. 6. *D. glaucescens* subsp. *oldhamii* (Hemsl.) Huang. A: Twig with matured fruit, and a fertile stamen (Wang s. n., MO); B: Abnormal flowers, two top views and three external views (Wang, s. n., MO); C: Ovary, longitudinal and cross sections (Wang s. n., MO); D: Staminate flower, stamen and anther in cross section (Wang s. n., MO); E: Staminate flower with staminodia (Wang s. n., MO); and F: Staminate flower with staminodia (Huang 2301, MO).

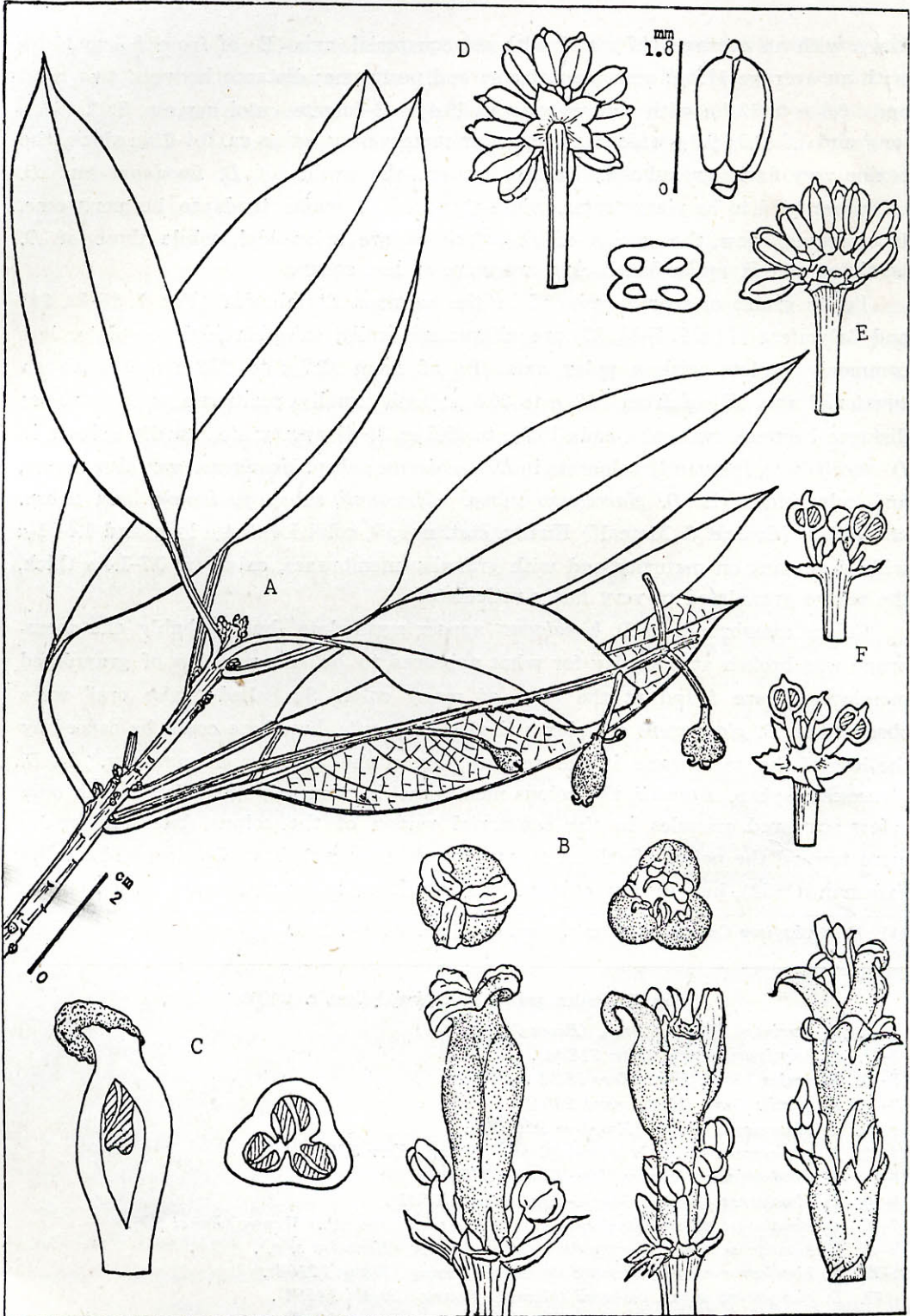


Fig. 6.

21.4 μ with an average 14.7 μ and with an equatorial axis (E) of from 8 μ to 16.1 μ with an average 11.9 μ ; amb pleurotreme and peritreme; distance between two colpi ends 6.6 μ to 13.4 μ with an average of 13.4 μ ; 3-colpate, colpi narrow, 8(12)16.1 μ long and 1.3 (3.2) 9.3 μ wide with granular membranes; exine ca. 0.4–0.9 μ thick, the sexine very finely granulated. In this section, the grains of *D. laurinum* and *D. calycinum* tend to be pleurotreme, while those of *D. majus* tends to be peritreme. In equatorial view, the grains of *D. calycinum* are spheroidal, while those of *D. laurinum* and *D. majus* Muell.-Arg are more or less square.

Pollen grains of species grouped in the sections *Staminodia* (Fig. 7, 15–22, 24) and *Calycifera* (Fig. 7, 7–14, 23) are characteristically subspheroidal to oblate, less commonly prolate with a polar axis (P) of from 10.7 μ to 25.7 μ and with an equatorial axis (E) of from 10.7 μ to 26.8 μ ; amb usually peritreme or gonotreme; distance between two colpi ends 10.7 μ to 29.5 μ ; 3(–4) aperturate, usually colpate in *D. parvifolium*, frequently colpate in *D. himalaense* subsp. *himalaense* var. *chartaceum*, and colpoidate in *D. glaucescens* subsp. *teijsmannii*, subsp. *paxianum*, and subsp. *atrabadium* (Croizat & Metcalf) Huang, stat. nov.⁽¹⁾, colpi 1.4–21.4 μ long and 1.4–11 μ wide depending on maturity and with granular membranes, exine ca. 0.7–1.4 μ thick, the sexine granulated to very finely reticulated.

Colpus membranes in *D. himalaense* appear egranulate, but probably the membrane was broken at maturity for what appeared to be the remains of granulated membranes were found at the edge of many colpi. So called "false ora" were observed in *D. glaucescens* complex and also *D. gracile*, but these could be caused by the loss of the membrane in the central part of the aperture at maturity. In *D. glaucescens* subsp. *oldhamii*, the colpus membrane is variously granulated with only a few scattered granules in the equatorial region of the colpus, but with many more toward the poles. Such an aperture was interpreted as 3-colpor(oid)ate by Erdtman (1952), but in my opinion this condition is not associated with complex

(1) *D. atrabadium* Croizat & Metcalf, Ling. Sci. Jour. 20: 108. 1941.

Fig. 7. Pollen grains of *Daphniphyllum*, c. $\times 1300$

- 1–2. *D. laurinum* (Benth.) Baill. (Baeea 7669).
- 3–4. *D. calycinum* Benth. (How 71894).
- 5–6. *D. majus* Muell.-Arg. (Kerr 1824).
- 7–8. *D. gracile* Gage (Kostermans 2184).
- 9–10. *D. glaucescens* Blume (Koorders 39027 β).
- 11–12. *D. glaucescens* subsp. *beddomei* (Craib) Huang (Kerr 3101).
- 13–14. *D. woodsonianum* Huang (Van Steenis 8654).
- 15–16. *D. himalaense* (Benth.) Muell.-Arg. (Biswas 6641).
- 17–18. *D. himalaense* subsp. *himalaense* var. *chartaceum* (Rosenth.) Huang (Rawat 99).
- 19–20. *D. himalaense* subsp. *macropodium* (Miq.) Huang (Kanehira s. n.).
- 21–22. *D. himalaense* subsp. *macropodium* (Miq.) Huang (Wang 12104).
23. *D. glaucescens* subsp. *oldhamii* (Hemsl.) Huang (Sasaki 14591).
24. *D. himalaense* subsp. *himalaense* var. *chartaceum* (Rosenth.) Huang (Stainton, Sykes & Williams 2500).

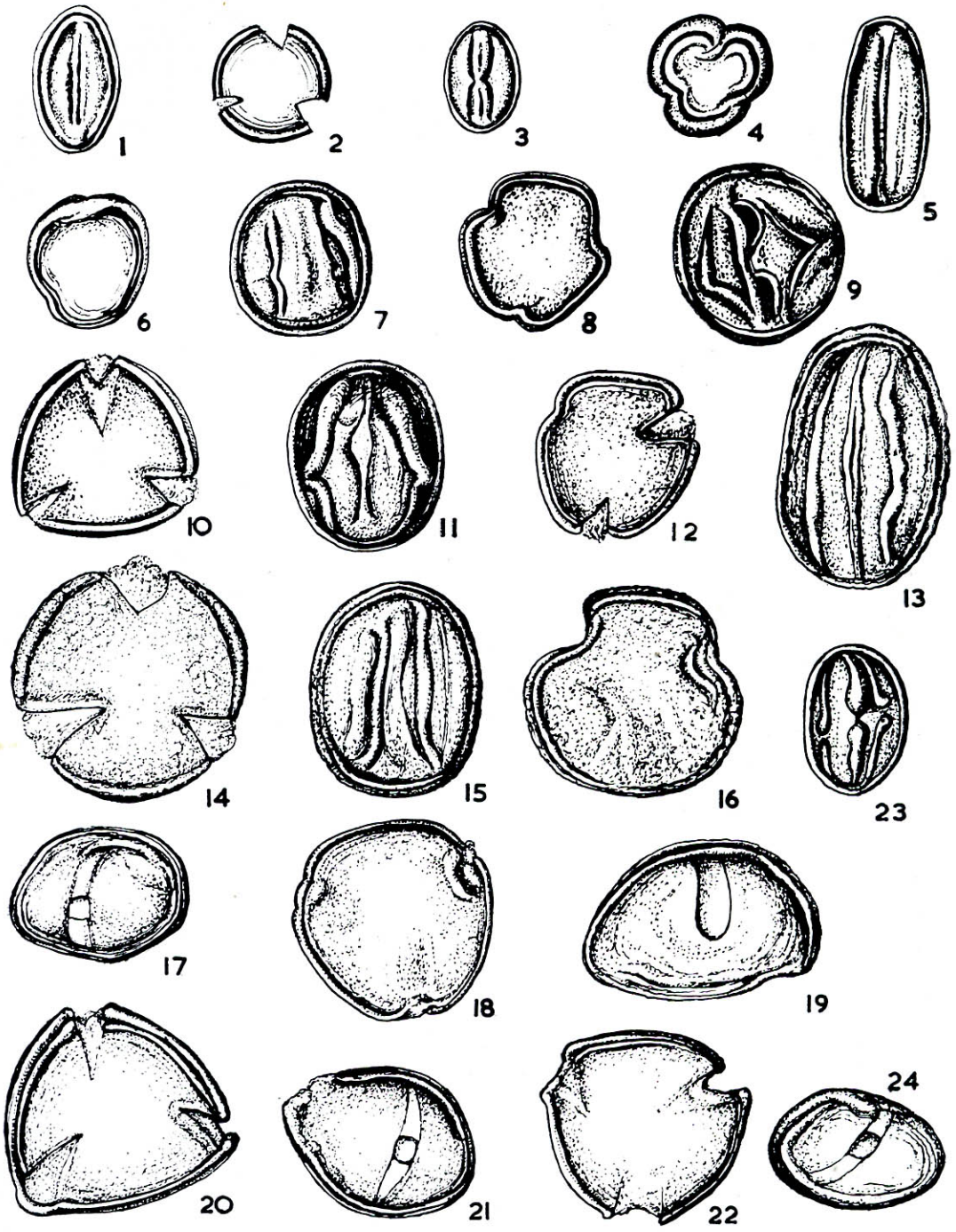


Fig. 7.

Table 3. Pollen collections and their morphology of *Daphniphyllum*

Species (#)	Collectors and Numbers	Locality	Vouchers	P(*) × 2.5 μ	E(*) × 2.5 μ	P/E	Aperture	Arm types
1(†)	Boesa 7381, 7669 Clemens 26822 Griffithi s. n.	Sumatra Borneo Malacca	A A GH	4.5(5.3)5.5	3(3.9)5	prolate subprolate 40%	3-colpate	pleurotreme
2(†)	How 71894 Hu s. n. Poilane 21927 Tsang 22143	Hainan Kiangsi Vietnam Kwangtung	A A UC A	5(5.3)6	3.5(5)6	prolate subprolate suboblate 20%	3-colpate	Pleurotreme (peritreme)
3a(†)	Kerr 1824, 3592	Siam	K	5.5(6.7)8	3(4.2)5.5	perolate prolate subprolate 20%	3-colpate	peritreme (Pleurotreme)
3c	Hance 19067 Pététot 4683 Pierre s. n.	Siam Indochina Kreyeh	BM NY E	4.5(4.8)5	3.5(4.4)5	subprolate suboblate 10%	3-colpate	peritreme (pleurotreme)
4	Brass 30190 Eyma 2040 (**) Hoagland & Pullen 5521 Kostermans 2184 Robins 425	New Guinea New Guinea New Guinea New Guinea New Guinea	NY L US L CANB	4.5(6.2)8	4(6)8.5	prolate subprolate suboblate oblate 20% 45% 28% 7%	3-colpate	peritreme (gonotreme)
5aa(†)	Koorders 39027β Van Steenis 5027	Java Java	L L	5.5(6.5)7.5	5(6.4)8	subprolate suboblate 50% 50%	3-colpate	peritreme (gonotreme)
5d	Taam 523, 543 s. coll. s. n.	Kwangtung Kwangtung	A A	4(5.6)7	4(5.9)7.5	prolate subprolate suboblate oblate 19% 25% 39% 17%	3-colpate	peritreme (gonotreme)
5ed	Moran 4985 Taquet 744 Wilson s. n., Wilson 8406	Okinawa Korea Hondo Hachijo	A A A A	4.5(5.9)7	5.5(8)9	subprolate suboblate oblate peroblate 15% 48% 29% 8%	3(4)-colp(oroïd)- ate	peritreme (gonotreme)
5f (**)	Henry 12657 A Tsai 55595	Yunnan Yunnan	A A	4(5.2)6	5(6)8	suboblate oblate 55% 45%	3-colpate	peritreme (gonotreme)

5g	Liang 65264 A	Hainan	A	5(5.8)6.5	5(6.2)7	subprolate suboblate	34% 66%	3-colporoidate	peritreme gonotreme
5h (†)	Sasaki 14591 Tanaka & Shimada 13531 Wilson 10207	Taiwan Taiwan Taiwan	TAIF NY A	5.5(5.9)7	6.5(7)8	subprolate suboblate	15% 85%	3-colp(or)ate(?)	peritreme (gonotreme)
5j	Kerr 3101	Siam	K	6.5(7)7.5	5(5)5	suboblate oblate	34% 66%	3-colpate	peritreme (gonotreme)
5n (†)	Clemens 10656, 30324, 51109	Borneo	NY?	6(7.6)9.5	4.5(5.6)8	perolate prolate subprolate suboblate	2.5% 50% 45% 2.5%	3-colpate	peritreme (gonotreme)
5q	Robinson s. n.	Selanque	BM	6(6.2)6.5	5(6)6.5	subprolate	100%	3-colpate	peritreme (gonotreme)
5r	Travancore s. n. Wight 2649	Ceylon Ceylon	K GH	5(6.8)9	6.5(7.3)8	subprolate suboblate oblate	50% 25% 25%	3-colpate	peritreme gonotreme
7 (†)	Van Steenis 8654	Sumatra	L	8.5(9.6) 10.5	5(7)8.5	perolate prolate subprolate	10% 30% 60%	3-colpate	peritreme (gonotreme)
8	Ramos & Edano 45687	Philippines	A	4.5(5.9)7	4(5.1)6.5	perolate subprolate suboblate oblate	20% 63% 7% 10%	3-colpate	peritreme (gonotreme, pleurotreme)
9aa	Biswas 6641	Lachen	A	7(8.4)9.5	6(7.1)8	prolate subprolate suboblate	25% 64% 11%	3-colpate	gonotreme (pleurotreme, peritreme)
9ae	Forrest 14505 Forrest 17505 King's collector s. n. Rawat 99 Stainton, Sykes, & Williams 2500	Yunnan Yunnan Assam India Nepal	BM E US A BM	4.5(5.9)8	4(7.1)10	prolate subprolate suboblate oblate	10% 15% 32% 53%	3-colp(or)ate	gonotreme (peritreme, pleurotreme)

9c	Kanehira s. n. Kanehira s. n. 1929 Keng 1118 Mizushima 1139 Wilson 8541	— Kyushyu Taiwan Japan Korea	US A A A A	5(7.2)9.5	6(7.9)10	prolate subprolate suboblate oblate	3% 25% 24% 48%	3-colpate	peritrema (gonotreme)
9c	Farges 1187 Wang 12104 Wilson s. n.	Szechuan Hunnan Szechuan	BM A K	5(6.4)9	7(8.3)10	subprolate suboblate oblate	3% 40% 57%	3-4-colpate 3-colporate	gonotreme (peritrema)

Based on IX, The Enumeration of Recognized Taxa

* Based on 10 measurements from each collection

** Presence of false osis

† Constricted colpi

Table. 4. Seed germination in *D. glaucescens* subsp. *oldhamii* (Hemsl.) Huang

Date planted (1962)	C°	Drupe	Mesocarp	Treatment	Germination (days)
October	21	fresh	present	none	55
October	21	fresh	present	none	66
November	29	fresh	absent	soaked in warm tap water for 5 hours	45
December	27	dry	prescent	soaked in warm tap water for 1/2 hour	64

apertures and only reflects a diverse granulation of the membranes. Constricted colpi are frequently observed in grains of *D. glaucescens* subsp. *glaucescens* and subsp. *borneense*.

Pollen grains of species in the sections *Calycifera* and *Staminodia* are very similar: they are commonly subspheroidal or oblate, less frequently prolate, size varies, and the sexine is granulated or finely reticulated. The elongated grains are often correlated with small pollen size as well as with small or narrow leaves in the sporophyte, eg., *D. glaucescens* subsp. *subverticillatum* and *D. parvifolium*. In the section *Staminodia*, pollen grains tend to be 3-colporate, while in the section *Calycifera*, they tend to be 3(-4)-colporoidate. Species in the section *Lunata* consistently have small, prolate grains with clearly outlined, very narrow and long, equatorially constricted colpi, and very finely reticulated sexines.

Pollen from one species of nine possibly related families, i.e., Buxaceae, Cericidiphyllaceae, Euphorbiaceae, Eupteleaceae, Hamamelidaceae, Pittosporaceae, Platanaceae, Stachyuraceae and Trochodendraceae has been studied. A brief account of this morphology is indicated below.

1. Buxaceae: *Buxus microphylla* var. *japonica* Rehd. & Wils., *Wilson* 8377 (MO), Japan.

Pollen medium(*); subspheroidal; (6-)7-porate (polyforate); sexine finely reticulated, O-L pattern.

2. Cericidiphyllaceae: *Cericidiphyllum japonicum* S. et Z., *Yokubuchi* s.n., April 1890, Japan.

Pollen medium; subprolate; 3-colpate; sexine finely reticulate. The sexine is identical to that seen for pollen in the Buxaceae and Eupteleaceae, but the apertures differ markedly.

3. Euphorbiaceae: *Aporosa leptostachya* Benth., *Tsui* 182 (MO), China.

Pollen small; subprolate; 3-colporate, the colpi long, the os narrowly rectangular; sexine distinctly reticulated, O-L pattern.

4. Eupteleaceae: *Euptelea polandra* S. et Z., *Palmer* s.n., April 1936 (MO), Japan.

Pollen medium; subspheroidal (3-)6-porate, granular; sexine finely reticulated, O-L pattern. Pollen grains are very similar to those in the Buxaceae.

5. Hamamelidaceae: *Hamamelis virginiana* var. *macrophylla* Pursh, *Demaree* 5611 (MO), Arkansas.

Pollen small; subspheroidal; 3-colpate, the colpi long, with distinct colpus membrane; sexine distinctly reticulate, O-L pattern. Pollen grains are almost identical to those of the Platanaceae and Trochodendraceae but flatter in shape. The sexine is similar to pollen in the Euphorbiaceae and Pittosporaceae.

6. Pittosporaceae: *Pittosporum tobira* Willd., *Huang* 2282, 2283 (MO), Taiwan.

* Pollen size (from Erdtman, 1952): small, to 25 μ ; medium, 25-50 μ ; large, 50-100 μ .

Pollen medium; elliptic, subprolate or prolate; 3(-4)-colporate, with long colpi, the ora small and laterally diffused; sexine distinctly reticulate, O-L pattern.

7. Platanaceae: *Platanus racemosa* Nutt, *Munz & Hitchcock 12,075* (MO), California.

Pollen small; subprolate; 3-colpate, the colpi long, with distinct colpus membrane; sexine distinctly reticulate, O-L pattern.

8. Stachyuraceae: *Stachyurus himalaicus* Hook. et Th., *Tsang 20674* (MO), China.

Pollen small; subprolate; 3-colporate; sexine granular, O-L pattern. The granulate sexine is similar to that observed for pollen in the Daphniphyllaceae.

9. Trochodendraceae: *Trochodendron aralioides* S. et Z., *Huang 2308* (MO), Taiwan.

Pollen small; subspheroidal; 3-colpate, the colpi long, with distinct colpus membrane; sexine distinctly reticulate, O-L pattern.

In aperture morphology, the pollen of Daphniphyllaceae is similar to that of the Cercidiphyllaceae, the Hamamelidaceae, the Platanaceae, and the Trochodendraceae (for additional species, cf. Erdtman, 1952), and the granular sexine clearly resembles that characteristic of the Stachyuraceae. By combining these two characters, the nature of the aperture and the sexine, the pollen of the Daphniphyllaceae can be distinguished from the pollen of all closely allied families.

FRUIT:—The fruit of *Daphniphyllum* is an ovoidal, elliptic-globose, obovoidal, and ellipsoidal drupe. The texture of the epicarp varies from smooth, rugose to tuberculate and the color may be brown to gray-black or sometimes glaucous. Hardness of the endocarp varies among taxa, e.g., the endocarp of *D. gracile* is harder than that of *D. calycinum*. Among members of the subsection Calycifera, the hardest endocarp is found for *D. glaucescens* subsp. *glaucescens* from southeastern Asia and the softest one for *D. glaucescens* subsp. *oldhamii* from northeastern Asia. This suggests that plants of *Daphniphyllum* generally produce harder endocarps in tropical regions than in the temperate zone. Tanniniferous canals were observed in the epicarp. The morphology of drupes may, sometimes, be used for identification, but when species are dioecious it is difficult to base classification solely on fruit characteristics. Thus for *D. gracile* as many as five varieties could be proposed on the basis of drupe morphology, but the flowering specimens could not be distinguished. Yet *D. glaucescens* subsp. *borneense* can be distinguished from the subsp. *dichotomum* by differences in drupe sizes and shapes and both subspecies are separable from the subsp. *glaucescens* on the basis of smooth versus tuberculate texture of the drupes.

SEED:—The seed is smooth and ellipsoidal, with an obtuse apex and a rotundate base. The size and shape of the seeds are correlated with the size and shape of the drupes. The seed coat is membranous. Usually only one seed develops leaving 3(-5-7) aborted ovules hanging either subapically or on incomplete septa. The funiculus of the undeveloped ovule is one-half as long as the ovule. The embryo, apical in position, is very small, ellipsoidal, white to yellow, with accumbent cotyledons, and a copious endosperm (Fig. 8).

Seed germination.—Table 4 gives the results of experiments on seed germination of *D. glaucescens* subsp. *oldhamii* at the Taiwan Forestry Research Institute. L. C. Huang (unpublished) found that when seeds from fresh drupes without mesocarp were soaked in warm water, they germinated more readily than did those subjected to different treatments. Seeds would also germinate rapidly when they were planted, then dug out of the soil, and re-planted. Nevertheless, seeds of *D. glaucescens* subsp. *oldhamii* require at least 45 days for germination. When a purple color appeared in the dissected embryos, seeds were found to be nonviable.

The cotyledons as illustrated in Fig. 8 are epigeal and paired, and each is oblong.

CHROMOSOME NUMBERS.—Sugiura (1928) recorded the chromosome number from pollen mother cells of *D. himalaense* subsp. *macropodum* as $n=16$ which has been verified by Sinoto (1929). Both examined material collected in Japan. Based on these counts, Darlington and Wylie (1956) suggested a basic number of $x=8$ for *Daphniphyllum*.

For this study, I have examined the chromosomes of *Daphniphyllum* from root tips of *D. glaucescens* subsp. *oldhamii* and the number is $2n=32$. According to my proposed infrageneric classification based on morphological characters, these species belong to different sections: *D. himalaense* subsp. *macropodum* to the section *Staminodia*. *D. glaucescens* subsp. *oldhamii* to the section *Calycifera*, but by both number and size the chromosome complements of these taxa are similar. No voucher specimen was mentioned by Sugiura (1928), and Sinoto (1929). The voucher specimens for the present study were collected by Mr. Lu (Lu 1-10), deposited in the several herbaria (A, MO).

In Table 5, the basic numbers known for eight families which have been associated with *Daphniphyllum* are given. Of these the chromosome complements of the Buxaceae, Cercidiphyllaceae, Eucommiaceae, Pittosporaceae, Platanaceae, and Trochodendraceae are most distinctly removed from *Daphniphyllum* while some complements of the Euphorbiaceae and Hamamelidaceae are also common to *Daphniphyllum*. Based on other evidences (pollen morphology and wood anatomy), the Hamamelidaceae are considered most closely allied to the Daphniphyllaceae and the basic number of $x=(8) 16$ found for *Liquidambar* (Hamamelidaceae) gives additional support to this conclusion.

IV. CHEMICAL COMPONENTS

The crucial chemical components of the Daphniphyllaceae are still not well known. Swain(1963) stated that *D. humile* Max. has seed fats with linoleic, oleic, linoleinic on conjugated polyethenoid acids as major components in common with that of the Euphorbiaceae, but the former differs from the latter by having other seed fats with palmitic, oleic and linoleic as major component acids. The chromo-

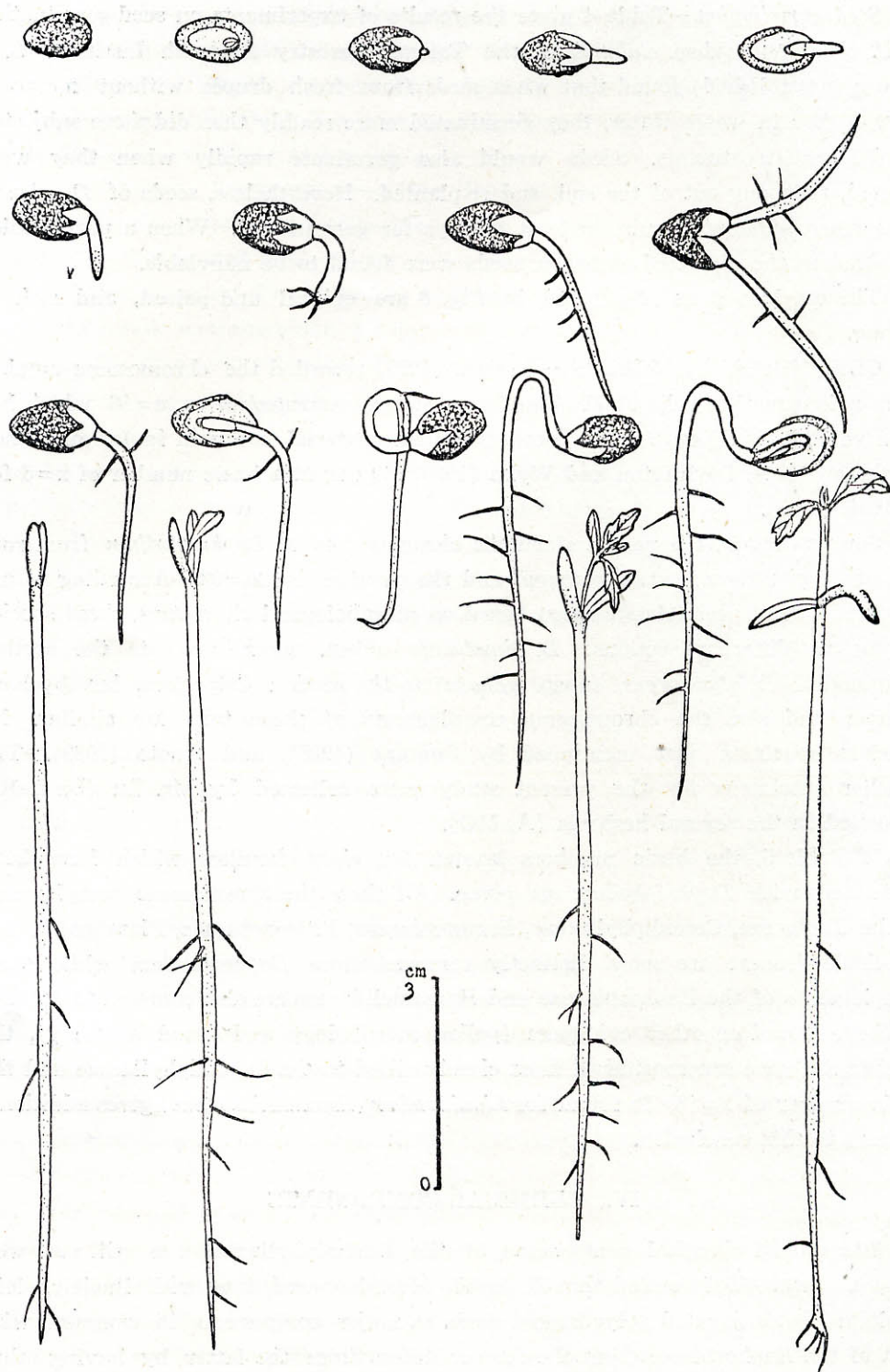


Fig. 8. Illustration of seed germination for *D. glaucescens* subsp. *oldhamii* (Hemsl.) Huang.

Table 5. Basic chromosome numbers for eight families thought to be related to the Daphniphyllaceae (Darlington and Wylie, 1956: Index to plant chromosome numbers, 1956-64).

Family	Number of Genera	Basic Numbers
Buxaceae	2	$x=(7) 14$
	1	$x=10$
Cercidiphyllaceae	2	$x=19$
Eucommiaceae	1	$x=7$
Euphorbiaceae	1 (<i>Euphorbia</i>)*	$x=6-10, 12, 16$
	6	$x=7$
	2	$x=8$
	8	$x=9$
	3	$x=10$
	9	$x=11$
	3	$x=12$
	7	$x=13$
	1	$x=15$
	6	$x=12$
Hamamelidaceae	1 (<i>Liquidambar</i>)	$x=(8) 16$
Pittosporaceae	1	$x=12$
Platanaceae	1	$x=(7) 14$
Trochodendraceae	1	$x=19$

* Excluding nine other genera with more than one basic number which vary from $x=7$ to $x=17$.

genic glycoside, asperuloside of *Daphniphyllum* (Swain, 1963), methylsalicylate of *D. glaucescens* Blume (Hegnauer, 1964), and the poisonous alkaloids, daphniphylline (*D. laurinum* Baill.) and daphnimacine (*D. macropodum* Miq.) in the bark and seeds (Burkill, 1935) are not reported in those families thought to be allied with the Daphniphyllaceae.

V. RE-EVALUATION OF TAXONOMIC POSITION

In an attempt to understand more clearly the classification of Daphniphyllaceae in relation to other taxa, I have studied members of the Buxaceae, Cercidiphyllaceae, Eucommiaceae, Euphorbiaceae, Eupteleaceae, Hamamelidaceae, Pittosporaceae, Platanaceae, Stachyuraceae and Trochodendraceae by comparative gross morphology, wood anatomy, cytology, pollen morphology, and chemical components. First, *Daphniphyllum* is characterized by small, dioecious flowers, by scalariform perforation plates in the vessels of the xylem, by tanniniferous canals in tissues and organs, by usually 3(-4)-colpate pollen grains with granulate membranes and an obscure sexine pattern, by incompletely septate ovary with a reduced subapical placentation, by small embryos, drupaceous fruits, by the possibly basic chromosome number $x=8$,

and by papillate and estipulate leaves. The subapical placentation indicates a development of the placentation from a parietal origin and, in my opinion, this negates a close relationship with either the Euphorbiales or the Hamamelidales in which the placentation is axile. Moreover, the incompletely septate ovary, the drupaceous fruits, the possibly basic chromosome number $x=8$, the papillate leaves, the small embryo, and non-reticulated sexines of the pollen of *Daphniphyllum* represent characteristics distinct from those of most members of these other orders. The wood of the Daphniphyllaceae also differs from that of the Pittosporales and the Euphorbiales (cf. discussion under III. Morphology). The chemical components of *Daphniphyllum*, namely, asperuloside, methylsalicylate and the poisonous alkaloids, are not reported in other families thought to be allied with the Daphniphyllaceae. Although the external gross morphology (Table 6) of *Daphniphyllum* is similar to that of the members of several families, especially to the Buxaceae, Cercidiphyllaceae, Eucommiaceae, Euphorbiaceae, Eupteleaceae, Platanaceae and Trochodendraceae, these

Table 6. Comparative study of the gross morphology of the Daphniphyllaceae and possibly related 10 families. The following are the abbreviations for the respective families: B, Buxaceae; C, Cercidiphyllaceae; E, Eucommiaceae; Eh, Euphorbiaceae; Et, Eupteleaceae; H, Hamamelidaceae; P, Pittosporaceae; Pl, Platanaceae; S, Stachyuraceae; and T, Trochodendraceae

Characteristics of the Daphniphyllaceae*	Families with characteristics resembling Daphniphyllaceae**	Families with characteristics different from Daphniphyllaceae**
1. Dioecious plants	B, C, E, Eh, Pl	B, Eh, Et, H, P, S, T
2. Estipulate	B, E, Et, P, T	C, Eh, H, Pl, S
3. Apetalous	C, E, Eh, Et, Pl, T	B, Eh, H, P, S
4. Anthers with longitudinal dehiscence	B, C, E, Eh, Et, P, Pl, S, T	Eh, H, P
5. Ovary superior	B, C, E, Eh, Et, P, Pl, S, T	H
6. Drupe	none	All 10 families
7. 2(-3-4)-carpellate	B, E, Eh, H, P	C, Eh, Et, P, Pl, S, T
8. Origin of parietal placentation	P	B, C, E, Eh, Et, H, Pl, S, T
9. Incompletely septate ovary	None	All 10 families
10. Endosperm copious	C, E, Eh, P, S	B, Et, H, Pl, T
11. Small embryo	Et, P, T	B, C, E, Eh, H, Pl, S

* 1-6, external gross morphology; 7-11, internal gross morphology

** According to Lawrence (1963)

families differ greatly from the Daphniphyllaceae by their internal gross morphology. Among the 10 families reputed to be allied to the Daphniphyllaceae, only member of the Pittosporaceae have estipulate leaves, parietal placentation, copious endosperm, and small embryos, and most resemble those of the Daphniphyllaceae in gross morphology.

Transferring these data to a meaningful classification, I suggest that *Daphniphyllum* be classified in a distinct order, the Daphniphyllales, as already proposed by Hurusawa (1954). With regard to the relationship and origin of the order Daphniphyllales, I believe that it was derived either directly from the primitive Magnoliales or from a more ancestral prototype. I cannot agree with Hurusawa (1954) that the order is closely related to the Euphorbiales nor that it evolved from the Rosales as proposed by Hutchinson (1959) or with the Pittosporales as Croizat believed. In my opinion, the Daphniphyllales are most closely related to the Hamamelidales and have both probably undergone a parallel evolution from a common primitive ancestor.

VI. SPECIATION

Foremost among the morphological diversities represented by species of *Daphniphyllum* is the variation in calyx size including its reduction and ultimate loss. In the section Calycifera, *D. gracile* of the subsection Longicalycifera Huang, subsect. nov. possesses a calyx longer than the androecium and gynoecium while the other species, *D. glaucescens* of the subsection Calycifera, has calyces shorter than the reproductive organs. *Daphniphyllum woodsonianum* and *D. philippinense* of the subsection Unicalycifera have lost their calyces in staminate flowers. A similar trend in size reduction is found in the section Lunata: *D. majus* has a long calyx, *D. calycinum* and *D. laurinum* have short calyces. The ultimate in calyx reduction is reached by *D. himalaense* and *D. parvifolium* of the section Staminodia in which the calyx is absent from pistillate flowers and usually from staminate flowers. When present in the later, the calyx lobes are reduced to 1 or 2 and are very narrow. Such reduction suggests to me that the section Staminodia is the most highly evolved in *Daphniphyllum* (at least in this respect).

Calyx size is of major significance in differentiating two specific complexes in the genus, i. e., *D. gracile* and *D. glaucescens*, the former with a long calyx, the latter with a short one.

Individuals of *D. gracile* (confined to New Guinea) are very variable in leaf, fruit, staminal and pistillate morphology. The *D. glaucescens* complex also possesses these morphological diversities, but each insular or otherwise geographically restricted population is much more homogeneous and I find that certain morphological expressions are largely restricted to certain specific areas. For example, in Ceylon the population is characterized by its obovate, roughened leaves, and its more or less smooth fruits with other variations for these characters represented by

only a few individuals. Similar trends in *D. glaucescens* exist elsewhere: in the Malaysian peninsula, the population is similar to that known in Ceylon but the plants have smooth leaves; in Ceram the leaves characteristically are elliptic and thin; and in Borneo the leaves of the subsp. *borneense* are similar to those of the subsp. *ceramense* except that they are thicker. Plants of the subsp. *dichotomum* with narrowly elliptic leaves differ from those of the subsp. *borneense* which have elliptic leaves, a difference correlated with altitude for on Kinabalu mountain in northern Borneo, the subsp. *borneense* occurs mostly between 2,000 to 4,000 m. whereas the subsp. *dichotomum* is found at 1,600 m. or lower.

What I wish to illustrate is that the populations of *D. glaucescens* are rather homogeneous within any one geographical or ecological area, especially on the islands surrounding Asia, and that the discontinuity between populations has resulted in the formation of many geographically distinct races. Such a geographical displacement is also found among the infraspecies of *D. himalaense*. In the past, these have been accepted as distinct species but I consider them as one, although consisting of numerous geographical and ecological subspecies. In addition there may possibly exist small populations established in certain continental regions through hybridization between infraspecific taxa with overlapping ranges.

Variations in fruit morphology correlated with geographical distribution for populations of the *D. glaucescens* complex are noteworthy. Generally, the size and shape of the fruit, the length of the fruiting axis, and the length of the style either from the pistillate ovary or fruit vary from south to north Asia with the largest sizes to the south and the smallest sizes to the north. Thus, the species population in Java, subsp. *glaucescens*, with its long fruiting axes is separable from those characterized by shorter fruiting axes in the Malaysian (subsp. *lanceifolium*) and in Sumatra (subsp. *sumatraense*). Likewise, while the style for individuals in the Java population is long, a gradual decrease in style length for plants found in Borneo and the Philippines is observable; an extreme is reached in subsp. *teijsmannii* in Japan which has a very short style. Furthermore, the fruit of individuals in the most southern range (Java) is large, but in the most northern range (Japan) the fruit is small. Fruit shape also varies: ellipsoidal to elliptic-globose in plants from Java to China, whereas from some parts of the Philippines, Borneo, and Japan the plants usually have elliptic-globose fruits and these are smaller.

I have already discussed the difference in calyx morphology between species of the section Calycifera (invariably present) and Staminodia (usually absent). On the other hand a few collections of some taxa segregated in different sections on the basis of calyx morphology, are strikingly similar in other respects. For example, some plants of *D. glaucescens* subsp. *teijsmannii* var. *iriomotense* (Hurusawa) Huang, comb. nov.⁽¹⁾ of the section Calycifera have the same leaf shape and texture as

(1) *D. teijsmannii* var. *iriomotense* Hurusawa, Jour. Jap. Bot. 18: 270. 1942.

observed for *D. himalaense* subsp. *macropodum* of the section *Staminodia*. For the same reasons, *D. glaucescens* subsp. *paxianum* is frequently misidentified as *D. himalaense*, but because individuals of the latter lack a calyx, I have maintained it in a different section. This is also true for *D. himalaense* subsp. *himalaense* var. *divaricatum* Huang, var. nov. versus *D. glaucescens* subsp. *beddomei* (Craib) Huang stat. nov.⁽¹⁾, *D. himalaense* subsp. *angustifolium* and subsp. *macropodum* vs. *D. longistylum* (cf. Croizat and Metcalf, 1941), and *D. himalaense* subsp. *macropodum* vs. *D. glaucescens* subsp. *oldhamii*.

Following a study of about 2,600 specimens covering the entire range of the genus, I shall present in the systematic treatment a new infrageneric classification for *Daphniphyllum*. Prior to this time the describing and naming of new taxa was

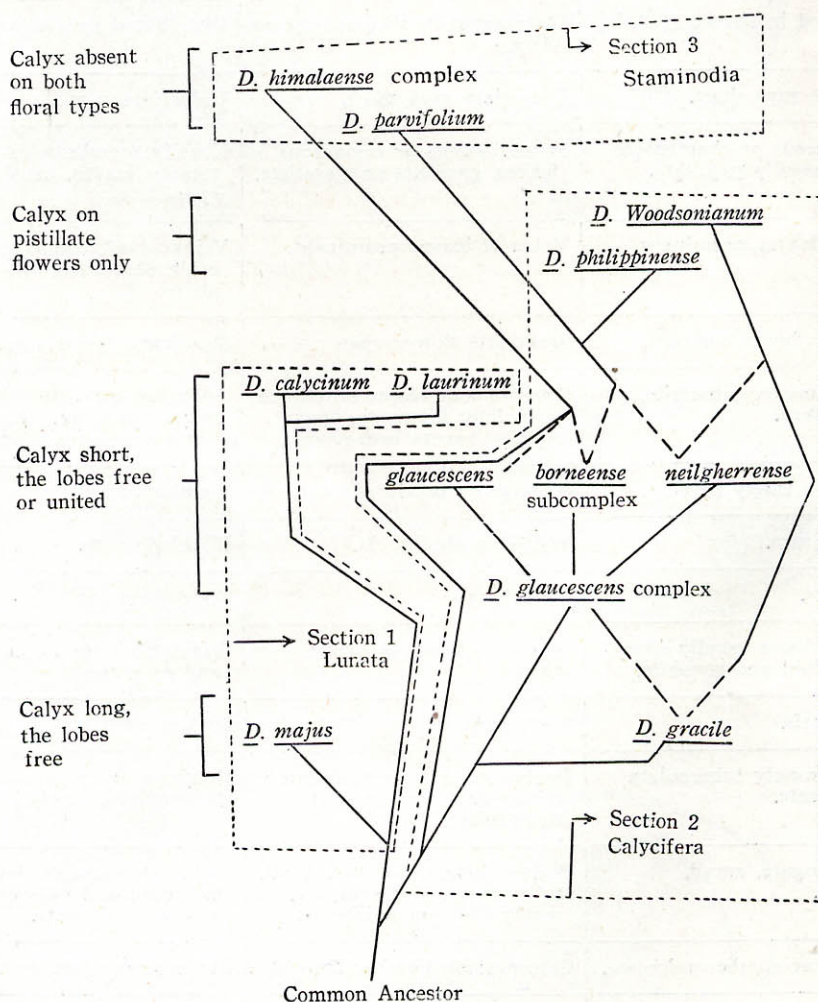


Fig. 9. Hypothetical trend of speciation in *Daphniphyllum*

(1) *D. beddomei* Craib, Kew Bull. 1916: 268. 1916.

based on incomplete regional collections, especially for New Guinea, and as such systematists failed to recognize the range of variation for most taxa beyond a restricted geographical area or a limited environmental condition. In my opinion, these limitations have influenced many workers in the recognition of many species in *Daphniphyllum*. My concept of the infraspecific taxa, particularly in the section

Table. 7. Sectional Characters of *Daphniphyllum*

Lunata	Calycifera	Staminodia
Growing on the lower elevation of sea shores to medium mountainous regions.	Growing on the lower elevation of sea shores to medium mountainous regions.	Growing on the high elevation of mountainous region.
Distributed in southeast Asia.	Distributed in all parts of east Asia.	Distributed in northeast Asia.
Uniseriate rays short.	Uniseriate rays short.	Uniseriate rays long.
Subcoriaceous or chartaceous leaves, usually papillate.	Subcoriaceous or coriaceous leaves, papillate or epapillate.	Usually membranous or chartaceous leaves, usually epapillate
Veins of leaves prominent.	Veins of leaves prominent.	Veins usually delicate, frequently obscure or impressed above
Staminate flower compact.	Staminate flower open	Staminate flower open.
Anthers lunate, subsessile, apex beaked.	Anthers compressed or oblique, with long filaments, apex various except beaked one.	Anthers compressed or oblique, with long filaments, apex various except beaked one.
Staminodia rarely present.	Staminodia partly present.	Staminodia frequently present.
Pistillode rare.	Pistillode absent (?).	Pistillode rare.
Style short.	Style long	Style short or long
Stigmatic lobes usually divaricate, discoid and revolute.	Stigmatic lobes variously shaped.	Stigmatic lobes radiate, and revolute
2(-3) carpels.	2(-3) carpels	2(-3-4) carpels
Drapes strongly tuberculate and glaucate.	Drapes smooth or moderately tuberculate, eglaucate if tuberculate.	Drapes usually moderately tuberculate, rarely glaucate.
Pollen elongate, small, 3-colpate.	Pollen elongate or flat, small to medium, 3(-4)-colpate, rarely 3(-4)-colporoidate.	Pollen elongate or flat, small to medium, 3(-4)-colpate, rarely 3-colporate.
Chromosome number unknown.	Chromosome number $2n=32$	Chromosome number $2n=32$.
Alkaloids unknown	Daphniphylline	Daphnimacine
3 species.	4 species.	2 species.

Calycifera, is novel, but by so recognizing the many described species in this section at a subspecific level, I am able to emphasize the gradation found geographically and ecologically within a single species complex.

My opinion of the hypothetical trend of speciation in *Daphniphyllum* is summarized in Fig. 9 and this is based on the following data which is summarized from Table 7.

1. Calyx length from long to short,
2. Calyx from free to united,
3. Calyx from present to absent,
4. Style from long to short,
5. Pollen grains from 3-colpate to 3-colporoidate or 3-colporate,
6. Wood rays from 2(-3)-seriate to uniseriate.

VII. GEOGRAPHICAL DISTRIBUTION AND ORIGIN

Daphniphyllum is confined to eastern Asia between about 46°N and 10°S, and 75°E and 150°E, and is found in New Guinea, Indonesia, Malaysia, the Philippines, Ceylon, India, Pakistan, Burma, Thailand, Cambodia, Vietnam, Laos, Sikkim, Bhutan, Nepal, China, Taiwan, the Ryukyu Islands, Korea and Japan.

Four species occur in restricted areas. *Daphniphyllum woodsonianum* is found only in Sumatra, *D. parvifolium* and *D. philippinense* are endemic to the Philippines, and *D. gracile* is known only in New Guinea. The five species with wide distribution are: *D. himalaense* in Vietnam, the Himalayan region, China, Taiwan, Korea, and Japan; *D. laurinum* in Sumatra, Borneo, and Malaysia; *D. calycinum* in Vietnam and China; *D. majus* in Cambodia, Thailand, Burma, Vietnam, Laos, and China; and *D. glaucescens* throughout all of eastern Asia except India, Pakistan, Sikkim, Bhutan, Nepal, and Thailand.

The absence of *Daphniphyllum* from south India (see Fig. 10) has been questioned by Dr. Owen Sexton, because *D. glaucescens* subsp. *neilgherrense* (Wight) Huang, stat. nov.⁽¹⁾ is reported from the continental island of Ceylon, which was at one time connected with south India. Perhaps, this can be explained by scanty collections from south India, or its destruction by human beings.

When the morphological characteristics and geographical distribution between species complex of *D. glaucescens* and *D. gracile* are compared, *D. glaucescens* subsp. *ceramense*, and the subsp. *celebense* (Rosenth.) Huang, stat. nov.⁽²⁾ show an intermediate geographical position (Fig. 11) and intermediate feature of calyces between the two above listed species complex. This is additional evidence for Darlington's proposal (1957) regarding the fauna of south Pacific Asia. Much as Darlington divided the fauna of the area, the flora can be divided into three regions: oriental flora extending eastward to the islands of Timor, Lombok, Borneo,

(1) *Gouphia neilgherrensis* Wight, Ic. Pl. Ind. Or. 5: 22. 1852.

(2) *D. celebense* Rosenth. in Engl., Pflanzenreich 68 (IV. 147a): 5. 1919.

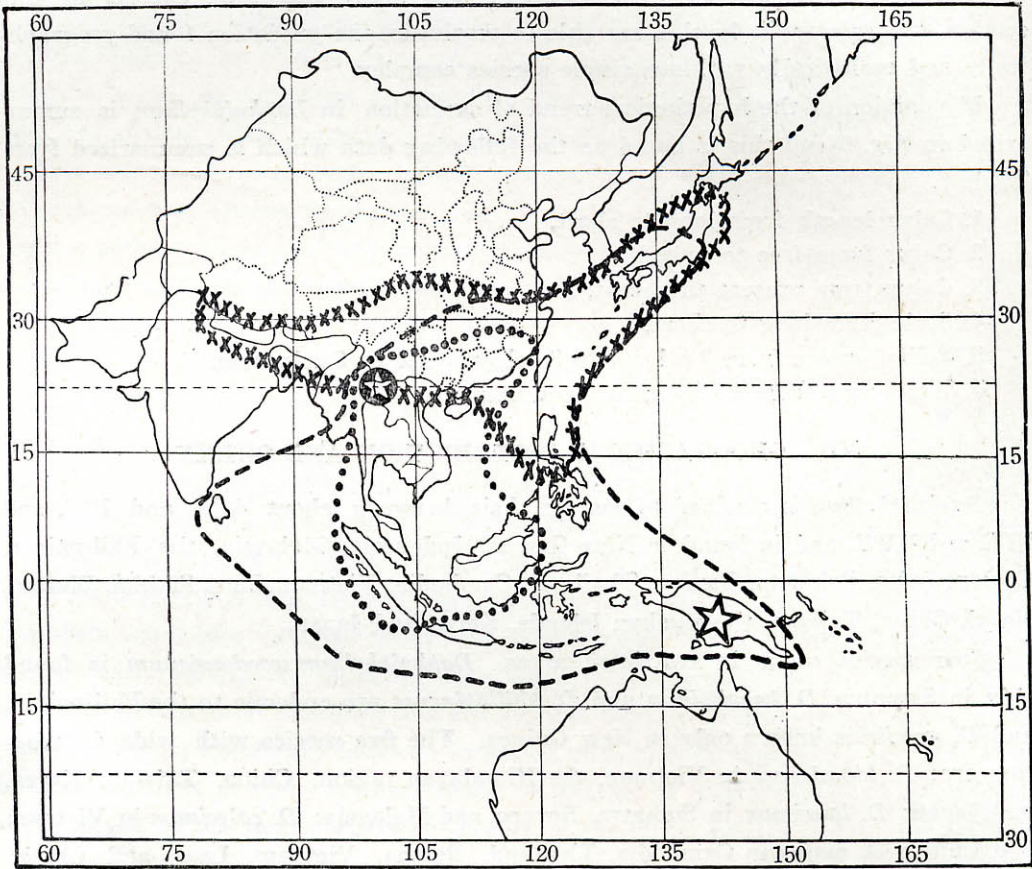
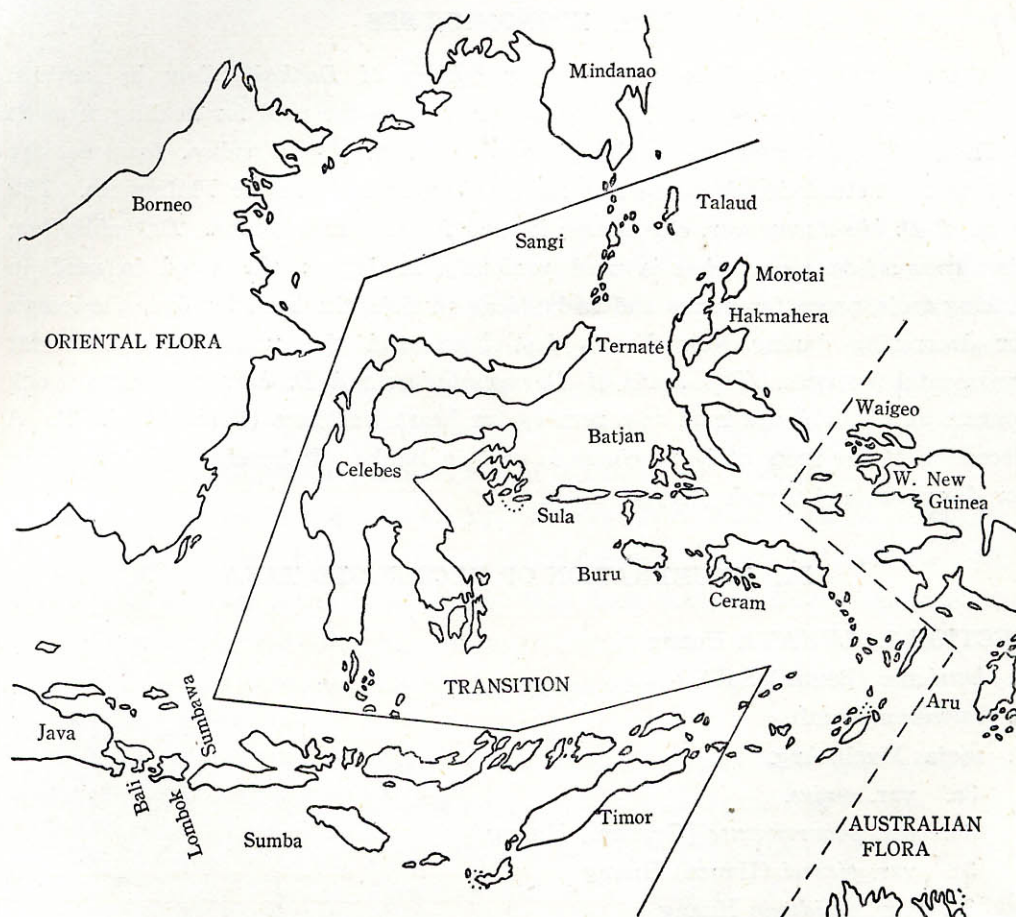


Fig. 10. Distribution of *Daphniphyllum*: section *Lunata* (···), section *Calycifera* (---), and section *Staminodia* (× × ×), noting possible center of origin (⊙) and center of survival (☆).

and Mindanao; Australian flora reaching westward to the islands of Aru, W. New Guinea, and Waigao; and a transitional flora occupying the islands of Celebes, Ceram, Ternate, Morotai, Sangi, and Talaud which lie between those of the oriental and the Australian flora.

Rosenthal (1916) stated that the "evolutionary center" of *Daphniphyllum* was in the Malaysian Archipelago. From there she theorized that two distributional branches stretched northward, one extending on a line through the eastern Asia islands to northern Japan, the other limited to the continent proper; the two branches uniting in China. Croizat and Metcalf (1941) concluded: "We may not doubt that it is an Austro-Malaysian phylum. Roughly speaking, *Daphniphyllum* occurs from Australia to India, extending as far north as Japan and Korea".

I consider that there are two possible present centers of morphological diversity in the genus (Fig. 10). The first, including the member of the section *Calycifera*, *D. gracile* probably arose and initially differentiated in New Guinea or her adjacent

Fig. 11. Floral Map of *Daphniphyllum*

areas, a differentiation which was enhanced following migration westward to Talaud, Sangi, Celebes, and Ceram. Perhaps New Guinea is a center of survival. The second center of diversity which includes members of sections *Lunata*, *Staminodia*, and *Calycifera* may have originated in southwestern China, northern Burma or northern Thailand from whence species migrated northward to China, Korea and Japan, and southward to Malaysia, Borneo, and Java.

Possibly the center of origin of the *Daphniphyllaceae* is in southwestern China, particularly in Yunnan province, for there exists here the greatest modern differentiation in the genus including the presence of members of the three systematic sections, the most diverse forms of members of the section *Staminodia*, and the most primitive member of the section *Lunata*. Sumatra, the Philippines, Indochina, and central China may represent secondary areas of speciation. Therefore, *D. woodsonianum* which is endemic in Sumatra, and *D. parvifolium* and *D. philippinense* which are restricted to the Philippines are considered recently evolved species rather than relics.

VIII. ECONOMIC USES

Certain uses have been reported for species of *Daphniphyllum* by several collectors. The leaves of *D. calycinum* soaked in wine are used for healing wounds in China. The decocted drupes and leaves of *D. glaucescens* subsp. *luzonense* are used to treat stomach aches and also for a poison antidote in the Philippines. The wood of *D. himalaense* var. *chartaceum* is used for timber in China. *Daphniphyllum himalaense* subsp. *macropodum* is used variously in Japan: the wood is used in making tools, props for mines and in building tunnels, the bark for dye, the leaves for decorating during New Year's festivities, and the trees are grown for ornamental purposes. The seeds of *D. macropodum* and *D. bancanum* Kurz which contain an alkaloid, are used as a remedy for heart weakness (Rosenthal, 1919). A decoction of the roots of *D. laurinum* is used in Banka (Indonesia) as a medicine for diarrhoea and thrush (Heyne, 1917).

IX. ENUMERATION OF RECOGNIZED TAXA

SECTION 1. LUNATA Huang

1. *laurinum* (Benth.) Baill.
2. *calycinum* Benth.
3. *majus* Muell.-Arg.
 - 3a. var. *majus*.
 - 3b. var. *phanrangense* (Gagnep.) Huang
 - 3c. var. *pierrei* (Hance) Huang
 - 3d. var. *deciduum* Huang

SECTION 2. CALYCIFERA Hurusawa

SUBSECTION 1. LONGICALYCIFERA Huang

4. *gracile* Gage
 - 4a. var. *gracile*.
 - 4b. var. *tuberculatum* Huang

SUBSECTION 2. CALYCIFERA

5. *glaucescens* Blume
 - 5a. subsp. *glaucescens*.
 - 5a(a). var. *glaucescens*.
 - 5a(b). var. *blumeanum* (Baill. ex Muell.-Arg.) Smith.
 - 5b. subsp. *lancifolium* (Hook. f.) Huang
 - 5c. subsp. *sumatraense* Huang
 - 5d. subsp. *subverticillatum* (Merr.) Huang
 - 5e. subsp. *teijsmannii* (Zoll. ex Teysm. & Binn.) Huang
 - 5e(a). var. *teijsmannii*.
 - 5e(b). var. *amamiense* (Hurusawa) Huang

- 5e(c). var. *iriomotense* (Hurusawa) Huang
- 5e(d). var. *buergeri* (Muell.-Arg.) Huang
- 5e(e). var. *hisautii* (Hurusawa) Huang
- 5f. subsp. *paxianum* (Rosenth.) Huang
- 5g. subsp. *atrobadium* (Croizat & Metcalf) Huang
- 5h. subsp. *oldhamii* (Hemsl.) Huang
 - 5h(a). var. *oldhamii*.
 - 5h(b). var. *longistylum* (Chien) Huang
 - 5h(c). var. *salicifolium* (Chien) Huang
- 5i. subsp. *celebense* (Rosenth.) Huang
- 5j. subsp. *beddomei* (Craib) Huang
- 5k. subsp. *luzonense* (Elmer) Huang
- 5l. subsp. *dichotomum* Huang
- 5m. subsp. *ceramense* Huang
- 5n. subsp. *borneense* (Stapf) Huang
- 5o. subsp. *timorianum* Huang
- 5p. subsp. *buchananii* (Hallier) Huang
- 5q. subsp. *scortechinii* (Hook.) Huang
- 5r. subsp. *neilgherrense* (Wight) Huang

SUBSECTION 3. UNICALYCIFERA Huang

- 6. *philippinense* Huang
- 7. *woodsonianum* Huang

SECTION 3. STAMINODIA Hurusawa

- 8. *parvifolium* Merr.
- 9. *himalaense* (Benth.) Muell.-Arg.
 - 9a. subsp. *himalaense*.
 - 9a(a). var. *himalaense*.
 - 9a(b). var. *triangulatum* Huang
 - 9a(c). var. *divaricatum* Huang
 - 9a(d). var. *longeracemosum* (Rosenth.) Huang
 - 9a(e). var. *chartaceum* (Rosenth.) Huang
 - 9b. subsp. *angustifolium* (Hutch.) Huang
 - 9c. subsp. *macropodum* (Miq.) Huang
 - 9c(a). f. *macropodum*
 - 9c(b). f. *crassifolium* (Hurusawa) Huang
 - 9c(c). f. *viridipes* (Hurusawa) Huang

X. ABBREVIATIONS

Loaned specimens were received from the following herbaria or institutions (abbreviations from Lanjouw and Stafleu's Index Herbarium, Part 1, Ed. 5, Regnum

Vegetabile 31. 1964, excepting TAF which is first proposed here).

- A Arnold Arboretum of Harvard University, Cambridge, Mass.
- BM British Museum of Natural History, London.
- BO Botanical Garden Bogorensse, Indonesia.
- CANB C. S. I. R. O. Herbarium, Canberra, Australia.
- E The Royal Botanic Garden, Edinburgh.
- F Chicago Natural History Museum, Chicago.
- GH Gray Herbarium of Harvard University, Cambridge, Mass.
- K The Herbarium, Royal Botanic Garden, Kew.
- L Rijksherbarium, Leiden, Netherlands.
- MICH University Herbarium, University of Michigan, Ann Arbor.
- MO Missouri Botanical Garden Herbarium, St. Louis.
- MOAR Morris Arboretum, University of Pennsylvania, Penn.
- NA United States National Arboretum, Washington.
- NY New York Botanical Garden, New York.
- P Museum National d'Histoire Naturelle, Laboratoire de Phanerogamie, Paris.
- PNH Philippine National Herbarium, National Museum, Manila, Philippines.
- TAF Forest Department, National Taiwan University, Taiwan.
- TAI Botany Department, National Taiwan University, Taiwan.
- TAIF Taiwan Forest Research Institute, Taiwan.
- TI Tokyo University, Tokyo, Japan.
- UC University of California Herbarium, Berkeley.
- US U. S. National Museum, Smithsonian Institution, Washington.

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