A MONOGRAPH OF DIPHYLLEIA (BERBERIDACEAE)

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DIPHYLLEIA Michaux is one of approximately 120 genera with members exhibiting the classic eastern Asian–eastern North American disjunction pattern. It was one of the first examples of this pattern that Asa Gray (1859) pointed out when he listed *D. grayi* F. Schmidt (as *D. cymosa* Michaux) as one of a number of taxa restricted to these two widely separated areas. Three species of *Diphylleia* (*D. cymosa, D. grayi,* and *D. sinensis* H. L. Li) are presently recognized, each occurring in separate, disjunct regions. Despite this well-known distribution pattern and the interest it has generated, there have been relatively few detailed studies of the taxa involved. The following account is an attempt to bring together the scattered information on *Diphylleia* and to point out areas where further studies might result in a better understanding of this disjunction pattern.

Floristically, eastern Asia and eastern North America are two of the largest and most complex relictual areas for the once-widespread Mixed Mesophytic Forests that circled the globe at middle and high latitudes in the Northern Hemisphere during the Tertiary (Wood, 1972). These forests and their floras become extinct in large intervening areas during the orogenies and climatic deterioration of the late Tertiary and the glaciations of the Pleistocene. *Diphylleia,* unknown in the fossil record, can be inferred from its present occurrence with dominant relictual Tertiary woody genera with well-documented fossil histories (e.g., *Fagus* L., *Liriodendron* L., *Magnolia* L., *Cercidiphyllum* Sieb. & Zucc., *Cornus* L. subg. *Thelycrania* Endl., *Tsuga* Carr.) to have been a member of these forests, even though the components of the present forest may have had very different histories. Although it might be argued that the current distribution of *Diphylleia* is the result of long-distance dispersal, it seems more likely that the berry fruits enabled a more continuous and widespread distribution during the Tertiary by dispersal over shorter distances. The present localized distribution of *D. cymosa* in the southern Appalachian Mountains of the southeastern United States is unexplainable. In cultivation plants of this species are able to grow far north of their present range. It may be that they are unable to compete in nature with other, better-adapted plants farther north, or that they have been unable to bridge intervening unsuitable habitats since the melting of the last continental glaciers to reach the seemingly suitable habitats occurring outside of their present range.

In addition to *Diphylleia,* other genera and species of Berberidaceae *s.l.* (*Caulophyllum* Michaux, *Jeffersonia* Bartram, *Podophyllum* L., and close relatives of *Berberis canadensis* Miller) are well known for their discontinuous

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distribution in eastern North America and eastern Asia. With the exception of *Berberis*, these genera are all perennial, rhizomatous herbs that grow in rich, moist soils in mixed deciduous forests.

ECOLOGY

The three species of *Diphylleia* occupy similar habitats in the eastern United States, Japan, and China. All are found on gentle to steep slopes in seepages or along streams. They grow in brown forest soils or podzols that are rich in organic matter and characteristically acidic (pH 4.5–7.0 for *D. sinensis* in the Shennongjia Forest District in central China (*Shennongjia Bot. Exped. 10276* and *25107*); 4.0–5.8 for *D. cymosa* in samples from Watauga County, North Carolina (*Boufford & E. W. Wood 16310*), and Rabun County, Georgia (*Boufford & E. W. Wood 17033*), in the United States). The plants are found in cool-temperate, mixed-deciduous broad-leaved forests, in mixed-deciduous broad-leaved and coniferous forests, and in nearly pure coniferous forests at high altitudes or latitudes. On Mount Jinfu Shan in southeastern Sichuan Province, *D. sinensis* is sometimes found growing in bamboo thickets. Plants characteristically associated with *Diphylleia* in each of the three disjunct regions are listed in TABLE 1. Hara (1959), Numata *et al.* (1972), and Numata (1974), without referring specifically to *D. grayi*, have discussed some of the associations in which it occurs in Japan.

Due to its use as a medicinal plant and to the destruction of its habitat, *Diphylleia sinensis* is becoming increasingly scarce. In Japan and the United States, however, large areas where *Diphylleia* grows are under protection in national forests and national parks, and the plants are in no danger of extirpation.

ECONOMIC IMPORTANCE

In China, where *Diphylleia sinensis* has long been used as a folk remedy, the rhizomes are collected during the summer or fall, cut into slices, and dried in the sun. An infusion of the rhizomes has been employed in the treatment of injuries from falls; chewing and swallowing the rhizome has been a remedy for stomach trouble. The rhizome, however, contains poisonous substances, and care should be taken in using it; it should not be taken during pregnancy (Fu, 1976; Anonymous, 1974). It has also been reported (Anonymous, 1974) that the rhizome has been employed in treating lumbago, rheumarthritis, "menoxenia," and gynecologic ailments, and that the roots are useful in lowering fever, detoxification, dissolving blood clots, and improving circulation.

Diphylleia grayi is occasionally cultivated as an ornamental plant in Japan. Lloyd and Lloyd (1887, p. 120), commenting on *D. cymosa*, stated "It is not an article of commerce, there being no demand for it."

CHEMISTRY

Murakami and Matsushima (1961) investigated chemical compounds in the rhizomes of *Diphylleia grayi*. They reported podophyllotoxin, picropodophyl-

lin, β-apopicropodophyllin, kaempferol, quercetin, diphyllin, and an additional substance that they assumed to have a 4-arylnaphthalene skeleton. They believed that the constituents picropodophyllin and β-apopicropodophyllin were formed from podophyllotoxin during separation.

Lloyd and Lloyd (1887) noted that after evaporation, alcohol extractions of the rhizomes of *Diphylleia cymosa* produced a bitterish, acrid-tasting resin similar to that obtained from *Podophyllum peltatum*. They also reported that *Diphylleia* extracts had no medicinal properties, in contrast to those of *Podophyllum*, and (p. 120) "careful investigations demonstrated that no trace of an alkaloid or other interesting constituent existed in the plant."

More recent investigations by Kimura (1963) revealed that extracts of *Diphylleia grayi* contain substances similar to colchicine and podophyllin that produce an antimitotic effect on cancer cells of MTK-sarcoma III, Yoshida-sarcoma, and Ehrlich ascites carcinoma: the cells die without progressing beyond metaphase, thereby causing regression in tumors. Toyokuni and Toyokuni (1964) used this evidence as a basis for a classification of the Podophyllaceae in which they recognized two subfamilies. One, the Podophylloideae, contains podophyllin or podophyllinlike substances that inhibit tumors; the other, the Glaucidioideae, contains no podophyllinlike substances and has no effect on tumors. They considered the Podophylloideae to contain two genera, *Podophyllum* (nine species) and *Diphylleia* (*D. cymosa* and *D. grayi*). The sole member of their Glaucidioideae is *Glaucidium palmatum* Sieb. & Zucc.

ANATOMY

Material used in this study consisted of flowers, buds, and vegetative parts of *Diphylleia cymosa* and *D. grayi*, and fruiting peduncles and pedicels of *D. sinensis*, all preserved in FAA. Voucher specimens are cited in APPENDIX 1. Methodology was the same as in Terabayashi (1983). For a more detailed description of the anatomy of *Diphylleia*, that paper should be consulted.

RHIZOME AND ROOT

Kumazawa (1930) discussed the anatomy of the rhizome and root in *Diphylleia grayi*. Our study confirms Kumazawa's findings and shows the root and rhizome anatomy of *D. cymosa* and *D. grayi* to be similar. Secondary xylem elements and an interfascicular cambium are not produced, and the phellogen in the rhizome is subepidermal in origin. The roots of *Diphylleia* are adventitious and about 1 mm in diameter. The stele of the roots in *D. grayi* and *D. cymosa* is usually tetrarch (see FIGURE 1), with secondary xylem elements rarely produced. According to Zhong Guo Yixui Gexui Yuan Yowu Lianjuoso (1979) the root of *D. sinensis* differs from those of the other two species in having a pentarch stele.

STEM

Studies of Harvey-Gibson and Horsman (1919), Himmelbaur (1913), Kumazawa (1930), and Worsdell (1908) showed that *Diphylleia* is among a small number of dicotyledonous genera having the monocotyledonous feature of

TABLE 1. **Plants characteristically associated with Diphylleia.***

CHINA **D. sinensis**	JAPAN **D. grayi**†	UNITED STATES **D. cymosa**
Abelia dielsii		
Abies fargesii	*Abies mairesii*	*Abies fraseri*
	Abies veitchii	
Acer caudatum	*Acer rufinerve*	*Acer pensylvanicum*
var. *multiserratum*	*Acer tschonoskii*	*Acer saccharum*
Acer tetramerum	*Acer ukurunduense*	*Acer spicatum*
Actaea asiatica	*Actaea asiatica*	*Actaea pachypoda*
		Aesculus octandra
		Arisaema triphyllum
Asarum caudigerum		
Athyrium fallaciosum	*Athyrium* spp.	*Athyrium asplenioides*
Athyrium filix-femina		
Betula albo-sinensis	*Betula ermanii*	*Betula alleghaniensis*
var. *septentrionalis*		*Betula lenta*
Betula fargesii		
Cacalia roborowskii	*Cacalia adenostyloides*	*Cacalia muhlenbergii*
Cardamine engleriana		*Cardamine clematitis*
Caulophyllum robustum	*Caulophyllum robustum*	*Caulophyllum thalictroides*
Chrysosplenium micro-spermum		
Cimicifuga foetida		*Cimicifuga racemosa*
Circaea alpina	*Circaea alpina*	*Circaea alpina*
subsp. *imaicola*	subsp. *alpina*	subsp. *alpina*
Clintonia udensis	*Clintonia udensis*	*Clintonia umbellulata*
	Coptis trifolia	
		Disporum lanuginosum
Dryopteris sinofibrillosa	*Dryopteris austriaca*	*Dryopteris austriaca*
	Dryopteris crassirhizoma	*Dryopteris intermedia*
	Fagus crenata	*Fagus grandifolia*
	Glaucidium palmatum	
Kingdonia uniflora		
	Kinugasa japonica	
Ligularia stenocephala		
	Lindera umbellata	*Lindera benzoin*
Liriodendron chinensis		*Liriodendron tulipifera*
Lonicera kungeana		
		Magnolia acuminata
		Magnolia fraseri
	Oxalis acetosella	*Oxalis acetosella*
Panax pseudo-ginseng		
var. *bipinnatifidus*		
Paris thibetica	*Paris polyphylla*	
	Paris tetraphylla	
Peracarpa carnosa	*Peracarpa carnosa*	
var. *circaeoides*	var. *circaeoides*	
Picea wilsonii	*Picea jezoensis*	*Picea rubens*
	Plagiogyria matsumureana	
Polygonatum roseum		*Polygonatum pubescens*
	Polystichum retrorso-paleaceum	*Polystichum acrostichoides*
Prunus gracilifolia	*Prunus grayana*	*Prunus serotina*
Pseudocystopteris spinulosa		

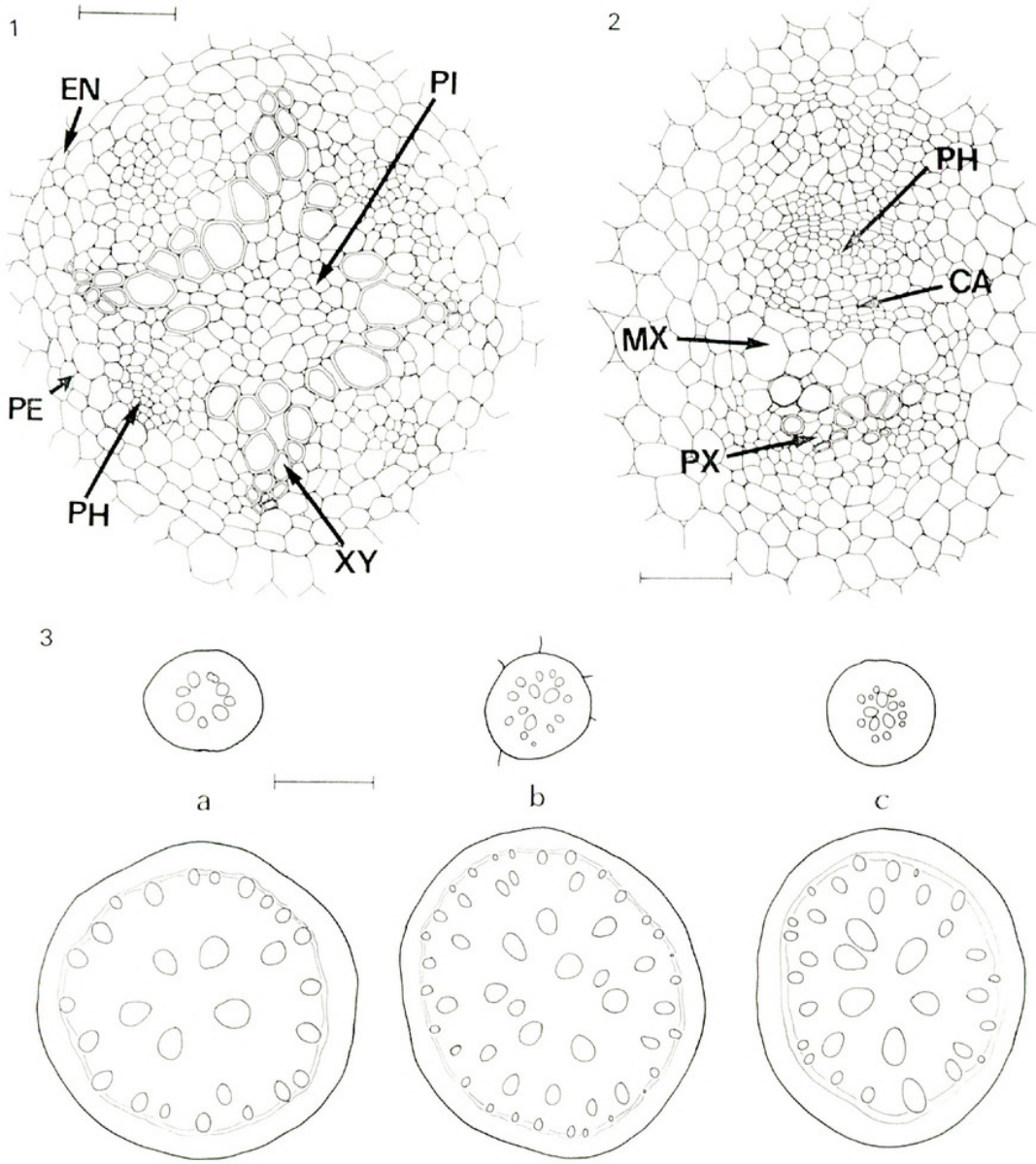
TABLE 1 *(continued).*

CHINA **D. sinensis**	JAPAN **D. grayi**†	UNITED STATES **D. cymosa**
Rhododendron concinnum		*Rhododendron maximum*
Rhododendron fargesii		*Rhododendron catawbiense*
Rhododendron purdomii		
Ribes glaciale		*Ribes rotundifolia*
Rosa omeiensis		
Salix cathayana		
		Saxifraga micranthidifolia
Schisandra incarnata		
Schisandra sphenanthera		
Sinarundinaria indica		
Smilacina henryi		*Smilacina racemosa*
Smilacina japonica	*Smilacina japonica*	
Sorbus koehneana		
	Streptopus streptopoides var. *japonicus*	*Streptopus roseus*
Thalictrum ichangense		*Thalictrum clavatum*
Thalictrum przewalskii		
Tiarella polyphylla	*Tiarella polyphylla*	*Tiarella cordifolia* subsp. *cordifolia*
		Tilia americana (incl. *T. heterophylla*)
	Trautvetteria japonica	*Trautvetteria caroliniana*
Trillium tschonoskii	*Trillium smallii*	*Trillium erectum*
		Trillium grandiflorum
		Trillium vaseyi
Triosteum himalayanum		
Tsuga chinensis	*Tsuga diversifolia*	*Tsuga canadensis*
Vaccinium japonicum var. *sinensis*	*Vaccinium japonicum* var. *japonicum*	*Vaccinium erythrocarpum*
Viburnum betulifolium		
Viola acuminata		

* Author names have been omitted to save space.

† Partially from Hara (1959), Numata (1974), and Numata *et al.* (1972).

scattered vascular bundles in the stem stele. The aerial stem in all three species is about 10 mm in diameter and contains 70 to 80 scattered vascular bundles in the portion below the leaves; between 40 and 50 vascular bundles occur in the internodal region (see FIGURE 4). The interior bundles are larger and mature earlier than those near the periphery. A sclerenchymatous ring, in which the phloem of the outer small bundles is embedded, is found near the periphery of the mature aerial stem. Kumazawa (1930, 1932) reported that the inner bundles give rise to the leaf traces in *D. grayi*. The same is true in *D. cymosa*. After the separation of traces to the upper leaf, a rearrangement of the vascular bundles occurs so that there are two concentric circles of vascular bundles in the peduncle. This configuration persists through the pedicel in *D. grayi* and *D. sinensis*, but in *D. cymosa* one circle is lost during branching of the inflorescence, so the stele of the pedicel consists of only a single circle of vascular bundles (FIGURE 3). Where two circles of vascular bundles occur, the bundles



FIGURES 1–3. Cross sections. 1, *Diphylleia grayi*, root, showing tetrarch stele (EN, endodermis; PE, pericycle; PH, phloem; PI, pith; XY, xylem; scale = 0.1 mm). 2, *D. grayi*, vascular bundle in stem (MX, metaxylem (slightly immature in this sample); PX, protoxylem; PH, protophloem; CA, inactive cambium; scale = 0.1 mm). 3, vasculature of peduncles (below) and pedicels (above), scale = 1 mm; a, *D. cymosa* (note single circle of vascular bundles in pedicel); b, *D. grayi*; c, *D. sinensis*.

in the inner circle are larger than those of the outer. A cross section of a single vascular bundle in the stem of *D. grayi* is shown in FIGURE 2.

LEAF

The petiole of *Diphylleia* is stemlike, with scattered vascular bundles. There are 40 to 50 vascular bundles in the petiole of the lower leaf, and 20 to 30 in

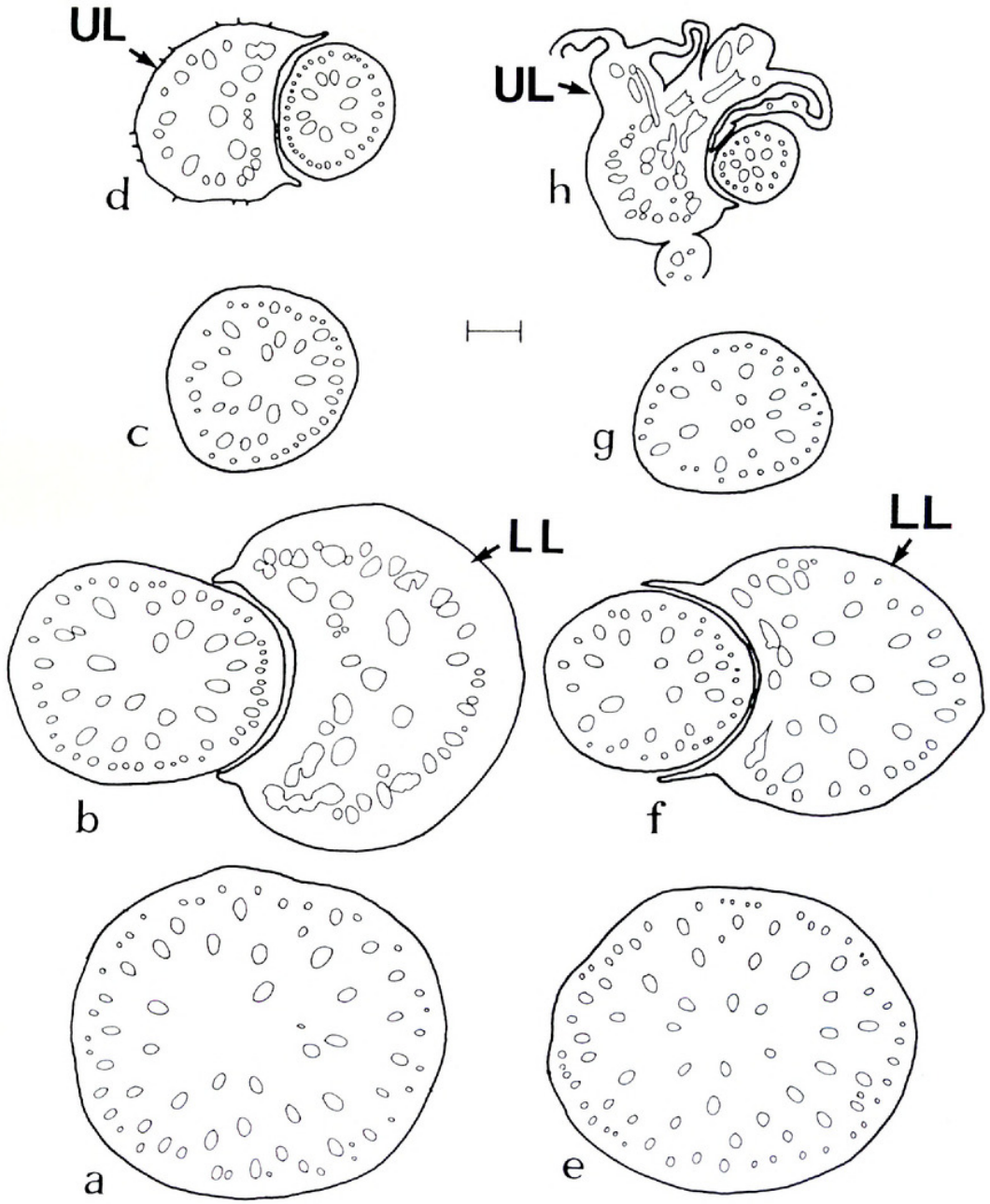


FIGURE 4. Cross sections of aerial shoots of *Diphylleia* showing vasculature: a–d, *D. cymosa*; e–h, *D. grayi* (note sessile upper leaf in h). a and e, near ground level; b and f, just above node of lower leaf; c and g, internodal region; d and h, just above upper leaf. Scale = 1 mm.

that of the upper leaf. The petioles are round in cross section from about the middle upward, but the lower portion shows dorsiventrality in both external and internal morphology (FIGURE 4).

The anatomy of the leaf blades in *Diphylleia grayi* and *D. cymosa* was studied by Oganozova (1974), who found the mesophyll of *D. cymosa* to be ca. 0.07 mm thick, with the palisade layer one cell thick and the spongy tissue four

cells thick. He reported the number of stomata of the lower epidermis to be 25 per mm^2 in *D. cymosa* and 24 per mm^2 in *D. grayi*.

The leaves are folded umbrellalike in bud in *Diphylleia*, as they are in *Podophyllum* and *Dysosma* Woodson. Kumazawa (1937) indicated that in *Podophyllum* and *Dysosma* the summit of the folded leaf is at the position of attachment to the petiole, although in *Diphylleia* the fold in the leaf is above the point of attachment.

FLOWER

Terabayashi (1983) examined the floral vasculature of *Diphylleia cymosa* and *D. grayi* in detail. Unfortunately, in both his study and ours flowering material of *D. sinensis* was unavailable for comparison. In *D. grayi* the double circle of vascular bundles in the pedicel continues into the receptacle; the inner circle contains the main bundles. In *D. cymosa*, where the pedicellate stele is composed of a single circle of vascular bundles, an outer circle of bundles arises from the stelar bundles at the lowest level of the receptacle, so the receptacle contains the two circles of bundles as in the peduncle and stem. No major differences are seen in the trace patterns to the sepals, petals, stamens, and pistils in the two species. The traces to the outer sepals originate mainly from the outer circle of vascular bundles, while those to the inner sepals, petals, and stamens usually derive from adjacent bundles in the inner circle. In exceptional cases, weak bundles from the outer circle may fuse with the petal traces. The pistil is traversed by a few ventral bundles and a dorsal bundle that extends to the stigmatic region. The ovary wall is covered by a network of veins. The ovular traces arise from ventral bundles, while those in the placental region originate from bundles other than ventral bundles.

Chapman (1936) and Kaute (1963) studied pistil anatomy in *Diphylleia* and interpreted the pistil as being pseudomonomerous. Kaute (1963) observed abnormally dimerous pistils with a single locule but with two placentas in *D. cymosa*. Such abnormally dimerous pistils were also observed in *D. grayi* by Terabayashi in this study. The monomerous pistil in *Diphylleia* may have been derived from a dimerous pistil through reduction.

EMBRYO

In *Diphylleia cymosa* the ovule is bitegmic and crassinucellate; embryo sac formation is of the Polygonum type, and pollen formation is simultaneous (Mauritzon, 1936). Terabayashi found the ovular morphology and embryo sac formation in *D. grayi* to be the same as in *D. cymosa*. The seed coat of *D. grayi* is exotestal, according to Corner's terminology (Corner, 1976; Takhtajan & Melikian, 1972).

SEEDLING

The seedlings of *Diphylleia* are characterized by long "cotyledonary tubes" (Himmelbaur, 1913; Terabayashi, in prep.). The cotyledon is two-parted, with the "cotyledonary tube" and an orbicular lamina. The plumule is hypogeal. The seedling does not produce foliage leaves during the first year after germination. The stele in the radicle and hypocotyl is diarch.

CYTOLOGY

The number and karyotype of the chromosomes of *Diphylleia grayi* are well known. Counts of $2n = 12$ have been reported in this species by Kurita (1956), Kuroki (1967), Matsuura and Suto (1935), Miyagi (1930), S. Noda and Fujimura (1970), Noguchi and Kawano (1974), and Soeda (1942). The anomalous count of $2n = 16$ attributed to Lee (1967) is in error. Lee reported $2n = 16$ for *Caulophyllum robustum* Maximowicz; this count was later mistakenly reported as being for *D. grayi* by Noguchi and Kawano (1974). As far as we have been able to determine, Lee did not examine chromosomes in *Diphylleia*.

The single report (Langlet, 1928) of $2n = 12$ for *Diphylleia cymosa* was determined from plants in cultivation in Europe. Langlet considered *Diphylleia* to be monotypic, with *D. cymosa* as the sole species. Although it can be assumed that the material he was working with—and probably the species in cultivation in Europe at the time—was *D. cymosa*, there is no way to prove this. Langlet did not cite vouchers for his cytological studies, and we saw no specimens collected or annotated by him among those that we examined. Until Langlet's report can be verified, it seems best not to attribute counts to *D. cymosa*.

No counts have been made of the Chinese *Diphylleia sinensis*. Chromosome counts of *Diphylleia* are summarized in TABLE 2.

Kurita (1956), Kuroki (1967), S. Noda and Fujimura (1970), and Noguchi and Kawano (1974) reported similar karyotypes in plants of *D. grayi* collected from widely separated populations in Hyogo, Iwate, and Tochigi prefectures, Japan. All reported two pairs of large (length 10.7–15.5 μm; all measurements from Kurita, 1956, and Kuroki, 1967), metacentric chromosomes, one pair of medium (length 9–11.1 μm), submetacentric chromosomes, and one pair of medium (length 8.4–10.8 μm), submetacentric chromosomes with a constriction at the midpoint of the shorter arm (Noguchi and Kawano (1974) reported the constriction to be at the distal end of the short arm, but their illustration shows it to be more nearly medial). Of the two remaining pairs, all of the authors reported them as being small (length 6.3–7.6 μm), with one pair being telocentric and the other having a subterminal constriction. Soeda (1942) found an additional constriction on the short arm of the small, telocentric chromosome, but none of the other authors mentioned this.

S. Noda and Fujimura (1970) also examined mitosis in developing seeds. In the plants in their study, they found that fruit-set was about 60 percent, but only 21.1 percent of the ovules developed into mature seeds. They (pp. 2549, 2551) attributed this high sterility to an ". . . asynchronization of mitosis" that they observed in endosperm tissue.

PALYNOLOGY[1]

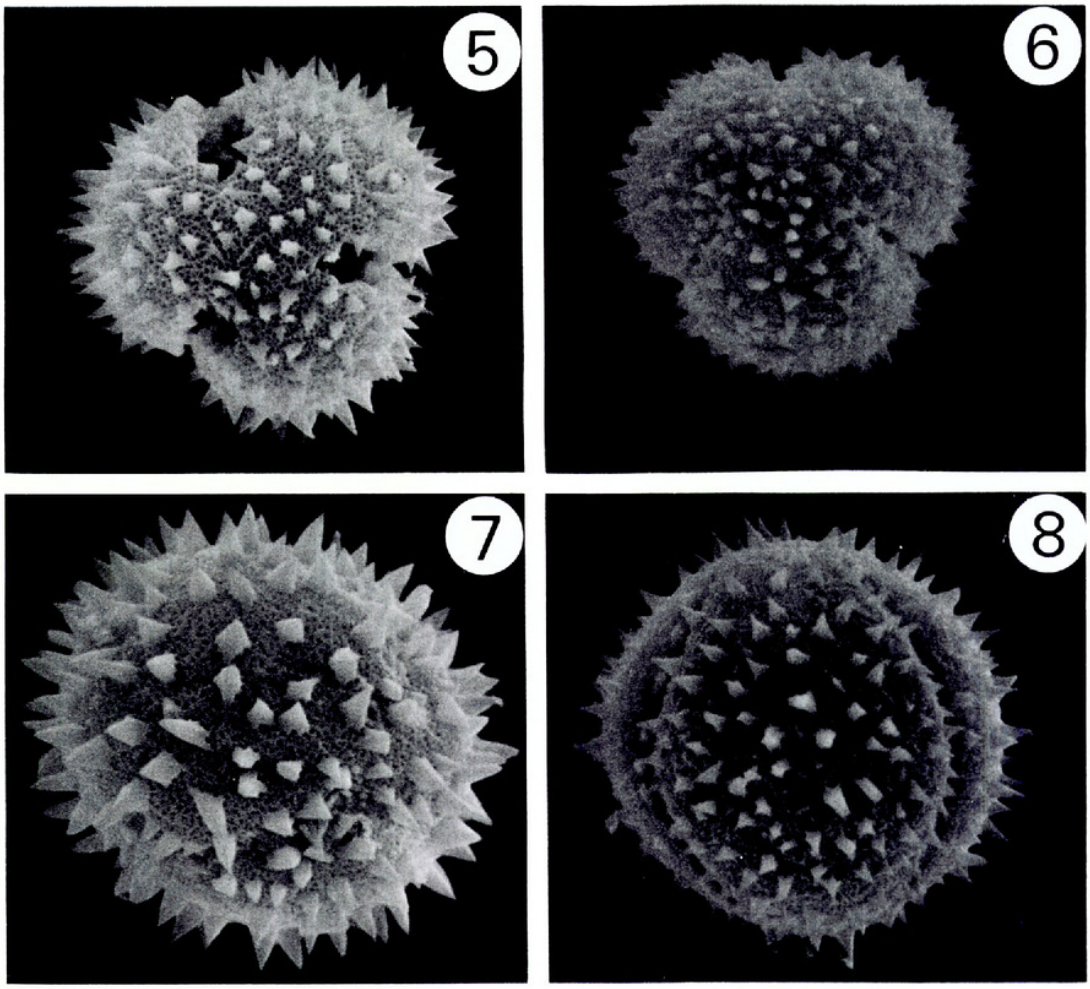
Pollen samples were collected from unopened buds or young flowers on herbarium specimens (see APPENDIX 2 for vouchers) of three sheets each of *Diphylleia cymosa, D. grayi,* and *D. sinensis*. The samples were acetolyzed

[1]Contributed by Masamichi Takahashi, Biological Institute, Faculty of Education, Kagawa University, Takamatsu-shi 760, Japan.

TABLE 2. **Reported chromosome counts for Diphylleia.**

TAXON	CHROMOSOME NUMBER	LOCALITY	REFERENCE	VOUCHER*
D. cymosa	$2n = 12$	U. S. A.†	Langlet, 1928	S
D. grayi	$2n = 12$	Japan, moist forest in mountains of N Japan	Miyagi, 1930	KIEL
	$n = 6$	Japan, Hokkaido, Ishikari Shicho, Mt. Moiwa	Matsuura & Suto, 1935	SAP
	$2n = 12$	Japan, Hokkaido	Soeda, 1942	SAPS
	$2n = 12$	Japan, Honshu, Tochigi Pref., Mt. Shirane	Kurita, 1956	Ehime Univ.
	$2n = 12$	Japan, Honshu, Iwate Pref., Hachimantai	Kuroki, 1967	Ehime Univ.
	$2n = 12$	Japan, Honshu, Hyogo Pref., Hyono-sen	S. Noda & Fujimura, 1970	?
	$2n = 12$	Japan, Honshu, Tochigi Pref., Nikko	Noguchi & Kawano, 1974	Toyama Univ.

* No voucher specimens were cited in any of the reports. If vouchers exist, they are probably in the herbaria indicated.
† See text.

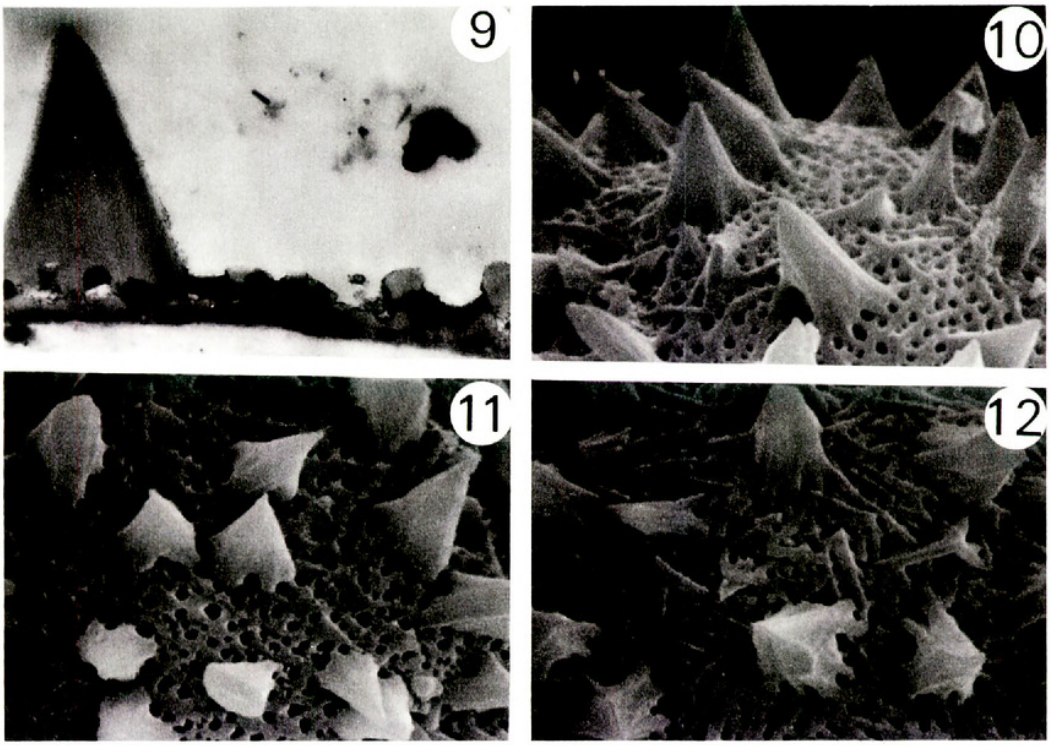


FIGURES 5–8. SEMs of pollen of *Diphylleia*, all × 1400: 5, *D. cymosa* (*J. K. Small s.n.*, 28–29 May 1892), polar view; 6, 8, *D. sinensis* (*Licent 5325*), polar and equatorial views; 7, *D. grayi* (3 July 1952, *A. Kimura & S. Sugaya s.n.*, 3 July 1952), inaperturate.

according to procedures outlined in Erdtman (1960), dehydrated in ethanol, transferred to amyl acetate, and critical-point dried. They were then coated with gold by using an ion sputtering apparatus (Damblon, 1975) and examined with an Akashi MSM-101 scanning electron microscope.

For transmission electron microscopy (TEM) the pollen was fixed in 1 percent osmium tetroxide, dehydrated in an ethanol–propylene oxide series, and embedded in a low-viscosity Epon mixture according to the method of Spurr (1969). Glass knives were used for sectioning on an LKB ultratome. The unstained sections were examined with a Hitachi H-500 transmission electron microscope.

Pollen of *Diphylleia* has been examined by Kumazawa (1936) and Ikuse (1956), who used light microscopy, and by Nowicke and Skvarla (1981), who used light microscopy and scanning and transmission electron microscopy, but none of these authors examined all three species. *Diphylleia* is unique in the Berberidaceae *s.l.* in having spinose pollen grains. Pollen features support other



FIGURES 9–12. Pollen surface ornamentation in *Diphylleia*. 9, TEM, *D. grayi* (*H. Takahashi 366*), section through spine, × 12,000. 10–12, SEMs, all × 3670: 10, *D. cymosa* (*Kologiski & Perino 165*); 11, *D. grayi* (*A. Kimura & S. Sugaya s.n.*, 3 July 1952); 12, *D. sinensis* (*Nan-shui–Bei-diao Team 7164*).

data that indicate a closer relationship between *D. cymosa* and *D. sinensis* than between either of these two and *D. grayi*. In gross morphology, pollen of *D. cymosa* and that of *D. sinensis* are basically the same (FIGURES 5, 6, 8): both are tricolpate or rarely hexarugulate. In contrast, the pollen of *D. grayi* (FIGURE 7) has irregular apertures, which is the same as that reported by Nowicke and Skvarla (1981) in several species of *Berberis* L. and *Mahonia* Nutt. Kumazawa (1936) reported finding some pollen grains of *D. grayi* that had less densely staining spineless, "round areas" containing densely staining "punctations" that he regarded as the germinating pores, while Ikuse (1956) found pollen of *D. grayi* to be polyforate, 34–36 μm in diameter, and with spines 2.5 μm long. In exine ornamentation, however, *D. cymosa* is more similar to *D. grayi* than to *D. sinensis*. The exine of the first two species is characterized by stout spines 1.5–4.5 μm long, while that of *D. sinensis* has slender spines 0.5–2.8 μm long. This difference between *D. cymosa* and *D. sinensis* was also noted by Nowicke and Skvarla (1981). FIGURES 9–12 show exine ornamentation of the pollen of the three species, while TABLE 3 gives pollen size of the samples examined in this study.

TAXONOMIC HISTORY

Diphylleia was first discovered by André Michaux in North Carolina and was described and illustrated in his *Flora Boreali-Americana* (1803). Plants of

TABLE 3. **Pollen size in Diphylleia.***

COLLECTION	POLLEN DIAMETER (μm)	SPINE LENGTH (μm)
D. cymosa		
Kologiski & Perino 165	36.7 ± 2.5 × 32.6 ± 2.7	1.5–4.5
J. K. Small s.n., 28–29 May 1892	32.5 ± 2.5 × 29.7 ± 2.0	1.5–3.7
Radford 5239	35.8 ± 2.4 × 31.1 ± 2.3	1.5–3.8
D. grayi		
Takahashi 366	34.9 ± 2.7 × 31.5 ± 2.2	1.5–4.2
Kimura & Sugaya s.n., 3 July 1952	37.7 ± 1.7 × 33.3 ± 2.2	1.5–4.7
Saito & Kaneko s.n., 18 May 1961	35.0 ± 2.2 × 30.5 ± 2.5	1.4–4
D. sinensis		
Delavay 3862	31.3 ± 2.3 × 30.2 ± 1.7	0.5–2.0
Nan-shui–Bei-diao Team 7164	30.1 ± 2.5 × 28.5 ± 2.6	0.7–2.5
Licent 5325	29.6 ± 2.1 × 28.4 ± 2.0	0.5–2.8

* Thirty pollen grains were measured from each specimen.

Diphylleia from Japan and Sakhalin were probably first collected around 1855 by C. Wright and J. Small; Asa Gray (1859) considered them to be conspecific with the North American *D. cymosa*—an opinion shared by Diels (1900). Schmidt (1868), however, recognizing the plants from Sakhalin to be different from Michaux's *D. cymosa*, described them as *D. grayi*, and Kitamura and Murata (1962) subsequently treated them as a subspecies of *D. cymosa*. Augustine Henry apparently first collected *D. sinensis* in 1888 in what is now the Shennongjia Forest District in northwestern Hubei Province (Henry *in* Thiselton-Dyer, 1889), but he believed the plants he found to be *D. grayi*. Authors subsequent to Henry treated these plants from central China as either *D. cymosa* or *D. grayi* until 1947, when Li described them as *D. sinensis*.

Since the characters that can be used to separate the three taxa are discontinuous, we prefer to treat them as three distinct species.

RELATIONSHIPS AND PLACEMENT OF DIPHYLLEIA

The familial placement of *Diphylleia* has been controversial. Schultz (1832) was the first to place *Diphylleia* in a separate family, the Diphylleiaceae (in which he also placed *Sarracenia*!), while Tischler (1902) proposed that the two genera *Diphylleia* and *Podophyllum* (which included the then-undescribed *Dysosma*) represented the family Podophyllaceae. In this, Tischler has been followed by Hutchinson (1969), Takhtajan (1969), and Airy Shaw (1965), although Hutchinson and Airy Shaw expanded the concept of the Podophyllaceae to include most or all of the herbaceous genera of Berberidaceae. Engler (1903) established a new subfamily in the Berberidaceae, the Podophylloideae, in which he placed *Diphylleia* and all other herbaceous members of the family.

His treatment was followed by Ernst (1964) and Thorne (1968). Cronquist (1968, p. 365) placed the Podophyllaceae (presumably including *Podophyllum* and *Diphylleia*) in his Ranunculaceae but later (1981, p. 126) returned them to the Berberidaceae.

Despite the controversy that exists over the familial placement of *Diphylleia*, there has been little doubt concerning its closest generic relatives. Based on chromosomal, anatomical, and chemical evidence, as well as on overall morphological similarity, *Diphylleia* unquestionably has its greatest affinities with *Podophyllum* and *Dysosma*. Meacham's (1980) study supports this view. However, Nowicke and Skvarla (1981), using palynological evidence, do not feel that these genera are particularly close.

POSSIBILITIES FOR FURTHER STUDIES

Perhaps one of the most interesting studies that could be undertaken with *Diphylleia* would be one dealing with reproductive biology. As far as we have been able to determine, there have been no investigations of this topic. The spinose pollen grains (like those of the Compositae) and the showy clusters of flowers that are held high above the forest floor in early spring strongly suggest insect pollination. However, as in many other herbaceous plants of mixed deciduous forests, the extensive rhizome system also suggests a degree of vegetative reproduction that might account for the large colonies encountered in *D. cymosa* and *D. grayi*. The plants occurring singly or in open colonies in *D. sinensis* possibly indicate a greater dependence on reproduction by seed than by vegetative means, especially since individuals are often found several meters apart. In connection with reproductive biology, it would be of interest to know whether plants are self compatible and, if so, to what extent outcrossing takes place. Study of inter- and intraspecific crosses and knowledge of chromosome behavior in any resultant hybrids are also desirable. Chromosome counts and karyotype analyses of *D. cymosa* and *D. sinensis* would enable comparison with the cytologically well-known *D. grayi*.

Chemical analysis and comparison of the three species could also provide useful information. Except for the above-mentioned work of Murakami and Matsushima (1961), Kimura (1963), and Toyokuni and Toyokuni (1964), we are unaware of any chemical studies involving *Diphylleia*. Comparative flavonoid studies might prove useful, especially in light of the differences among the three taxa revealed by other comparative studies. Comparative evidence from any of the above areas would improve our understanding of the relationships of the three species and could also make possible more detailed comparisons between *Diphylleia* and other genera of the Berberidaceae.

TAXONOMIC TREATMENT

Diphylleia Michaux, Fl. Bor.-Amer. **1**: 203. *pls. 19, 20.* 1803.

Perennial herbs with thickened, creeping rhizomes and coarse, fibrous roots, the rhizomes formed of distinct annual increments, producing stout, 2- (rarely

3-)leaved stem that separates at base in autumn along marked articulation, leaving broad, bowllike excavation on rhizome. Leaves alternate; blade petiolate and peltate (except upper leaf in *Diphylleia grayi*, which is sessile or subsessile and attached at sinus), transversely oblong to reniform-orbicular, 2-cleft with divisions shallowly to coarsely lobed and prominently dentate, palmately veined with main veins connected by secondary, reticulate veins, pubescent or sparsely pubescent with unicellular hairs. Inflorescence a terminal, pedunculate (peduncle rarely branched below), usually many-flowered cyme or umbel, the branches glabrous or pubescent. Flowers pedicellate, actinomorphic, 3-merous; sepals 6 in 2 (rarely 3) whorls, white or pale green, deciduous prior to or just at anthesis; petals 6 in 2 whorls, white; stamens 6, antipetalous, the anthers basifixed, longitudinally dehiscent, the thecae separating from connective and ultimately attached only at apex, the pollen conspicuously spiny; ovary superior, ellipsoid, unilocular, the style absent or very short and thickened, the stigma peltate, cristate, the placentation parietal near base of ovary, the ovules 2 to 11, anatropous. Fruit a globular or broadly ellipsoid berry, dark blue, glaucous, to 1 cm broad, borne on thickened, disclike, lobed receptacle. Seeds oblong to ovoid, rounded on all sides or flattened to concave ventrally, straight or slightly curved, surface minutely rippled and microscopically striate. Embryo straight or slightly curved, ca. 2–4 mm long, with 2 cotyledons, embedded in endosperm. Chromosome number: $n = 6$.

TYPE SPECIES. *Diphylleia cymosa* Michaux.

A genus of three species, with one in each of three widely disjunct areas: the southern Appalachian Mountains of the southeastern United States; central and northern Japan, Sakhalin, and the southern Kuril Islands (Kunashiri Island); and central and southwestern China.

KEY TO THE SPECIES OF DIPHYLLEIA

1. Inflorescence glabrous; ovules 2 to 4; leaves glabrous or sparsely pubescent. ..... 1. *D. cymosa.*
1. Inflorescence pubescent; ovules 5 to 11; leaves pubescent.
   2. Upper leaf distinctly petiolate, the petiole more than 2.5 cm long; petals less than 9 mm long and 6 mm wide; flowers usually 15 or more. ..... 2. *D. sinensis.*
   2. Upper leaf sessile or with petiole less than 1 cm long; petals more than 8 mm long and 6 mm wide; flowers usually 12 or fewer. ..... 3. *D. grayi.*

1. **Diphylleia cymosa** Michaux, Fl. Bor.-Amer. **1:** 203. 1803. FIGURE 13.

Plants 4–12 dm tall, growing in dense or loose colonies, occasionally as scattered individuals. Petiole 7–22 cm long in lower leaf, 3–15 cm long in upper; blade peltate, suborbicular, reniform or transversely oblong, deeply cleft at apex and base, 14–30 by 19–47 cm in lower leaf and 9.5–33 by 13–42 cm in upper, deeply cut to lobed at margin and coarsely doubly serrate, sparsely pubescent along main veins beneath or glabrescent, usually glabrous above or with few hairs along main veins. Peduncle solitary, occasionally bifurcate, 0.6–3.3 cm long, glabrous; inflorescence 7.5–41 cm long including peduncle, 3.7–

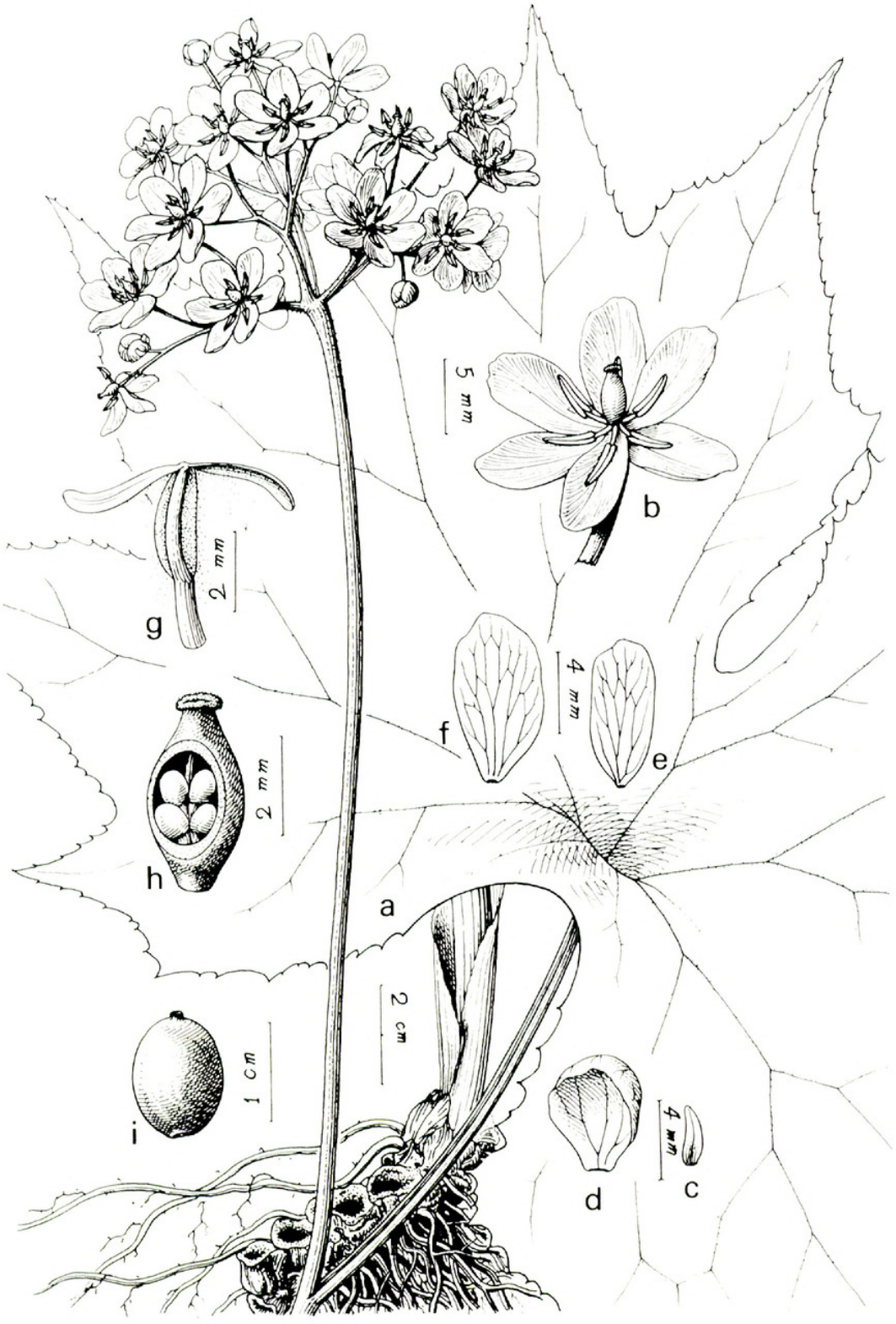


FIGURE 13. *Diphylleia cymosa* (based on *Chinese-Amer. Exped. 853*, PE): a, upper leaf, inflorescence, rhizome, roots; b, flower; c, outer sepal; d, inner sepal; e, outer petal; f, inner petal; g, stamen; h, ovary; i, fruit.

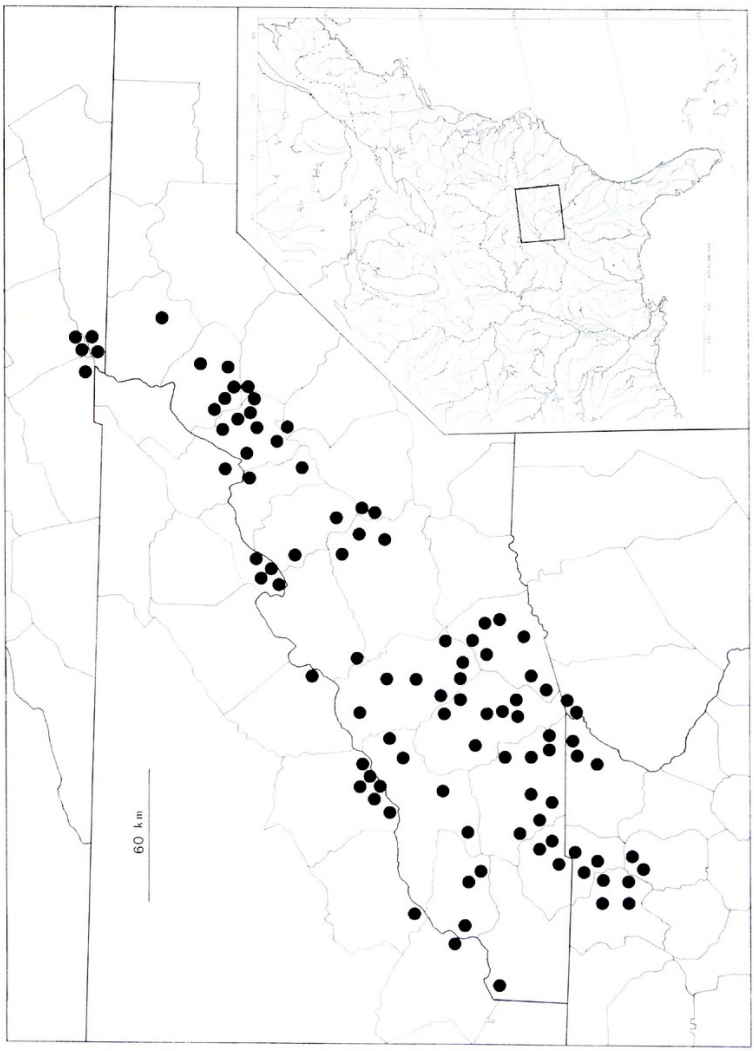
14 cm wide, glabrous (rarely with few scattered hairs when young). Flowers (6 to) 14 to 70 or more; pedicels 0.8–4 cm long; outer sepals lanceolate, oblanceolate to spatulate, or reduced and scalelike, ca. 1.7–4.5 by 0.4 mm; inner sepals obovate to suborbicular, 2.5–6 by 3.5–4 mm; outer petals narrowly obovate, 9–11 by 4.5–6 mm; inner petals elliptic-obovate to obovate, 10–13 by 6–7 mm; stamens 3.6–4.5 mm long, filaments 1–2 mm long, anthers ca. 2 by 1.2 mm; ovary ellipsoid, 3.5–5 by 2–2.5 mm, style ca. 0.3 mm long, stigma ca. 0.5 by 1 mm. Berry globular to very broadly ellipsoid, 0.5–1.2 cm broad, blue, glaucous, on pedicel 1–3.8 cm long. Seeds 2 to 4, ± oblong, 3.9–7 by 2–4.7 mm, rounded dorsally, flattened to concave ventrally. Chromosome number: $n = 6$ (but see under cytology above).

TYPE. United States, mountains of North Carolina, 1786?, *A. Michaux s.n.* (lectotype, P, photo A; isolectotype, P).

DISTRIBUTION AND ECOLOGY. Moist places in mixed deciduous and coniferous forests, often along seepages and small streams, 1000–1650 m alt. United States: southwestern Virginia, western North Carolina, and eastern Tennessee to northeastern Georgia and extreme northwestern Oconee County, South Carolina; restricted to Blue Ridge of southern Appalachian Mountains. (MAP 1.)

SPECIMENS EXAMINED. **United States.** GEORGIA. Rabun Co.: Rabun Bald, 34°57′N, 83°18′W, *Boufford & E. W. Wood 17033* (NCU); along Darnell's Creek SE of Dillard, *Duncan & McDowell 10852* (GA); 2 mi N of Clayton, *Pyron & McVaugh 847* (GA). Towns Co.: N-facing slope, Hogpen Gap, Richard Russell Scenic Hwy., *Coile 346* (NCU); N-facing ravine just N of summit of Hightower Bald, *Duncan 7597* (GA). Union Co.: 3 mi W of Vogel State Park, *Hardin 259* (GA); Brasstown Bald, *Howell 407* (US); Sosbee Cove, above Vogel State Park, *Kral 59676* (VDB); 1.5 mi from top of Brasstown Bald, *Lord 364* (NCU); cove E of Wolfpen Gap, *Pyron & Duncan 46* (GA); Blairsville, Lock Gap, *I. Stuckey s.n.* (VDB). White Co.: 2.5 map mi above jct. of Chattahoochee R. and Spoibine Creek, *Duncan & Hardin 16361* (GA); Hogpen Gap, off hwy. 348, *Wohlers 122* (GA). NORTH CAROLINA. "Mountains of North Carolina," *A. Michaux s.n.*, 1786? (Michaux herb. at P, IDC 6211. 47: I. 2, 3). Iron Mt., *Canby s.n.*, Sept. 1876 (NY). Ashe Co.: Bluff Mt., *Radford 44012* (NCU). Avery Co.: 1.2 mi SSW of Minneapolis on U.S. 19E, *Ahles & Ashworth 39451* (NCU); NNW of Linville, 1 mi SSW of jct. N.C. 184 and 105 on 105, *Ahles & Duke 43632* (NCU); Grandfather Mt., *Blomquist 3681* (DUKE), *Heller s.n.*, 22 July 1890 (LE, NY), *Mohr s.n.*, 28 July 1894 (US), *Mullen 81* (NCSC), *Seymour 91 8 13* (DUKE); ca. 7 mi ENE of Linville along U.S. route 221, *McVaugh 8937* (GA, NCU, VDB); 2 mi E of Linville along U.S. route 221, *Robertson & Umber s.n.*, 3 June 1973 (GH); vic. of Banner Elk, *Steele 18* (US); Linville Falls, *Weiss s.n.*, 30 May 1959 (VPI); NE of Linville, 3 km E of U.S. route 221 on county road 1514 (Edgemont Road), *E. W. Wood & Boufford 4150a* (BM, CM, KYO). Buncombe Co.: Craggy Mt., *Biltmore Herb. 1213*[b] (BM, GH, L, NCU, NY, US, W); Pisgah Natl. Forest, ca. 10 mi SE of Dillingham, *Boufford et al. 14417* (NCU); S flank Black Mt., *N. L. & Mrs. Britton s.n.*, 18 Sept. 1885 (NY); Black Mt., *Canby s.n.*, June 1868 (NY); Blue Ridge Pkwy. at Craggy Gardens, *Freeman 58196* (NY); wet woods in Craggy Gardens, *Hicks & Bartley 2248* (GH); Black Mts., *LeRoy s.n.* (NY), *Rugel 243* (BM); Graybeard Mt., *Pollard s.n.*, 16 May 1901 (US); Craggy Mts., *Rydberg 9446* (LE, NY). Burke Co.: near Linville, *Barkley & Hicks 2031* (NY, US). Caldwell Co.: NW corner of Caldwell Co. on U.S. 221, hwy. to Grandfather Mt., *Radford & Stewart 1575* (NCU). Cherokee Co.: 2.3 mi E of Tennessee state line on Tellico R. Road, *Pittillo & Floyd 5710* (WCUH). Clay Co.: near Perry Gap, ravine at end of U.S. Forest Service Road along Buck Creek (N of U.S. route 64), *Boufford et al. 14165* (NCU), *17001* (BM); ca. 15 mi E of

Haysville, Chunky Gal by U.S. route 64, *Kral 60290* (VDB); Chunky Gal Mt., W of Rainbow Springs on U.S. 64, *Pittillo et al. 4289* (WCUH); Buck Creek near U.S. 64, 2 mi SW of Clay-Macon Co. line, *Radford 12162* (NCU); Perry Gap Road above Buck Creek, 4 mi N of U.S. 64, *Fox & Godfrey 5056* (NCSC). Graham Co.: 5.1 mi N of jct. of Cherokee Co. roads 1391 and 1399 on U.S. Forest Service Road 423, *Boufford et al. 14518* (NCU); 4 mi E of Fontana, *Radford 11870* (NCU, VDB); 4 mi S of Robbinsville, *Radford 14196* (NCU); Joyce Kilmer Mem. Forest, *Tucker & Pittillo 141* (WCUH). Haywood Co.: Junaluska Mt., *Batchelder 5081, 5082* (GH); Junaluska Mt., Lake Junaluska, *Blomquist 3682* (DUKE); ca. 1.6 mi S of Sunburst on N.C. 215 along West Fork Pigeon R., *Boufford et al. 15041* (NCU); Mt. Sterling, *Caughey 716* (NCSC); Bill Camp Cove, *Couch s.n.*, 24 July 1926 (NCU); Jonathan Creek, *Pyron 63* (GA); Eagles Nest, *Ruth 367* (GH); Blue Ridge Pkwy. at Frying Pan Gap, *Smathers s.n.*, 25 June 1958, 22 June 1959 (WCUH); Balsam Mt., *J. D. Smith s.n.*, 11 Aug. 1882 (US); near Waynesville, Eagles Nest, *Standley 5459* (US); county road 1334 2.8 mi N of intersection with county road 1335, *Wyatt 267* (DUKE); Crabtree Bald, county road 1505 ca. 5 mi NE of intersection with N.C. route 209, *Wyatt et al. 598* (DUKE). Jackson Co.: 14.7 mi NW of N.C. route 215 on Blue Ridge Pkwy., *Boufford et al. 13529* (NCU); Balsam, *Braun s.n.*, 14 July 1911 (US); 5.2 mi S of Dillsboro on county road 1371, *Bryson 47* (WCUH); Tuckaseegee R., ½ way from Sylva to Cashiers, *Coker s.n.*, 21 Aug. 1939 (NCU); 10 mi S of Cullowhee P.O. on N.C. 107, *Crisp s.n.*, 29 June 1965 (WCUH); E of Glenville, Slatten Creek, *Godfrey & O'Connell 51951* (DUKE, NCSC); Soco Falls, *Hendrix B-22* (DUKE); 14 mi SSE of Cullowhee P.O. on N.C. route 107, *Hoffman 70* (WCUH); Mull Creek, *Murtagh 230* (WCUH); Nantahala Natl. Forest, N.C. route 107 at pipeline from Lake Thorpe, *Pittillo 2876* (E, FARM, GA, GH, NCU, NY, VDB, WCUH); Rough Butt Bald Mt., *Ramseur 389* (NCU); Wet Camp Gap, *W. B. & M. B. Schofield 8527* (DUKE); ca. 4 mi S of Thorpe Power Sta. on N.C. route 107, *Sharpe 26* (WCUH); above Glenville Power Plant, *B. Smith s.n.*, 10 May 1953 (WCUH); 15.1 mi S of Cullowhee P.O. on N.C. route 107, *Taylor 38* (WCUH). Macon Co.: Satulah, *L. B. s.n.*, 24 May 1934 (NCU); near Highlands, *Biltmore Herb. 1213* (GH, LE, NY, P, US, W), *1213*[c] (FI, G); under Dry Falls, *Coker & party s.n.*, 28 Aug. 1932 (NCU); near Rainbow Springs, *D. S. Correll 3522* (DUKE); 4.5 mi W of Fish Checking Sta. on Nantahala Forest Road, *Fox & Godfrey 3081* (NCSC); U.S. route 64 at Glade Gap, *Freeman 59143* (NCU); Highlands, *Gibbes s.n.*, July 1882 (NY), *Harbison s.n.*, 13 July 1901 (GH); county road 1678 2.2 mi from jct. with county road 1679, *Metheney 076* (WCUH); Cullasaja R. at Dry Falls, *Oosting 34427* (DUKE); Highlands, *Palmer 42502* (NY); county road 1001 S of Cullowhee Gap to Wildcat Road, E to Bryson Branch, *Pittillo 4050* (WCUH); 13 mi N of U.S. route 64 on Rainbow Springs–Aquone Forestry Road, *Radford 5239* (NCU); 4 mi N of Highlands, Cole Mt. Road, *Radford 6123* (NCU); Cullasaja Gorge, High Falls, *W. B. Schofield 8776* (DUKE); Crow Creek ca. 0.5 mi below Cullasaja Falls, *Stewart & Hechenbleikner s.n.*, 25 July 1938 (NCU); Stewart Trail between Bearpen and Albert Mt., *Stewart & Hechenbleikner s.n.*, 12 Aug. 1938 (NCU). Madison Co.: 0.2 mi N of Betsy Gap and Haywood Co. line on N.C. 209, *Bozeman et al. 9102* (GA, GH, NCU, NY, VDB). McDowell Co.: near Big Craggy on Blue Ridge Pkwy., *Ahles & Bell 17697* (NCU); Blue Ridge, *W. F. s.n.*, 1872 (GH). Mitchell Co.: Roan Mt., *Canby s.n.*, June 1868, June 1879 (NY), *Chickering s.n.* (US), *J. D. Smith s.n.*, 15 Sept. 1884 (GH, US), *Shallert s.n.*, 1927 (DUKE); Spruce Pine, *Hyams s.n.*, June 1878 (US); Little Roan, *Merriam s.n.*, 1 Sept. 1892 (US). Swain Co.: Great Smoky Mts. Natl. Park, Round Bottom Road from Heitooga Overlook, *Athey s.n.*, 16 May 1973 (VDB); 3.4 mi from N.C. hwy. 28 on Mica Knob Road, *Bell 3117* (NCU); Nantahala Gorge, 3 mi SE of Beechertown, *Radford et al. 8021* (NCU); Great Smoky Mts. Natl. Park, Smokemont, foot of Hughes Ridge, *Jennison 445* (GSMNP, TENN); Great Smoky Mts. Natl. Park, upper Chasteen Creek, *Jennison & J. G. Smith 2291* (GSMNP, TENN); Brookside, Rich Mt., *Hunnewell 10337* (GH). Transylvania Co.: Whitewater R. near jct. with Bohaynee Road bridge, *Bannister & Anderson 432* (NCU); near head of Davidson R. near Fish Rearing Sta., Pisgah Ranger Distr., *Beaman 50026* (NCSC); 2.7 mi N of N.C. 215 on Courthouse Creek Road (U.S. Forest Service



MAP 1. Distribution of *Diphylleia cymosa* in the United States.

Road 140), *Boufford & E. W. Wood 16283* (NCU); W Fork French Broad R., jct. U.S. 64 near Rosman, *Bozeman et al. 9122* (BM, TENN); on trail, Black Rock to Sapphire, *Coker s.n.*, 18 Aug. 1910 (NCU); Blue Ridge Pkwy. between Wagon Road Gap and Beech Gap, *Freeman 57326* (NCU); Pink Beds, *House 4008* (GH); road from Mt. Pisgah to Brevard, *Oosting 34686* (DUKE); Pisgah Ridge, U.S. route 276 1.8 mi below jct. with Blue Ridge Pkwy., *Roberts & Keil 7416* (VDB); Sapphire, NE-facing cove on Hogback Mt., *Ware & White 3055* (NCU, VDB). Watauga Co.: 1.2 mi E of Bamboo on road to Triplett, *Ahles & Ashworth 39619* (NCU); Blowing Rock, *H. L. B. 3680* (DUKE); Rich Mt. NW of Boone, N-facing cove near lookout tower, *Boufford & E. W. Wood 16310* (WCUH), *Chinese-Amer. Bot. Exped. 853* (KUN, NAS, PE, WH); Linville Road, *Churchill s.n.*, 1899 (TENN); along Long Hope Creek on W slope of Old Field Bald, *Hardin 13255* (NCSC); upper end of Long Hope Creek, *Hardin 13273* (NCSC); Potato Hill, N of jct. of state roads 1324 and 1306, *Kologiski & Perino 165* (GH, NCSC); 2.5 mi SE of Aho, *Radford 11111* (NCU); Rich Mt., *Radford 45373* (NCU, USCH); NW slope of Hanging Rock Ridge, *Rohrer 1790* (NCU); Grandfather Mt., *Seymour 91 8 13* (GH); 5 mi W of Blowing Rock, *J. K. Small & Heller s.n.*, 1891 (G, GH). Yancey Co.: 3.4 mi NW of Swiss, *Ahles & Duke 50705* (GH); Mt. Mitchell, *Palmer 42540* (GH), *Rhoades s.n.*, 1932 (GH), *Shallert s.n.*, 1923 (DUKE). SOUTH CAROLINA. Oconee Co.: near S.C. route 107 near North Carolina line, *Batson & Swails s.n.*, 1956 (SCUH); Ellicott Wilderness Area of Sumter Natl. Forest, E fork of Chatooga R., *Kirkman & Ellis 1201* (GA). TENNESSEE. Doe R. Valley, *Ball s.n.*, Sept. 1884 (US). Blount Co.: Great Smoky Mts. Natl. Park, trail to Gregory's, *Cain s.n.*, 3 Aug. 1929 (TENN). Carter Co.: Roan Mt., 1 mi below Cold Spring, *D. M. Brown 27* (DUKE); Roan Mt., below Carver's Gap, *Cannon 146* (NY, US); along old hacktrail leading to summit of Roan Mt., *Wofford 81-36* (TENN). Cocke Co.: near Lemon's Gap, *Kearney 610* (NCU, NY, US). Greene Co.: near summit of Cold Spring Knob, *Sharp & D. K. Smith s.n.*, 23 Sept. 1973 (TENN). Monroe Co.: Cherokee Natl. Forest, Citico Creek WSA, Falls Branch Scenic Area, *Malter 53107* (TENN); Cherokee Natl. Forest, near Beech Gap, *Sharp 715* (TENN). Sevier Co.: Great Smoky Mts. Natl. Park, Newfound Gap along U.S. route 441, *Boom 39435* (L); Great Smoky Mts., "Spruce Flat," Roaring Fork, *Braun s.n.*, 25 April 1927 (US); Chimney Caps, *Cain s.n.*, 12 June 1933 (TENN); Greenbrier, Lester Prong, *Cain & Duncan 401:2* (TENN); Great Smoky Mts. Natl. Park, Chimney Caps Trail, *Duncan 406* (GA); Lester Prong, *Duncan 901* (NCU); Great Smoky Mts. Natl. Park, 1 mi E of Seilers Bald, *Fosberg 18718* (NCSC); Mt. LeConte, *Iltis 1355* (NCSC); Smoky Mts., Balsam Point, *Hunnewell 14997* (GH); Little Pigeon R., *Hunnewell 14178* (GH); W fork of Little Pigeon R., ca. 1 mi W of Chimneys Campground, *Hypio 453* (VDB); Great Smoky Mts., Greenbrier, near Ramsey Prong Creek, *Jennison 39* (GSMNP, TENN); near Jakes Gap, *Jennison 2828* (GSMNP); trail up Mt. LeConte, *T. Jones s.n.*, 4 May 1935 (TENN); Mt. LeConte, *Ramseur 1662* (NCU), *Underwood 2669* (TENN); Double Springs Gap, *W. B. Schofield 10038* (DUKE); Mt. LeConte, Roaring Fork, *Sharp 640* (TENN); Great Smoky Mts., Elkmont, *Whmeyer 350* (GA). Unicoi Co.: E side of Rich Mt., valley of Higgins Creek, *E. H. Cooley et al. 8855* (TENN); Big Bald Mt., *James s.n.*, 5 Sept. 1955 (TENN); along U.S. route 23, Flag Pond, *James 16579* (TENN); Unaka Mt. near Beauty Spot, *Price 702* (DUKE); near Bald Mt., *Price 756* (USCH). VIRGINIA. Grayson Co.: Pine Mt., Solomon Branch, *Sheffey s.n.*, 18 May 1974 (FARM); White Top Mt., *Britton et al. s.n.*, 1892 (G, NY), *Roller s.n.*, 1939 (VPI), *Sharp 20496* (TENN), *Stevens & Harvill 25604* (FARM), *Uttal 11182* (VPI); Mt. Rogers, *Massey s.n.*, 1946 (VPI), *Nicely 826* (VPI), *Reedy 65-4* (EHCV), *C. E. Wood, Jr., 1403* (GH, VPI). Smyth Co.: White Top Mt., *Camp 1564* (NY), *Core (Moldenke) 6846* (NY), *J. K. Small s.n.*, 28–29 May 1892 (GH, US), *Stevens & Harvill 25656* (FARM); Mt. Rogers, *Kral 11684* (NCU, VDB). Washington Co.: Taylor's Valley, *Jervis s.n.*, 9 Aug. 1967 (EHCV).

In addition to the two sheets of *Diphylleia cymosa* in the Michaux Herbarium at P (IDC 6211. 47: I. 2, 3), there are also two sheets in the general herbarium at P that are most likely part of the original collection and represent type

material. Both of the latter sheets are annotated "Herb. Richard," and both also bear labels with "Herbarium Drake." Background information on the role of L. C. Richard in the authorship of *Flora Boreali-Americana* and on the history of the Richard and Drake herbaria support this contention, as outlined below.

Gray (1882a, p. 183), commenting on specimens in the "older herbaria," said of Michaux's *Flora Boreali-Americana* (1803), "It is known through tradition that this work was prepared by L. C. Richard, from the collections of the elder Michaux; but he wholly withheld his name, which therefore cannot be cited." Gray (1882b) also mentioned that Richard's herbarium contained an almost complete set of the plants described in that work. Previous to Gray, Hooker (1842, p. 432) had written that "Richard is the anonymous author of the *Flora Boreali-Americana* of Michaux, in 2 vols. 1803." It is of interest to note that Fedchenko (1937), in his treatment of the Berberidaceae for *Flora SSSR*, cited the authorship of *Diphylleia* as "L. C. Richard in A. Michaux."

Louis Claude Richard's son, Achille Richard, continued his father's botanical work and inherited his father's herbarium (Gray, 1882b). The Richard herbarium later came into the hands of De Franqueville (Roze, 1891) and was eventually obtained by Drake del Castillo, who, according to Bureau (1904), acquired many of the larger private herbaria in Europe during the latter part of the 1800's. In summarizing the contents of the Drake herbarium, Bureau mentioned that A. Michaux's collections from North America were among them. Stafleu and Cowan (1976, p. 872) also mentioned the fact that the herbaria of L. C. and A. Richard are now at P through the De Franqueville and Drake herbaria. It appears obvious that the two specimens at P that are annotated "Herbarium Richard" are part of Michaux's original collections of *Diphylleia* from North America and were among the material available to L. C. Richard when he prepared *Flora Boreali-Americana*. These two sheets, in addition to the two in the Michaux Herbarium, must therefore be considered in the designation of a lectotype.

The protologue of *Diphylleia cymosa* Michaux includes a description of all above-ground parts of the plant plus two plates (*tt. 19, 20*). One plate (*t. 19*) illustrates the habit of a plant in fruit (including a rhizome that more closely resembles that of *Podophyllum peltatum* L.); the other shows only the upper portion of a stem with the upper leaf and the inflorescence. Neither illustration exactly matches any of the four sheets of original material, although one sheet in the Michaux Herbarium (IDC 6211. 47: I. 2) and one in the general herbarium at P are quite similar to the illustration in *t. 20* of *Flora Boreali-Americana*. The Michaux Herbarium specimen, however, is in fruit (as is IDC 6211. 47: I. 3), while each of the two sheets in the general herbarium at P has both flowers and fruits. One of these sheets is labeled (in Michaux's handwriting?) with essentially the same information as in the original description. The characteristics of the attached specimens agree with the original description in *Flora Boreali-Americana*, and we designate the flowering material on this sheet as the lectotype of *D. cymosa* Michaux.

Although the three species of *Diphylleia* are remarkably alike, *D. cymosa* appears to be most similar in overall morphological features to *D. sinensis*, of

central and southwestern China. Both have a petiolate, peltate upper leaf, smaller flowers, more abundantly flowered inflorescences, and tricolpate or hexarugulate pollen—characters not found in *D. grayi*, of Japan. The inflorescences are commonly cymose in *D. cymosa* and *D. sinensis* but are frequently umbellate in *D. grayi*. However, *D. sinensis* and *D. grayi* are similar in the pubescent inflorescence, the greater number of ovules per ovary, and the exine ornamentation of the pollen. It is difficult, if not impossible, to say with certainty which species is most primitive.

2. **Diphylleia sinensis** H. L. Li, J. Arnold Arbor. **28:** 442. 1947. FIGURE 14.

Diphylleia cymosa Michaux subsp. *sinensis* (H. L. Li) T. Shimizu, Hikobia Suppl. **1:** 450. 1981.

Plants 4–10 dm tall, growing in dense to loose colonies or individually. Petiole of lower leaf 7–20 cm long, of upper (2.5–)6–13 cm long; blade peltate, reniform or reniform-orbicular to transversely oblong, 19–40 by 20–46 cm in lower leaf and 6.5–31 by 19–42 cm in upper, 2-cleft with divisions undulate or shallowly 3- to 6-lobed, margin irregularly dentate with teeth apiculate, pubescent with whitish hairs beneath, sparsely so or subglabrous above. Peduncle 3.5–28 cm long, solitary, occasionally bifurcate; inflorescence 4.2–35 cm long including peduncle, 3.5–10 cm broad, branches pubescent or glabrescent in fruit. Flowers (8 to) 15 to 51; pedicels 0.4–3.7 cm long; outer sepals lanceolate to linear-lanceolate, 2.3–3.5 by 0.7–1.2 mm; inner sepals very broadly elliptic to subcircular, 4–4.5 by 3.8–4 mm; outer petals narrowly to broadly obovate, 5–8 by 2.5–5 mm; inner petals narrowly elliptic to narrowly obovate, 5.5–8 by 2.5–3.5 mm; stamens ca. 4 mm long, laminar filaments 1.7–2 mm long, anthers ca. 2 by 0.6 mm; ovary ellipsoid, 3–4 by 1.8–2 mm, ovules 5 to 11, style absent or represented by slight constriction at summit of ovary, stigma ca. 0.3 by 1 mm. Berry globular to broadly ellipsoid, 10–15 by 6–10 mm broad, dark blue or purple-black, on pedicel 1–3 cm long. Seeds 2 or 3, ovoid, ca. 5.5 by 3.5 mm, ± rounded on all sides or only slightly flattened ventrally. Chromosome number: unknown.

TYPE. China, western Sichuan Province, July & August 1908, *E. H. Wilson 814* (lectotype, GH (the fruiting element); isolectotype, US).

DISTRIBUTION AND ECOLOGY. Moist deciduous and coniferous forests, sometimes bamboo thickets, 1880–3700 m alt. China: western Hubei, southern Shaanxi, southern Gansu, Sichuan, and northwestern Yunnan. (MAP 2.)

SPECIMENS EXAMINED. **China.** GANSU: Zhouchu Xian, *P. Z. Guo 5148, 5561* (WUK), *S. Zhang 00406* (PE), *W. J. Zhou 294* (NWTC); Zhang Xian, *Y. S. Lian 790160* (NWTC); Dang Chang Xian, *Y. S. Lian 790971* (NWTC); Die Bu Xian, *Y. S. Lian 800328* (NWTC), *C. R. Wang 15643* (WNC); Liou h'ia tien ze, col du Koan Chan, *E. Licent 5325* (BM, K, P), *5335* (K), *5336* (K); Tianshui Xian, *J. M. Liu 10182* (PE), *Z. W. Zhang 151* (WUK); Ming Xian, *J. C. Wang 200* (NWTC), *Xu-Mo-Tin Team 387* (WNC); Longde Xian, *Z. P. Wang 13120* (WUK); Xigu Xian, *Z. P. Wang 15159* (PE, WUK); Jing Yuan, *Z. P. Wang 17074* (PE); Wu Shan Xian, *without collector 324* (NWTC). HUBEI: Badong Xian, *F. H.*

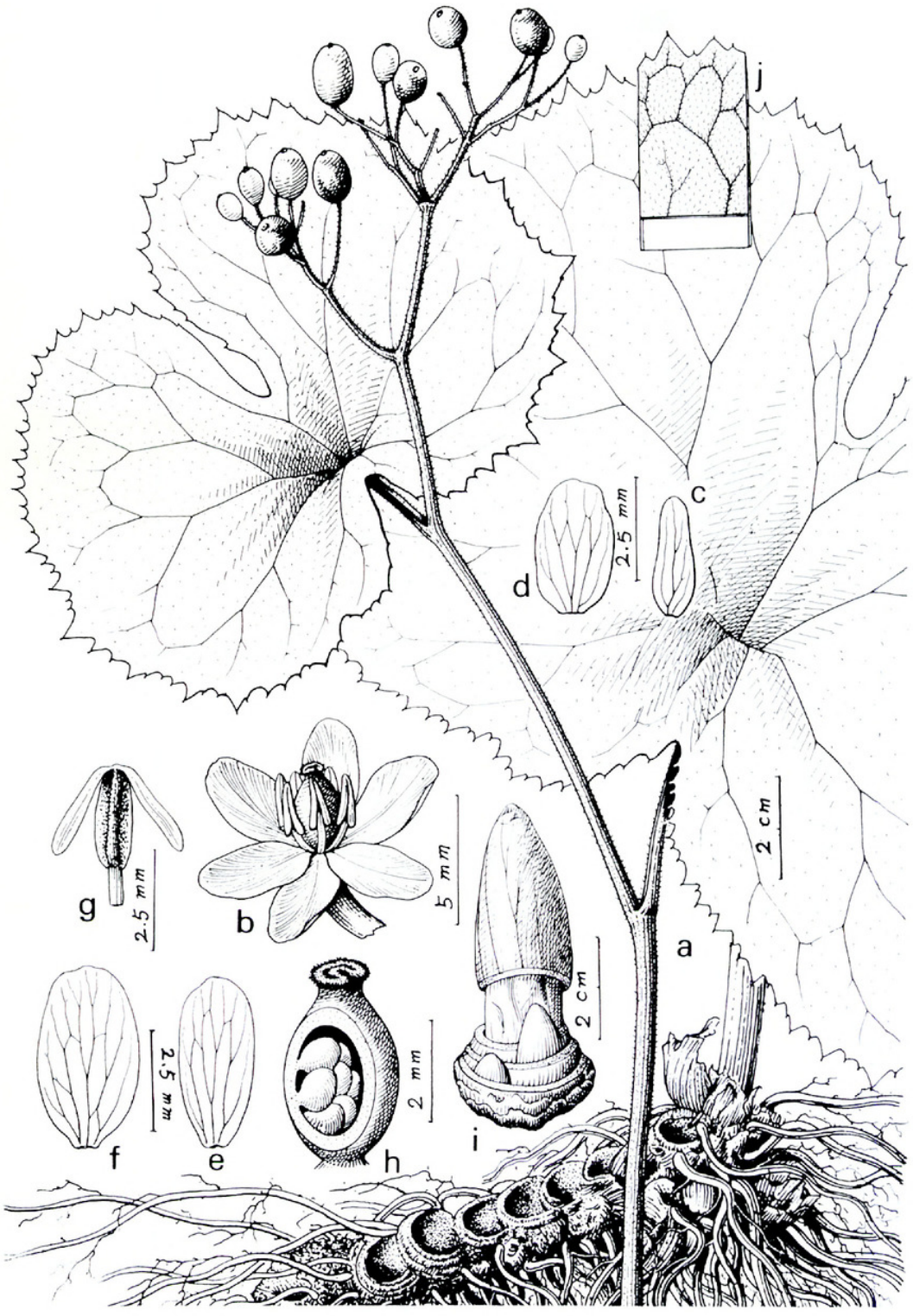


FIGURE 14. *Diphylleia sinensis* (based on *Nan-shui–Bei-diao Team 7164, G. X. Fu 1062, Shennongjia Bot. Exped. 10276*; all PE): a, upper portion of plant, rhizome, roots; b, flower; c, outer sepal; d, inner sepal; e, outer petal; f, inner petal; g, stamen; h, ovary; i, apical bud of young plant (from top of rhizome); j, undersurface of leaf.

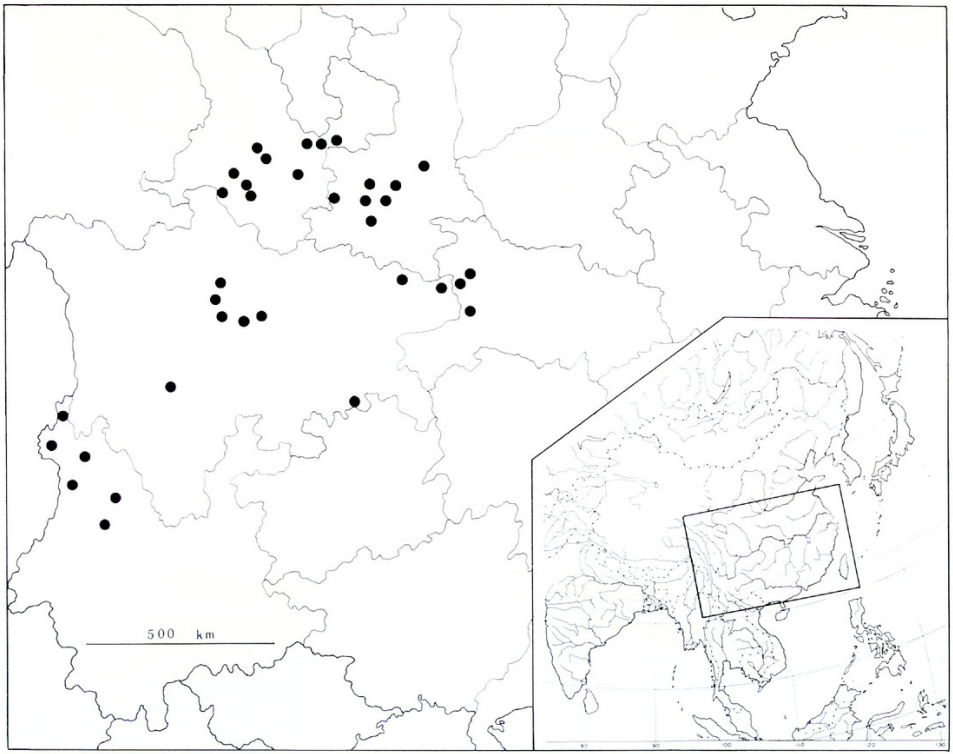
Chen 5132 (HIB), *G. X. Fu 1062* (PE), *R. H. Wang 307* (HIB); Fang, *A. Henry 6820* (BM, E, G, GH, K, NY, US), *E. H. Wilson s.n.* (W); Shennongjia Forest Distr., *Shennongjia Bot. Exped. 10276, 22868, 25107, 31388, 32451* (HIB, PE); Shennongjia Forest Distr., Xiaoshennongjia, *Shennongjia Bot. Exped. 10599* (A, HIB, PE); Shennongjia Forest Distr., vic. of Dalongtan and Xiaolongtan, *1980 Sino-Amer. Bot. Exped. 910* (A, HIB); "W Hupeh," *E. H. Wilson 2112* (W). SHAANXI: Mei Xian, *Central Shaanxi Team 85* (WUK), *Z. P. Wang 19976* (WUK); Feng Xian, *K. J. Fu 8306, 12299, 13285* (WUK); Tiabai Shan, *K. J. Fu 4452, 9424* (WUK), *P. Y. Li 5199* (WUK), *Y. M. Liang 125* (WUK), *T. N. Liou & P. C. Tsoong 330* (PE, WUK), *2263* (PE), *Qinling Team 300* (WUK), *C. L. Tang 1491* (WUK), *Z. P. Wang 15741* (WUK), *G. P. Wei 1492* (WUK); Gua-in-san, *G. Giraldi 1867* (FI); Kin-tou-san, *G. Giraldi 6004* (FI); Thae-pei-san, *G. Giraldi 6274* (FI); Hu Xian, *P. Z. Guo 386* (KUN, PE); Fuping Xian, Daping, *B. G. Guo 1421* (PE, WUK), *1769* (A, PE); Weinan, *Z. P. Wang 15632* (PE). SICHUAN: Tchen-keou Xian, *T. R. Dai 101090* (SZ), *R. P. Farges 581*[2] (K (2 sheets), P (3 sheets)). Kangding Xian, *B. C. Gao et al. 111455* (SZ); Heishui Xian, San-dao-gou, *Heishui Team 1075* (A), *1354* (PE), *X. Li 73212, 73389* (PE); Li Xian, *Z. Ho 13376* (PE), *Z. R. Wu 33348* (PE); Jinfu Shan, *Z. Y. Lau 780390* (PE), *G. F. Li 62274* (PE); Maowen Xian, *Maowen Team 2642* (PE); Heishui Xian, *Nan-shui–Bei-diao Team 01525* (PE); Mealo Xian, Ly-su-gou, *Nan-shui–Bei-diao Team 7164* (A, PE); "W Szechuan" [Wenchuan Xian, near Wasi], *E. H. Wilson 814* (GH, K, US). YUNNAN: Ma-cul-chan, *Delavay 3862* (A, P (2 sheets)[3]), *s.n.* (K); "Yun-nan," *Delavay s.n.* (A, P), *G. Forrest 30037* (BM, E); Chungtien Plateau, *Feng 1457* (KUN); Deching Xian, *Feng 6382* (KUN, PE); Lichiang Range, NW flank, *G. Forrest 10488* (BM, E, L); Chungtien Plateau, *G. Forrest 12524* (BM, E); "duplicate of 1913–1914," *G. Forrest 15458* (E, K); "duplicate of 1917," *G. Forrest 18709* (E, US); Landsang-djiang (Mekong) & Lu-djiang (Salween), vic. of Tseku, *H. F. Handel-Mazzetti 8921* (K, W (2 sheets)); Lichiang Xian, *Lichiang Bot. Gard. 100267* (PE); Mt. Fu-Chuan, *H. D. McLaren's coll. 203* (E); Lichiang Range, *H. D. McLaren's coll. 203d* (BM); Yangtse watershed, Lichiang Snow Range, *J. F. Rock 4230* (E, US); Mt. Fu-Chuan, SW of Wei-Hsi, Mekong-Salween, *J. F. Rock 16971* (E, GH, NY, US).

The type of *Diphylleia sinensis* (*Wilson 814*, GH) is based on specimens—one in flower and one in fruit—collected at different times of the year and mounted on the same sheet. The single label bears two dates, "7/08 + 8/08." Li (1947) did not indicate a choice of elements in designating the type, but in 1951 he annotated as "isotype" a duplicate of *Wilson 814* (US) consisting only of fruiting material. Since flowering and fruiting material are about equally represented on the GH specimen and each applies equally well to the original description, we have chosen the fruiting material as the lectotype.

Although no locality more exact than "Western Szechuan" is given on the label of *Wilson 814*, it is probable that Wilson's collections of *Diphylleia sinensis* came from the area in Wenchuan Xian near Wasi ("Wa-ssu") at about 31°28′N, 103°28′E (see Clausen & Hu, 1980; Howard, 1980). This is based on the fact that Wilson's numbers *813* and *815* (*Rubus pileatus* Focke and *R. giraldianus* Focke) were both collected at that locality (Rehder, 1913; Sargent, 1916).

[2]*Farges 581* ranges from plants in bud to plants with mature fruits; the specimens were obviously collected over several months and later lumped under a single number.

[3]The specimen at A is in flower, while the 2 specimens at P are in fruit. The date on the labels is 6 August 1889, obviously an error on the A sheet.



MAP 2. Distribution of *Diphylleia sinensis* in China.

3. **Diphylleia grayi** F. Schmidt, Mem. Acad. Imp. Sci. Saint Pétersbourg **12**(2): 109. 1868. (Reis. Amurl. 109. 1868). FIGURE 15.

Diphylleia grayi F. Schmidt var. *typica* H. Takeda *in* H. Takeda & K. Tanabe, Kozan Shokobutsu Shashin-jushu, 95. *figs. 134–136.* 1931.

Diphylleia grayi F. Schmidt var. *incisa* H. Takeda *in* H. Takeda & K. Tanabe, Kozan Shokobutsu Shashin-jushu, 96. *figs. 137–139.* 1931. TYPE: no specimens were cited in the original description, and we have seen no specimens collected or annotated by Takeda as var. *incisa.* In lieu of a specimen, we designate *fig. 139* in Takeda and Tanabe (1931) as the lectotype.

Diphylleia grayi F. Schmidt var. *rotundata* H. Takeda *in* H. Takeda & K. Tanabe, Kozan Shokobutsu Shashin-jushu, 97. *fig. 140.* 1931. TYPE: no specimens were cited in the original description, and we have seen no specimens labeled as var. *rotundata* by Takeda. In the absence of a specimen, we designate *fig. 140* in Takeda and Tanabe (1931) as the lectotype.

Diphylleia cymosa Michaux subsp. *grayi* (F. Schmidt) Kitamura *in* Kitamura & Murata, Acta Phytotax. Geobot. **20:** 202. 1962.

Diphylleia cymosa Michaux subsp. *grayi* (F. Schmidt) Kitamura var. *incisa* (H. Takeda) T. Shimizu, Hikobia Suppl. **1:** 450. 1981.

Plants 2.5–9 dm tall, the stems with scattered, curled, white pubescence; growing in dense to loose colonies or sometimes individually. Lower leaf with petiole 1–25 cm long, blade 9.2–35 by 11–44 cm; upper leaf sessile or occasionally with short petiole to 1 cm long (very rarely up to 5.8 cm long), blade attached at sinus, not peltate or only slightly so, 3.9–27 by 4.8–35 cm; blades of both leaves orbicular to reniform-orbicular, margin doubly serrate and sometimes deeply lobed, pubescent beneath, sparsely so above. Peduncle 0.8–7 cm long, to 16 cm long in fruit, pubescent, sometimes densely so; inflorescence 2.2–21 cm long including peduncle, 2–8 cm broad, branches pubescent. Flowers (2 to) 4 to 16, on pedicels 0.8–3.2 cm long; outer sepals lanceolate to linear-lanceolate, 4–7.2 by 0.6–1.2 mm; inner sepals broadly elliptic, 4–9 by 3–5.4 mm; outer petals broadly obovate, 8–15 by 6–11 mm; inner petals broadly obovate, 8–15 by 4.8–11 mm; stamens ca. 4 mm long, filaments ca. 0.7–1.5 mm long, anthers ca. 2–3.2 by 0.8–1.4 mm; ovary ellipsoid, 2.5–5 by 1.7–2.8 mm, ovules 5 to 11, style 0.3–0.8 mm tall, stigma 0.2–0.7 by 0.8–1.5 mm. Berry ellipsoid to subglobose, 9–18 by 8–16 mm, blue, on pedicel 0.9–4 cm long. Seeds (3 to) 5 to 7 (to 10), ovoid to oblong, ca. 6–6.5 by 3.3–4.5 mm, rounded on all sides. Chromosome number: $n = 6$.

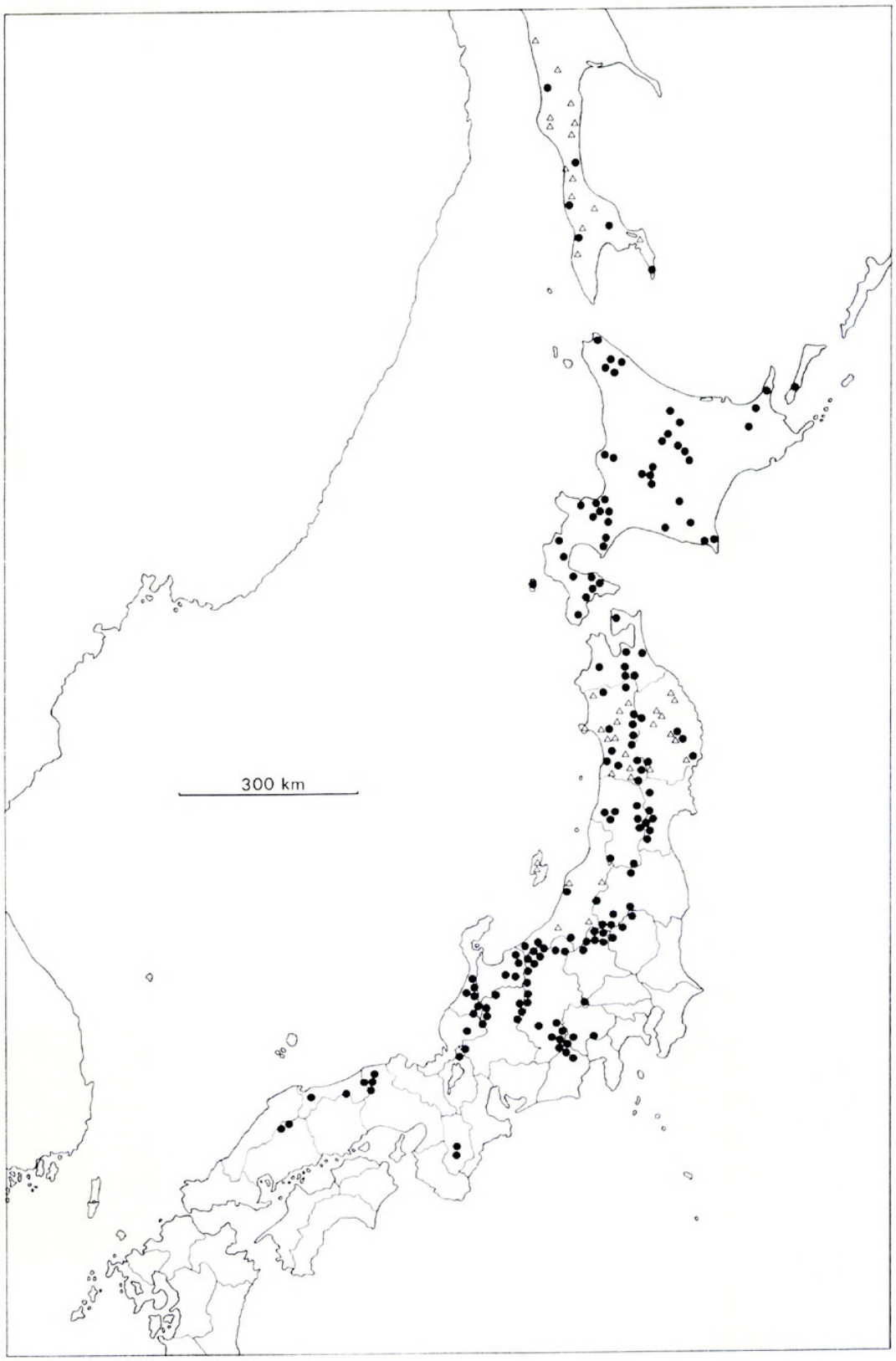
TYPE. Schmidt (1868) cited the following specimens (all from Sakhalin), which we have not seen, in his description of *Diphylleia grayi*: Arkai, 27 May 1861, *Glehn s.n.*, beginning of August 1860, *Glehn s.n.*; Dui, beginning of June 1860, and 21 July, *Glehn s.n.*; Estaing Bay, July, *Brylkin s.n.*; Kussunai, 25 April 1861 and mid-May, *Brylkin s.n.*; Manue, mid-August 1860, *without collector or number.* All are syntypes and are presumably at LE, where Glehn's and Brylkin's specimens are deposited (Holmgren, Keuken, & Schofield, 1981; Lanjouw & Stafleu, 1957; Stafleu & Cowan, 1976).

DISTRIBUTION AND ECOLOGY. Moist places in cool deciduous and coniferous forests, usually along small streams and seepages; from near sea level in the

FIGURE 15. *Diphylleia grayi* (based on *Brooks 661*, PE): a, upper portion of plant, rhizome, roots; b, flower; c, outer petal; d, inner petal; e, stamen; f, ovary.

north to 2700 m in the south. U.S.S.R. (Sakhalin, below 50°N), Japan (from Hokkaido (throughout) to southwestern Honshu (mostly limited to western side)), Kuril Islands (Kunashiri). (MAP 3.)

SPECIMENS EXAMINED. **Japan.** HOKKAIDO (Hokkaido Prefecture). "Southern Hokkaido," *W. D. Brooks 661* (PE). Abashiri Shicho: Shirataki-mura, Mt. Taira-yama, *K. Ito s.n.* (SAP); Shari-cho, Raus-daira, *S. Kobayashi s.n.*, 20 July 1967 (MAK); Shari-cho, Mt. Shari-dake, *S. Kobayashi s.n.*, 31 July 1967 (MAK); Takinoue-cho, *S. Okamoto s.n.*, 22 July 1952 (KYO); Mombetsu city, Shokotsu, *S. Okamoto s.n.*, 5 Aug. 1954 (KYO). Hidaka Shicho: Hiratori-cho, Shoya, *K. Ito s.n.*, 11 May 1963 (SAP); Shizunai-cho, Mt. Petekari-dake, *H. Koyama & N. Fukuoka 3256* (TNS); Hiratori-cho, Mt. Horoshiri-dake, *H. Koyama et al. 3591* (TNS); Samani-cho, *M. Tatewaki 9242* (SAP); Erimo-cho, Sarurusando, *M. Tatewaki 42844* (SAP), *Y. Tokubuchi s.n.*, 14 Aug. 1892 (NY, SAP). Hiyama Shicho: Okushiri-cho, Okushiri Is., *K. Miyabe & Tokubuchi s.n.*, 28 July 1890 (K, SAP), *K. Togashi 21821* (SAP). Iburi Shicho: Muroran city, Mt. Washibetsu, *S. Kawano 444* (SAP); Shiraoi-cho, Mt. Orofure, *S. Kawano 530* (SAP). Ishikari Shicho: Sapporo city, Mt. Soranuma-dake, *S. Akiyama s.n.*, 19–20 June 1932 (NY), *H. Hara s.n.*, 18 June 1937 (TNS), *Y. Yokomizo s.n.*, 22 June 1958 (SAP); vic. of Sapporo, *S. Arimoto s.n.*, 26 May 1903 (GH, MO); Sapporo city, Jozankei, *S. Kurosawa & Y. Tateishi s.n.*, 2 June 1975 (KYO, TI, TUS), *J. Ohwi 4662* (KYO), *S. Terabayashi 588* (KYO); Eniwa city, Mt. Eniwa, *K. Miyabe s.n.*, 7 Aug. 1902 (SAP); Sapporo city, Mt. Teine-yama, *S. Saito 456* (GH), *H. Yanagishima s.n.*, 1 June 1912 (SAP); Sapporo city, *H. Takeda s.n.*, 13 May 1909 (BM, E, K, US); Mt. Moiwa-yama, *H. Takeda s.n.*, 6 June 1923 (SAP). Kamikawa Shicho: Kamikawa-cho, Mt. Taisetsu-san, *N. Kitagawa 1153* (KYO), *T. Nakai s.n.*, Aug. 1928 (TI), *J. Ohwi s.n.*, 9 Sept. 1928 (TNS), *S. Okuyama s.n.*, 18 July 1941 (TNS); Minamifurano-cho, Mt. Yubari-dake, *G. Murata & T. Yahara 37461* (KYO, SAP); Otoineppu-mura, *G. Murata et al. 38447* (KYO); Furano city, Furano, *S. Nishida s.n.*, 25 July 1916 (SAP); Kamikawa-cho, Mt. Yui-ishikari-dake, *J. Samejima & T. Misumi s.n.* (SAP). Kushiro Shicho: Teshikaga-cho, Mt. Mashu-dake, *K. Takita 297* (KYO). Nemuro Shicho: Nemuro city, Nosappu, *H. Toda s.n.*, 15 July 1954 (TUS). Oshima Shicho: Ono-cho, Naruka Valley, *F. C. Greatrex 236* (SAP); Matsumae-cho, Mt. Daisengen-dake, *T. Ishiyama 229* (SAP); Kamiiso-cho, Moheji, *S. Kaminago s.n.*, 25 May 1906 (SAP); Hakodate, *C. J. Maximowicz s.n.*, 1861 (BM, FI, G, GH, K, L, NY, US); Assabu-mura, Uzura R., *T. Nakai & Maruyama s.n.*, 22 May 1950 (TNS); Nanae-cho, Mt. Yokotsu-dake, *H. Takeda s.n.*, 21 July 1977 (KYO, TI), *I. Yamamoto 566* (SAP); Fukushima-cho, Mt. Daisengen-dake, *K. Takeda s.n.*, 24 July 1977 (NCU); Nanae-cho, Onuma, *M. Tatewaki 44602* (SAP); Yakumo-cho, Kiootoshike, *M. Tatewaki et al. s.n.*, 25 May 1955 (SAP); Oshamanbe-cho, Inaho Pass, *Y. Tokubuchi s.n.*, 16 July 1888 (SAP). Rumoi Shicho: Horonobe-cho, Toikanbetsu, *H. Koyama 1688* (KYO); Horonobe-cho, Mt. Chikoma-dake, *M. Tatewaki s.n.*, 12 July 1931 (SAP); Mashike-cho, Mt. Shokanbetsu-dake, *I. Yamamoto 5474, 5475* (SAP). Shiribeshi Shicho: Otaru, mountain gorges, *U. Faurie 201* (P), *Takenouchi s.n.*, 28 May 1928 (L); Niki-cho, Nakanosawa, *S. Ishikawa s.n.*, 2 July 1893 (SAP); Mt. Tenguyama, *Kawata s.n.*, 12 May 1935 (SAP); Shimamaki-mura, along Tomari R., *T. Misumi & J. Igarashi s.n.*, 28 June 1954 (SAP); Iwaoto, *B. Yoshimura & H. Yokoyama s.n.*, 19 June 1938 (SAP). Sorachi Shicho: Ashibetsu city, Mt. Kirigishi-yama, *E. Ishizuka & M. Tohyama s.n.*, 26 July 1970 (SAP); Ashibetsu city, Mt. Ashibetsu-dake, *H. Koidzumi 67192* (TNS); Uryu-cho, Mt. Minamishokan-dake, *G. Murata et al. 38644* (CM, KYO, SAP), *38695* (KYO, SAP); Yubari city, Mt. Yubari-dake, *J. Ohwi 5041* (KYO), *K. Sugawara s.n.*, 13 July 1969 (TUS); Yubari, *Y. Tokubuchi s.n.*, 11 Aug. 1892 (GH). Soya Shicho: Nakatonbetsu-cho, *M. Yamanoi s.n.*, 28 May 1972 (TNS); Cape Soya, *C. Wright s.n.*, 15 July 1853–1856 (GH, NY). Tokachi Shicho: Shikaoi-mura, near Lake Shikaribetsu, *M. Wakabayashi 738* (KYO). HONSHU. Mirosaki, *U. Faurie 574* (WU). Akita Prefecture: Senboku-gun, Tazawako-machi, Hachimantai, *H. Hara s.n.*, 20 July 1953 (TI), *S. Kurosawa s.n.*, 4 Aug. 1951 (TI); Senboku-gun, Tazawako-machi, Mt. Komagatake, *H. Hara s.n.*, 8 July



MAP 3. Distribution of *Diphylleia grayi* in Japan and the U. S. S. R. Dots based on specimens; triangles based on literature reports (Board of Education of Iwate Prefecture, 1970; Muramatsu, 1932; M. Noda, 1969; Sugawara, 1937).

1958 (TI), *H. Muramatsu s.n.*, 7 Aug. 1928 (TI); Yuri-gun, Chokai-machi, Mt. Chokai, *T. Kaneko s.n.*, 15 Aug. 1962 (TUS); Kitaakita-gun, Ohta-machi, Mt. Yakushi, *Kurata s.n.*, 3 June 1978 (Akita Pref. Mus.); Kazuno-gun, Kosaka-machi, Mt. Shirozi-yama, *R. Mochizuki s.n.*, 20 July 1969 (herb. Mochizuki); Hiraka-gun, Sannai-mura, Nango, *R. Mochizuki s.n.*, 3 May 1977 (herb. Mochizuki); Yuri-gun, Ouchi-machi, Shirouchi, *R. Mochizuki s.n.*, 7 May 1977 (herb. Mochizuki); Honjo city, Kitanomata, *R. Mochizuki s.n.*, 11 May 1980 (herb. Mochizuki); Senboku-gun, Nishisenboku-machi, Osawago, *R. Mochizuki s.n.*, 6 June 1981 (herb. Mochizuki); Kitaakita-gun, Tashiro-machi, Mt. Tashiro-dake, *R. Oikawa s.n.*, 25 May 1968 (TNS); Kitaakita-gun, Ohta-machi, Kitamahiru, *Takada s.n.*, 7 June 1978 (Akita Pref. Mus.); Ogachi-gun, Minase-mura, Mt. Toragayama, *Tohoku Univ. Bot. Gard. Staff s.n.*, 23 July 1970 (MO, TUS); Ogachi-gun, Ugomachi, Karuizawa, *Tsuchida s.n.*, 10 May 1974 (Akita Pref. Mus.); Ogachi-gun, Minasemura, Mt. Kiji-san, *Tsuchida s.n.*, 10 May 1974 (Akita Pref. Mus.); Akita city, Mt. Ohira-yama, *Yoshikawa s.n.*, 15 June 1955 (Akita Pref. Mus.). Aomori Prefecture: Aomori, *U. Faurie 574* (BM); Mt. Hakkoda, *U. Faurie 926* (FI), *928* (G), *13072* (MO, P); Aomori city, Hakkoda Mts., Mt. Odake, *T. Fujita & E. Nakagawa s.n.*, 1 July 1908 (TUS), *A. Kimura & S. Sugaya s.n.*, 1 July 1953 (TUS); Kamikita-gun, Towadako-machi, Hakkoda Mts., Sarukura, *K. Hasegawa s.n.*, 30 June 1964 (TI), *S. Sugaya et al. s.n.*, 2 July 1955 (TUS); Kamikita-gun, Noheji-machi, Mt. Eboshi-dake, *K. Hosi s.n.*, 17 June 1951 (KANA); Shimokita-gun, Sai-mura, *O. Mori 31* (MAK); Kamikita-gun, Towadako-machi, Mt. Towada-yama, *T. Naito 7750* (TUS); Minamitsugaru-gun, Hiraga-machi, Mt. Kushigamine, *Osawa Senior High School Students 128* (TNS); Nakatsugaru-gun, Iwaki-machi, Mt. Iwaki-san, *S. Narita s.n.*, 19 June 1910 (MAK), *H. Sakurai s.n.*, Sept. 1885 (TNS); Kamikita-gun, Tohoku-mura, Kochi, *Z. Tashiro s.n.*, 1 July 1948 (KYO). Fukui Prefecture: Katsuyama city, Tani-toge Pass, *G. Koidzumi s.n.*, 7 July 1921 (KYO); Ono city, Mt. Beko-san, *Z. Tashiro s.n.*, 20 June 1937 (TNS); Nanjo-gun, Imajo-machi, Yashagaike Pond, *N. Fukuoka 4889* (KYO), *K. Ueda 508* (A, KYO, MO, TI); Katsuyama city, Mt. Tottate-yama, *S. Watanabe s.n.*, 16 May 1964 (KYO). Fukushima Prefecture: Yama-gun, Inawashiro-machi, Mt. Azuma-yama, *G. Nakahara s.n.*, June 1904 (TNS), *S. Okuyama 3558* (TNS); Minamiazumi-gun, Hinoemata-mura, Mt. Hiuchi, *G. Nakai 2587* (KYO); Minamiazumi-gun, Tateiwa-mura, Mt. Tashiro-yama, *S. Okuyama 6800* (TNS); Minamiazumi-gun, Tadami-machi, Mt. Asakusa-dake, *M. Suzuki s.n.*, 12 July 1960 (TNS); Nishishirakawa-gun, Nishisata-mura, Mt. Asahi-dake, *H. Utsumi s.n.*, 29 July 1958 (TNS); Onuma-gun, Showa-mura, Komado, *without collector or number*, 10 May 1905 (MAK). Gifu Prefecture: Ibi-gun, Sakauchi-mura, SW of Mt. Sobatsubu-yama, *N. Fukuoka 5793* (KANA, KYO); Ono-gun, Shirakawa-mura, Hirase, *M. Hashimoto 382* (KANA); Ono-gun, Shokawa-mura, Tenbu Pass, *J. Hatasa s.n.*, 25 July 1968 (TNS); Ibi-gun, Kasugamura, E of Mt. Ibuki-yama, *M. Hutch 23487* (KYO), *Y. Satake & S. Okuyama s.n.*, 24 May 1942 (TNS); Ono-gun, Takane-mura, Nomugi Pass, *H. Kanai s.n.*, 13 June 1958 (MAK), *H. Kanai & H. Ohashi 731217* (TNS); Ibi-gun, Sakauchi-mura, Kawakami, *H. Kanai & T. Morita 0259* (TI); Masuda-gun, Kasako-cho, NW of Mt. Ontake-san, *G. Murata 10670* (KYO); Yoshiki-gun, Mannami, *Y. Nagai s.n.*, 31 May 1972 (KANA, MAK), *N. Naruhashi 3616* (KANA); Gujo-gun, Takawashi-mura, Mt. Daihi-dake, *S. Ueno s.n.*, 22 July 1970 (TNS). Gunma Prefecture: Shimizu-toge Pass, *U. Faurie 2396* (MO); Tone-gun, Kaashina-mura, Oze, *T. Harazawa s.n.*, 1 Aug. 1910 (MAK), *M. Mizushima 1121* (TI), *G. Nakai 2628* (KYO), *S. Okuyama s.n.*, 21 July 1934 (TNS), *M. Ono s.n.*, 2 June 1954 (TI); Tone-gun, Minakami-machi, Mt. Tanigawa, *M. Furuse s.n.*, 16 June 1958, 6 June 1961 (A), *K. Hasegawa s.n.*, 15 July 1966 (TI), *K. Hisauchi 489* (TI), *H. Kanai 3368* (TI), *T. Miyamae s.n.*, 30 May 1969 (TNS), *R. Noguchi s.n.*, 24 June 1934 (TNS), *S. Okuyama 13055* (TNS), *T. Yamazaki s.n.*, 24 June 1944 (TI); Tone-gun, Minakamimachi, Mt. Hotaka, *H. Kanai s.n.*, 5 July 1957 (TI); Tone-gun, Minakami-machi, Mt. Hiraga-take, *H. Kanai s.n.*, 1 Aug. 1959 (TI); Azuma-gun, Himekoi-mura, Hiramata, *K. Matsuda 378* (TNS); Tone-gun, Kaashina-mura, Mt. Shirane, *H. Ohba & S. Akiyama 1317* (A, KYO, TI); Tone-gun, Niiharu-mura, Mikuni Pass, *S. Okuyama et al. s.n.*, 11

July 1957 (TNS). Hiroshima Prefecture: Hiba-gun, Mt. Sarumasa-yama, *G. Akiyama s.n.*, 23 May 1976 (TNS); Mt. Omaki-san, *S. Takafuji 583* (KYO). Hyogo Prefecture: Kinosaki-gun, Hidaka-cho, Mt. Sofugatake, *E. Araki 3123* (KYO); Mikata-gun, Muraoka-cho, Mt. Torokawa-yama, *E. Araki s.n.*, 12 July 1931, 31 August 1931 (KYO), *M. Hashimoto 9223* (KYO), *G. Koidzumi s.n.*, July 1927 (KYO), *G. Murata 20902* (KYO); Mikata-gun, Onsen-cho, Mt. Ogino-sen, *S. Hosomi s.n.*, 31 July 1968, 4 May 1969 (KYO); Yabu-gun, Sekinomiya-cho, Mt. Hyono-sen, *G. Murata & K. Iwatsuki 700* (KYO, TNS), *J. Ohwi s.n.*, 6 July 1927 (TNS), *S. Terabayashi 60* (KYO), *Y. Yoneda s.n.*, 13 May 1933 (KYO). Ishikawa Prefecture: Kanazawa city, Komagaeri-Kurotani, Mt. Takasaburo-yama, *N. Fukuoka 7658* (KYO); Kanazawa city, Mt. Takao, *H. Kaneko s.n.*, 20 May 1962 (KANA, MAK); Ishikawa-gun, Shiramine-mura, Mt. Haku-san, *U. Faurie? 2798* (P), *M. Hotta 5707, 5936, 5950* (KYO), *G. Koidzumi s.n.*, 8 July 1921 (KYO), *J. Ohwi s.n.*, 25 April 1929 (TNS), *S. Terabayashi 73, 74* (KYO), *K. Urabe s.n.*, Aug. 1908 (KYO); Ishikawa-gun, *H. Nakagawa 372* (KANA); Kanazawa city, Mt. Ioh-sen, *N. Satomi s.n.*, 27 May 1951 (TI); Ishikawa-gun, Oguchi-mura, Iwama Hot Spring, *N. Satomi s.n.*, 16 June 1952 (KANA). Iwate Prefecture: Shimohei-gun, Kawai-mura, Mt. Hayachine, *R. Endo s.n.*, 31 July 1951 (TUS), *E. Ito & M. Togashi 38* (TNS), *G. Murata & H. Tabata 222* (KYO), *J. Murata et al. 5827* (TI), *Y. Ogura s.n.*, 19 June 1910 (MAK), *S. Okuyama 12807* (TNS), *K. Sohma 3241* (MO); Iwate-gun, Mt. Iwate, *M. Honda s.n.*, 27 July 1927 (TI), *G. Nakahara s.n.*, 26 July 1907 (TI), *Y. Ogura s.n.*, 4 Aug. 1915 (TI), *H. Sakurai s.n.*, 29 July 1908 (A); Waka-gun, Iwasaki-mura, Mt. Ushigata-yama, *K. Hosoi s.n.*, 20 July 1948 (KANA); Iwate-gun, Shizukuishi-machi, Mt. Komagatake, *H. Iwabuchi 2379* (TUS); Kamaishi city, Mt. Goyo-san, *H. Koyama & M. Hotta 2270* (TNS), *H. Koyama & S. Sasamura 2539* (KYO, TNS); Nambu, *Tschonoski s.n.*, 1865 (GH, K). Miyagi Prefecture: Katta-gun, Zao-machi, Mt. Zao, *K. Endo s.n.*, 12 June 1900 (MAK), *H. Kanai 742732* (A, BM, E, KYO, L, NY, TNS, WU), *M. Kato 54* (MAK); Natori-gun, Akiu-machi, Mt. Daito-dake, *H. Ohashi s.n.*, 3 May 1959 (TUS); Natori-gun, Akiu-machi, Mt. Takakura-yama, *H. Ohashi 3348* (TI, TUS); Izumi city, Mt. Izumigatake, *K. Saito & T. Keneko s.n.*, 18 May 1961 (TUS); Tamatsukuri-gun, Naruko-machi, Kawatabi, *K. Sugawara 8517* (TUS); Shibata-gun, Kawasaki-machi, Sasaya, *S. Sugaya et al. s.n.*, 26 May 1971 (TUS); Kurokawa-gun, Yamato-machi, Mt. Funagata, *M. Yashima & H. Ohba 717011* (TUS). Nagano Prefecture: Minamisaku-gun, Kawakami-mura, Jumonji Pass, *H. Asuyama s.n.*, 11 July 1930 (TNS); from Mitsumata to Mt. Jonen-dake to Mt. Choga-dake, *D. E. Boufford et al. 19951* (MO); Kamiminochi-gun, Togakushi-mura, Mt. Togakushi, *S. Ito 132* (TNS), *H. Koidzumi 67178* (TNS), *S. Matsuda s.n.*, 28 July 1893 (KYO), *H. Takeda s.n.*, 19 July 1904 (E, K), *C. Wright s.n.*, 1853–1856, (K); Kamiminochi-gun, Kinasa-mura, Okususobana, *S. Ito 152* (TNS); Minamiazumi-gun, Azumi-mura, Mt. Norikura-dake, *T. Ito s.n.*, 19 Aug. 1891 (TI); Kamiina-gun, Hase-mura, Mt. Senjo-dake, *K. Iwatsuki et al. 120* (KYO), *G. Murata 8275* (KYO), *T. Yamazaki s.n.*, 3 Aug. 1949 (TI); Kiso-gun, Oshika-mura, Mt. Akaishi-dake–Mt. Osawa-dake, *K. Iwatsuki & H. Koyama 183* (KYO); Shimoina-gun, Achi-mura, Mt. Ena-san, *H. Kanai s.n.*, 29 July 1957 (TI); Shimotakai-gun, Yamanouchi-cho, Shigakogen, *H. Kanai 7607* (TI); Shimoina-gun, Oshika-mura, Ogawara, *T. Kawamata 65* (TNS); Minamiazumi-gun, Azumi-mura, Tokugo Pass, *G. Koidzumi s.n.*, 31 May 1928 (KYO), *T. Nakai s.n.*, 11 July 1927 (TI); Minamiazumi-gun, Azumi-mura, Kamikochi, *K. Kojima s.n.*, 6 July 1934 (KYO), *K. Ueda et al. 19* (KYO); Kiso-gun, Oshika-mura, Sanpuku Pass, *F. Konta 10326* (KYO), *J. Sugimoto 4915* (TI); Nishikomaga-dake, *M. Kume 2595* (A); Kitaazumi-gun, Hakuba-mura, Mt. Shirouma, *T. Makino s.n.*, Aug. 1918 (MAK), *N. Maruyama s.n.*, 2 Aug. 1950 (TNS), *M. Sugiyama s.n.*, 29 June 1968 (TI), *S. Terabayashi 306, 793* (KYO), *F. Tomihisa s.n.*, 16 Aug. 1923 (KYO), *Y. Yabe s.n.*, 26 Aug. 1902 (TI); Kitaazumi-gun, Hakujo-mura, to Sarukura from Futamata, foot of Mt. Shirouma, *M. Furuse s.n.*, 25 May 1958 (A); Kiso-gun, Minamishinano-mura, Mt. Hijiri-dake, *H. Matsuda s.n.*, 17 June 1954 (TI); Omachi city, Taira-mura, *T. Mimoro et al. 1492* (TNS); Shimotakai-gun, Kijimadaira-mura, Kayanodaira, *M. Mizushima s.n.*, 16 June 1966 (A, KYO, MAK, TI); Kiso-gun, Oshika-mura, Mt. Otaka-san, *M. Muramatsu 1487* (TNS); Ki-

taazumi-gun, Otari-mura, Mt. Amakazari, *D. E. Boufford & E. W. Wood 19145* (A), *G. Murata et al. 30378* (KYO), *S. Terabayashi 767* (KYO), *S. Tsugaru 3389* (MO); Minamiazumi-gun, Hotaka-mura, Mt. Tsubakuro, *Y. Ogura s.n.*, 25 June 1918 (TI), *Y. Satake s.n.*, 13 July 1941 (TNS); Kamiina-gun, Hase-mura, Mt. Kitaarakawa-dake, *Y. Okada s.n.*, 12 Aug. 1923 (TNS); Chino city, Mt. Yatsuga-take, *C. Okawa s.n.*, 4 July 1977 (TNS), *Y. Yabe s.n.*, 20 Aug. 1902 (TI); Minamiazumi-gun, Azumi-mura, Mt. Otaki, *S. Okuyama et al. s.n.*, 18 Aug. 1954 (TNS); Kamiina-gun, Hase-mura, Mt. Komaga-take, *H. Sakurai s.n.*, 10 Sept. 1884 (TNS); Kiso-gun, Oshika-mura, Mt. Toyoguchi-san, *T. Yamazaki s.n.*, 29 July 1953 (TI); Kiso-gun, Agematsu-mura, Mt. Kisokoma-dake, *without collector or number*, July 1935 (MAK). Nara Prefecture: Mt. Sanjogatake–Mt. Inamuragatake–Gyojagaeri, *H. Hara s.n.*, 15 July 1955 (TI), *M. Hotta et al. 55* (KYO), *G. Murata & K. Iwatsuki 72* (KYO), *Y. Momiyama s.n.*, 16 July 1955 (TI); Yoshino-gun, Tenkawa-mura, Omine Mts., Mt. Misen-Gyojagaeri, *M. Hotta et al. 74* (KYO), *M. Hotta & N. Fukuoka 258* (KYO), *G. Koidzumi s.n.*, 14 July 1922 (KYO), *G. Murata & T. Shimizu 88* (KYO), *H. Okada et al. 1370* (KYO), *S. Tanaka s.n.*, 17 July 1933 (K, TNS), *Yokohama Nursery Co. s.n.*, Aug. 1907 (E). Niigata Prefecture: Nishikanbara-gun, Yahiko-mura, Mt. Yahiko, *N. Fukuoka 1828* (KYO); Nishikubiki-gun, Myokokogen-cho, Mt. Kurohime-yama, *N. Fukuoka 2158* (KYO); Nishikubiki-gun, Myokokogen-cho, Mt. Myoko-san, *S. Matsuda s.n.*, 27 July 1894 (KYO), *G. Murata 6834* (KYO); Nishikubiki-gun, Myokokogen-cho, Sasagamine, *A. Nitta 10681* (KYO); Nakauonuma-gun, Tsunami-mura, Mt. Naeba, *S. Okuyama s.n.*, 19 July 1936 (TNS), *Y. Satake & H. Ito s.n.*, 12 July 1951 (TNS). Shiga Prefecture: Higashiasai-gun, Asai-cho, Takayama-Torigoe Pass, *Y. Inamasu & N. Fukuoka 82* (KYO); Ika-gun, Suino-mura, Mt. Tsuchigura, *Y. Inamasu & N. Fukuoka 205* (KANA, KYO); Higashiasai-gun, Ibuki-cho, Mt. Ibuki, *G. Koidzumi s.n.*, 26–27 June 1922 (KYO); Higashiasai-gun, Asai-cho, Mt. Kanakuso, *G. Murata & N. Fukuoka 1020* (E, K, KANA, KYO, MAK, MO, TNS); Takashima-gun, Imazu-cho, Mt. Miedake, *S. Watanabe s.n.*, 26 June 1927 (KYO). Shimane Prefecture: Iishi-gun, Yoshida-mura, Mt. Omaki-san, *Y. Moriyama s.n.*, 5 Aug. 1961 (MAK). Shizuoka Prefecture: Shizuoka city, Mt. Hakkorei, *F. Konta et al. 309* (KYO); Shizuoka city, Mt. Senmai, *H. Matsuda s.n.*, 7 July 1954 (TI); Shizuoka city, Higashimata, *H. Matsuda s.n.*, 22 July 1954 (TI). Tochigi Prefecture: Nikko city, Mt. Shirane-yama, *J. Bisset 4027* (E), *Hattori s.n.*, 1 July 1922 (TI), *T. Makino s.n.*, 17 July 1924 (MAK), *H. Sakurai s.n.*, 16 July 1887 (TNS); Shioya-gun, Fujiwaramachi, Mt. Takahara-yama, *H. Kanai s.n.*, 25 May 1959 (TI); Nikko city, Yumoto, *S. Kobayashi 45870* (MAK), *G. Murata 18205* (KYO), *N. Shibusa s.n.*, 2 July 1966 (TNS), *S. Suzuki s.n.*, 21 June 1931 (KYO); Nikko, *Yokohama Nursery Co. s.n.*, Aug. 1906 (E). Tottori Prefecture: Saihaku-gun, Daisen-cho, Mt. Daisen, *S. Hori s.n.*, 4 Aug. 1889 (MAK), *N. Kinashi s.n.*, 7 June 1917 (KYO), *G. Koidzumi s.n.*, 3 July 1924 (KYO); Yazu-gun, Sajimura, Kitadani, *G. Murata et al. 298* (KYO). Toyama Prefecture: Shimoshinkawa-gun, Asahi-cho, Mt. Iburi, *H. Kanai s.n.*, 1 Aug. 1958 (TI); Higashitonami-gun, Minoya-mura, *H. Kaneko s.n.*, 19 May 1963 (KANA, TI); Nakashinkawa-gun, Kaminoichi-cho, Mt. Takamine-yama, *N. Kurosaki 1601* (KANA, KYO); Nakashinkawa-gun, Tateyama-cho, Mt. Tateyama, *S. Matsuda s.n.*, Aug. 1893 (KYO), *G. Nakai 4000* (KYO); Higashitonamigun, Kamitaira-mura, Bunao Pass, *T. Mimoro & S. Tsugaru 11846* (MO, TNS), *G. Murata 30018* (KYO, TNS); Higashitonami-gun, Kamitaira-mura, Hosoo Pass, *N. Mino s.n.*, 21 May 1964 (KANA); Shimoshinkawa-gun, Unazuki-cho, Mt. Karamatsu, Baba-dani valley, *G. Murata & T. Shimizu 1904* (KYO), *J. Ohwi 7107* (KYO), *S. Okamoto s.n.*, 23 July 1935 (KYO); Higashitonami-gun, Nawaga-ike Pond, *N. Satomi 10150* (KANA, MAK, TNS). Yamagata Prefecture: E of Higashine city, Makino to Mt. Shiragami, *D. E. Boufford et al. 22281* (GA, GH); Yamagata city, Yamadera, *K. Doi s.n.*, 10 Aug. 1966 (TNS), *H. Ohashi s.n.*, 20 May 1960 (TUS); Higashitagawa-gun, Tachikawa-machi, Mt. Gassan, *R. Endo s.n.*, 28 July 1914 (TUS); Nishimurayama-gun, Nishikawa-machi, Mt. Asahi-dake, *Hara s.n.*, 7 July 1959 (TI); Nishiokitama-gun, Oguni-machi, Mt. Iide, *M. Ito 407* (KYO, MO), *G. Koidzumi s.n.*, 15 Aug. 1910 (TI), *H. Ohba et al. 73071* (A, TI, TUS), *T. Yamazaki s.n.*, 3 Aug. 1943 (TI), *T. Yamazaki et al. 15* (TI); Higashitagawa-gun, Asahi-mura, Kamina, *K. Mori s.n.*, 30 July 1950 (TI); Nishiokitama-gun, Oguni-machi, Oishisawa,

S. Terabayashi 828 (KYO); Akumi-gun, Yuza-machi, Mt. Chokai, *Univ. Tokyo Staff s.n.*, 28 July 1888 (TI); Nishimurayama-gun, Nishikawa-machi, Mt. Yudono, *Univ. Tokyo Staff s.n.*, 23 July 1882 (G, TI); Yonezawa city, Mt. Azuma-san, *Yoshida s.n.*, 6 Aug. 1915 (MAK). Yamanashi Prefecture: Kitakuma-gun, Shirasu-cho, Mt. Kanno-dake, *S. Kitamura s.n.*, 28 July 1931 (KYO), *H. Matsuda s.n.*, 22 July 1954 (TI), *Y. Ogura s.n.*, 28 July 1920 (TI); Kitakuma-gun, Shirasu-cho, Mt. Komaga-take, *G. Murata 11976* (KYO); Nakakuma-gun, Ashiyasu-mura, Mt. Kita-dake, *H. Terao 895* (KYO); "Fudzi yama" [Mt. Fuji-san], *Tschonoski s.n.*, 1864 (BM, P, UPS, W). **Kuril Islands.** KUNASHIRI: *without collector or number*, 1935? (KYO). **U.S.S.R.** SAKHALIN. Without further locality: *Augustinowicz 18591* (BM), *Augustinowicz s.n.* (G, GH, K). Maoka Province: Maoka-gun, Mt. Maoka-san, *T. Miyake s.n.*, 4 June 1907 (SAP); Katada-gun, Mt. Nota-san, *T. Miyake s.n.*, 28 June 1907 (SAP). Motodamari Province: Motodamari-gun, Mt. Tasso-san, *M. Nagai & S. Iwadera s.n.*, 23 July 1927 (SAP). Odomari Province: Nagahama-gun, Shiretoko-mura, Mt. Shiretoko, *T. Miyake s.n.*, 11 July 1908 (SAP, TNS). Shikika Province: Sanko-gun, Funadomari, *M. Tatewaki 22705, 22961* (KYO, SAP). Tomari Province: Nayoshi-gun, Nayoshi-mura, Kitakosawa, *M. Henmi 63* (MAK). Toyohara Province: Toyohara-gun, Mt. Suzuya-dake, *T. Miyake s.n.*, 27 July 1907 (SAP), *M. Sato s.n.*, 19 July 1932 (TI).

We have seen no collections of *Diphylleia* from the Amur region of the Soviet Far East. The reports of its occurrence there by Kumazawa (1930), Li (1947), and others appear to be based on the title of the publication in which *D. grayi* was first described (*Reisen in Amur-lande und auf der Insel Sachalin*), rather than on actual specimens. Fedchenko (1937), in his treatment of the Berberidaceae for *Flora SSSR*, attributed *Diphylleia* to only Sakhalin in the Soviet Union.

Takeda (*in* Takeda & Tanabe, 1931) named plants with very deeply lobed leaves *Diphylleia grayi* var. *incisa*, and those with the lobes essentially lacking var. *rotundata*. The degree of lobing of the leaves in *D. grayi* is variable and continuous; plants with both deeply lobed and nearly unlobed leaves can be found intermixed in single populations. *Kanai 742732* represents plants with lobed and unlobed leaves. There seems to be no basis for the recognition of these plants as infraspecific taxa.

Takeda (*in* Takeda & Tanabe, 1931) did not cite specimens or indicate types in his descriptions of *Diphylleia grayi* vars. *incisa* and *rotundata*, and we have seen no specimens annotated or collected by him with these varietal names. In lieu of specimens, we wish to designate the illustrations accompanying the original descriptions of these two varieties as the lectotypes.

In the more than 200 specimens of *Diphylleia grayi* that we examined, seven had upper petioles longer than 1 cm (1.2 cm, 1.3 cm, 1.4 cm, 1.6 cm, 2.1 cm, 4.4 cm, and 5.8 cm). The most logical explanation for these aberrant plants is that although they have only two leaves, they represent forms transitional between plants with two and plants with three leaves. In the occasional plants with three leaves, the uppermost leaf is sessile or subsessile while the next lower leaf is petiolate.

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APPENDIX 1. **Voucher specimens of Diphylleia used in anatomical studies.**

TAXON	VOUCHER
D. cymosa	U. S. A., North Carolina, Avery County, *E. W. Wood & Boufford 4150a* (BM, CM, KYO)
	U. S. A., North Carolina, Watauga County, *Boufford & E. W. Wood 20954* (CM, KYO)
D. grayi	Japan, Honshu, Hyogo Prefecture, Mt. Hyonosen, *S. Terabayashi 60* (KYO)
	Japan, Honshu, Ishikawa Prefecture, Mt. Haku-san, *S. Terabayashi 73, 74* (KYO)
	Japan, Honshu, Nagano Prefecture, Mt. Shirouma, *S. Terabayashi 793* (KYO)
	Japan, Honshu, Yamagata Prefecture, Mt. Iide, *M. Ito 40* (KYO)
D. sinensis	China, Hubei Province, Shennongjia Forest District, *Wan Jiziang* (material in fruit; no voucher collected)

APPENDIX 2. **Voucher specimens of Diphylleia used for pollen observations.**

TAXON	VOUCHER
D. cymosa	U. S. A., North Carolina, Watauga County, Potato Hill, N of jct. of state roads 1324 and 1306, *Kologiski & Perino 165* (GH)
	U. S. A., Virginia, Smyth County, NE slope of White Top Mt., *J. K. Small s.n.*, 28–29 May 1892 (GH)
	U. S. A., North Carolina, Macon County, 13 mi N of U.S. 64 on Rainbow Springs–Aquone Forestry Rd., *Radford 5239* (NCU)
D. grayi	Japan, Honshu, Iwate Prefecture, Mt. Hakkoda, *A. Kimura & S. Sugaya s.n.*, 3 July 1952 (TUS)
	Japan, Honshu, Miyagi Prefecture, Mt. Izumi, *K. Saito & T. Kaneko s.n.*, 18 May 1961 (TUS)
	Japan, Honshu, Nagano Prefecture, Minamiazumi-gun, *H. Takahashi 366* (TUS)
D. sinensis	China, Gansu Province, "SE Gansu," *Licent 5325* (BM)
	China, Sichuan Province, Mealo Xian, Lysugou, *Nan-shui–Beidiao Team 7164* (PE)
	China, Yunnan Province, "Ma-cul-chan," *Delavay 3862* (A)

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ADDENDUM. **Lectotypification of Diphylleia grayi F. Schmidt.**

Since this paper went to press, one of us (D. E. B.) has had the opportunity to examine the following specimens from Sakhalin, U. S. S. R., that were cited by Schmidt (1868) in his original description of *Diphylleia grayi*: no further locality, *Glehn s.n.*, beginning of August 1860; Dui, *F. Schmidt s.n.*, June 1860 (Schmidt did not indicate in the protologue that his collections were among those used in the original description, but the specimen cited as "Dui Anf. Juni 1860" is probably this one), *Glehn s.n.*, 21 July 1860; Arkai, *Glehn s.n.*, 27 May 1861; Kussunai, *Brylkin s.n.*, May 1860, *Brylkin s.n.*, 25 April 1861 (all at LE).

There are two plants on the sheet collected by *Glehn* on 21 July 1860, and both are atypical of the vast majority of *Diphylleia grayi* in having a petiolate upper leaf. It is almost certain, however, that Schmidt based his description of the fruits of *D. grayi* on this specimen, since none of the other specimens contains mature fruits. Of the other specimens, *Brylkin s.n.*, 25 April 1861, is a sterile plant, and the *Schmidt* specimen has no flowers and only very young fruits. *Glehn s.n.*, beginning of August 1860, is a mixed collection containing an upper leaf and infructescence (berries lacking) from one plant and the upper portion of another plant with two leaves and flowers, which must have been collected in the spring and not on the date indicated on the label. The specimen collected at Kussunai, *Brylkin s.n.*, May 1860, has only a single late flower and several very immature fruits and could not have been the source for Schmidt's description of floral characters. The remaining sheet, *Glehn s.n.*, 27 May 1860, collected at Arkai, contains two very young plants with flowers in various stages of development; these were clearly the basis for Schmidt's comments on the sepals, and for his comparison of them with those of *D. cymosa* Michaux, in his original description. There is also a small packet on this sheet that contains what appear to be portions of the roots of one of the plants.

Of the two specimens on this sheet, the one on the right is the more complete, and it is this one that I wish to designate as the lectotype of *Diphylleia grayi* F. Schmidt. Photographs of the lectotype have been deposited at A, KYO, and PE.

I am grateful to the director and curators at LE for making these specimens available to me on loan.—D. E. B.