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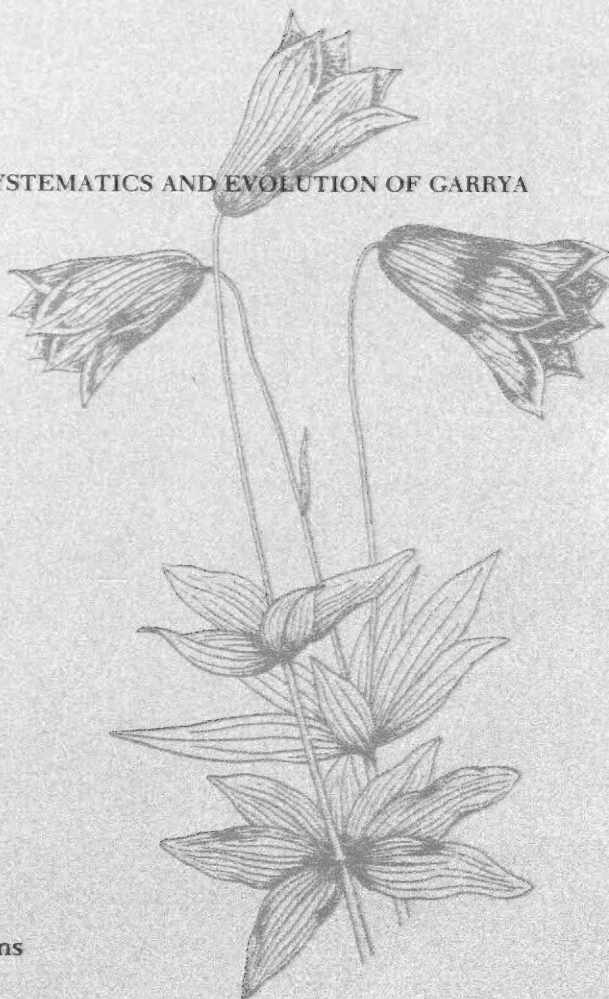
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SYSTEMATICS AND EVOLUTION OF GARRYA



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SYSTEMATICS AND EVOLUTION OF GARRYA

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# SYSTEMATICS AND EVOLUTION OF GARRYA

GERALD V. DAHLING<sup>1</sup>

## HISTORY

For many centuries the medicinal properties, charm, and aesthetic beauty of 'Esawana' were known to the Indians of southeastern Mexico. However, the plant was not discovered by white explorers until 1826 when David Douglas, an early explorer-naturalist, found *Garrya* in the Pacific Northwest. Seeds and cuttings were sent to the London Horticultural Society for propagation and within a few years it was flourishing in the Botanical Garden. Lindley (1834) used these plants, along with the Douglas collection, to first describe the order Garryaceae, named in honor of Nicholas Garry Esq., the first secretary of the Hudson Bay Company. The single species represented was *Garrya elliptica* and was designated the type of the genus. Thus the rich and varied taxonomic history of *Garrya* began (Table 1). The group was first allied with several families of the Amentiflorae because of the highly reduced nature of the flowers and the bracteate inflorescences. Included were the Piperaceae, Cupuliferae, Chloranthaceae, Urticaceae, Euphorbiaceae, and the Mensloviaceae. Endlicher (1836-1841), in his *Genera Plantarum*, also classified *Garrya* in a similar fashion. Considering Garryaceae and other amentiferous families to be primitive, he placed them directly after the gymnosperms. *Garrya*, in his treatment, was specifically related to the cupuliferous and chloranthaceous members of the class Juliflorae.

A much broader concept of Garryaceae became possible after the Mexican expedition of Theodor Hartweg in 1836. Several new species were discovered and subsequently described by Bentham in *Plantae Hartwegiana*.

Endlicher (1847) constructed a segregate genus *Fadyenia* for these new species but retained the original genus *Garrya* for *G. elliptica*. His familial division was based on the differences in the inflorescences and floral bracts.

Lindley revised his original classification in 1847, and established the order Garryales for the Garryaceae and Helwingiaceae. He also suggested that a progression from the Gnetales to the Amentales, Urticales, and Euphorbiales was so obvious that no explanation was required. He believed that the Garryales and Quernales represented neighboring groups which were epigenous forms of the Euphorbiales alliance. This Garryales-Euphorbiales relationship was strengthened by the putative approach of Garryaceae to Helwingiaceae, another Euphorbiales-related group included in the Garryales. To make the

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TABLE 1. TAXONOMIC HISTORY

Lindley (1834, 1847)	Founder of the genus, family, and order; related <i>Garrya</i> to Euphorbiales, Urticales, Quernales, Menispermiales, and Gnetales.
Endlicher (1837, 1847)	Placed Garryaceae within the Apetalae; related the group to Cupuliferae and Chloranthaceae; constructed <i>Fadyenia</i> as a segregate genus.
Bentham & Hooker (1867)	Lowered the taxonomic rank and placed <i>Garrya</i> within the Cornaceae.
DeCandolle (1869)	Placed Garryaceae near Salicaceae within the Amentiferae; sections <i>Eugarrya</i> and <i>Fadyenia</i> with nine and one species, respectively, were recognized.
Baillon (1879)	Related Garryaceae to Cornaceae; suggested an <i>Aucuba-Garrya</i> affinity.
Harms (1898)	Established the subfamily Garryoideae within the Cornaceae.
Wangerin (1906)	Rejected the Baillon classification and placed <i>Garrya</i> among the Amentiferae.
Wangerin (1910)	Monographed and considered <i>Garrya</i> an aberrant member of the Cornaceae; sixteen species were listed.
Faure (1924)	Anatomically compared Garryaceae with the Cornaceae and rejected a relationship; Garryales was placed next to Salicales.
Engler & Gilg (1924)	Garryales was related to the Amentiferae and placed near Salicales.
Bacigalupi (1924)	Maintained the order Garryales and provisionally positioned it near the Cornaceae.
Hallock (1930)	Based on morphology, Garryaceae was placed in the Umbelliflorae next to the Cornaceae.
Moseley & Beeks (1955)	Anatomically related Garryaceae with the Cornaceae.
Eyde (1964)	Suggested an affinity between <i>Garrya</i> and the Cornaceous genera <i>Aucuba</i> and <i>Griselinia</i> .
Present revision (1974)	Family rank maintained; Garryaceae placed next to the Cornaceae; subgenera <i>Garrya</i> and <i>Fadyenia</i> with six and eight species, respectively, are recognized.

trend complete, in Lindley's system *Garrya* was also related to the Menispermiales which followed the Garryales. Thus *Garrya* represented a single step in the 'obvious' progression from Gymnosperms to Dicots.

Lindley's position was attacked by Bentham and Hooker (1867), who lowered the taxonomic rank, dropped the segregate genus *Fadyenia*, and placed *Garrya* in the Cornaceae. Within two years, however, this was disputed by Alphonse DeCandolle (1869) and *Garrya* was again given a family rank and placed among the amentiferous groups. On the basis of stelar characters, *Garrya* was divided into sections *Eugarrya* and *Fadyenia*. This was an extremely artificial division of the genus and resulted in the formation of unrelated species groups. To add further confusion, section *Eugarrya* was divided into two parts, but without formal recognition. Although the names are similar, sections *Eugarrya* and *Fadyenia* of DeCandolle do not corre-

spond and are less satisfactory than the genera *Garrya* and *Fadyenia* of Endlicher (1847). The treatment of DeCandolle is completely artificial, without merit, and justifiably has never been followed.

Baillon (1874, 1879) studied living *Garrya* flowers from the Botanical Garden of Paris and concluded that an alliance with the Cornaceae was indicated. His opinion was based on morphological study and on the successful grafting of *Garrya* and *Aucuba japonica* of the Cornaceae. This relationship was maintained by Harms (1898) who constructed the subfamily Garryoideae within the Cornaceae.

Wangerin (1906), in an involved discussion, rejected Baillon's classification and included *Garrya* in the Amentaceae. This was rather short-lived, for in his monograph a few years later he reversed himself and placed it in the Cornaceae, but as an extremely aberrant form (Das Pflanzenreich, 1910). This conclusion failed to win support from Faure (1924) in his study of the Garryaceae and Cornaceae. After a detailed morphological investigation, a relationship with the Cornaceae was rejected in favor of an alliance with the Amentiferae. The order Garryales was maintained and placed next to the Salicales because both were interpreted as having superior ovaries. A similar conclusion was drawn by Engler and Gilg (1924), who also considered *Garrya* to represent a separate order near the Salicales. This was disputed in the same year, however, when Bacigalupi (1924) provisionally placed the order near the Cornaceae.

Modern studies and investigations have repeatedly demonstrated a Garryaceae-Cornaceae relationship. Hallock (1930) studied the reproductive structures of *Garrya* and clarified the morphology of the fruits and seeds. Careful developmental analysis, stressing the cytological events associated with the pre- and post-fertilization periods, also supported the separation of *Garrya* from the amentiferous groups. In addition, many anatomical features relating *Garrya* to the Cornaceae were discovered. As a result, Hallock placed Garryaceae in the Umbelliflorae next to the Cornaceae.

The most thorough phylogenetic investigation of *Garrya* was completed by Moseley and Beeks (1955). Eleven species were studied and compared to 23 families which were at one time considered to be related to *Garrya*. Concentrating on wood anatomy, they demonstrated profound differences between Garryaceae and the amentiferous families. Significant differences in wood anatomy were found in almost all the families except the Cornaceae. An analysis of other characteristics, including the phloem, and the nodal, floral, and pollen anatomy, also demonstrated trends which are common in the Cornaceae but are lacking in the other families compared. Developmental anatomy, cytology, paleobotany, and phytochemistry also were considered, allowing for a broadly based phylogenetic interpretation. The main

conclusion drawn from this was that the cumulative comparative evidence favored a relationship with the Cornaceae. It was also shown that, where similar structures are lacking, sequences of specialization from the Cornaceae to the Garryaceae are evident. Moreover, the Garryaceae was hypothesized to have differentiated by reduction from pro-umbellifloreal ancestral members which were cornaceous in nature.

The relationship between *Garrya* and the Cornaceae was supported and expanded by a critical examination of the ovary by Eyde (1964). Previously the ovary was variously interpreted, accounting for the vacillation in the placement of Garryaceae between the Amentiferae and the Cornaceae. Eyde suggested that a floristic relationship exists between *Garrya* and the Cornaceae, especially *Aucuba* and *Griselina*. While an alliance with *Aucuba* was previously recognized (Baillon, 1879), the suggestion of a *Garrya*-*Griselina* affinity was novel. Considering *Griselina* closest to the primitive condition, he further suggested the possible derivation of *Garrya*, *Aucuba*, and *Griselina* from common ancestral stock via reduction.

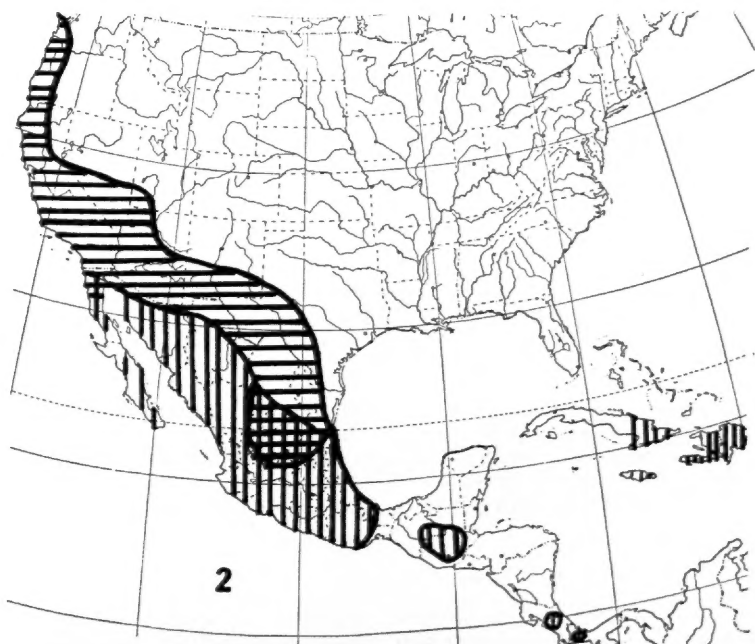
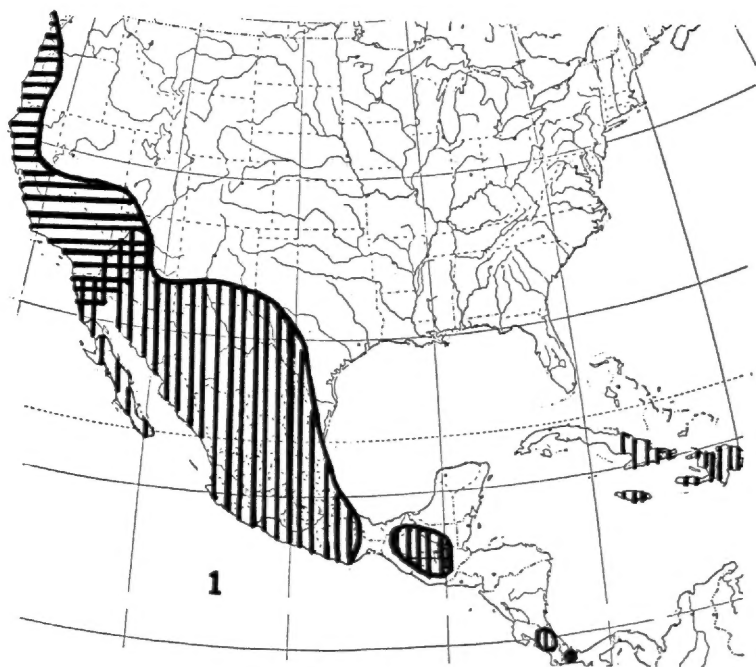
The present treatment maintains the rank of family for the Garryaceae and places it next to the Cornaceae. The subgenera *Garrya* and *Fadyenia*, with six and eight species respectively, are also recognized.

#### DISTRIBUTION

The genus *Garrya* is confined to the New World and ranges from the Pacific Northwest of North America to the volcanic peaks of Panama. As shown in Figure 1, subgenus *Garrya* generally occurs in northern areas ranging from Washington to Baja California and eastward to Sonora in Mexico, Arizona, Utah, and Nevada. A major exception to this otherwise close-knit and geographically related group is *G. corvorum*, an isolated representative found in central Guatemala. Subgenus *Fadyenia* is comprised of closely related species and generally occurs in more southerly areas. The species of this group range from Arizona, New Mexico, and Texas to western Panama and the Greater Antilles.

#### TAXONOMIC LIMITS

The generic limits of *Garrya* are readily definable and do not pose serious questions, but the taxonomic rank is more controversial. While a relationship with the Cornaceae appears well-documented (Hallock, 1930; Moseley & Beeks, 1955; Eyde, 1964), there exist sufficient differences in the floral morphology to warrant the recognition of it as a distinct family. The bracteate and amentiferous nature of the



FIGS. 1-2. 1, Distribution of the subgenera: horizontal lines—subgenus *Garrya*; vertical lines—subgenus *Fadyenta*. 2, Distribution of trichome types: horizontal lines—rough ridged trichomes; vertical lines—smooth ridged trichomes.

inflorescences, in addition to the much reduced flowers, serve to remove *Garrya* from the Cornaceae, supporting the recognition of it as a separate family. Moreover, while the Garryaceae and Cornaceae share certain glycosides and flavonoids, their phytochemical relationship, as outlined in a later section, is not close, thus helping to justify the retention of family status. The species form two infrageneric groups which are here recognized and designated as subgenus *Garrya* and subgenus *Fadyenia*. These subgenera can be readily characterized by their morphology (Table 2).

The taxa of subgenus *Garrya* are characterized by flowers borne in groups of three and with unbranched, condensed, and compact female inflorescences. The floral bracts are fused laterally and at the base forming cup-like structures which house and protect the floral clusters. The successive cup-like bracts are not leafy but overlap and appear imbricated. The ovaries are nude or occasionally bear small paired perianth remnants which alternate with, and arise near, the base of the paired styles. The smooth, terete, and elongated styles often equal, and frequently exceed, the length of the ovary in young material. Members of subgenus *Garrya* are usually shrubs, but small trees have also been observed.

Taxa of subgenus *Fadyenia* are characterized by bearing solitary flowers and the female inflorescences are branched, lax, and loosely spreading. Floral bracts are free, or fused only at the base, and appear expanded and distinctly leaf-like. The successive floral bracts are free and not overlapping or imbricated. Ovaries appear nude or sometimes bear minute bracteate appendages which are variably adnate and arise opposite and near the base of the paired styles. Being rough, thick, and short, the styles appear less delicate than those of subgenus *Garrya*.

TABLE 2. COMPARISON OF THE SUBGENERA

<i>Garrya</i>	<i>Fadyenia</i>
Inflorescences not branched	Inflorescences branched, at least at the base
Female inflorescences condensed, compact and straight	Female inflorescences lax and loosely spreading
Successive floral bracts closely spaced and frequently overlapping and imbricate	Successive floral bracts separate, free, and not overlapping
Paired floral bracts fused at base and laterally to form a cup-like structure	Paired floral bracts free or fused only at the base
Female floral bracts reduced and not leaf-like	Female floral bracts expanded and distinctly leaf-like
Flowers in groups of three	Flowers solitary
Ovary nude or bearing paired perianth remnants near base of styles	Ovary nude or bearing a minute pair of adnate bracts
Small trees and shrubs from 2-20 feet tall	Large trees and shrubs from 3-40 feet tall
Confined mostly to the far western United States	Mostly throughout Mexico, Central America, and the Greater Antilles

Large trees are common in subgenus *Fadyenia* although some species are distinctly shrubby. While a few species are found in the southwestern United States, most of them are geographically located in Mexico, Central America and the Greater Antilles.

### MORPHOLOGY

**Habit.** The plants of *Garrya* have numerous crown sprouts, in size they range from small shrubs to large trees, and appear distinctly bushy and clumped. In arboreal members the crown sprouts ring the trunk and are clearly secondary to the main stem axis, contrasting with the more shrubby members where the crown sprouts approach or sometimes exceed the main stem, giving a bushy appearance.

Within subgenus *Garrya*, the growth habit is variable even within given species. *Garrya elliptica* is a low shrub when growing near the coast but it often becomes arboreal inland, attaining heights of over 20 feet. *Garrya veatchii* is predominantly shrubby but occasionally small gnarled tree-like forms are observed. The latter has also been seen in *G. fremontii*, which sometimes also takes on the bushy character of *G. buxifolia*. The habit of *G. flavescens* is influenced by the availability of water and ranges from bushes to 20 foot trees. The Guatemalan *G. corvorum* is almost always arboreal.

Most species of subgenus *Fadyenia* are arboreal but *Garrya wrightii*, *G. grisea*, *G. ovata* ssp. *ovata*, and *G. ovata* ssp. *goldmanii* are exceptions. The latter is a small 2-5 ft. shrub and shows the most reduced habit of the genus. The other taxa mentioned are clumped and bushy, ranging from 6 to 15 feet. Species with an arboreal habit include *G. laurifolia*, *G. longifolia*, *G. salicifolia*, *G. glaberrima*, *G. fadyenii*, *G. ovata* ssp. *mexicana*, and *G. ovata* ssp. *lindheimeri*. The latter is rather shrubby in the northern part of its range and contrasts with *G. laurifolia* which often exceeds 35 feet in height. In general, an arboreal habit is most prevalent in subgenus *Fadyenia* while a shrubby habit is most frequent in subgenus *Garrya*.

**Root.** Root morphology in *Garrya* is quite uniform with little significant variation (Faure, 1924). Rows of cork along with a less-developed phelloderm, a narrow cortex, and a wide pericycle are present in all species. Circular vessel elements are prominent in the xylem as are sclerenchymatous rays. Calcium oxalate crystals and secretory cells are also common in the root parenchyma.

Although *Garrya flavescens* shows minor variation in the pericycle width, the general systematic and evolutionary importance of comparative root morphology appears to be very limited. This is especially true since the narrow pericycle of *G. flavescens* is an isolated occurrence that fails to correlate with other characters.



**Stem.** While the shape, color and pubescence of *Garrya* stems are important, the internal morphology yields little systematic information. Faure's comparative anatomical study (1924) demonstrated a general uniformity in stem structure although some variation was noted. The species examined contained cork, an inner and outer cortex, and a continuous or incomplete cylinder of fibres which borders the wood. As in the roots, calcium oxalate crystals are abundant in the parenchyma.

Growth rings in the secondary wood are usually distinct but rather narrow, indicating slow growth. This is not surprising since *Garrya* inhabits areas which are somewhat arid and generally unfavorable for rapid plant growth.

Wood and phloem anatomy has been studied in detail (Moseley & Beeks (1955); Metcalfe & Chalk, 1950) and is summarized here. Imperforate elements, such as tracheids and fiber tracheids, are common in *Garrya* wood and range from 210 to 1470  $\mu\text{m}$ . in length. The average is 762  $\mu\text{m}$ . which is moderately short as defined by the Committee on the Standardization of Terms of Cell Size (1937). Also, the wood is mostly ring porous and shows a solitary distribution of vessels although small clusters and chains are sometimes observed.

The average vessel diameter for *Garrya* is 34.2  $\mu\text{m}$ ., or very small as defined by Chalk (1938). Their perforation plates are scalariform showing from 1 to 13 bars and the end walls are quite oblique, ranging from 50-70° off the vertical. Pitting is opposite to alternate or transitional in most species. The average vessel length in *Garrya* is 562  $\mu\text{m}$ . or medium-sized, as defined by the Committee on the Standardization of Terms of Cell Size (1937).

Both uniseriate and multiseriate rays are present in *Garrya* and while compound rays are not found, a definite trend toward aggregation of rays is evident except in *G. elliptica* and *G. veatchii*. This may be systematically significant since both *G. elliptica* and *G. veatchii* are closely related. In contrast, no significance should be attached to ray and wood parenchyma type since both are highly variable even within taxa.

Phloem in *Garrya* is divided into wedge-shaped masses and is composed of sieve tubes, companion cells, phloem rays, and phloem fibres. The sieve tubes are arranged in radial rows and range from 120 to 400  $\mu\text{m}$ . in length and have extremely oblique walls with scalariform compound sieve plates. In most species the phloem fibres are arranged in bands but in *G. laurifolia* and *G. ovata* ssp. *lindheimeri* the fibres are solitary or sometimes absent. This may be significant because of their close systematic relationship. Large druses are sometimes found associated with the phloem rays, but are not common in the genus as a whole.

Vascular anatomy traditionally has been useful in phylogenetic studies, but, at the level of species its systematic importance is doubtful or at least diminished. This is also the case in *Garrya*, where exterior stem characters are more important and diagnostic than the internal morphology. It should be emphasized that this is only the case when questions of phylogeny are not considered.

**Leaf.** The leaves in *Garrya* are thick, persistent, and uniformly coriaceous, ranging from oblong, oval, ovate, to obovate in shape. On the exterior they appear opposite but, as shown by Moseley and Beeks (1955), the trilacunar vascular traces for one leaf become distinct from the stele before the traces for the other. Therefore, the arrangement is actually sub-opposite even though the leaves appear to occupy opposite positions at the nodes. The bases of the petioles are connate and adnate to the stem, which is characteristic of the genus. The angle of fusion with the stem is distinct and shows considerable variation among taxa (Plate 1). Leaf surfaces, variably covered with unicellular trichomes of differing shapes and arrangements, appear reticulate-rugose, especially within subgenus *Fadyenia*.

The internal anatomy of *Garrya* leaves was reported by Paliwal and Kakkar (1970) and is summarized here followed by my own observations. The upper epidermis, which is composed of a single layer of rectangular cells, is covered by a well-developed cuticle. The lower epidermal surface is double, with the inner layer often becoming sclerotic. A prominent hypodermis is found beneath the upper epidermis and is composed of large circular cells which contrast with the 2-3 layers of palisade parenchyma which are below. While usually retaining their nuclei and cytoplasm, they sometimes sclerify as do the isodiametric parenchyma cells in the spongy layer. In addition to collenchyma, brachysclereids are also found near the midrib and major veins. Sclereids are therefore produced in almost all areas of the leaf, accounting for their frequency and wide distribution.

The venation pattern of *Garrya* is distinctive and easily observed in cleared specimens. In the present study, leaf material was cleared in the usual way (Foster, 1949), mounted, and examined. Three vascular traces enter the leaf, with the outer two branching to form the midrib at the base of the lamina. A series of lateral or primary veins are produced and are directed toward, but never reach, the leaf margins. Secondary veins from the laterals connect neighboring veins, forming smooth loops which are quite prominent. Anastomoses of the secondaries produces numerous areoles which enclose terminal vein endings. As reported earlier by Paliwal and Kakkar (1970) filiform, stellate-polymorphic, and brachysclereids are common in the areoles, veins, and terminal vein endings. Filiform sclereids have narrow lumens and thick striated walls. The stellate-polymorphic sclereids are found

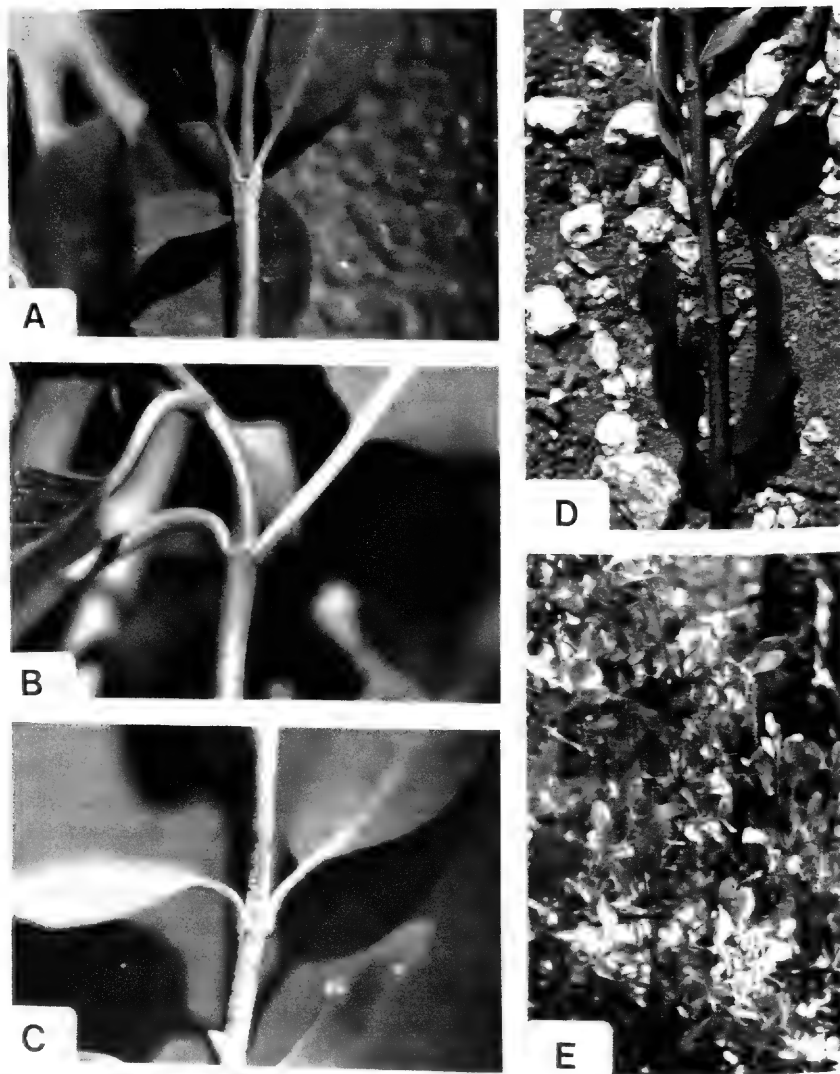


PLATE 1. Node, petiole, and leaf differences in *Garrya* species. A, *G. wrightii*, Dahling 543; B, *G. fremontii*, Dahling 1007; C, *G. huxifolia*, Dahling 1081; D, *G. laurifolia* ssp. *laurifolia*, Dahling 329; E, *G. fremontii*, Dahling 1007.

near the midrib, vein endings and leaf margins but are also widely scattered throughout the mesophyll. They are vertically oriented and have thick striated walls with a nucleus and cytoplasm. Brachysclereids, isodiametric cells with thick striated walls and small lumens, are chiefly confined to the midrib and lateral vein areas.

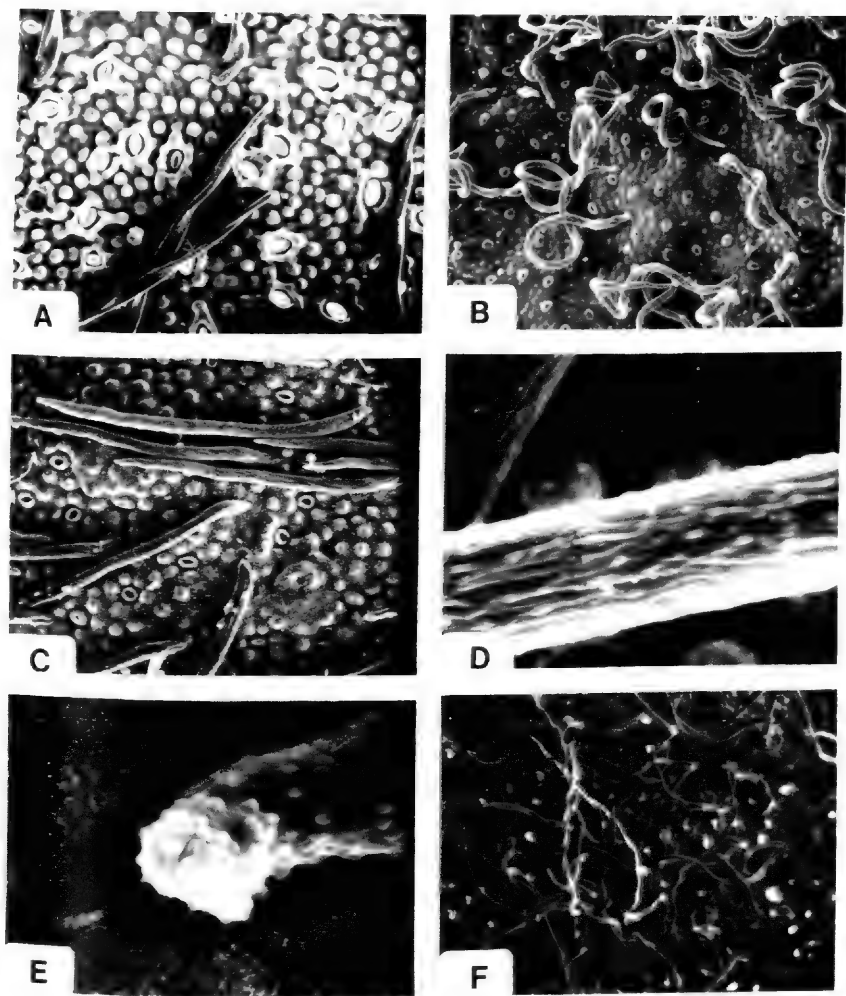


PLATE 2. Epidermal and trichome differences in *Garrya* species: A. *G. flavescens* ssp. *pallida*, Dahling 1426, 150 $\times$ ; B. *G. ovata* ssp. *lindheimeri*, Dahling 113, 75 $\times$ ; C. *G. grisea*, Wiggins and Demaree 4903, 150 $\times$ ; D. *G. urightii*, Dahling 1208, 1350 $\times$ ; E. *G. ovata* ssp. *lindheimeri*, Dahling 113, 2000 $\times$ ; F. *G. elliptica*, Dahling 369, 75 $\times$ .

Epidermal characters in *Garrya* are important systematic indicators and are quite significant (Plate 2A, B, C). Stomata are uniformly paracytic and confined to the lower leaf surface in all taxa. Their size and shape varies along subgeneric lines (Table 3) with the larger stomata being found in subgenus *Garrya*. *Garrya elliptica*, *G. fremontii*, and *G. flavescens* show the largest and most pronounced stomata

TABLE 3. STOMATAL APPARATUS

Subsidiary cells undulate	Subsidiary cells not undulate or wavy	
<i>G. elliptica</i> (least wavy)*	<i>G. corvorum</i> *	<i>G. grisea</i>
<i>G. veatchii</i> *	<i>G. ovata</i> ssp. <i>ovata</i>	<i>G. glaberrima</i>
<i>G. fremontii</i> *	<i>G. ovata</i> ssp. <i>lindheimeri</i>	<i>G. fadyenii</i>
<i>G. flavescens</i> ssp. <i>flavescens</i> *	<i>G. ovata</i> ssp. <i>goldmanii</i>	<i>G. longifolia</i>
<i>G. flavescens</i> ssp. <i>pallida</i> *	<i>G. ovata</i> ssp. <i>mexicana</i>	<i>G. laurifolia</i>
	<i>G. wrightii</i>	

\*Subgenus *Garrya*

while those of *G. corvorum* and *G. veatchii* are somewhat smaller but exceed those of subgenus *Fadyenia*. The stomata of subgenus *Fadyenia* are smooth, not undulate, and rather small. They are clearly wavy in *G. elliptica*, but less undulate than others in the subgenus. Subsidiary cells of *G. corvorum* are smooth and appear very similar to those of subgenus *Fadyenia*, indicating a possible distant relationship between *G. corvorum* and the other members of subgenus *Garrya*. Species of subgenus *Fadyenia* have subsidiary cells which are smooth, uniformly not undulate, and not wavy.

Epidermal surfaces range from papillate, as in most *Garrya* species, to muricate in *G. fremontii*. The papillae are most dense in *G. corvorum*, *G. ovata* ssp. *ovata*, *G. ovata* ssp. *mexicana*, *G. longifolia*, and *G. laurifolia*. While not as dense in other *Garrya* taxa, they are usually prominent and highly developed. Papillae in *G. fremontii* are smaller and less numerous than those of other taxa. Variation in the epidermal surfaces appears greatest in subgenus *Garrya*, since both maximum and minimum papillae development are represented in *G. corvorum* and *G. fremontii* respectively. Size variation in papillae crosses subgeneric lines. The largest are found in *G. flavescens*, *G. corvorum*, *G. wrightii*, *G. grisea*, *G. salicifolia*, and *G. longifolia*. The remaining *Garrya* species show prominent but smaller papillae with the smallest being found in *G. fremontii*.

Leaf sizes are quite variable in *Garrya* (Tables 4 and 5). Petiole length (PL $\bar{X}$ ), blade length (BL $\bar{X}$ ), total length (TL $\bar{X}$ ), and width (W $\bar{X}$ ) were measured and expressed as averages for natural populations. The figures were also expressed as proportions for calculating the petiole length:blade length (PL/BL), petiole length:total length (PL/TL), width:blade length (W/BL), and width:total length (W/TL) ratios.

*Garrya corvorum* has uniformly small leaves, shows little intraspecific leaf variation and is easily distinguished by the leaf length and width from the other members of subgenus *Garrya* (Table 4). The small amount of intraspecific leaf variation within *G. corvorum* is

TABLE 4. AVERAGES OF LEAF DIMENSION (cm.) AND PROPORTION FOR SUBGENUS GARRYA

Species	P $\bar{X}$	BL $\bar{X}$	W $\bar{X}$	TL $\bar{X}$	P/BL	P/L	W/BL	W/TL
<i>G. elliptica</i>	0.632	5.239	3.034	5.871	0.120	0.107	0.579	0.517
<i>G. veatchii</i>	0.530	4.242	1.959	4.773	0.125	0.111	0.461	0.410
<i>G. buxifolia</i>	0.603	3.568	1.791	4.172	0.169	0.144	0.502	0.429
<i>G. fremontii</i>	1.061	4.943	2.330	6.004	0.214	0.176	0.471	0.388
<i>G. flavescens</i>								
ssp. <i>flavescens</i>	0.891	4.890	2.491	5.781	0.182	0.154	0.509	0.430
<i>G. flavescens</i>								
ssp. <i>pallida</i>	0.916	4.494	3.324	5.410	0.203	0.169	0.517	0.429
<i>G. flavescens</i>								
ssp. <i>congdonii</i>	0.538	5.259	1.940	5.787	0.102	0.092	0.368	0.335
<i>G. corvorum</i>	0.362	3.070	1.266	3.433	0.118	0.148	0.412	0.368

TABLE 5. AVERAGES OF LEAF DIMENSION (cm.) AND PROPORTION FOR SUBGENUS FADYENIA

Species	P $\bar{X}$	BL $\bar{X}$	W $\bar{X}$	TL $\bar{X}$	P/BL	P/TL	W/BL	W/TL
<i>G. ovata</i> ssp. <i>ovata</i>	0.825	4.441	2.458	5.266	0.185	0.156	0.553	0.466
<i>G. ovata</i> ssp. <i>goldmanii</i>	0.630	3.485	1.768	4.115	0.180	0.153	0.507	0.429
<i>G. ovata</i> ssp. <i>lindheimeri</i>	1.083	5.250	2.616	6.334	0.206	0.171	0.498	0.413
<i>G. ovata</i> ssp. <i>mexicana</i>	1.466	8.328	3.717	9.795	0.176	0.149	0.446	0.379
<i>G. wrightii</i>	0.563	3.679	1.748	4.243	0.153	0.132	0.475	0.411
<i>G. grisea</i>	0.600	3.766	1.550	4.366	0.159	0.137	0.411	0.354
<i>G. salicifolia</i>	0.739	5.609	1.763	6.348	0.131	0.116	0.314	0.277
<i>G. glaberrima</i>	1.003	6.718	2.937	7.722	0.149	0.129	0.422	0.367
<i>G. fadyenii</i>	0.812	6.601	2.057	6.823	0.135	0.119	0.342	0.301
<i>G. longifolia</i>	1.210	10.567	4.091	11.777	0.114	0.102	0.387	0.347
<i>G. laurifolia</i>								
ssp. <i>laurifolia</i>	1.218	8.698	3.573	9.916	0.140	0.122	0.410	0.360
<i>G. laurifolia</i>								
ssp. <i>macrophylla</i>	1.339	9.673	5.122	11.012	0.138	0.121	0.529	0.465
<i>G. laurifolia</i>								
ssp. <i>racemosa</i>	1.925	13.684	4.312	15.609	0.140	0.123	0.315	0.276
<i>G. laurifolia</i>								
ssp. <i>quichensis</i>	1.202	8.502	3.039	9.704	0.141	0.123	0.357	0.313

not surprising since it grows in a restricted area where presumably the temperature and the precipitation are relatively constant from one site to the next. The other larger-leaved members of subgenus *Garrya* do, however, show considerable inter- and intraspecific variation in leaf size. Although leaves of *G. elliptica*, *G. fremontii*, and *G. flavescens* are larger than those of *G. veatchii* and *G. buxifolia*, the leaf size within a species frequently varies extensively, depending on moisture, and the edaphic and general climatic conditions for growth. Intraspecific variation in the petiole length was also noted. On the average, the longest petioles are found in *G. fremontii* and *G. flavescens*.

Variation in the leaf size ratios (Table 4) for members of subgenus *Garrya* is not extensive but there are some differences among the taxa. The smallest petiole length:blade length ratios are found in *G. elliptica*, *G. veatchii*, *G. corvorum*, and *G. flavescens* ssp. *congdonii*. Their ratios are quite similar, ranging from .102 to .125. *Garrya fremontii*, *G. buxifolia*, *G. flavescens* ssp. *flavescens* and *G. flavescens* ssp. *pallida* have larger and less uniform petiole:blade length ratios which range from .169 to .214. In addition, these taxa also have larger petiole length:total length ratios than do *G. elliptica*, *G. veatchii*, and *G. flavescens* ssp. *congdonii*. Within subgenus *Garrya* the width:blade length ratios are quite similar with the exception of *G. flavescens* ssp. *congdonii*, *G. corvorum*, and *G. elliptica*. The two former taxa show small ratios of .368 and .412 respectively. The latter shows a ratio of .579 which is the largest width:blade length ratio within *Garrya*. The width:total length ratios generally parallel the width:blade length ratios and will not be discussed further.

The largest leaves are found within subgenus *Fadyenia* (Table 5). The average petiole lengths of *Garrya laurifolia*, *G. longifolia*, *G. glaberrima*, *G. ovata* ssp. *mexicana*, and *G. ovata* ssp. *lindeheimeri* contrast with the shorter lengths of the remaining taxa. Also, the average leaf blade lengths and widths of the large-leaved *G. laurifolia*, *G. longifolia*, and *G. ovata* ssp. *mexicana* stand out from the smaller leaved species. The latter include *G. wrightii*, *G. grisea*, and *G. ovata* ssp. *goldmanii* with small leaves; and *G. ovata* ssp. *ovata*, *G. ovata* ssp. *lindheimeri*, *G. salicifolia*, *G. glaberrima*, and *G. fadyenii* with leaves of intermediate size.

As with members of subgenus *Garrya*, leaf ratios within subgenus *Fadyenia* are fairly uniform. The petiole length:blade length and petiole length:total length ratios are largest in *G. ovata*. The ratios of the remaining members of subgenus *Fadyenia*, however, are smaller and show little significant variation. The largest width:blade length ratios are found in *G. ovata* ssp. *ovata* and *G. laurifolia* ssp. *macrophylla*; the smallest are found in *G. salicifolia* and *G. laurifolia* ssp. *racemosa*. Thus very large and very small ratios are found within the same species. Because interspecific leaf variation is nearly continuous, data of this sort must be cautiously applied if valid systematic conclusions are to be drawn.

**Trichomes.** The diagnostic value of trichomes in identifying *Garrya* species was recognized early. Taxonomic keys (Eastwood, 1903; Wangerin, 1910; and Bacigalupi, 1924) relied heavily on the trichome arrangement on abaxial leaf surfaces. From my own observations in the field and with the scanning electron microscope, this is not without justification. As was discovered, trichome arrangement and their fine structure yield information of considerable systematic and evolutionary significance.

Trichomes of *Garrya* are unicellular and are found in all species except *G. glaberrima* which, as the name implies, completely lacks an indumentum. The trichomes are not confined to the leaves, but commonly occur on the stems, flowers, and fruits as well. However, the SEM investigations concentrated on the leaf trichomes because of their accessibility and ease of preparation.

**Method:** Mature leaves appearing normal in size, shape, and color were selected and labeled. Small square leaf portions were excised with a sharp razor blade and then transferred to aluminum pedestals coated with silver paint. The leaves, with the adaxial surfaces down, were placed in the paint and allowed to dry in a flat position. After 20 minutes, additional silver paint was applied to the specimen corners, insuring a firm attachment to the pedestal. Next, the specimens were evacuated to  $10^{-4} - 10^{-5}$  torr. in a Varian Vacuum Evaporator VE 10, coated with carbon and then gold-palladium. They were then placed in an AMR Model 900 scanning electron microscope and examined. The results were recorded photographically.

**Discussion:** The trichomes of *Garrya* are delicate and quite susceptible to electron beam damage (Plate 2D). They are roughened by ridges and furrows which are oriented in a counterclockwise direction. In some species, the ridges bear small protuberances which stand out in high relief (Plate 2E). In species lacking the protuberances, the smoother trichomes bear only ridges and furrows. The rough-ridged trichomes appear on all species of subgenus *Garrya* except *G. corvorum* (Figure 2). *Garrya corvorum* has smooth-ridged trichomes which are characteristic of subgenus *Fadyenia*. This extremely interesting finding indicates a possible early evolutionary divergence from the ancestral stock of subgenus *Garrya*. The peculiar isolated Guatemalan distribution of *G. corvorum* also supports this view. With other species confined to the far western United States, *G. corvorum* is spatially isolated, making a close relationship with the western members difficult to explain. Flavonoid investigations show only loose affinities with the other taxa and *G. corvorum* appears chemically intermediate between the two subgroups, also suggesting an early divergence from ancestral types common to both subgenera.

Only *Garrya ovata* and *G. wrightii* of subgenus *Fadyenia* show the rough-ridged trichomes. Since both taxa are northern and show moderate specialization within the subgenus, the development of trichomes of a different sort is not unexpected.

Within subgenus *Garrya*, trichome variation in both arrangement and detail is striking. Trichomes of *Garrya elliptica* (Plate 2F) densely cover the abaxial leaf surfaces and appear short, curly, and intertwined. The counterclockwise distribution of ridges and furrows is prominent as are the small protuberances which appear to be confined to the tops of the ridges (Plate 3A). *Garrya veatchii* (Plate 3B) has trichomes



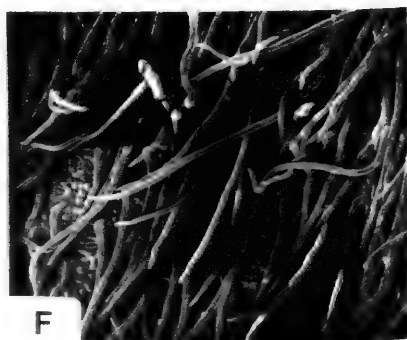
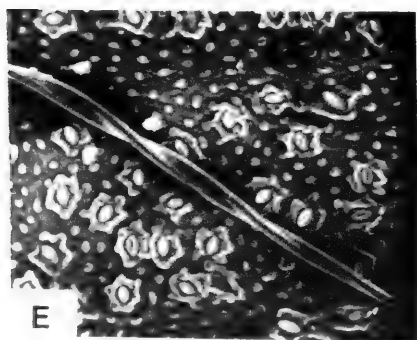
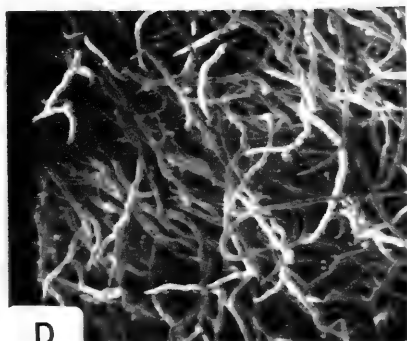
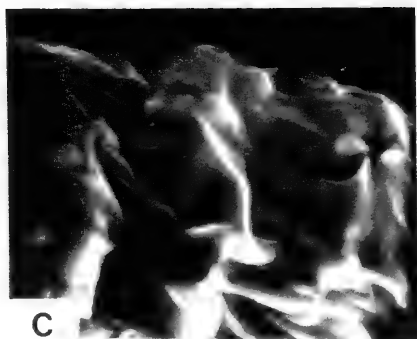
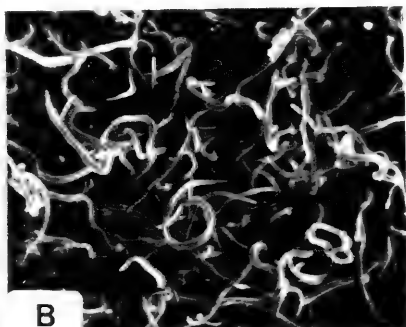


FIGURE 1. Trichome differences in *Garrya* species. A, *G. elliptica*, Dahling 1369, 150 $\times$ ; B, C, *G. recticollis*, Dahling 1512, B 75 $\times$ , C 3375 $\times$ ; D, *G. buxifolia*, Dahling 1512, 75 $\times$ ; E, *G. fremontii*, Dahling 1078, 75 $\times$ ; F, *G. flavescentis* ssp. *flavescentis*, Dahling 1637, 75 $\times$ .

which are extremely curly and interwoven, forming a dense mat-like covering on the underside of the leaf. They are shorter and much more dense and curled than those of *G. elliptica*. In addition to the characteristic ridges and furrows, the trichome surface shows a series of rather large vertical valleys (Plate 3C). Thus, two systems of ridges

and furrows running in opposite directions are present on the trichomes. Trichomes of *G. buxifolia* (Plate 3D) are wavy to straight and upwardly appressed forming a dense silky covering of the leaf abaxial side; the surfaces are covered with the customary ridges and furrows. Again protuberances are numerous and are located on the ridges. *Garrya fremontii* (Plate 3E) normally shows few trichomes on its leaves, but those present are striking. In addition to the ridges and furrows, the entire trichome is twisted in a counterclockwise direction. Thus in this taxon, the trichomes have taken on a compound counterclockwise orientation. Numerous protuberances are present, chiefly occurring on the ridges but occasionally protuberances in the furrows have been observed. Trichomes of *G. flavescens* ssp. *flavescens* are more or less straight and upwardly appressed to the lower leaf surface (Plate 3F). They form a dense and silky white covering that appears soft and fine. Upon closer examination, several trichomes reveal a compound counterclockwise orientation similar to that of *G. fremontii*. This compound orientation is especially pronounced in *G. flavescens* ssp. *pallida* (Plate 4A). These trichomes appear upwardly appressed but are wavy, coarse, and only sparsely cover the underside of the leaf. Ridges and furrows (Plate 4B) are oriented in a counterclockwise direction with protuberances confined chiefly to the ridges. They appear similar in size and shape to those of *G. flavescens* ssp. *flavescens* (Plate 4C). The size and design of the stomatal apparatus of *G. fremontii* (Plate 3E), and both subspecies of *G. flavescens*, are similar and distinctive, suggesting a close relationship. *Garrya corvorum* (Plate 4D) has trichomes which are long, straight, and generally upwardly appressed. They are white and soft, giving the leaf undersides a light silky appearance, and they glisten in the sun. Lacking protuberances (Plate 4E), the trichomes are smoother and more uniform than those of other members of the subgenus. The usual ridges and furrows are present (Plate 4F) but the protuberances so characteristic of subgenus *Garrya* are not.

Members of subgenus *Fadyenia* show a high degree of trichome variation. All subspecies of *Garrya ovata* have a dense trichome cover on the leaf undersurface. Trichomes of *G. ovata* ssp. *ovata* are moderately appressed to the surface and appear somewhat tangled and curly. *Garrya ovata* ssp. *goldmanii* (Plate 5A) has short, curly, crinkly, grossly entangled leaf trichomes, forming a dense mat on the leaf undersurface and, in younger material, on the adaxial surface as well. Ridges and furrows, bearing extremely large protuberances, are oriented in a counterclockwise direction (Plate 5B). The protuberances are much larger than those of other species and stand out in high relief. Leaves of *G. ovata* ssp. *lindheimeri* appear woolly, due to their short, highly coiled, crinkly, curly trichomes (Plate 5C). Also,

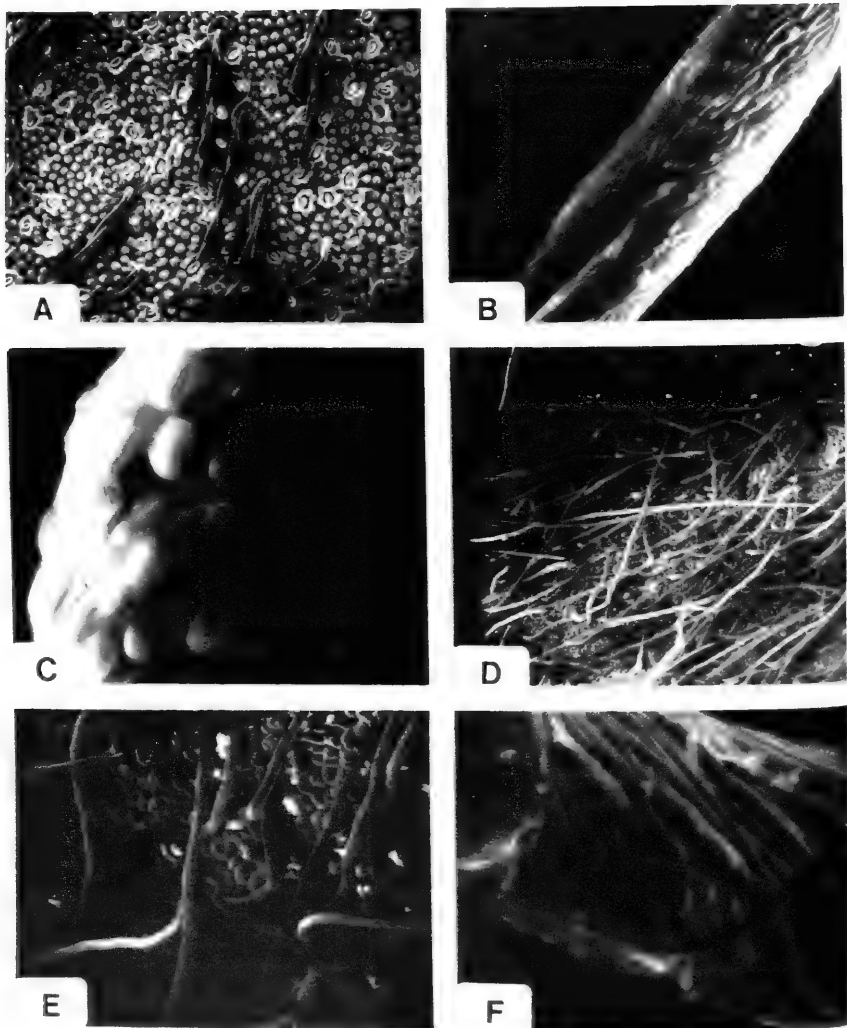


PLATE 4. Trichome differences in *Garrya* species. A-B *G. thalassensis* ssp. *pallida* Dahling 1426. A-25 $\times$ , B-1350 $\times$ . C-D *G. thalassensis* ssp. *thalassensis* Dahling 1637. C-375 $\times$ , D-25 $\times$ . E-F *G. corchorum* Hammewell 17196. E-25 $\times$ , F-75 $\times$ .

a system of shallow ridges and furrows (Plate 5D) bearing large protuberances is present. The protuberances are numerous and cover the trichome surface almost to the tip (Plate 2E). Trichomes of *G. ovata* ssp. *mexicana* show similar ridges, furrows, and protuberances but are less curly (Plate 5E). They also appear appressed and entangled but less numerous. Trichomes of *G. wrightii* are usually sparse or

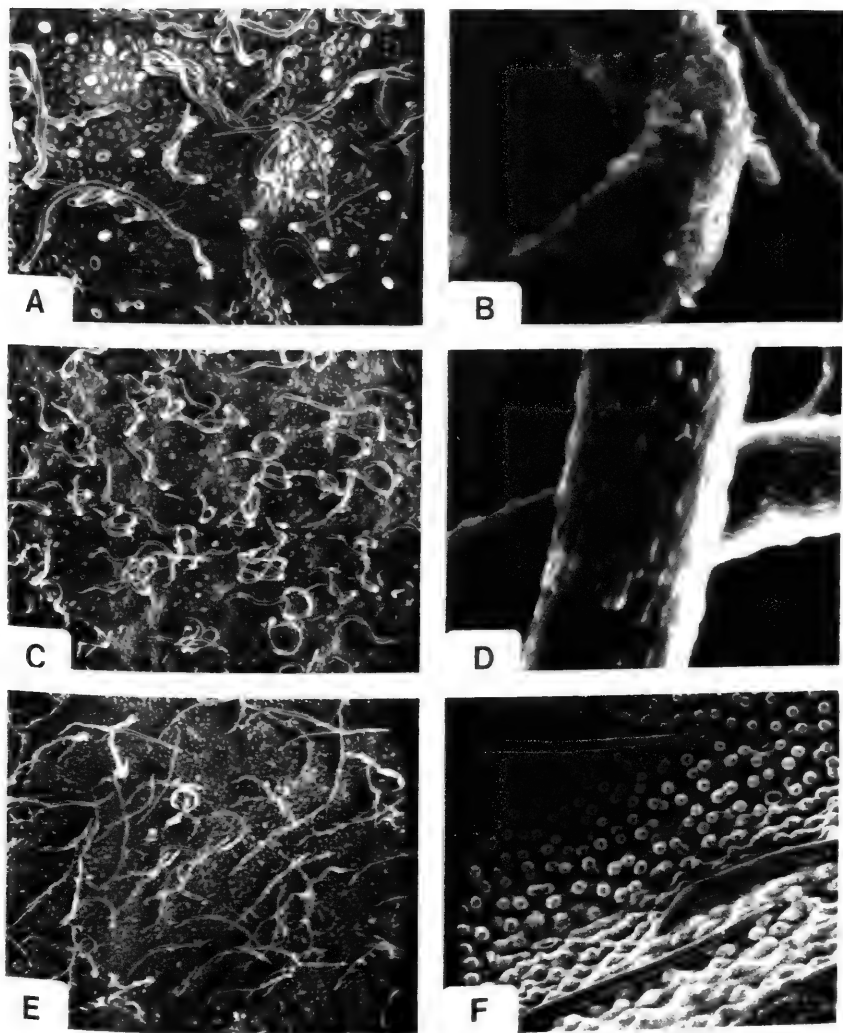


PLATE 5. Trichome differences in *Garrya* species: A, B, *G. ovata* ssp. *goldmanii*, Dahling 1414, A-75 $\times$ , B-1350 $\times$ ; C, D, *G. ovata* ssp. *lindheimeri*, Dahling 333, C-25 $\times$ , D-1350 $\times$ ; E, *G. ovata* ssp. *mexicana*, Dahling 126, 25 $\times$ ; F, *G. wrightii*, Dahling 1208, 150 $\times$ .

absent, but those present are short, straight, and upwardly appressed (Plate 5F). The system of ridges and furrows, with numerous protuberances, is gently oriented in a counterclockwise direction (Plate 6A). The protuberances are confined to the ridges and are smaller than those of *G. ovata*. Leaves of *G. grisea* are densely covered with short, straight, and upwardly appressed trichomes on both the abaxial and

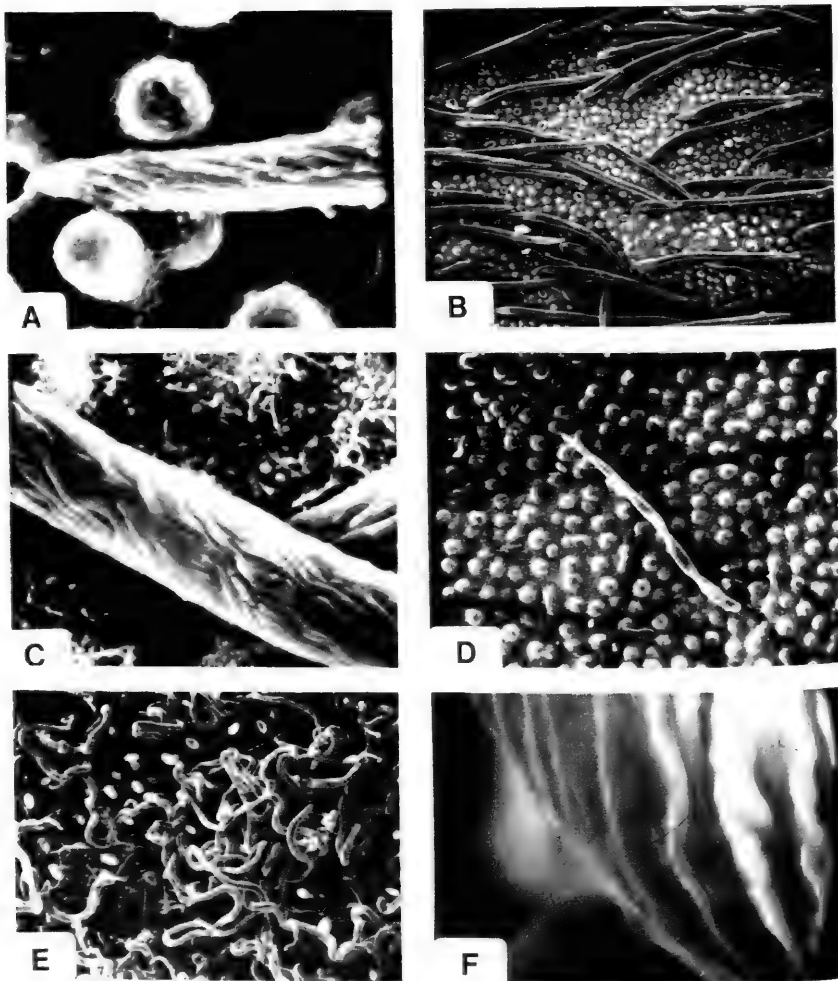


PLATE 6 Trichome differences in *Garrya* species. A. *G. wrightii*, Dahling, 1208, 1350 $\times$ ; B, C, *G. grisea*, Wiggins and Demaree 4903, B-75 $\times$ , C-1350 $\times$ ; D. *G. salicifolia* Nelson and Goldman 7458, 150 $\times$ ; E, F. *G. fadyenii*, Rehder 2-10-1903, E, 75 $\times$ , F 3375 $\times$ .

adaxial surfaces (Plate 6B). The ridges and furrows are coarse, as in *G. wrightii*, but the protuberances are essentially lacking (Plate 6C). They are barely perceptible and are represented by minor areas of swelling on the tops of ridges. *Garrya salicifolia* is the only member of subgenus *Fadyenia* with a pronounced compound counterclockwise orientation of leaf trichomes. The trichomes are extremely sparse, but the structural twisting in those present is evident (Plate 6D).

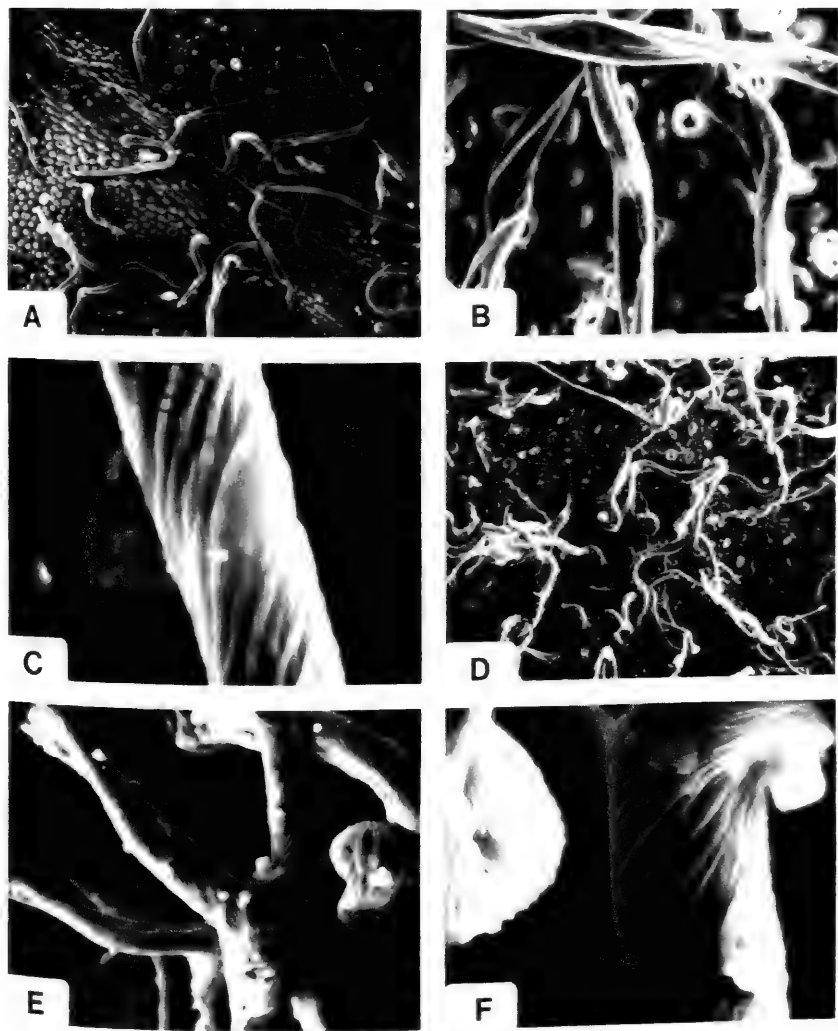


PLATE 7. Trichome differences in *Garrya* species: A, B, C, *G. longifolia*, Dahling 2121, A-75 $\times$ , B-350 $\times$ , C-1350 $\times$ ; D, E, F, *G. laurifolia*, Dahling 3838, D-75 $\times$ , E-350 $\times$ , F-1350 $\times$ .

Ridges and furrows line the trichome surface but there are no protuberances. *Garrya fadyenii* shows abaxial leaf trichomes which are dense, curly, tangled, and more or less erect (Plate 6E). They are moderately long and form an intertwining mat on younger leaves. Ridges and furrows line the trichome surfaces and appear widely spaced and rather coarse (Plate 6F). No protuberances have been observed. The

leaf trichomes of *G. longifolia* are short, curly, and more or less appressed (Plate 7A). Some have a compound counterclockwise orientation (Plate 7B), but the structural twisting appears gentle and not as severe as that seen in *G. salicifolia*. The ridges and furrows are coarse and completely lack protuberances (Plate 7C). The leaf undersides of *G. laurifolia* are covered by moderately long, curly, tangled and more or less erect trichomes (Plate 7D). They form a woolly mat in *G. laurifolia* ssp. *laurifolia* and *G. laurifolia* ssp. *macrophylla* but the trichomes are rapidly lost in *G. laurifolia* ssp. *racemosa* and *G. laurifolia* ssp. *quichensis* as the leaves mature. The trichomes appear relatively smooth even though ridges and furrows are present because of the absence of protuberances (Plate 7E). They are oriented in the usual fashion and appear fine and more delicate than those of *G. longifolia* (Plate 5F).

**Inflorescence.** The morphology of the inflorescence (Reeve, 1943) varies according to subgeneric lines and is an important source of systematic characters. The inflorescence is essentially an axis bearing oppositely arranged bracts which subtend highly reduced flowers (Plates 8C, D). Frequently the weight of the inflorescence causes it to droop and resemble an ament, accounting for the earlier placement of *Garrya* among amentiferous groups (Table 1).

Within subgenus *Garrya*, both the male and female inflorescences are unbranched and of variable lengths. They are linear and compact with reduced decussate bracts closely spaced, overlapping, and imbricate. The paired bracts are connate both at the base and laterally, forming cup-like structures which house ternate flowers. The fasciculate inflorescences are borne at the ends of the branches and are usually pendulous, although in *Garrya fremontii* they may also be semierect. At maturity the inflorescences are sometimes less compact, especially the male inflorescences, where internodes between the floral bracts are often visible.

The inflorescences within subgenus *Fadyenia* are pendulous, branched, bear solitary flowers, and are borne in clusters at the ends of the branches. The female inflorescences are lax, with the decussate floral bracts connate only at the base, and not imbricate as in subgenus *Garrya* (Plates 8A, F). The bracts are expanded and distinctly leaf-like in *G. laurifolia* (Plates 9A, C). They are reduced and much smaller than the foliage leaves in other species of the subgenus (Plate 9B). While most of the flowers are subtended by a single bract, the terminal flowers are subtended by a partially adnate bract pair.

A strong trend toward reduction in lateral branching of the inflorescence is evident within subgenus *Fadyenia*. Branching is common in *Garrya laurifolia* and *G. longifolia*, but is restricted and reduced in *G. wrightii*. *Garrya laurifolia* has long branches but those of *G.*

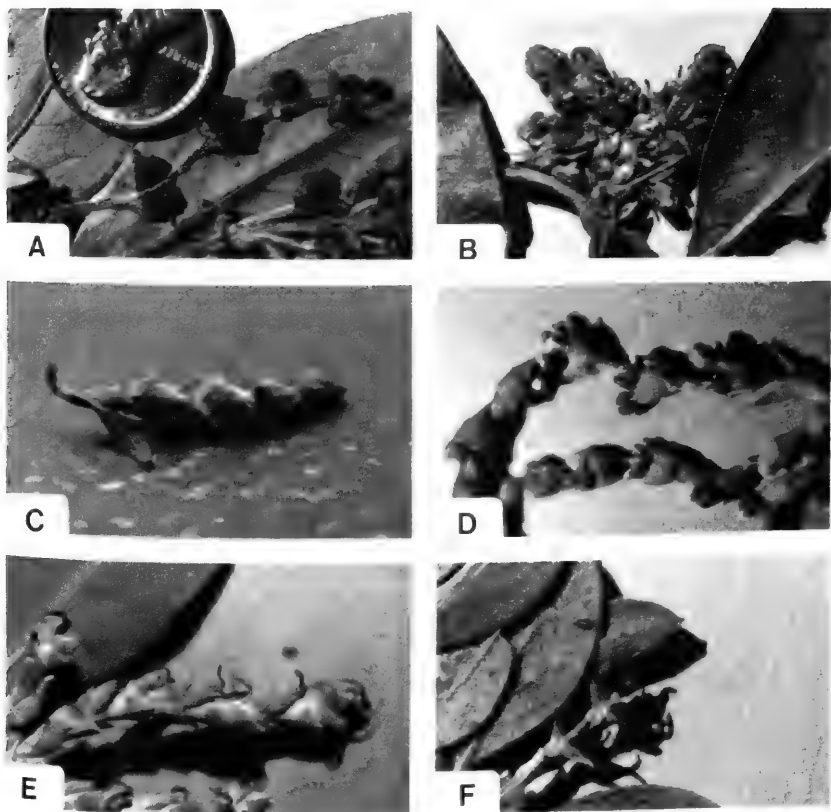


PLATE 8 Inflorescence and floral differences in *Garrya* species: A, *G. longifolia*, Dahling 2120; B, *G. ovata* ssp. *lindheimeri*, Dahling 331; C, *G. flavescens* ssp. *flavescens*, Dahling 781; D, *G. fremontii*, Dahling 1150; E, *G. flavescens*, Dahling 918; F, *G. ovata* ssp. *lindheimeri*, Dahling 325.

*wrightii* are short and have only terminal flowers. These are generally subtended by a pair of bracts, making their recognition easy and definite. Short lateral branches with several flowers are also present in *G. wrightii* but are confined to the bases of the inflorescences, as is seen in *G. ovata*. The number, position, and length of the lateral branches in the former species have become suppressed until only terminal flowers are represented in branches above the base. A continuation of the evolutionary trend leads to the complete suppression of branching, as is found in the inflorescences of subgenus *Garrya*.

The pendulous male inflorescences are shorter and more condensed than their female counterparts. The inflorescence branches are short and only bear a few flowers although branching is common near the base. Terminal male flowers are also subtended by a pair of bracts,



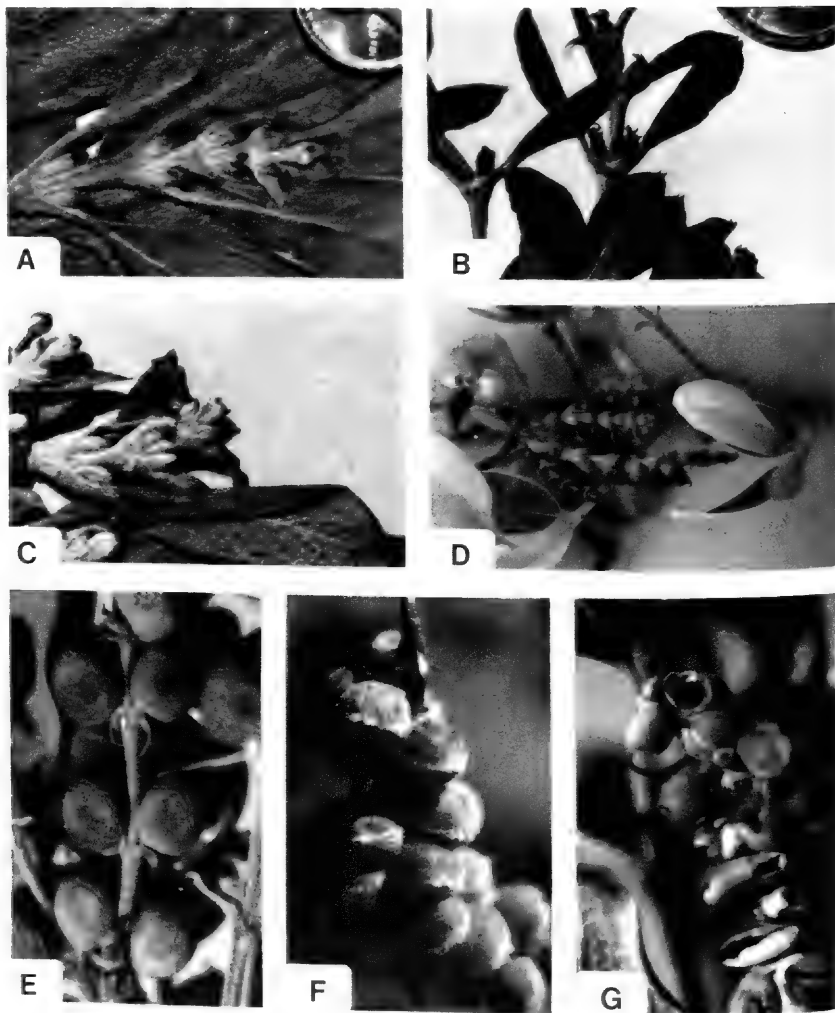


PLATE 9. Floral and fruit differences in *Garrya* species: A, *G. laurifolia* ssp. *racemosa*, Dahling 118; B, *G. urightii*, Dahling 1206; C, *G. laurifolia* ssp. *macrophylla*, Dahling 280; D, *G. buxifolia*, Dahling 1050; E, *G. longifolia*, Dahling 2130; F, *G. elliptica*, Dahling 1361; G, *G. flavescens* ssp. *flavescens*, Dahling 1635.

and are easily distinguished from the lateral flowers. The bracts are uniformly reduced and are less expanded or leaf-like than the female structures.

The male inflorescence of *Garrya longifolia* is an important taxonomic feature because of the prominent branching and lax character. The flowers are not crowded and appear widely spaced, as they are

in the female inflorescences. Hence, *G. longifolia* may serve as the starting point in a series of reductions that lead to the condensed male inflorescences which characterize other members of the genus (Plate 8A).

**Flowers.** The reduced nature of *Garrya* flowers has been responsible for the phylogenetic confusion surrounding the group. The female flowers have been variously interpreted as having superior or inferior ovaries, dramatically affecting the classification of the genus (Table 1).

The minute female flowers are represented by an ovary subtended by a single bract or sometimes by a pair (Plate 9). The ovary is bicarpellate (rarely tricarpetate) with two persistent styles, and produces a pair of subterminal anatropous ovules. The perianth is reduced or lacking in older material making the ovary appear superior. However, careful examination sometimes reveals small paired appendages at the base of the styles. Typically one pair of appendages, but sometimes two, are present and situated at about the same level. They are variably adnate to the ovary and show considerable variation in size.

Paired ovarian appendages are found in both subgenus *Garrya* and subgenus *Fadyenia* but their orientations are quite different, an observation first recorded by Eyde (1964). The appendages of subgenus *Garrya* are alternate, while those of subgenus *Fadyenia* are opposite the styles. In addition, the ovarian appendages of subgenus *Fadyenia* are restricted to the terminal flowers of the inflorescences or inflorescence branches. Pronounced differences in vasculature suggest that the appendages are not homologous and therefore not comparable.

Each carpel contains a dorsal and two ventral or marginal vascular bundles (Eyde, 1964). At lower levels in the ovary the lateral bundles of adjacent carpels fuse, forming two large compound ventral bundles which are oriented opposite each other. Near the top of the ovary the compound ventral bundles bifurcate and proceed, with the dorsals, to the base of the styles and then terminate. The styles are not vascularized in either subgenus. Each ovule is supplied with a single vascular strand which connects to the compound ventral at about the level of bifurcation. If the vascular connection is above the point of bifurcation, two strands diverge from each ventral bundle, later fusing to form the single ovular supply.

Within subgenus *Garrya*, the paired ovarian appendages sometimes lack a vascular supply. However, when present it consists of a single vascular bundle which is fused, at least procambially, with the compound ventral bundle. Ovarian appendages of subgenus *Fadyenia* are variably situated on the ovary and are also not always vascularized. The appendages borne near the styles are less leaf-like than those in a lower position, which show a prominent midrib and reticulate

venation. When present, the vascular supply consists of a single strand which, although aligned with the dorsal bundle, does not unite with it but rather extends independently into the pedicel. Therefore, the paired ovarian appendages in subgenus *Fadyenia* are leaf-like in character and are fundamentally bracts. Those of subgenus *Garrya*, as demonstrated by their vasculature, are intimately associated with the carpels and represent perianth remnants. These reduced segments are adnate and in a terminal position making the ovary clearly inferior. It can also be inferred that the perianth has been completely lost by members of subgenus *Fadyenia*. The ovary would then appear superior accounting for the earlier erroneous descriptions.

The floral characters in *Garrya* are generally not important systematically because of the reduced nature and similarity of the flowers. However, the styler characters are important and provide useful information for the characterization of subgenera and even certain species. Within subgenus *Garrya*, the styles are smooth, elongated and terete. In *G. fremontii* the pair of styles is strongly divergent, curly, and appears distinctly mustache-like and wavy, contrasting with the more erect styles of *G. flavescens* (Plate 8E). The styles of the species in subgenus *Fadyenia* are quite uniform, appearing short, thick and somewhat fleshy (as in *G. laurifolia*). Minor papillae are sometimes present but lack systematic importance.

The male flowers are minute, and consist of four anthers and four ovate-oblong perianth segments. These segments are connate at their tips, forming slits or windows for the alternately arranged anthers (Plate 8B). They often appear yellow-green to red and brown. While the pedicels are generally short, they are almost lacking in some populations of *Garrya longifolia* and appear somewhat longer in *G. elliptica* and other members of subgenus *Garrya*. The perianth segments are variably pubescent, especially near the connate tips, but are essentially glabrous on the adaxial side. Normally the flowers of *G. glaberrima* are entirely glabrous, although sometimes a single row of stiff trichomes is found on the perianth borders. The anthers are oblong-elliptic, introrse, open by longitudinal slits, and are basifixed to extremely short filaments which barely exceed the length of the anthers. The presence of a degenerate or obsolete ovary within the male flowers has been periodically reported, but my own observations have not verified this.

The male flowers in *Garrya* are fairly uniform in size, but those of *G. wrightii* and *G. grisea* appear smaller than in other species. During development and early anthesis they are semi-enveloped by the subtending bracts whose adaxial surface curls upward and partially encloses the flower. This offers, in addition to the reduction in floral size, a greater protection from desiccation and represents an adaptation

to arid and semiarid environments. The length of the anthers and the filaments of several taxa were measured, but because significant results were not obtained, this approach was abandoned. As with female flowers of *Garrya*, the general reduction, simplicity of design, and uniformity of male flowers severely limits their significance and taxonomic usefulness.

**Fruit.** *Garrya* fruits are two-seeded berries which persist on the parent plants for long periods of time. When young, the fruits appear green and fleshy (Plates 9D, E, F) but this condition gradually gives way to the dry and brittle form seen at maturity (Plate 9G). Pairs of persistent styles grace the tops of the nearly globose fruits. The color ranges from dark blue to brown or white, but is not of taxonomic importance.

Hallock's investigation (1930) of the internal anatomy of the fruit revealed several distinct cell layers and my own observations in both the field and laboratory supplement these findings. In longitudinal section, the outside of the ovary wall forms a large circle with two bulges representing the bases of the styles and the pedicel. The fruit wall is composed of nine cell rows making up three distinct layers. Cells of the four outer rows are rounded and more or less irregular, with the outside row being heavily cutinized. The fifth or middle row is made up of deeply pitted stone cells, which demarcate the remaining inner rows which contain flattened cells of variable lengths. The row of stone cells diverts outward, forming a semicircle around the fibrovascular bundles which frequent the area. This displaces the outer cells, forcing them to curve outward forming the veins which are visible on the fruit exterior. Two, or rarely three, pendulous ovules with parietal placentation normally occur in a subterminal position and partially fill the ovarian chamber. Much of the flesh of the fruit is derived from the outer layer of the single massive integument. In drying, this flesh gradually withdraws, forming a thin papery covering around the seeds. At maturity, two-thirds of the fruit remains hollow with the seeds occupying only the terminal portion.

Herbarium material was used to examine the size and shape of *Garrya* fruits. A calibrated dissecting microscope was used and both the length and the width of the fruits were measured. A comparison of dimension averages (in millimeters) is given in Table 6. The fruit shape is expressed as the width/length (W/L) proportion. If the quotient is less than 1.00, the fruits are longer than they are broad, and if the quotient is greater than 1.00 the fruits are broader than long. An exact value of 1.00 indicates a perfectly globose fruit with the width and length being equal.

Fruit size within subgenus *Garrya* is relatively uniform and offers little information of systematic interest. *Garrya elliptica* has the largest

TABLE 6. FRUIT DIMENSIONS (mm.), AVERAGES, AND SHAPES IN SUBGENUS GARRYA

Species	$L\bar{X}$	$W\bar{X}$	W/L
<i>G. elliptica</i>	8.20	7.16	0.873
<i>G. veatchii</i>	7.24	6.32	0.852
<i>G. buxifolia</i>	6.74	5.72	0.849
<i>G. fremontii</i>	7.08	6.30	0.900
<i>G. flavescens</i> ssp. <i>flavescens</i>	6.39	4.98	0.778
<i>G. flavescens</i> ssp. <i>pallida</i>	7.67	6.53	0.851
<i>G. flavescens</i> ssp. <i>congdonii</i>	7.70	6.25	0.810
<i>G. corvorum</i>	7.41	6.58	0.887

fruits but this is of questionable significance when the total range of fruit dimensions of the other taxa is considered. Even *G. corvorum*, highly isolated geographically and strongly divergent in other characters, shows fruit dimensions similar to the other species of the subgenus. Fruit shape is also rather uniform, with the W/L ratios varying from 0.77 to 0.90. All fruits appear subglobose and are longer than they are wide. *Garrya flavescens* ssp. *flavescens* is the most elongated, showing a ratio value of 0.77 while *G. fremontii* is nearly round with a ratio value of 0.90. Because of the almost continuous distribution of shapes between these minimum and maximum values, the taxonomic importance of fruit shape is, at best, minimal.

The fruit dimensions within subgenus *Fadyenia* (Table 7) are more variable than those of subgenus *Garrya*. *Garrya laurifolia* ssp. *racemosa* has the largest fruits of the entire genus, with an average length of 10.30 and width of 8.38 mm. This contrasts with the small fruits of *G. salicifolia* and *G. grisea*, with widths of 5.50 mm. and lengths of 5.91 and 6.30 mm. respectively. The fruit dimensions of other taxa in the subgroup are intermediate (Table 7). Fruit shape is of greater interest because of the definite differences among taxa. *Garrya ovata*, *G. wrightii*, *G. grisea*, *G. salicifolia*, and *G. fadyenii* have

TABLE 7. FRUIT DIMENSIONS (mm.), AVERAGES, AND SHAPES IN SUBGENUS FADYENIA

Species	$L\bar{X}$	$W\bar{X}$	W/L
<i>G. ovata</i> ssp. <i>ovata</i>	8.07	7.03	0.870
<i>G. ovata</i> ssp. <i>goldmanii</i>	6.84	6.34	0.927
<i>G. ovata</i> ssp. <i>lindheimeri</i>	7.73	7.24	0.935
<i>G. wrightii</i>	6.21	6.08	0.979
<i>G. grisea</i>	6.30	5.50	0.873
<i>G. salicifolia</i>	5.91	5.50	0.929
<i>G. fadyenii</i>	6.70	6.11	0.911
<i>G. longifolia</i>	8.70	6.94	0.797
<i>G. laurifolia</i> ssp. <i>laurifolia</i>	8.38	6.92	0.825
<i>G. laurifolia</i> ssp. <i>macrophylla</i>	8.26	6.76	0.818
<i>G. laurifolia</i> ssp. <i>racemosa</i>	10.30	8.38	0.806

nearly globose fruits with shape ratios ranging from 0.87 to 0.97. *Garrya glaberrima*, *G. longifolia*, and all subspecies of *G. laurifolia* have more elongated fruits, with shape ratios ranging from 0.79 to 0.82. Of these species, *G. laurifolia* and *G. longifolia* appear closely related in other respects. *Garrya glaberrima* is isolated within the genus, but shows an affinity with *G. laurifolia* in pollen and leaf dimension. Within this group of species, *G. ovata*, *G. wrightii*, and *G. grisea* appear related, but the inclusion of *G. salicifolia* and *G. fadyenii* is more difficult. They show an affinity with *G. laurifolia*, but they are each geographically well isolated. *Garrya salicifolia* occurs in southern Baja California and *G. fadyenii* is found in the Greater Antilles. It seems likely that these taxa originated from isolated colonial or peripheral populations of laurifoliate ancestors. The chance fixation of smaller and more globose fruits in such populations would not prove difficult because the gene pool would be constricted.

*Garrya* fruits are indehiscent and have no abscission layer separating them from the parent plants. The action of the wind and rain opens them and gradually wears holes in the walls, exposing the seeds. Insects also burrow into the walls and weaken or actually crack the brittle fruits in half. The seeds are quite hard and do not appear to suffer from such insect intrusion. However, this is not always the case since some fruits show a small hole, lack seeds, and are filled with insect larvae. The wood rat, *Neotoma fuscipes annecteur* Elliot (Hallock, 1930), also eats *Garrya* fruits.

**Seeds.** *Garrya* fruits produce from one to three seeds. However, three seeds are found only in plants with tricarpeolate ovaries, which are rare. The seeds are subglobose and are borne in a subterminal position on parietal placentae. During development, one seed is pushed down and to the side, making the pair appear somewhat asymmetric. The embryology of *Garrya* has been investigated by Kapil and Moshang (1966) and also by Rao (1963). The minute embryos of *Garrya* are embedded in a copious green endosperm which gradually becomes purple and hard. The arilloid structure (Hallock, 1930) develops early, with the outer cells of the integument absorbing water, bulging outward, and forming a silvery transparent layer which divides periclinally. After the first division, the inner layer divides periclinally again producing a third layer. Cells of the outer layer do not divide but become greatly elongated, cubical, and 10 to 15 times their original size. The translucent arilloid structure becomes purple and quite fleshy during seed development, but dries out at maturity and appears thin, wrinkled and membranous. However, this is reversible since, when wet, the arilloid structure regains its thickness and again covers the seed. Within subgenera *Garrya* and *Fadyenia*, the seed size and shape are relatively uniform. Minor variation in seed size and coat appears

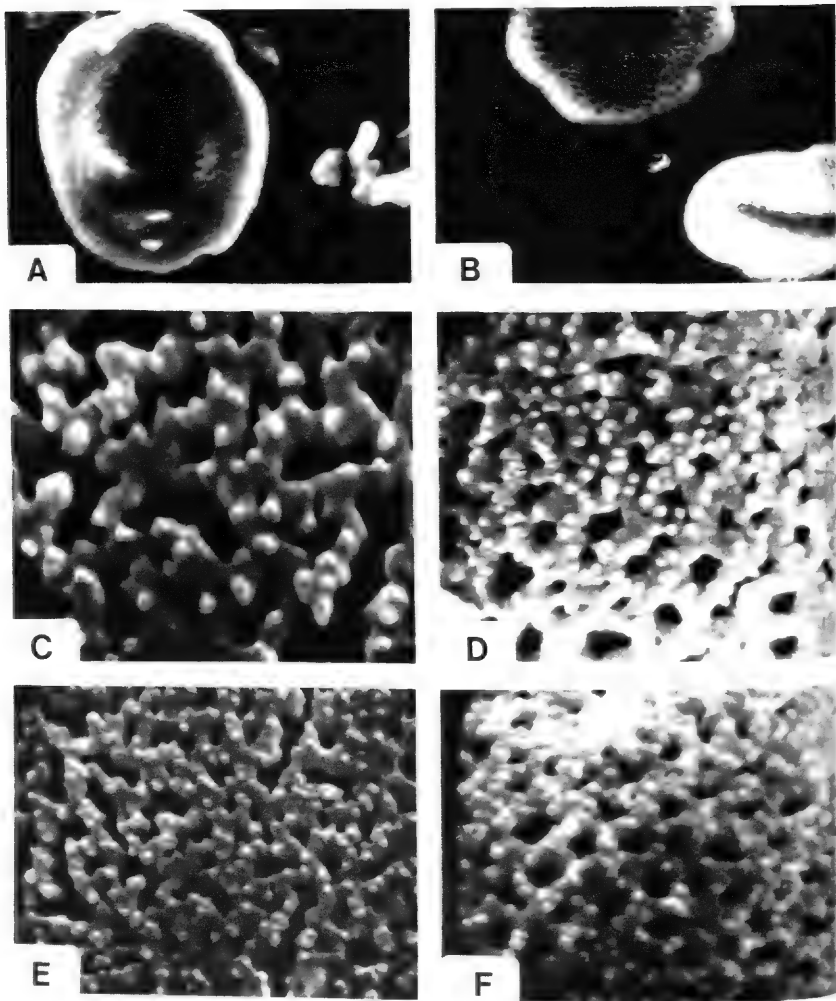


PLATE 10. Pollen differences in *Garrya* species: A, B, unacetolysed *Garrya* pollen, 675 $\times$ ; C, *G. flavescens* ssp. *flavescens* (acetolysed), Cottam 6780, 6725 $\times$ ; D, *G. ovata* ssp. *goldmanii* (acetolysed), Johnson 10756, 6725 $\times$ ; E, *G. glaberrima* (acetolysed), Dahling 38, 6725 $\times$ ; F, *G. laurifolia* ssp. *racemosa* (acetolysed), Dahling 111, 6725 $\times$ .

to reflect growth conditions rather than genetic differences between taxa. The seeds have fairly large diameters, ranging from 2 to 3 mm., but the dimensions fail to show significant differences that can be used for taxonomic purposes.

**Palynology.** *Garrya* pollen is copious and is yellow-green to orange in color. It is small to medium in size, and is small enough to be effectively transported by wind. The shape of the pollen is subspherical

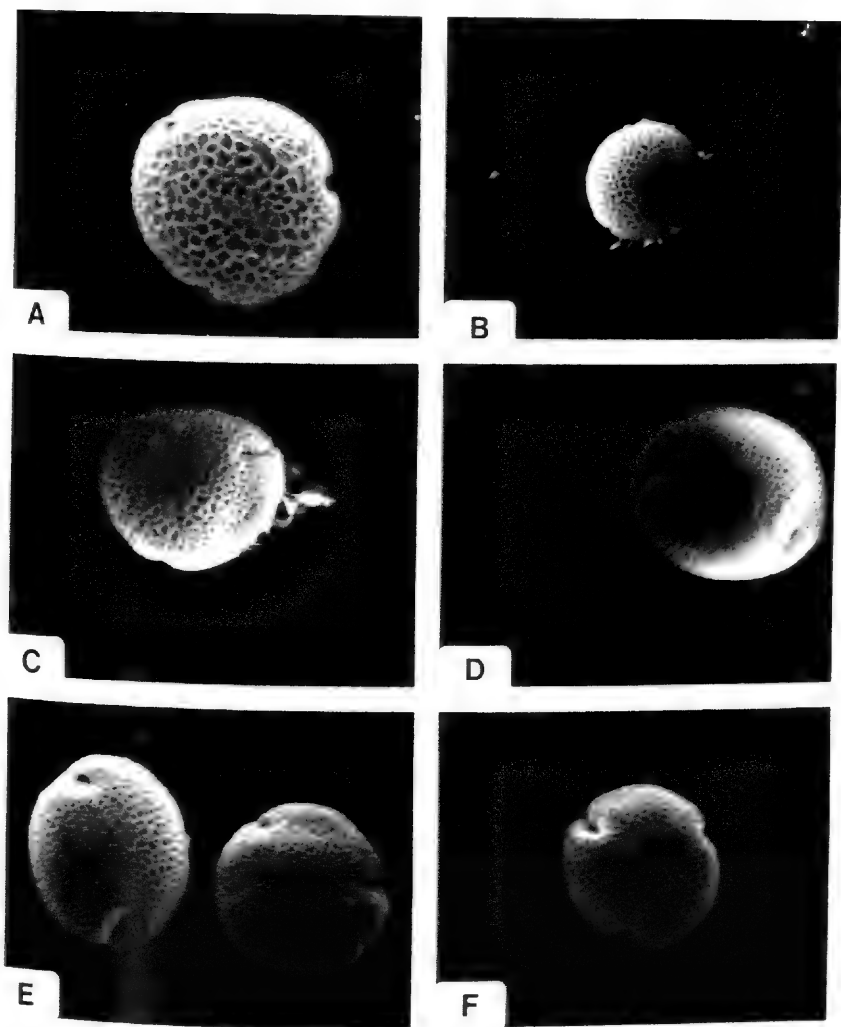


PLATE 11. Pollen differences in *Garrya* species. A. *G. ovata* ssp. *lindheimeri*, Warnock 46012, 1350 $\times$ ; B. *G. ovata* ssp. *mexicana*, Dahling 511, 675 $\times$ ; C. *G. laurifolia* ssp. *laurifolia*, Dahling 11, 1350 $\times$ ; D. *G. laurifolia* ssp. *macrophylla*, Dahling 16, 1350 $\times$ ; E. *G. laurifolia* ssp. *racemosa*, Dahling 45, 1350 $\times$ ; F. *G. wrightii*, Peebles 1457, 1350 $\times$ .

dal ranging from oblate-spheroidal to prolate-spheroidal. This interpretation differs from that of Erdtman (1952) who describes it as suboblate to oblate spheroidal. The differences are probably attributable to the use of different mounting media and to my having examined a larger number of samples. The exine is thick and quite roughened by minute processes. The sexine is thinner than the nexine and



reticulate with muri simpli- or duplibaculate. *Garrya* pollen is tri-colporate with the colpi being rather short (Plate 11D).

Pollen data are often important in the resolution of systematic questions, and thus a survey of *Garrya* pollen was undertaken. Comparisons were made of pollen size, shape and the polar area index for the various *Garrya* taxa.

**Method:** Pollen samples were obtained from herbarium material. Small amounts were placed in the center of microscope slides and then washed five times with ethyl alcohol. This was done by applying one or two drops of alcohol to the sample and allowing it to dry. The oils and resins were removed with a small piece of gauze after each application. Then a small quantity of diaphane mounting medium was placed on the sample, and, with the aid of a dissecting needle, the polleniferous material was evenly spread over the slide. After positioning a cover glass, the samples were examined. A light microscope was calibrated allowing for the expression of equatorial and polar diameters in microns. The Polar Area Index (Kapp, 1969), defined as the ratio of the distance between adjacent furrows and the equatorial diameter, was calculated for all taxa. Pollen shape was examined and measured as the ratio of polar to equatorial diameter (P/E).

**Discussion:** With few exceptions, pollen size of *Garrya* species is rather uniform. Equatorial and polar diameters range from 21–38 and 22–39  $\mu\text{m}$ , respectively. The polar furrow distance varies from 15–30  $\mu\text{m}$ . Measurement averages (Table 8) afford a convenient method of comparing taxa. With the exception of *G. flavescens* and *G. laurifolia*,

TABLE 8. AVERAGE POLLEN SIZE ( $\mu\text{m}$ .)

<i>Garrya</i>	Equatorial Diameter	Polar Diameter	Polar Furrow Distance
buxifolia	26.689	27.423	19.770
elliptica	29.380	29.400	21.687
veatchii	27.985	29.184	20.913
fremontii	28.444	30.057	21.375
flavescens ssp. flavescens	31.702	33.355	24.187
flavescens ssp. pallida	30.084	31.756	22.833
corvorum	26.611	29.162	20.076
salicifolia	28.350	29.137	22.398
wrightii	27.612	29.164	20.160
grisea	27.918	28.464	20.650
ovata ssp. ovata	26.268	27.232	19.627
ovata ssp. lindheimeri	27.749	28.723	20.846
ovata ssp. mexicana	25.258	26.616	18.892
fadyenii	25.987	26.334	18.985
longifolia	26.535	26.550	20.713
laurifolia ssp. laurifolia	31.224	31.741	26.621
laurifolia ssp. racemosa	32.400	33.300	27.450
laurifolia ssp. macrophylla	30.776	30.746	25.082

most equatorial and polar diameter averages are similar. Species within subgenera *Garrya* and *Fadyenia* are not distinguishable by their pollen. Taxa showing size variation belong to both groups, including *G. flavescens* and *G. laurifolia*, which show equatorial and polar diameter averages of 30 and 33  $\mu\text{m}$ . respectively. The remaining *Garrya* taxa have smaller equatorial and polar diameters ranging from 25–29 and 26–29  $\mu\text{m}$ . Polar furrow distance averages also show a general uniformity (Table 8) with the exception of *G. flavescens* ssp. *flavescens* and *G. laurifolia*. Both of these taxa have higher polar furrow distances which correspond to their large equatorial and polar diameters. Since these species are not closely related to each other, the significance of their increased pollen size is not evident.

Variation in polar area index (PAI) is less continuous than other dimensions of *Garrya* pollen. Both the largest and smallest PAI values (Table 9) are found in subgenus *Fadyenia*. *Garrya longifolia*, *G. salicifolia*, and *G. laurifolia* show large PAI averages ranging from 0.79 to 0.85. This contrasts sharply with *G. grisea* of the same subgenus, which has a PAI average of 0.68, the smallest of the family. Remaining taxa of both subgenera show intermediate PAI averages ranging from 0.72 to 0.76. It is interesting to note that taxa sharing large PAI values also appear morphologically related in other ways and may represent a separate line of specialization within the genus.

There is no significant variation in the shape of *Garrya* pollen, which is almost identical in all species (Table 9). What variation there is (P/E ratios), is extremely limited, ranging from 0.99 to 1.12, and is not of taxonomic importance.

TABLE 9. POLAR AREA INDEX AND POLLEN SHAPE

Garrya	PAI	P/E
buxifolia	0.7407	1.1245
elliptica	0.7381	1.0006
veatchii	0.7473	1.0428
fremontii	0.7301	1.0560
flavescens ssp. flavescens	0.7629	1.0546
flavescens ssp. pallida	0.7590	1.0555
corvorum	0.7532	1.0941
salicifolia	0.7900	1.0277
wrightii	0.7300	1.0562
grisea	0.6802	1.0362
ovata ssp. ovata	0.7277	1.0367
ovata ssp. lindheimeri	0.7513	1.0351
ovata ssp. mexicana	0.7450	1.0496
fadyenii	0.7305	1.0133
longifolia	0.7805	1.0005
laurifolia ssp. laurifolia	0.8521	1.0165
laurifolia ssp. racemosa	0.8472	1.0277
laurifolia ssp. macrophylla	0.8015	0.9989

**SEM Pollen Morphology.** Examination of pollen by means of the scanning electron microscope (SEM) was carried out to survey the fine structure of the exine.

**Method:** Polleniferous material was obtained from herbarium specimens and divided into two samples. One was acetolyzed and the other was not. The acetolysis procedure was as follows: polleniferous material was placed in 40 ml. glass centrifuge tubes, covered for two minutes with 100% glacial acetic acid, and then centrifuged for three minutes. After decanting, 20 mls. of acetolysis mixture, composed of nine parts of electronic grade acetic anhydride and one part concentrated sulfuric acid, was added to the samples. The sample tubes were then placed in a water bath, heated to 100° C, and stirred for three minutes. Following centrifugation and decanting, the material was put through a 100% and 50% glacial acetic acid series. After the final centrifugation, 20 ml. of distilled water was added and the samples were centrifuged and decanted once more. This procedure was repeated four times to insure the removal of all traces of acid. The final polliniferous sediments were resuspended in 15 ml. of distilled water and stored in small vials. Samples were then placed on aluminum pedestals applying double stick scotch tape and then several drops of pollen suspension. Next, the pedestals were transferred to a slide warmer and allowed to dry for 12 hours. Untreated pollen was applied to the taped pedestal surfaces dry. Pollen samples were evacuated in a Varian Vacuum Evaporator VE 10 to  $10^{-4}$ – $10^{-5}$  torr. and then coated with both carbon and gold-palladium. The samples deteriorated after coating, so the specimens were immediately placed in an AMR Model 900 SEM and examined. The maximum resolution of the SEM employed was 100–200 Å.

**Discussion:** Most untreated *Garrya* pollen tends to be distorted or completely collapsed, making observation and photographing under high magnification almost impossible (Plates 10A, B). Untreated pollen also tends to shatter when exposed to the electron beam. These problems are almost eliminated when acetolyzed material is used (Plate 10C), and although chemical treatment expands the individual grains to a degree, the pollen becomes much more workable. The increase in pollen size is more than compensated for by the expansion of collapsed grains and the removal of surface depressions.

The size of *Garrya* pollen shows great uniformity, but there are several interesting variations in the fine structure of the exine. All species bear minute processes which are borne on the reticulate sculptural elements, but the frequency of these processes is variable. Within subgenus *Fadyenia*, *G. ovata* displays the greatest frequency, showing many processes on the surface of the grains (Plate 10D). *Garrya glaberrima* follows with a lesser, but impressive, number of

processes (Plate 10E). *Garrya laurifolia* shows only moderate sculptural development and resembles *G. fadyenii*, *G. salicifolia*, *G. grisea*, and *G. wrightii* (Plate 10F), in this respect contrasting with *G. longifolia*, which shows the least number of processes. In subgenus *Garrya*, the pollen of *G. fremontii*, *G. flavescens*, and *G. corvorum* is most densely covered with the minute processes. Because of their ability to hybridize in nature, the similarity between *G. fremontii* and *G. flavescens* is especially noteworthy. The pollen of *G. corvorum* also approaches the former taxa, but that species is isolated and not closely related. Although the remaining species of the subgenus, *G. buxifolia*, *G. elliptica*, and *G. veatchii*, display a low frequency of sculptural processes, only *G. elliptica* and *G. veatchii* appear to be closely related on other grounds.

The size and shape of the lacunae are variable and are important taxonomic indicators for some species. In subgenus *Fadyenia*, *Garrya ovata* ssp. *lindheimeri* (Plate 11A) and *G. ovata* ssp. *mexicana* (Plate 11B) show the largest lacunae. They appear almost square and are of diagnostic importance because identification can be made from pollen alone. Pollen of *G. laurifolia* (Plates 11C, 11D, and 11E), *G. salicifolia*, *G. fadyenii*, and *G. wrightii* (Plate 11F) display lacunae which, though moderately large, are smaller than those of *G. ovata*. In addition, they are less angular and more rounded making them easily distinguishable. An intermediate condition between *G. ovata* and *G. laurifolia* is demonstrated by *G. glaberrima* (Plate 12A) where the relatively angular lacunae are larger than those of *G. laurifolia*, but smaller than *G. ovata*. Apparently pollen of *G. glaberrima* is not as different from the *Garrya* mainstream as is that of *G. ovata*. This is peculiar since other evidence (Figure 4) suggests that *G. glaberrima* is strongly isolated from other members of the genus. Pollen of *G. grisea* approaches *G. wrightii* in size, and is distinguished from the other taxa by the presence of elongated lacunae (Plate 12B). Lacunae of *G. longifolia* are small and mostly round (Plate 12C), and so reduced that in some areas the muri appear confluent.

Within subgenus *Garrya*, pollen lacunae range from very large and square, as in *G. elliptica*, to small and round, as in *G. veatchii* (Plate 12D). The intermediate condition is shown in *G. flavescens* ssp. *pallida* and *G. fremontii* which have smaller and angular to subround lacunae (Plate 12E). Pollen of *G. flavescens* ssp. *flavescens* differs from *G. flavescens* ssp. *pallida* by the smaller more rounded lacunae, not unlike those of *G. corvorum*. Lacunae of *G. buxifolia* are similar to *G. veatchii* in size but appear more rounded (Plate 12F).

Compared with other families (Moseley & Beeks, 1955), the pollen of *Garrya* strongly resembles that of the Cornaceae. *Aucuba japonica* (Erdtman, 1952), long reputed to be an ancestor of *Garrya*, has

tricolporate pollen, which is prolate spheroidal with an average polar and equatorial diameter of 43 and 39  $\mu\text{m}$ . respectively. The shape of the *Aucuba* pollen is similar to that of *Garrya*, but is larger and has a pilate sexine which is thinner than the exine. *Griselina litoralis*, another putative ancestor (Eyde, 1964), has pollen less similar to *Garrya* than does *Aucuba*. It has tricolporate pollen, which is prolate in shape, with an average polar and equatorial diameter of 31.0 and 20.5  $\mu\text{m}$ . respectively. The sexine is the same thickness as the exine and is tegillate (Erdtman, 1952). The basic features of cornaceous pollen, as seen in *Aucuba* and to a lesser extent in *Griselina*, do not controvert a relationship with *Garrya*, although the pollen is not similar in every aspect.

**Breeding System.** Generally the barriers between gene pools in *Garrya* may be easily breached, although isolation in some species is definitive. The speciation is of the geographic type (Grant, 1971) and is associated with only weakly formed reproductive barriers. In addition, both subgenus *Garrya* and subgenus *Fadyenia* have a uniform chromosome number of  $n = 11$  (Turner, 1960), thus eliminating some of the cytogenetic aberrations which result from interspecific crosses where chromosome numbers are different. With a few notable exceptions, speciation and gene pool integrity in *Garrya* are dependent on geographic separation rather than on specific chromosome or genetic incompatibilities.

*Garrya* is well-adapted for wind pollination, a beneficial strategy in arid regions. Moreover, the pendulous, cryptic, and catkin-like inflorescences are ideally suited for anemophily. The structures are blown by the wind and clouds of yellow pollen are visibly dispersed. Once caught by the air currents, the pollen is easily transferred to the receptive stigmas of the female inflorescences, which are pendulous at the ends of the shoots and are readily exposed to the pollen bearing wind.

The male floral morphology is also well-adapted for wind pollination. Since the stamens are opposite the four slits or windows of the partially connate perianth, the anthers are directly exposed. When air passes through the flowers, the pollen is blown out of the slit and into the air stream. In addition, the passage of the wind over the subtending and partially enveloping bract causes suction which forcibly removes the pollen from the perianth chamber. Formed from the terminally fused perianth segments (Plate 8B), the perianth chamber is of considerable significance. Anther dehiscence is introrse by means of longitudinal slits so that during anthesis the pollen is unable to fall to the ground. When there is no wind, it is stored in the shaded chambers and protected from excessive desiccation which otherwise might occur in the semiarid *Garrya* habitats. When the air currents

return, the pollen in the chambers is quickly sucked out and freed.

The breeding system of *Garrya* is designed for maximum outcrossing and genetic variability. Its dioecious condition prevents selfing and insures a gene pool with sufficient variability for successful divergence under arid conditions (Stebbins, 1950, 1952). In addition, variability is also stimulated by anemophily which allows for gene flow between spatially isolated populations. This accounts for the blurring of infraspecific and specific taxa within *Garrya*, especially when the weak interspecific reproductive barriers characteristic of the genus as a whole are considered. Therefore, many infraspecific taxa reach the level of semispecies but fail to achieve complete isolation and attain specific status.

Such a condition may indicate a relatively recent evolutionary origin for the group, and it may be supposed that complete divergence will eventually occur. However, it might be argued also that such systems themselves may be selected for in order to maintain the genetic variability that is advantageous in harsh environments. Although the question is still open, with respect to *Garrya*, the latter is the most convincing.

The problem of delineating the intergrading *Garrya* species was recognized early by several authors (Eastwood, 1903; Bacigalupi, 1924). Interspecific hybridization does occur in *Garrya*, but not to the extent that would be the case if the presently recognized infraspecific taxa were given specific rank. The early taxonomic history of *Garrya* was characterized by the splitting and erection of "species" which naturally intergraded with other "species." Examples of these problematic taxa include *G. rigida*, *G. pallida*, *G. congdonii*, *G. mollis*, *G. lindheimeri*, *G. goldmanii*, *G. macrophylla*, *G. oblonga*, *G. racemosa*, and *G. gracilis*. Such taxa as are represented by these names are better considered to be infraspecific taxa of polytypic species. Intergradation, where it occurs, is thus accounted for in a more satisfactory manner.

The most extensive hybridization in subgenus *Garrya* is between *G. fremontii* and *G. flavescens* ssp. *pallida*. They intergrade in leaf, trichome and epidermal characters, making their distinction sometimes difficult. Evidence for hybridization and introgression are also provided by chemical data (Figure 4). While delineation is problematic in local areas, these taxa are sufficiently distinct in most regions to justify their retention in specific rank. Since intermediates are occasionally observed, it is also likely that *G. flavescens* and *G. veatchii* hybridize, but not extensively.

Hybridization in subgenus *Fadyenia* exceeds that of subgenus *Garrya*. *Garrya ovata* ssp. *mexicana* and *G. laurifolia* hybridize in northern Mexico where their ranges overlap, and morphologically intermediate specimens are common in this area. *Garrya ovata* ssp.

*ovata* and *G. ovata* ssp. *lindheimeri* also hybridize with *G. laurifolia* but less frequently. *Garrya glaberrima* is of particular interest because, although sympatric with both *G. ovata* and *G. laurifolia* ssp. *macrophylla*, no intermediates or putative hybrids have been found. The assumption is that breeding barriers are present which provide for genetic isolation. The distinctiveness of *G. glaberrima* is supported by phytochemical data (Figure 4) which suggest that it is not closely related to other taxa. Genetic isolation is rare in *Garrya* which is a tightly knit group that generally shows reproductive flexibility.

While appearing distinct where geographically isolated, *Garrya longifolia* and *G. laurifolia* ssp. *racemosa* hybridize in areas where their ranges meet. They are closely related, with only weak isolating barriers. Intermediates are numerous at the contact points, but the degree of swamping is insufficient to warrant changing their taxonomic status. Most of the populations of *G. longifolia* are biochemically and morphologically distinct, lending additional support for the retention of their specific status (Figure 6). Interspecific hybridization does not affect *G. fadyenii* because of its complete geographical isolation in the Greater Antilles. The same is true for *G. salicifolia* and *G. grisea* of southern and northern Baja California respectively.

**Phytochemistry.** Discovery of the chromogenic glycoside aucubin (Herissey & Lebas, 1910) launched the chemical investigation of *Garrya*. The same glycoside (Figure 5) also occurs in *Aucuba japonica* (Bouquelot & Herissey, 1910; Lebas, 1911), often resulting in the conclusion that a *Garrya-Aucuba* alliance exists. Aucubin is not restricted to either subgenus and has been reported in the seeds, stems, leaves, and fruits of *G. elliptica*, *G. laurifolia* ssp. *macrophylla*, and in the hybrid *G. elliptica* X *G. laurifolia* (Herissey & Lebas, 1910). These occurrences provide little information about species affinity, and are mainly cited as supporting evidence for a Garryaceae-Cornaceae relationship. Since aucubin is rarely found in other than gamopetalous families (Swain, 1963), the isolated occurrence in *Garrya* and *Aucuba* may prove important.

Diterpenoid alkaloids are characteristic of several *Garrya* species (Oneto, 1946; Wiesner et al., 1952; Moselting, 1961). Leaf extracts of *G. fremontii* and *G. buxifolia* contain amorphous basic nitrogenous residues which react positively with general alkaloid reagents (Table 10). The crystalline salts of alkaloids have also been isolated and studied in some detail from *G. elliptica*, *G. veatchii*, and *G. wrightii*. Analysis of the leaf and bark extracts of *G. veatchii* reveals that the concentration of alkaloids is greatest in the bark; in *G. wrightii* the concentration in the bark and leaves is approximately equal. Six alkaloid constituents, garryine, veatchine, garryfoline, isogarryfoline, cuau-chichicine, and isocuauchichicine have so far been characterized. The

TABLE 10. DISTRIBUTION OF ALKALOIDS

Species	Leaves	Bark	Alkaloids Present
<i>G. fremontii</i>	+		Amorphous basic nitrogenous residues reacting positively with alkaloid reagents. No crystalline salts produced.
<i>G. buxifolia</i>	+		Amorphous basic nitrogenous residues reacting positively with alkaloid reagents. No crystalline salts produced.
<i>G. flavescens</i>	-	-	No alkaloidal material found.
<i>G. elliptica</i>	+		Garryine and veatchine. Both isolated as crystalline salts.
<i>G. veatchii</i>	+	+	Garryine and veatchine. Both isolated as crystalline salts. Highly concentrated in the bark.
<i>G. wrightii</i>	+	+	Garryine and veatchine. Both isolated as crystalline salts. Slightly more concentrated in leaves.
<i>G. laurifolia</i>		+	Garryfoline, isogarryfoline, cuauchichicine, and isocuauchichicine.

latter four were isolated from *G. laurifolia* (Djerassi et al., 1955) and bear a close isomeric relationship to each other and to veatchine and garryine. Oneto (1946) reports that *G. flavescens* completely lacks alkaloidal constituents but this has not been verified by other investigators. The *Garrya* alkaloids bear a structural resemblance to atisine (Pelletier, 1960) and are probably derived from the phytol part of chlorophyll (Robinson, 1967).

The present work gives a brief comparative survey of the flavonoid content within *Garrya* and selected genera of the Cornaceae in order to determine the biochemical affinity between *Garrya* species and to investigate suggested phylogenetic relationships to the Cornaceae (Hallock, 1930; Moseley & Beeks, 1955; Eyde, 1964, 1967).

Flavonoids consist of two phenol units linked together by a three carbon chain and are one of the most common constituents of vascular plants (Alston & Turner, 1963; Hegnauer, 1966; Gibbs, 1974). While the biosynthetic pathways for specific flavonoids remain obscure, much is known of the biogenesis of flavonoid compounds in general (Geissman, 1969; Robinson, 1967; Seshadri, 1962; Griseback & Patschke, 1960). Although data suggesting a physiological importance have been presented, the functional role of flavonoids in plants is still the subject of much speculation. Flavonoids may be involved in the formation of reproductive barriers (Kuhn & Low, 1949) and also in the regulation of plant growth and development (Furuya et al., 1962; Mumford et al., 1961; Hendershott & Walker, 1959). In addition, since some flavonoids are synthesized in response to injury or parasitic attack, a protective role has also been suggested (Hadwiger, 1966).

**Method:** Plant material was collected in the spring and summer



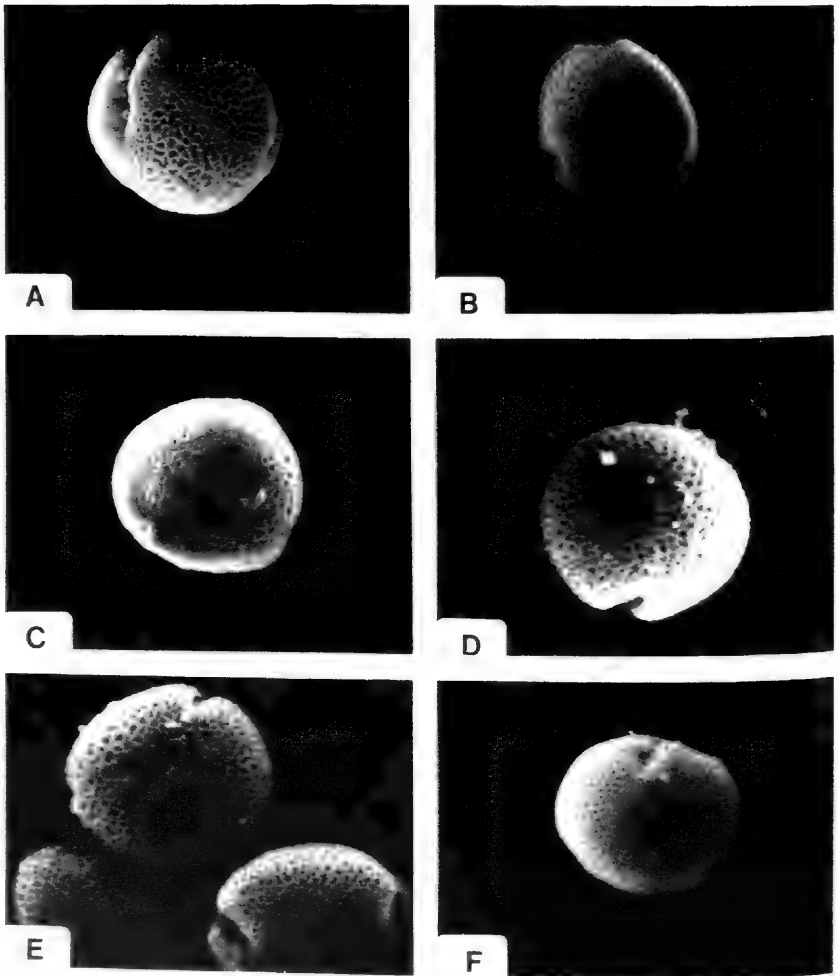


PLATE 12. Pollen differences in *Garrya* species: A, *G. glaberrima*, Dahling 38, 1350 $\times$ ; B, *G. grisea*, Brandegee 12013, 1350 $\times$ ; C, *G. longifolia*, Dahling 2233, 1350 $\times$ ; D, *G. veatchii*, Dahling 1674, 1350 $\times$ ; E, *G. fremontii*, Sikesdorf 6426, 1350 $\times$ ; F, *G. buxifolia*, Henderson 5716, 1350 $\times$ .

of 1972 and 1973 respectively. Approximately twenty-five leaves from individuals of a population were ground in a Waring blender for 2-3 minutes, until powdered. In every case mature nonsenescent leaves from the previous season's growth were used and unusual or distorted leaves were eliminated. A small portion (about 0.3 grams) was extracted in .1M HCl in methanol at room temperature for 24 hours. The extracts were immediately applied to a Watmann No. 3 mm. chromatographic paper as 2 cm. streaks. Electronic grade solvents were used, which

included benzene-acetic acid-water (4:4:2 v/v) and isopropanol-ethyl acetate-water (7:1:2 v/v).

The latter was the most satisfactory, especially when preceded by a benzene prerun which eliminated streaking and tailing. When the solvents reached a height of 35.5 cm. the chromatograms were air-dried and examined in the presence of ammonia, first in natural and then in ultraviolet light. The chromatograms were done in triplicate and independently scored to eliminate error or variation. Once separated, compounds were assigned reference numbers. Those compounds appearing identical in color and position were given the same number. In this way the flavonoid content of different species could be compared.

A combined total of 82 flavonoid compounds were found in *Garrya*. The number per species varied from 8 to 20, with an average of 15. All the species were compared by calculating the coefficient of association for species pairs. This was done by dividing the number of common compounds by the total number of compounds in the species pair. A score of 1.00 indicates complete compound correspondence while 0 indicates no agreement and presumably no biochemical relationship. The Paired Affinity Index (PAI) (Ellison et

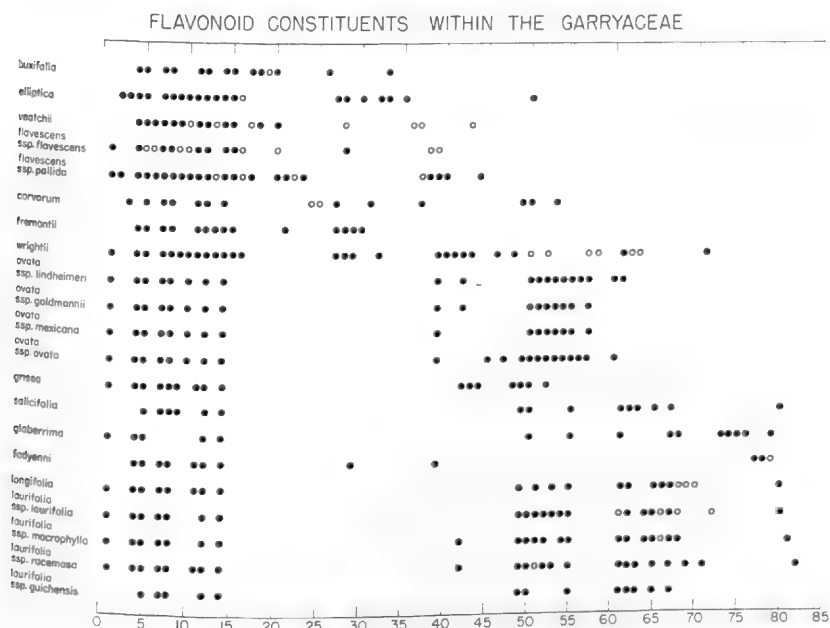


FIG. 3. Black dots—presence of individual flavonoids; white dots—trace amounts or questionable presence of individual flavonoids. Lower scale indicates flavonoids by number.

al., 1962) was obtained by expressing the coefficient of association as a percentage—that is, multiplying the value by 100. These indices can be expressed as polygonal graphs (Ellison et al., 1962) allowing for a rapid quantitative comparison of species. The center of the circular graphs (Figure 4) represents a PAI value of 0, while the periphery represents a value of 100, with intermediate values along the radii. Taxa are assigned different radii so that each graph compares one taxon with the others. At least one PAI value per graph will equal 100 because one radius represents the taxon in question. It is also possible to quantitatively express the relationship of one taxon to the others as a group. The Group Affinity Index (GAI) (Ellison et al., 1962) is obtained by adding the various PAI values of a taxon. Thus, each PAI graph takes on a numerical value indicating the general group relationship. For the 27 taxa considered, the maximum possible GAI is 2700, but only if one taxon completely corresponds to all other taxa. Conversely, if a taxon failed to correspond in any way to the other taxa, the GAI would be 100, the lowest value possible.

Consideration of unique compounds (those occurring in only one taxon) is also valuable. The Isolation Value (Ellison et al., 1962) is found by dividing the number of unique compounds by the total number of compounds of the taxa under consideration and expressing the value as a percentage. A large isolation value indicates extensive biochemical isolation and may also suggest an early evolutionary divergence. Smaller values probably result from adaptation to specific habitats or environments.

*Discussion:* The distribution of flavonoids in *Garrya* indicates a chemical division which corresponds quite well to the subgenera *Garrya* and *Fadyenia*, as shown in Figure 3. Flavonoid constituents of subgenus *Garrya* are numbered and located in the upper left while those of subgenus *Fadyenia* are in the lower right of the graph. Note that several compounds are common to both subgenera and that compound number 12 is universal, occurring in all species. Since the taxa share a similar genetic background, the occurrence of common compounds is expected.

The flavonoids of two species, *Garrya corvorum* and *G. wrightii*, deserve particular attention. *Garrya corvorum*, an isolated Guatemalan member of subgenus *Garrya*, shows a chemical similarity and shares certain morphological characteristics with members of subgenus *Fadyenia*. It probably diverged quite early from ancestral stock of subgenus *Garrya* and has followed an independent evolutionary course. It appears nearly as close chemically to subgenus *Fadyenia* as to subgenus *Garrya*. *Garrya wrightii*, a northern member of subgenus *Fadyenia*, shows an abundance of compounds found in subgenus *Garrya* but also contains compounds of its own subgenus. This is

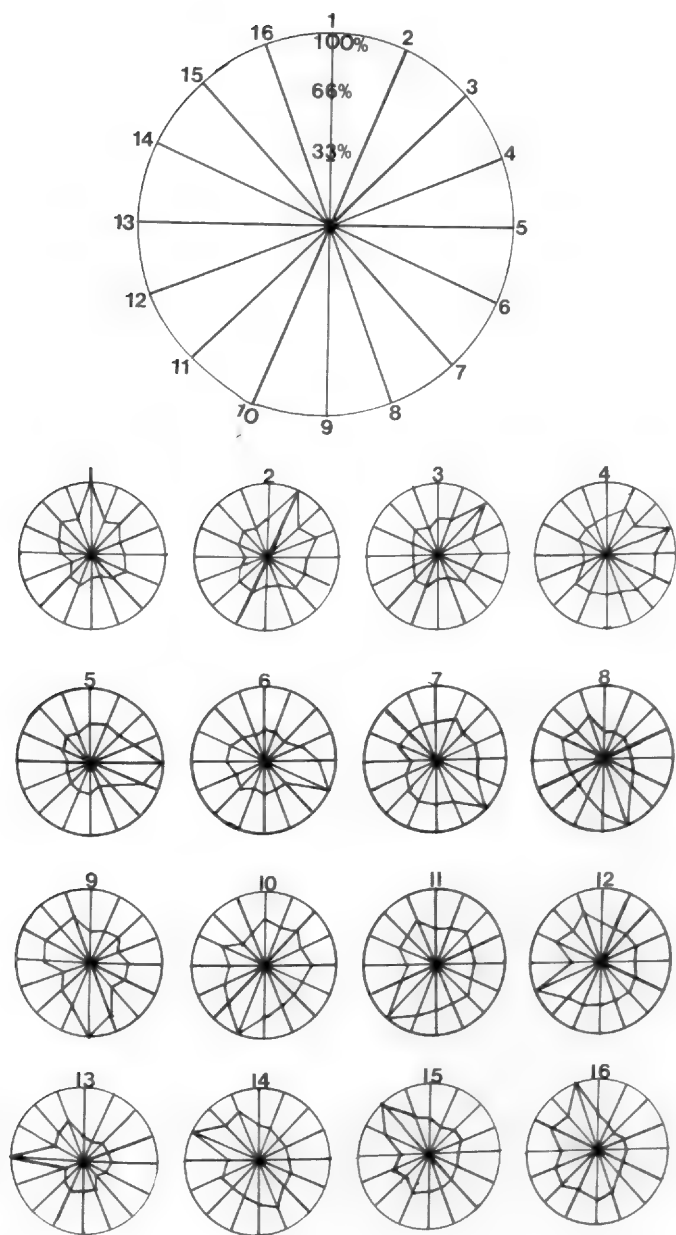


FIG. 4. Paired affinity indices (coefficients of association expressed as percentages). *Garrya buxifolia*, 1; *G. elliptica*, 2; *G. veatchii*, 3; *G. fremontii*, 4; *G. flavescens* ssp. *flavescens*, 5; *G. flavescens* ssp. *pallida*, 6; *G. corvorum*, 7; *G. ovata* ssp. *lindheimeri*, 8; *G. ovata* ssp. *goldmanii*, 9; *G. wrightii*, 10; *G. grisea*, 11; *G. salicifolia*, 12; *G. glaberrima*, 13; *G. fadyenii*, 14; *G. longifolia*, 15; *G. laurifolia* ssp. *laurifolia*, 16.

peculiar, since morphologically *G. wrightii* does not appear to be intermediate, but rather a derived member of the *Fadyenia* line.

An examination of PAI's (Figure 4) reveals a closer chemical relationship within rather than between subgenera. *Garrya buxifolia* and *G. veatchii* appear chemically distinct, while *G. fremontii* shows a relationship to *G. elliptica* and *G. flavescens*. It is not surprising that the two subspecies of *G. flavescens* show a close affinity, but the approach of *G. flavescens* ssp. *pallida* to *G. fremontii* is of interest. The two taxa intergrade morphologically, indicating hybridization and introgression, and their similar flavonoid constituents add support for this supposition.

Several species within subgenus *Fadyenia* show chemical affinities. All subspecies of *Garrya ovata* share similar flavonoid constituents and closely approach each other. In addition, a chemical relationship with *G. fadyenii*, *G. wrightii*, and *G. laurifolia* is indicated. Populations of *G. wrightii* vary chemically depending on their location. In the extreme eastern parts of the range, the flavonoid content is similar to *G. ovata* while in the south and west populations approach the flavonoid content of *G. grisea*. *Garrya salicifolia* appears closely related to *G. laurifolia* and *G. fadyenii* while the latter approaches *G. ovata*, *G. longifolia*, and *G. laurifolia*. *Garrya glaberrima* is of special interest because chemically it does not show a strong affinity towards other species. It is endemic to northern Mexico and appears to be well isolated reproductively. Although it is sympatric with *G. ovata* and *G. laurifolia*, no intermediates or hybrids have been found. Thus, *G. glaberrima*, because it maintains a unique gene pool, could follow an independent evolutionary path resulting in the development of flavonoids not shared by other members of the genus. *Garrya glaberrima* is not only isolated from the species of subgenus *Garrya*, but from members of its own subgenus as well. This is not the case, however, with *G. longifolia*, which appears chemically related to both *G. fadyenii* and *G. laurifolia*. While all *G. laurifolia* subspecies bear high PAI's with each other, they also chemically approach *G. fadyenii*, *G. longifolia*, and *G. ovata*. In general, most of the species show strong chemical relationships with the other species of the genus. This is not always the rule, however, as is demonstrated by *G. buxifolia* and *G. glaberrima* (Figure 4).

The GAI quantifies the relationship of one taxon to the group of taxa being considered. Indices of *Garrya* taxa (Table 11) range from approximately 1300-860. With the exception of *G. corvorum* and *G. glaberrima*, lower GAI's generally are found in subgenus *Garrya*. *Garrya corvorum*, chemically intermediate between subgenera *Garrya* and *Fadyenia*, has a high GAI of 1272, showing a close relationship with the *Garrya* species as a whole. The reverse situation, indicating

TABLE 11. GROUP AFFINITY INDEX

Species	GAI	Species	GAI
<i>Garrya wrightii</i>	1303.7	<i>G. flavescens</i> ssp. <i>pallida</i>	1110.5
<i>G. laurifolia</i> ssp. <i>racemosa</i>	1302.6	<i>G. fremontii</i>	1108.2
<i>G. fadyenii</i>	1292.4	<i>G. veatchii</i>	1089.7
<i>G. ovata</i> ssp. <i>mexicana</i>	1272.9	<i>G. buxifolia</i>	1083.5
<i>G. corvorum</i>	1272.1	<i>G. elliptica</i>	1060.9
<i>G. laurifolia</i> ssp. <i>laurifolia</i>	1262.4	<i>G. glaberrima</i>	0864.7
<i>G. ovata</i> ssp. <i>lindheimeri</i>	1245.2	<i>Griselina scandens</i>	0579.0
<i>G. ovata</i> ssp. <i>ovata</i>	1245.1	<i>G. ruscifolia</i>	0577.7
<i>G. grisea</i>	1244.5	<i>Aucuba japonica</i>	0569.7
<i>G. ovata</i> ssp. <i>goldmanii</i>	1212.5	<i>Griselina racemosa</i>	0543.0
<i>G. salicifolia</i>	1179.6	<i>Aucuba chinensis</i>	0428.7
<i>G. laurifolia</i> ssp. <i>macrophylla</i>	1163.4	<i>Griselina litoralis</i>	0388.5
<i>G. longifolia</i>	1158.9	<i>Macrocarpum officinalis</i>	0161.2
<i>G. flavescens</i> ssp. <i>flavescens</i>	1114.8		

biochemical divergence from the group is demonstrated in *G. glaberrima* with a GAI of only 864. Indices of the other *Garrya* species are larger and show a continuous distribution which makes the gap of *G. glaberrima* especially striking.

Some flavonoids are found in only one species, indicating a biochemical divergence. Only 12 taxa show unique flavonoid constituents and these are mostly members of subgenus *Fadyenia* (Table 12). *Garrya glaberrima* contains 26.6% of unique constituents, again demonstrating biochemical divergence and singularity. A smaller percentage of unique compounds, 11.7%, is found in *G. fadyenii*. It is isolated geographically so the occurrence of unique compounds is not particularly surprising. The remaining species, probably as the result of adaptation to specific habitats or environmental conditions, developed only 5.0–8.7% unique constituents.

Eyde (1964) suggested that *Garrya* is closely related to *Aucuba* and *Griselina* of the Cornaceae. A phylogenetic relationship between

TABLE 12. UNIQUE FLAVONOID CONSTITUENTS

Species	Percent
<i>G. buxifolia</i>	7.6
<i>G. elliptica</i>	8.7
<i>G. flavescens</i> ssp. <i>pallida</i>	8.0
<i>G. salicifolia</i>	6.6
<i>G. fadyenii</i>	11.7
<i>G. ovata</i> ssp. <i>ovata</i>	5.0
<i>G. ovata</i> ssp. <i>lindheimeri</i>	5.0
<i>G. longifolia</i>	6.2
<i>G. glaberrima</i>	26.6
<i>G. laurifolia</i> ssp. <i>laurifolia</i>	5.7
<i>G. laurifolia</i> ssp. <i>racemosa</i>	5.8
<i>G. laurifolia</i> ssp. <i>macrophylla</i>	7.6

Garryaceae and Cornaceae was suggested (Bentham, 1867), based on the morphology and the presence of aucubin in *Garrya* and *Aucuba*. Current investigations of flavonoid constituents of *Garrya*, *Aucuba*, and *Griselina* show only small degrees of similarity. Only herbarium material of the cornaceous genera was available. Leaf material from approximately ten individuals of a particular cornaceous species was ground, extracted, chromatographed, and numbered in the manner already described. The results indicate a close chemical relationship between *Aucuba japonica* and *A. chinensis*. *Griselina ruscifolia* and *G. scandens* also have similar flavonoid constituents and appear chemically close. *Aucuba* and *Griselina* species share few common compounds with *Macrocarpium officinalis*, indicating a more distant relationship. The emerging pattern suggests a loose but definite chemical affinity among the cornaceous taxa examined (Figure 5).

The flavonoids of *Garrya*, in comparison with those of the Cornaceae, do not reveal a striking chemical affinity. Of the combined total of 135 compounds discovered in *Garrya* and the Cornaceae, only two are present in both groups (Figure 5). *Macrocarpium* does not share any flavonoid compounds with *Garrya* and appears more closely allied with *Aucuba* and especially with *Griselina*. Since some flavonoids are ubiquitous and are found in widely separated plant groups, the occurrence of only two common constituents in *Garrya* and the Cornaceae scarcely suggests a genuine affinity. Also, the PAI's of *Garrya* and members of the Cornaceae are very low (Table 13), and with less than 1.5% of the total compounds found in both groups, relationships based on flavonoid constituents are not significant.

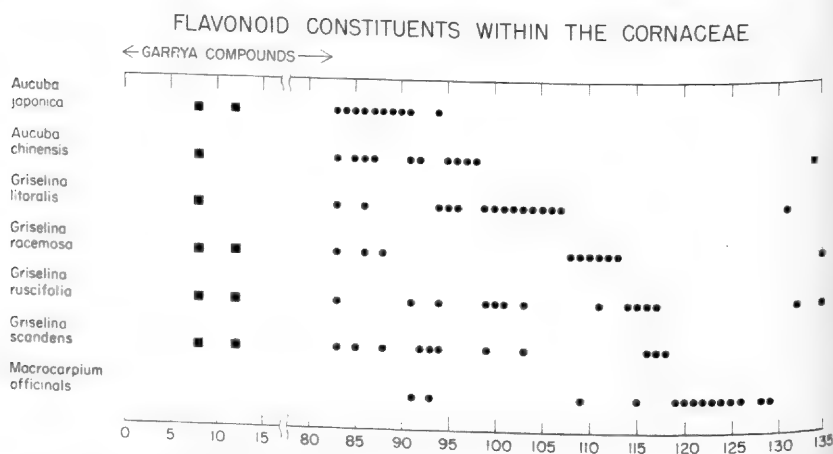
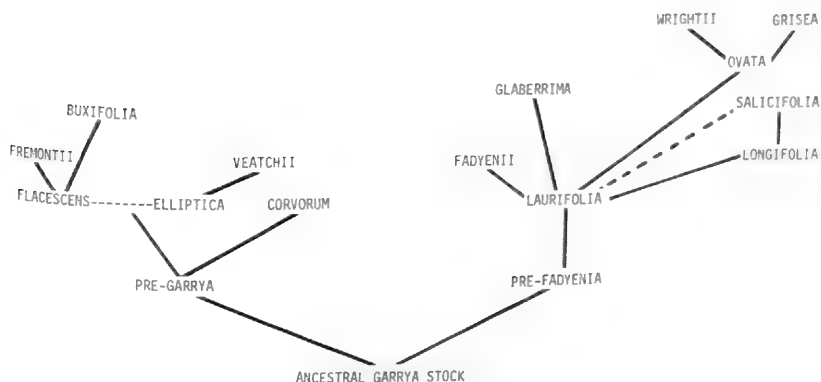


FIG. 5. Squares—presence of individual flavonoids in both the Garryaceae and the Cornaceae. Dots—presence of individual flavonoids in the Cornaceae only. Lower scale indicates flavonoids by number.

TABLE 13. COEFFICIENTS OF ASSOCIATION FOR FLAVONOID CONSTITUENTS\*

Garrya	Aucuba japonica	Aucuba chinensis	Griselina litoralis	Griselina racemosa	Griselina ruscifolia	Griselina scandens
wrightii	.137	.074	.064	.148	.129	.142
laurifolia ssp. racemosa	.129	.068	.060	.137	.121	.132
fadyenii	.129	.068	.060	.137	.121	.132
ovata ssp. mexicana	.129	.068	.060	.137	.121	.132
corvorum	.148	.080	.068	.160	.137	.153
laurifolia ssp. laurifolia	.129	.068	.060	.137	.121	.132
ovata ssp. lindheimeri	.129	.068	.060	.137	.121	.132
ovata ssp. ovata	.129	.068	.060	.137	.121	.132
grisea	.132	.071	.062	.142	.125	.137
ovata ssp. goldmanii	.121	.064	.057	.129	.114	.125
salicifolia	.137	.074	.064	.148	.129	.142
laurifolia ssp. macrophylla	.148	.080	.068	.160	.137	.153
longifolia	.137	.074	.064	.148	.129	.142
flavescens ssp. flavescens	.129	.068	.060	.137	.121	.132
flavescens ssp. pallida	.129	.068	.060	.137	.121	.132
fremontii	.148	.080	.068	.160	.137	.153
veatchii	.160	.086	.074	.173	.148	.166
buxifolia	.153	.083	.071	.166	.142	.160
elliptica	.137	.074	.064	.148	.129	.142
glaberrima	.068	.000	.000	.074	.064	.071

\*Macrocarpum officinalis is .000 for all the Garrya species above.

FIG. 6. Probable lines of relationship within *Garrya*.



Studies of unique flavonoid constituents of the taxa of the Cornaceae (Table 14) indicate that they, with the exception of *Griselina ruscifolia* and *G. scandens*, have moderately high values and are well-differentiated. *Griselina ruscifolia* and *G. scandens* have the lowest percentages of unique compounds, 6.2 and 7.6% respectively. In contrast, 64.2% of the flavonoid constituents of *Macrocarpium officinalis* are unique. Other taxa of the Cornaceae show intermediate unique compound percentages ranging from 21.4 to 41.2%.

Group Affinity Indices (Table 11) of cornaceous genera range from approximately 161 to 579. *Griselina litoralis*, adapted to a coastal habitat, appears chemically differentiated from other species of the genus. A large gap in the distribution of GAI's separates *Garrya* from the cornaceous taxa. If the isolated *G. glaberrima* is excluded, the gap is about 500 points. Even when *G. glaberrima* is included, the gap is substantial—approximately 300 points. Therefore, the GAI's also indicate how chemically well-defined and different *Garrya* is compared to the cornaceous genera.

**Conclusions:** 1. The flavonoid constituents are more variable on an individual level than on a population level and the degree of flavonoid differences are greater between interspecific than intraspecific populations.

2. The flavonoid content of *Garrya* indicates a chemical division of the genus corresponding closely to the morphologically based subgenera *Garrya* and *Fadyenia*.

3. *Garrya* species show a high group affinity and form a well-integrated group.

4. *Garrya glaberrima* appears to be the most chemically differentiated species of the genus and shows the greatest divergence from the *Garrya* mainstream.

5. *Garrya* species share few flavonoid constituents in common with

TABLE 14. PERCENTAGE OF UNIQUE FLAVONOID CONSTITUENTS IN THE CORNACEAE

Genus	Species	Total Compounds	Unique Compounds	% Unique Compounds
Aucuba	japonica	14	3	21.4
	chinensis	12	3	25.0
Griselina	litoralis	16	5	31.2
	racemosa	12	5	41.6
	ruscifolia	16	1	6.2
	scandens	13	1	7.6
Macrocarpium	officinalis	14	9	64.2
Garrya	laurifolia	17	15	88.2
	all species	82	80	97.5

*Aucuba*, *Griselina*, and *Macrocarpium* of the Cornaceae.

6. As indicated by the Paired and Group Affinity Indices, *Aucuba*, *Griselina*, and *Macrocarpium* are chemically more closely related to each other than to *Garrya*.

## ECOLOGY

**Habitat.** *Garrya* is a highland genus, found in both the chaparral and coniferous forests above the lowland deserts. It generally grows in semiarid regions, although some species have adapted to coastal or near-coastal conditions. *Garrya elliptica*, occurring from central Oregon to Santa Cruz Island, California, is one such species and is frequently found within a few meters of the sea. In the southern part of the range, populations also occur inland and at higher elevations. This is especially true near San Francisco where several collections have been made on Mt. Tamaulpais and the hills surrounding Berkeley and other nearby places. In the northern part of the range, *G. elliptica* is almost always confined to coastal positions. *Garrya fremontii*, ranging from southern Washington to central California, is characteristic of the Sierra Nevada and Cascade ranges where moisture is plentiful, but it also extends (although less commonly) into the arid transition zone at lower elevations. *Garrya veatchii* is a typical member of the chaparral community and is quite tolerant of arid and semiarid conditions. It is frequently found in extremely sandy soil in the transition zone on the lower mountain slopes along rivers, dry runs, and canyons of southern California and Baja California. A population also exists on Cedros Island, located about twenty miles west of mainland Baja California. From the coastal ranges and the Sierra Nevada of central California, *G. flavescens* is distributed southward to Baja California and eastward to Nevada, Utah, and Arizona. *Garrya flavescens* ssp. *flavescens* is found both in semimesic canyons and on mountain slopes. Although sometimes extending into the transition zone, it is less characteristic of the more arid canyons and slopes than *G. flavescens* ssp. *pallida*. *Garrya flavescens* ssp. *congdonii* is also Upper Sonoran but shows less tolerance for aridity than does *G. flavescens* ssp. *pallida* which is found predominantly in the arid transition zone. *Garrya buxifolia* is a chaparral component of the transition zone but is also found in disturbed areas and at higher moist locations in association with *Pinus*. It has a restricted distribution and is confined to a six county area of northern California and southern Oregon. *Garrya corvorum* is a limestone endemic of the high Cordilleran mountain forests of central Guatemala and is isolated from the other species of subgenus *Garrya* by over two thousand miles.

Species within subgenus *Fadyenia* show a southern distribution

and are adapted to a variety of highland soils and conditions. *Garrya wrightii* ranges from Arizona to west Texas and south throughout northern Mexico, growing on arid, open, and rocky slopes of the Upper Sonoran and transition zones. It is extremely tolerant of arid conditions and prospers in environments where most other plants cannot. Moreover, it shows a greater tolerance for aridity than the other *Garrya* taxa, often growing between rocky crevices and boulders of the lower mountains. *Garrya ovata* is adapted to limestone outcroppings and is common in the mountains above the lowland deserts in Arizona, New Mexico, Texas, and northern Mexico, with the distributional center in the Texas-Chihuahua-Nuevo Leon area. *Garrya glaberrima*, an isolated species with a limited distribution, is found in a few scattered mountain localities of southern Coahuila, Nuevo Leon, and Tamaulipas, growing between the lowland deserts and the highland coniferous forests. It is found at the edge of the shrub zone where conditions are not wholly arid. *Garrya laurifolia* is known from the Sierra Madre Oriental, Sierra Madre Occidental, the volcanic slopes surrounding Mexico City, and the mountain systems of southern Mexico, Guatemala, Costa Rica, and Panama. Although the range extends into Central America, the center of distribution appears to be central Mexico. *Garrya laurifolia* ssp. *laurifolia* and *G. laurifolia* ssp. *macrophylla* are shrub community members and are well-adapted to semiarid conditions. Contrasting with the other subspecies, *G. laurifolia* ssp. *racemosa* is adapted to moist mountain forests where it commonly forms an understory in association with *Pinus*. It also inhabits the steep, moist banks of ditches, gullies, and ravines. *Garrya longifolia*, a closely related species of southern and southwestern Mexico, ranges from Jalisco south to the mountains of Oaxaca. Although *G. longifolia* commonly inhabits volcanic slopes, it is not confined to the pedregal, and is frequently found on moist mountain slopes. It often inhabits ravines at the lower edge of coniferous forests but sometimes it is associated with *Quercus* and grows on wooded slopes above streams. *Garrya salicifolia*, of southern Baja California, is found on sandy loam soils while *G. fadyenii* of the Greater Antilles appears well-adapted to limestone. *Garrya grisea* is a member of the dry Upper Sonoran and transition communities of northern Baja California. Although it is tolerant of the semiarid conditions, it is less so than the closely related *G. wrightii*.

**Altitude.** *Garrya* is a highland genus, generally adapted to high elevations. Subgenus *Garrya* includes species growing at both the highest and lowest elevations of the genus. *Garrya elliptica* ranges from 10-2750 feet, contrasting with the high mountain species, *G. corvorum*, with elevations of 9900-11700 feet. *Garrya fremontii* is found at 500-9000 feet, the most common interval being 3400-5500

feet. *Garrya veatchii* also shows a wide altitudinal range (750–8550 feet) with the most frequent elevation being approximately 3500 feet. *Garrya buxifolia* occurs at lower elevations, ranging from 200–7000 feet, with 2000 feet being the most common for the species. Divergence within *G. flavescens* appears related to both altitude and aridity. *Garrya flavescens* ssp. *flavescens* grows from 2600–9000 feet while *G. flavescens* ssp. *pallida* has adapted to the drier, lower elevations, ranging from 1500–7753 feet.

Within subgenus *Fadyenia*, the highest elevation is attained by *Garrya laurifolia* ssp. *quichensis* with a range of 4500–11700 feet. *Garrya laurifolia* ssp. *racemosa* closely follows, growing at altitudes of 3600–10000 feet, the most common being approximately 7500 feet. *Garrya laurifolia* ssp. *laurifolia* and *G. laurifolia* ssp. *macrophylla* grow at lower elevations, ranging from 2000–9000 feet and 3500–8850 feet respectively. *Garrya glaberrima* also grows at high elevations, ranging from 4880–9000 feet. *Garrya longifolia* shows an altitudinal range of 4200–8700 feet, with the most common interval being 6000–7000 feet. The remaining species within subgenus *Fadyenia* occur at lower elevations: *Garrya fadyenii* at 2000–8130 feet; *G. salicifolia* at 5100–6000 feet; *G. ovata* ssp. *lindheimeri* at 2000–6600 feet; and *G. ovata* ssp. *ovata*, *G. ovata* ssp. *goldmanii*, and *G. ovata* ssp. *mexicana* ranging from 4800–8000 feet, 4550–7800 feet, and 4000–8400 feet respectively. *Garrya wrightii*, which grows in arid areas, is found at elevations of only 3000 feet. However, the maximum elevation is about 7000 feet, with 5000–6000 feet being the most common interval. The closely related *G. grisea* requires more moisture and occurs at higher altitudes, ranging from 4500–7950 feet.

#### ETHNOBOTANY

*Garrya elliptica*, *G. fremontii*, and *G. veatchii* are used as ornamental shrubs in many areas throughout the world (Howes, 1974; Usher, 1974). The graceful, elongated catkins and the stately contour of the shrubs give it an aesthetic quality.

*Garrya laurifolia* is also used medicinally as an antidiarrhetic throughout rural Mexico (Martinez, 1959; Armendariz, 1895; Garcia, 1886). An extract is prepared from the stem, diluted with alcohol, and ingested. The treatment is said to yield quick and positive results, but since experiments have shown that *Garrya* extracts are extremely toxic, the antidiarrhetic properties should be held suspect. Stem extracts of *G. laurifolia* were prepared and injected into the peritoneum or veins of dogs in an effort to determine pharmacological properties (Martinez, 1959; Olguin Hermida, 1932). At first the dogs became highly stimulated, suffering convulsions and general muscular con-

tractions. Depending upon the dosage, a gradual paralysis of the central nervous system develops, resulting in complete respiratory collapse and death. The same physiological aberrations were induced when pure alkaloid extracts were injected. Additional pharmacological studies of *Garrya* are also reported by Langman (1964).

According to legend, bark extracts of *Garrya* species were used by western American Indians to treat fever. It was this legend that led Oneto (1946) to begin characterizing *Garrya* alkaloids chemically for preliminary tests as possible antimalarials.

Informal experiments in Mexico have investigated the effects of smoking *Garrya*. The stems, leaves, and fruit material of *Garrya laurifolia* and *G. longifolia* were ground into a coarse powder. Using ordinary pipes, five 18–22 year old male volunteers slowly smoked small quantities of the plant powder over a period of five hours. The volunteers recorded their observations. These, along with their feelings, showed a general similarity and were discussed after the experiment was completed.

No differences between *Garrya* material were noted, and the volunteers reported that the smoke was sweet and quite similar to *Cannabis*. Two of the volunteers experienced the same dryness of the mouth that is associated with smoking *Cannabis*. However, whether this was the result of *Garrya* or autosuggestion remains questionable. All the volunteers became very relaxed and tranquil as *Garrya* was smoked. After about 30 minutes, most reported a feeling of well-being, and were noticeably tranquil but not euphoric or in a stupor. Several volunteers also reported a tingling sensation up and down their spines that gradually gave way to a dull pain in the back of the head and neck. In addition, muscle twitches and minor pain in the hands, feet, and stomach were reported. The pain, resulting from muscle contractions which were mild and of short duration subsided and disappeared when the smoking was interrupted. When they resumed, the pain returned but the volunteers were so tranquil and contented that few complaints were noted. In all cases, the experiment was interrupted and eventually terminated when contractions or pains were reported. The volunteers stated that smoking *Garrya* was a pleasant experience, but it should be noted that two of them experienced miscellaneous pain and a temporary loss of sexual appetite following the experiment. No hallucinations were reported. While acknowledging the many side effects, *Garrya* still may hold potential for the future as a tranquilizing agent in medicine.

#### PALEOBOTANY-PHYLOGENY

Paleobotanical information about *Garrya* is scarce, making phylogenetic relationships and proposed historical reconstructions difficult.

The Old World fossils, which have recently been discovered and assigned to *Garrya*, are of interest. *Garrya tsushimense*, from the lower Tertiary, was discovered near Kushi and Saraura of the Tsushima Islands of Japan (Matsuo, 1971). However, only leaf material was discovered, so no firm conclusions as to the authenticity of the putative *Garrya* fossils can be reached. Only the reproductive structures can provide definite answers to the question of fossil affinity and identification, and, if they are eventually discovered, the argument for an early evolutionary relationship between *Garrya* and *Aucuba* will be strengthened.

It seems apparent that, in the past, *Garrya* had a greater distribution than it does today (Axelrod, 1944, 1950, 1958, 1964; Wolfe & Barghoorn, 1960). *Garrya axelrodi* (Wolfe, 1964) was discovered in Miocene deposits of southwest Nevada while *G. idahoensis* (Axelrod, 1964) of the middle Miocene, was found in southern Idaho. The latter is well outside the range of extant *Garrya* but nevertheless corresponds to modern members in vegetative features. Unfortunately a subgeneric assignment is not possible because the reproductive structures are lacking. A similar situation is found in *G. masoni* (Dorf, 1930), a Pliocene species found in Sonoma County, California.

Fossil leaves, seeds, and an inflorescence of *Garrya* have been discovered in Pleistocene to Recent deposits at Willow Creek, Carpinteria, and Tomales Bay, California (Chaney & Mason, 1934, 1934a; Mason, 1934). The fossils have been identified as *G. elliptica* because they are similar to it in appearance and were found within its range. *Garrya* pollen has also been identified in Pleistocene to Recent deposits in Arizona (Gray 1960, 1961). Apparently the pollen is resistant to decay and is easily identified.

No paleoevolutionary conclusions concerning *Garrya* can be reached because of the incomplete fossil record. The fossils from the early Tertiary are dubious. The genus probably arose in North America during the middle Tertiary and underwent rapid evolution as a result of aridity and climatic change. However, the question of area of origin remains unsettled unless verified fossils of *Garrya* are found in the Old World. For the present, the evidence is strongest for a New World origin.

On the basis of morphology, and the evident trends of reduction, it is probable that subgenus *Fadyenia* most closely reflects the primitive condition. Members of subgenus *Garrya* have inflorescences which are more reduced and floral bracts which show a greater fusion than those of subgenus *Fadyenia*. Also, most of the members of subgenus *Garrya* are shrubs and are distinctly less tree-like than members of subgenus *Fadyenia*. The presence of a rudimentary perianth in the female flowers of subgenus *Garrya* is anomalous but absent in subgenus *Fadyenia*. However, this may not be significant if allowances

are made for the fact that the evolution of different features proceeds at different rates, permitting the various organs to reach different levels of specialization. On the whole, most of the characters associated with subgenus *Garrya* appear to be more specialized than the corresponding ones of subgenus *Fadyenia*. Because the morphological and phytochemical differences between the subgenera are pronounced, an early evolutionary divergence within the genus is indicated (Figure 6).

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## TAXONOMIC TREATMENT

### GARRYACEAE

Diocious evergreen trees and shrubs, bushy, 2-40 feet high. Crown sprouts numerous, often well-developed and indistinguishable from the main stem axis. Tap root long, with many secondaries. Young stems with ridges and grooves, becoming rounded with age, glabrous and densely covered with silky, appressed, sometimes hispid trichomes, typically gray, tan, green, or reddish-brown. Branching decussate. Stipules absent. Leaves simple, petiolate, decussate, elliptical, ovate, lanceolate, sometimes obovate, rarely oblong, stiff, coriaceous. Petioles 2-30 mm. long; opposite petioles connate at the base and adnate to the stem. Leaf blades 1.0-20.0 cm. long and 1.0-10.2 cm. wide; apices acute, acuminate, mucronate, or obtuse; bases frequently attenuate, sometimes cuneate, obtuse, or suboblique; margins entire, variably undulate; upper surfaces variably pubescent, frequently glabrate, often sparsely villous, pilose, sericeous or tomentose, typically shades of green, yellow, gray, or blue, often lustrous; lower surface rarely glabrous, typically velutinous, villous, pilose, hirsute, strigose, tomentose-lanate, often with appressed and ascending trichomes, green, yellow, gray, or blue, sometimes whitish-gray or silver, becoming less pubescent with age; papillae common and well-developed; midrib, major veins, and minor reticulation sometimes impressed, visible, or obscured above, hidden by pubescence below, midrib usually visible in high relief. Stomata paracytic, numerous, confined to lower leaf surfaces; subsidiary cells with wavy, undulate, or straight, plane outlines. Trichomes unicellular, uniformly showing counterclockwise orientation of ridges and furrows; protuberances frequently present and restricted to the ridges; occasional structural twisting results in a compound counterclockwise orientation. Staminate inflorescences catkin-like or racemose, branching or unbranching, usually fasciculate and pendulous at the tips of branches, sometimes axillary and solitary, lax or compact, densely flowered with short or elongated internodes. Staminate floral bracts connate at the base and laterally forming cup-like structures, or connate only at the base, frequently lanceolate, ovate, elliptical, or linear-oblong, apices straight or recurved, bases typically cuneate, obtuse or sometimes truncate. Staminate flowers solitary or ternate, in the axils of the partially enveloping bracts. Pedicels abbreviated or elongated. Perianth segments four, oblong-ovate, connate at the apices forming a semi-enclosed chamber with four openings, variably pubescent on the abaxial surface, typically glabrous on the adaxial surface, white, yellow-green, or red-brown. Stamens four, free, short, opposite the chamber openings. Anthers oval to oblong, basifixed, introrse, opening by longitudinal slits. Filaments abbreviated. Pollen tricolporate, reticulate, yellow-green to yellow-brown, copious, wind disseminated. Pistillate inflorescences catkin-like or racemose, branching or unbranching, rarely sub-erect, usually fasciculate and pendulous at branchlet tips, sometimes axillary and solitary, variable in length, lax or compact, sometimes densely flowered and imbricate, frequently with elongated conspicuous internodes. Pistillate floral bracts connate at the base and laterally forming cup-like structures, or connate only at the base, frequently ovate-elliptical to oblong, sometimes linear-lanceolate, often markedly foliaceous, green, gray, or brown. Pistillate flowers solitary, or ternate in the axils of bracts. Pedicels minute, rarely lacking. Ovaries bicarpellate, rarely tricarpetate, unilocular, subovoid to oblong-elliptical, subsessile, inferior, nude or sometimes bearing variably adnate paired perianth remnants alternating with and near the base of the styles, frequently with variably adnate bracts opposite and near the base of the styles, variably pubescent or glabrate. Styles two, rarely three, persistent, terete, elongate or frequently short, thick, fleshy and variously divergent. Ovules two, rarely three, subterminal, pendulous on parietal placentas, anatropous. Fruit a modified berry, globose to ovoid, glabrate or variously pubescent, compact or lax on the infructescences, green and fleshy, at maturity becoming dark blue, black or whitish-gray, dry and brittle. Dehiscence irregular, seeds two, rarely three, globose to ovoid-elliptical with a silver ariloid structure, becoming membranous at maturity, typically dark blue-black. Embryo minute, embedded in massive endosperm. Seeds scatter by weathering and fragmentation of persistent fruits.

The Garryaceae is a New World family of highland areas and consists



of a single genus with two subgenera. Both the genus, which was discovered and named by David Douglas in 1826, and the family were described by John Lindley in 1834. Subgenus *Garrya* consists of six species and is generally confined to the western United States and northern Baja California with the exception of *G. corvorum*, a central Guatemalan endemic. Subgenus *Fadyenia* contains eight species and is found in the southwestern United States, throughout Mexico and Central America, and in the Greater Antilles.

#### GARRYA DOUGLAS EX LINDLEY

*Garrya* Dougl. ex Lindl., Bot. Reg. **20**:1686. 1834. TYPE SPECIES: *Garrya elliptica* Dougl. ex Lindl.

*Fadyenia* Endl., Gen. Suppl. **IV**:38. 1847. TYPE SPECIES: *Fadyenia Hookeri* Endl., based on *Garrya fadyentii* Hook.

Characters of the family.

#### KEY TO THE SPECIES

- A. Inflorescences catkin-like and not branching. Floral bracts connate at the base and laterally forming cup-like structures which bear ternate flowers in the axil. Pistillate inflorescences compact, bracts not leaf-like, often imbricate obscuring the internodes when in fruit. Mostly shrubs . . . . . Subgenus *Garrya*.
- B. Lower leaf surfaces densely covered with strongly curled, woolly, or villous trichomes. Ovary densely pubescent.
  - C. Leaves ovate to broadly elliptical, ranging from 3.1–12.4 cm. long and 1.5–6.7 cm. wide, coriaceous and dark green in color. Margins strongly undulate, rarely plane. Leaf undersides densely covered with a tomentum of curly, intertwined trichomes, the uppersides glabrous and lustrous. Mostly coastal shrubs but sometimes arboreal inland . . . . . 1. *G. elliptica*.
  - C. Leaves ovate to ovate-elliptical ranging from 2.3–8.3 cm. long and 1.0–3.2 cm. wide, strongly coriaceous, light green. Margins plane. Leaf undersides densely covered by a mat of short, curled, interwoven bright, white trichomes. Upper surfaces covered with short, curly trichomes. Mostly shrubs or rarely gnarled trees in sandy arid regions . . . . . 2. *G. veatchii*.
- B. Lower leaf surfaces glabrous, slightly or densely covered with straight or somewhat wavy upwardly appressed trichomes. Ovary glabrous, sparsely or densely pubescent.
  - D. Lower leaf surfaces glabrous or very sparsely covered with pilose trichomes when young. Adult leaves oblong to ovate, 2.8–11.4 cm. long and 1.4–4.9 cm. wide, coriaceous, glabrous, bright green above, gray-green below. Ovaries sparsely pilose at the apex, typically glabrous at maturity. Female inflorescences semi-erect. Mostly shrubs in highland areas . . . . . 3. *G. fremontii*.
  - D. Lower leaf surfaces more or less covered with straight, wavy, or silky upwardly appressed trichomes. Rare individuals may show both glabrous leaf undersides and silky pubescent ovaries.
    - E. Lower leaf surfaces densely covered with long, silky, white, upwardly appressed trichomes. Leaves oblong to oblong-elliptical, 2.7–4.6 cm. long and 0.9–1.5 cm. wide. Trees confined to limestone areas in central Guatemala . . . . . 4. *G. corvorum*.
    - E. Lower leaf surfaces more or less covered with straight or wavy upwardly appressed trichomes. In glabrous leaf forms, ovaries are silky or moderately pubescent.
    - F. Ovaries glabrous. Lower leaf surfaces densely covered with silky appressed silver-gray trichomes. Leaves thick, coriaceous, usually glabrous above, 2.3–6.5 cm. long and 1.0–3.0 cm. wide. Mostly low shrubs . . . . .

- ..... 5. *G. buxifolia*.
- F. Ovaries silky pubescent. Lower leaf surfaces glabrous or covered with straight or wavy upwardly appressed trichomes. Leaves coriaceous, glaucous above, white and shiny below, oblong to elliptical, 3.3–9.5 cm. long, 1.3–4.4 cm. wide. Shrubs or small trees ..... 6. *G. flavescens*.
- A. Inflorescences racemose, branching at the base. Floral bracts connate at the base, appearing leaf-like although sometimes smaller than the foliage leaves, bearing solitary flowers in the axils. Pistillate inflorescences loose and spreading, bracts distinctly leaf-like, internodes prominent during fruiting. Trees and shrubs ..... Subgenus *Fadyenia*.
- G. Plants entirely glabrous or rarely with a sparse row of trichomes along the edge of the pistillate floral bracts. Leaves 6.0–9.8 cm. long, 2.2–4.0 cm. wide. Shrubs and small trees at high elevations. .... 7. *G. glaberrima*.
- G. Plants variously pubescent especially young stems, leaves, and floral bracts. Lower leaf surfaces usually densely covered with trichomes when young.
- H. Leaves elliptical to ovate-elliptical, mostly less than twice as long as broad. Usually leaf surfaces of mature leaves glabrous, nearly glabrous, or densely covered with short upwardly appressed or curly, woolly, or matted trichomes. Yellow-green, green, or gray-green shrubs and small trees.
- I. Leaves densely covered with curly, woolly, and coiled trichomes often forming a whitish-gray mat. Leaves plane or markedly undulate. Ovaries glabrous. Pistillate floral bracts mostly small, oblong-elliptical. Small shrubs and trees, frequently on limestone. .... 8. *G. ovata*.
- I. Leaves glabrous or densely covered with short upwardly appressed trichomes. Leaves plane. Ovary sparsely sericeous becoming glabrous with age. Pistillate floral bracts mostly small and linear to oblong-elliptical. Yellow-green to gray-green shrubs mostly in arid regions.
- J. Mature leaves essentially glabrous or rarely the lower surface covered with short upwardly appressed trichomes. Leaf surfaces yellow, green, or rarely light gray on the underside. Lowermost pistillate floral bracts sometimes foliaceous. Shrubs to small trees in semiarid regions. .... 9. *G. wrightii*.
- J. Mature leaves covered by short upwardly appressed trichomes on both surfaces. Leaves uniformly gray-green or rarely bright green. Pistillate floral bracts much smaller than foliage leaves. Mostly shrubs confined to the arid transition zone of northern Baja California ..... 10. *G. grisea*.
- H. Leaves oblong, elliptical-oblong, oblanceolate, lanceolate, and ca. 2–4 times as long as broad. Leaf under surfaces covered with curly trichomes when young but frequently glabrous with age. Leaves dark green to yellow with lustrous, usually glabrous upper surfaces. Shrubs to large trees.
- K. Bracts of the infructescences linear-oblong to linear-lanceolate and smaller than the foliage leaves. Upper leaf surfaces usually glabrous. Lower leaf surfaces glabrous or with sparse, appressed, villous, or densely woolly trichomes.
- L. Leaves glabrous or with sparse appressed trichomes on the lower surface. Leaves lanceolate to oblong-lanceolate. Mostly shrubs from Baja California ..... 11. *G. salicifolia*.
- L. Leaves densely covered with trichomes producing a woolly, curly, pilose, or villous under surface. Leaves lanceolate or elliptical. Mostly trees.
- M. Leaves elliptical, densely covered with woolly, curly, intertwined trichomes. Leaves plane, dark green above and gray below. Trees commonly found in limestone areas of the Greater Antilles ..... 12. *G. fadyenii*.
- M. Leaves oblong to oblong-elliptical, pilose to villous or sparsely so. Leaves frequently somewhat undulate, yellow-green, green, and reticulate. Staminate inflorescences lax with few flowers and prominent internodes. Staminate floral bracts often shorter than the flowers. Mostly trees. .... 13. *G. longifolia*.
- K. Bracts of the infructescences expanded and often as large as foliage leaves. Lower leaf surface covered with curly, woolly trichomes becoming glabrous with age. Leaves elliptical, ovate, or oblanceolate. Upper surfaces glabrous and lustrous. Shrubs to large trees. .... 14. *G. laurifolia*.

## SUBGENUS GARRYA

Inflorescences catkin-like and unbranched. Floral bracts connate at the base and laterally forming cup-like structures subtending the flowers. Female inflorescences compact, bracts often imbricate and not foliaceous, internodes short and inconspicuous. Ovaries bear minute partially adnate perianth appendages alternating with and near the base of the two styles. Styles elongate, slender, terete, often divergent and reflexed, sometimes erect. Mostly shrubs.

TYPE SPECIES. *Garrya elliptica* Dougl. ex Lindl., Bot. Reg. 20:1686. 1834.

1. *Garrya elliptica* Douglas ex Lindley

*Garrya elliptica* Dougl. ex Lindl., Bot. Reg. 20:1686. 1834. ISOTYPE: plentiful in rocky situations on the seashore near the confluence on the Columbia, on the south bow and in California more abundant, *Douglas 1838* (CH).

Low shrubs or small trees, 3–25 feet high. Crown sprouts numerous. Stems short, villous to pilose, becoming glabrate with age; reddish-brown, black, or greenish-white. Decussate branching. Stipules absent. Leaves simple, petiolate, decussate, elliptical oval, or oval-lanceolate, thick, coriaceous, persistent. Petioles (0.2–)0.4–1.0–(1.3) cm. long; opposite petioles connate at the base, adnate to the stem. Leaf blades (2.8–)4.0–9.5–(11.1) cm. long, (1.5–)2.0–4.0–(6.7) cm. wide; apices acuminate to mucronate; bases cuneate to broadly obtuse; margins entire, strongly undulate or revolute; glabrous, lustrous above, lanate below with curly trichomes; papillae developed; midrib and major veins visible above, prominent, in relief below. Staminate inflorescences catkin-like, unbranched, fasciculate, pendulous on branchlets, densely flowered, 5–30 cm. long. Staminate floral bracts ovate-elliptical, mucronate, acuminate, ca. 5 mm. long, villous; opposite bracts connate for half their lengths. Flowers ternate in bract axils. Pedicels short, sometimes extending beyond involucre. Perianth segments four, oblong, about 5 mm. long, connate at apices, abaxial sides silky pubescent, adaxial sides glabrous. Stamens free, short, alternating with the perianth segments. Anthers oblong-elliptical, 2–3 mm. long, basifixed, introrse, opening by longitudinal slits. Filaments minute. Pollen tricolporate, reticulate, yellow-brown to green. Pistillate floral bracts ovate-elliptical, acuminate, villous; opposite bracts connate for half their lengths. Flowers ternate in the bract axils. Pedicels short. Ovaries bicarpellate, rarely tricarpellate, unilocular, subglobose, inferior, sometimes with adnate perianth remnants alternating with and near the base of the styles, tomentose, green or dark blue at maturity. Styles two, rarely three, persistent, terete, subulate, divergent. Fruit a berry, subglobose, 7–8 mm. in diameter, densely pubescent and yellow-green when young, dark blue to black, dry at maturity. Dehiscence irregular. Seeds two, rarely three, globose to oval, subterminal, parietal placentas, dark blue to black.

Flowering from early December to late February at elevations of 10–2750 feet, mainly along the coast but sometimes inland from central Oregon to near Ventura County, California (Map 1).

REPRESENTATIVE SPECIMENS. **California.** Alameda Co.: Temesial Canyon, *Bioletti 2/18/92* (DS); Alameda, *Skolton 3/15/03* (CH). Contra Costa Co.: Oakland and Berkeley hills, *Belshaw 1420* (CH,UC); Mt. Diablo, NW corner of basin of the NE fork of Sycamore Creek, *Bowerman 1082* (UC); head of San Leandro Creek, Oakland hills, *Duran 3375A* (CH,ORE,UC); Berkeley, *Greene 2/17/88* (NY); Berkeley hills, Grizzley Peak, *Howell 5304* (CH,POM); Oakland hills, *McMinn 1397* (CH). **Del Norte Co.:** Requa, on ocean, *Duncan 428* (DS); Del Monte, *Heller 6800* (CH); Smith River near the sea, *Howell 6/10/84* (CH); 3 mi. S of Crescent City, *Wiggins 5883* (DS,POM,UC). **Humboldt Co.:** sea flubbs at mouth of Matole River, *Benson 1657* (POM); along Hwy. 1, about 10 mi. N of Trinidad, *Dahling 1229* (CH); mouth of Luffenholtz Creek near Trinidad, *Kildare 2550* (DS);

Trinidad, on cliffs near the ocean, *Parks* 4287 (GH,UC); Patrick's Point State Park, *Thorne* 19021 (RSA); Blue Slide on Van Duzen River, *Tracy* 16203 (GH,UC); Big Lagoon, *Tracy* 17441 (NY,UC,WTC). **Marin Co.:** San Francisco hills, *Bolander* 1863 (NY); Tomales Bay State Park, near the picnic and beach area, *Dahling* 819 (GH); Pt. Reyes Station, *Dahling* 1050 (GH); Mt. Tamalpais, *Eastwood* 3169 (GH), 1/97 (UC), 5/11/91 (ORE); Tomales Bay, 5 mi. S of Marshall Coastal Bluffs, *Everett* 18591 (RSA); Inverness ridge, NW of Inverness, *Hoover* 4745 (UC); above Hentfield, Eldridge Grade, *Raven* 1265 (RSA). **Mendocino Co.:** along Hwy. 1 about 1 mi. S of Little River State Beach, *Dahling* 050 (GH); sand dunes, 3 mi. N of Fort Bragg, *Mason* 5403 (UC); 1-1/2 to 2 mi. W of Haven's Neck, *Thorne & Everett* 34235 (GH); 1.2 mi. S of Garcia River Bridge on Coast Rd., *Wolf & Johnson* 6177 (UC,WTC). **Monterey Co.:** Pico Blanco, near summit, *Davy* 7333 (UC); Seaside, *Elmer* 4933 (ORE,UC); NE of Bouchers Gap Camp, Santa Lucia Mts., *Haasis* 47.59 (CAS); N of Pine Canyon, W side of Salinas Valley near Spreckels, *Hoover* 1183 (CAS); 5 mi. E of Monterey, *Rose* 44301 (GH,RSA); SW slope of ridge, W of Big Sur Camp, *Steward* 198 (UC). **Napa Co.:** near Four Corner, Adam & Eve Ridge, Howell Mt., *Jepson* 399 (UC). **San Luis Obispo Co.:** 1-1/2 mi. SE of the mouth of Little Falls Canyon, *Bolt* 565 (UC); summit rd. along S fork of Las Tablas Creek on Klau-Cambria Rd., Santa Lucia Mts., *Ferris* 9789 (DS,GH); Price Canyon, *Hoover* 7268 (CAS); 2.3 mi. NE of Slide Hill, Arroyo Grande, *Lee* 386 (UC). **San Mateo Co.:** NE side of Coal Mine Ridge, *Barry* 222 (DS); near La Honda, *Benson* 833 (POM,WTC); Los Tancos Woods, *Demaree* 7312 (GH,NY,WTC); San Mateo Ravine by the road to Santa Cruz Peninsula, *Dudley* 005 (GH); Portola, *Elmer* 4469 (NY,ORE,UC); up hill from Trillium Gulch, San Bruno Mt., *McClintock* 519683 (CAS); 3-1/2 mi. N of La Honda, Santa Cruz, *Sindel* 336 (UC). **Santa Barbara Co.:** N side of Devil's Backbone Peak, Cueva Valdaze, Santa Cruz Island, *Beeks* 3 (RSA); main N ridge E of Picacho Diablo, Santa Cruz Island, *William* 55 (UC). **Santa Clara Co.:** Saratoga, *Davy* 388 (UC); Black Mt., Santa Cruz Mts., *Dudley* 34 (GH,NY,ORE,WTC); canyon of Permanente Creek, Santa Cruz Peninsula, *Dudley* 116708 (RSA); foothills W of Los Gatos, *Heller* 7220 (GH,UC). **Santa Cruz Co.:** Santa Cruz, *Anderson* 160016 (GH); 4 mi. NW of Watsonville, *Rose* 55037 (NY); Pine Mt. Basin, Redwoods State Park, *Thomas* 37325 (DS). **Sonoma Co.:** 10 mi. N of Fort Ross along Hwy. 1, *Thorne* 34218 (GH,RSA). **Tehama Co.:** Tehama, *Heller* 13000 (GH). **Oregon. Coos Co.:** cliffs at Bandon Beach, *Abrams & Benson* 10617 (DS,ORE); Charleston, *Scuffen* 6/6/26 (UC); North Slough, *Smith* 3403 (DS); Crawford Pt., *Smith* 3660 (NY). **Curry Co.:** Brookings, *Henderson* 5717 (ORE); by the sea, Chetco, *Howell* 6/12/84 (NY,ORE,WTC); Huntas Creek near Pistol River, *Kildare* 6/65 (DS). **Douglas Co.:** Douglas, *Jones* 213 (GH); S of Florence on Hwy. 101, *Steward* 6006 (DS,GH). **Lane Co.:** Tahkinitch Creek, *Detling* 2406 (ORE,WTC); Siltcoos Outlet, *Eastwood* 1524 (GH), 1525 (GH); 1 mi. N of Cape Perpetua, *Peck* 10626 (GH); along Hwy. 101, 1 mi. S of Sea Lion, *Steward* 7282 (DS,NY).

*Garrya elliptica* is frequently found growing on the sandy, shrub-covered hills and ridges along the seacoast from central Oregon to Ventura County, California. Although it is best adapted to the humid coastal conditions, it has the capacity for growth at higher elevations inland. There its habit is more arboreal, contrasting with the shrubby habit found when it grows on the coast.

Undulate and revolute leaf margins are typical of *Garrya elliptica*, but the leaves of some individuals or populations are more or less plane. The degree of marginal leaf undulation is variable throughout *Garrya* and is not particularly significant systematically. Arboreal specimens from Tomales State Park, California, show nearly plane margins as do specimens from Santa Cruz Island. This condition is sporadic but not infrequent, and should not be given systematic recognition.

*Garrya elliptica* sometimes resembles other *Garrya* species. For example, in the southern and more arid parts of its range, *G. elliptica* has rather small leaves and resembles *G. veatchii*. Populations of *G. flavescens* ssp. *congdonii* superficially resembling *G. elliptica* have been discovered at higher elevations in Glenn, Lake, and Tehama Counties. Members of these populations approach *G. elliptica* in appearance because their leaves are weakly or sometimes strongly undulate with a covering of woolly and somewhat wavy trichomes on the underside. Although it is tempting to suggest that these populations of *G. flavescens* ssp. *congdonii* are inland forms of subspecies of *G. elliptica*, this is not well-supported when the entire distribution and variation patterns of both *G. elliptica* and *G. flavescens* are examined. Therefore these inland populations are best excluded from *G. elliptica* and referred to *G. flavescens*.

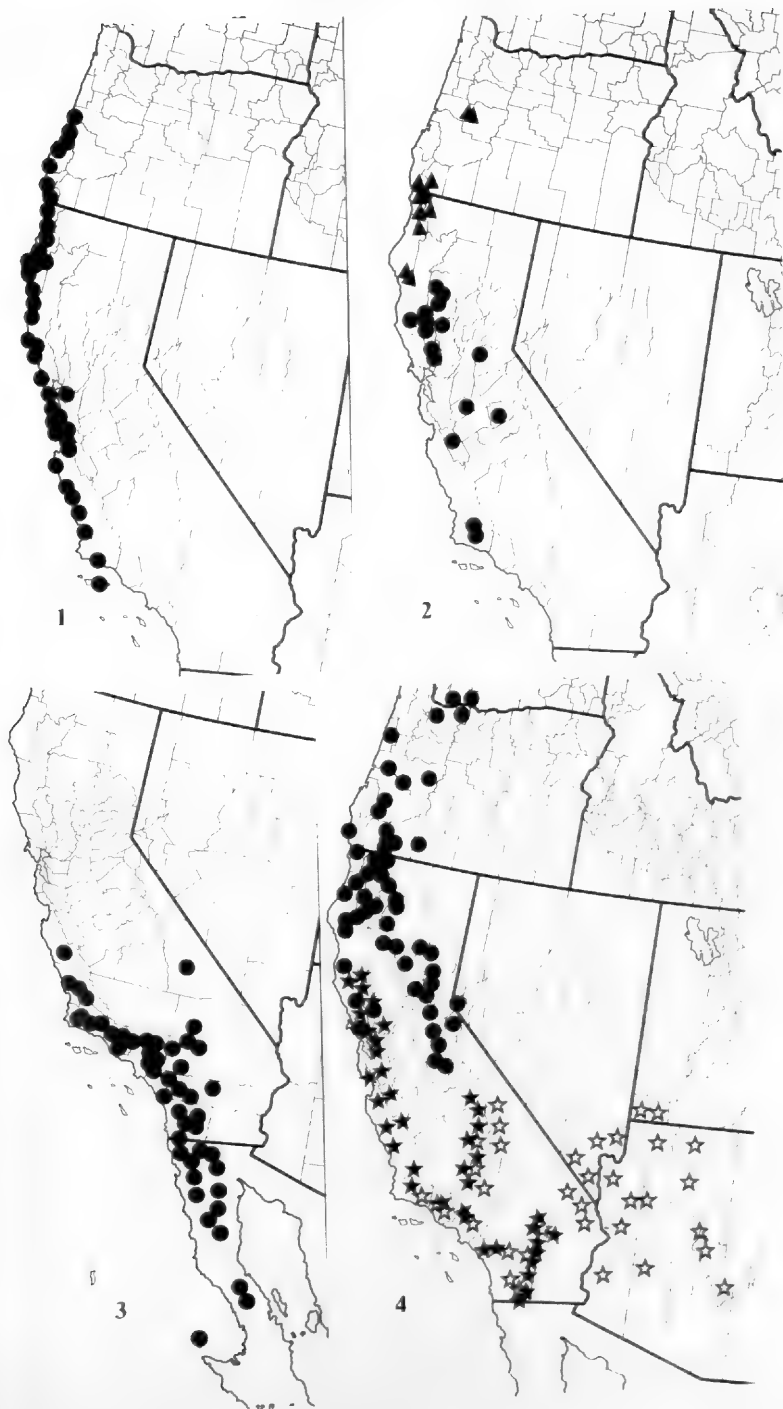
## 2. *Garrya veatchii* Kellogg

*Garrya veatchii* Kell., Proc. Calif. Acad. V:40. 1873. HOLOTYPE: Cedros Island, Veatch 569 (CAS). ISOTYPE: GH.

*Garrya veatchii* var. *undulata* Eastw., Bot. Gaz. 36:458. 1903. HOLOTYPE: Mt. Love, Echo Mt., Los Angeles Co., California, Grant 568 (CAS).

3 *Garrya flavescens* var. *palmeri* Wats., Bot. Calif. 1:276. 1876. HOLOTYPE: south part of San Diego County, California, 1875, Palmer 117 (GH).

Low shrubs or gnarled trees, 8–16 feet high. Crown sprouts well-developed. Young stems with short intertwined pubescences, becoming glabrate with age; yellow-tan, reddish-brown. Branching decussate. Stipules absent. Leaves simple, petiolate, decussate, narrow lanceolate-ovate or ovate-elliptical, coriaceous, stiff, persistent. Petioles short, (0.3–)0.4–1.0(–1.3) cm. long; opposite petioles connate at the base, adnate to the stem. Leaf blades (2.0–)3.0–6.0(–7.0) cm. long and (1.0–)1.5–3.0(–3.2) cm. wide; apices mucronate, acute or obtuse; bases mostly obtuse or subobtusate; margins entire, slightly undulate or revolute; upper surface with short, curly, white trichomes, light green and dull; lower surface with semiappressed, short, interwoven, bright gray-white trichomes; papillae well-developed; midrib and major leaf veins visible above, hidden below except for the midrib. Staminate inflorescences catkin-like, unbranched, fasciculate, pendulous at tips of branchlets, or axillary and solitary, densely flowered, 3–10 cm. long, internodes obscured by flowers. Staminate floral bracts truncate, sometimes weakly keeled, acuminate or apex recurved and aristate, densely tomentose or floccose; opposite bracts connate over half their lengths. Flowers ternate in the bract axils. Pedicels short, not exceeding the involucre. Perianth segments four, oblong-elliptical, 2–4 mm. long, connate at apices, silky pubescence on abaxial sides, adaxial sides glabrate. Stamens free, short, alternating with the perianth segments. Anthers oval to oblong, 1–3 mm. long, basifixed, introrse, opening by longitudinal slits. Filaments minute. Pollen tricolporate, reticulate, yellow-green or yellow-brown. Pistillate inflorescences catkin-like, unbranched, fasciculate at ends of branchlets, sometimes axillary and solitary, pendulous or suberect, many-flowered, 2–6 cm. long, compact with internodes mostly hidden. Pistillate floral bracts 5 mm. long, truncate, apex acuminate or recurved and aristate, tomentose to floccose; opposite bracts connate for over half



their lengths. Flowers ternate in axils of bracts. Pedicels minute. Ovaries bicarpellate, rarely tricarpetate, unilocular, subglobose, subsessile, inferior, sometimes with adnate paired perianth remnants alternating with and near the base of the styles, with long, white, woolly trichomes when young, less densely covered with age. Styles two, rarely three, persistent, terete, subulate, longer than ovary when young, divergent or erect. Fruit a berry, subglobose, 6-7 mm. in diameter, pubescent, dark blue to brown, at maturity brittle. Dehiscence irregular. Seeds two, or rarely three, globose to oval, subterminal, parietal placentas, dark blue to black.

Flowering from January to early May at elevations of 750-8550 feet, mainly in southern California from San Luis Obispo to San Bernardino county and southward into Baja California (Map 3).

REPRESENTATIVE SPECIMENS. **Mexico. Baja California:** San Pedro Martir, *Brandege* 173278 (UC); N slope of Cerro el Sauco, *Moran* 10248 (DS,UC); NW slope of Cedros Mt., Cedros Island, *Moran* 10649 (RSA,SD); Cerro Blanco, Sierra San Pedro Martir, *Moran* 10945 (DS,UC); Arroyo Agua Caliente, N of Cerro Chato, Sierra San Pedro Martir, *Moran* 11098 (DS,SD); Cañada el Duranzo, *Moran* 11383 (DS,SD,UC); W peak of Cerro Santa Marta, Sierra San Borja, *Moran* 13104 (SD,UC); 3 mi. S of La Hechicera, Sierra Juarez, *Moran* 14916 (TEX,UC); summit of Cerro Piñon, 3 mi. N of El Alamo, *Moran* 17649 (SD); E slope of Cerro Bola, *Moran* 17806 (SD); uppermost SW fork of Guadalupe Canyon, about 8 mi. E of Lagun Hansen, *Olmsted* 4860 (RSA); hillside on E side of summit, 6-8 mi. W of Ojos Negros Rancho, *Wiggins & Gillespie* 4068 (DS,GH,MICH,MO,US). **California. Inyo Co.:** ridge above junction of the two forks of Tuttle Creek, 8-1/2 mi. WSW of Lone Pine, *Olmsted* 609 (RSA). **Los Angeles Co.:** Lone Pine Canyon, San Gabriel Mts., *Abrams & McGregor* 671 (DS,GH); San Antonio Canyon, near Claremont, *Baker* 3651 (GH); foothills of San Gabriel Mts. above Monrovia, *Beach* 21874 (CAS); trail between Haines Canyon and Mt. Lukens, San Gabriel Mts., *Howell* 3342 (CAS,GH); San Antonio Mts., *Parish* 11975 (UC); Calabasas, Saddle Peak, Santa Monica Mts., *St. John* 79 (UC); Clear Creek branch of Big Tujunga Canyon, *Thorne* 40612 (CAS,RSA). **Monterey Co.:** S trail to Cone Peak, Santa Lucia Mts., *Munz* 20932 (RSA). **Riverside Co.:** Hemet to Idyllwild, San Jacinto Mts., *Balls* 20972 (RSA); across the valley from Santa Rosa Springs, Santa Rosa Mts., *DeBuhr* 529 (UC); Palms to Pines hwy., San Jacinto Mts., *McKelvey* 5049 (GH,UC); Santa Rosa Plateau, *Thorne* 39331 (RSA); Oak Lodge, mouth of San Jacinto Canyon, *Wolf* 1490 (RSA). **San Bernardino Co.:** Lytle Creek Canyon, *Abrams* 2805 (GH,WTC); S of Cajon Pass, *Bell* 1195 (UC); Lytle Creek area, *Dahling* 354 (GH); near Cajon summit and nearby slopes, *Dahling* 920 (GH); Lone Pine Canyon, about 2-3 mi. W of Hwy. 138, *Dahling* 1300 (GH); San Bernardino, *Howell* 2488 (GH); between San Bernardino and summit to Victorville, *McMinn* 3141 (UC); San Bernardino Mts., *Parish* 10793 (GH); **San Diego Co.:** Warners Springs, *Couchs* 43391 (CAS); San Diego, *Eastwood* 9435 (GH); Japatul Valley, 6 mi. SE of Descanso junction, *Gander* 587 (SD,UC); Campo, *Hall* 171022 (UC); La Posta beyond Beichman Springs, *Harvey* 13014 (SD); Cuyamaca, McGinty Mt., *Jensen* 100 (UC); Mt. Springs, *Parish* 10824 (GH); Bankhead Springs, 1 mi. E of Mistletoe Ridge, *Wiggins* 2349 (DS). **San Luis Obispo Co.:** main crest of Santa Lucia Range due SSE of Cuesta Pass, *Bacigalupi & Heckard* 8825 (WTC); 3.8 mi. W of Paso Robles on Peachy Rd., *Dahling* 944 (GH); 4 mi. W of Paso Robles on Peachy Canyon Rd., *Ferris* 9792 (GH,POM,UC,WTC); ridge, NW of Cuesta Pass, *Thorne* 31589 (GH,RSA); San Luis Obispo, *Thorne & Everett* 32140 (GH). **Santa Barbara Co.:** 4 mi. NE of Refugio Pass, Lompoc, *Axelrod* 158 (UC); El Camino Cielo Rd. E of junction with Depression Drive, La Cumbre Mt., *Beeks* 289 (WTC); Santa Barbara, *Eastwood* 63 (GH); Santa Ynez Mts., *Elmer* 3770 (DS,UC); Rattlesnake Canyon between La Cumbre Peak and Santa Barbara, *McMinn* 447 (UC); Nojoqui Park, Gaviota Pass Region, *McMinn* 4349 (UC). **Ventura Co.:** between Pipe and Sespe Creeks, just S of Oat Mt., *Ferris* 10641 (GH,RSA); Matilija Canyon, *Pollard* 75074 (SD,UC); Ventura, *Simontacchi* 10856 (GH).

*Garrya veatchii* is common to the chaparral of southern California

and Baja California. For the most part it is a natural and easily recognized taxon, distinct from the other *Garrya* species. Minor intergrading with *G. flavescens* and *G. elliptica* does occur, but not to a sufficient degree to support a change in status.

The holotype of *Garrya veatchii* was collected by Veatch on Cedros Island, several miles off Baja California, and is somewhat atypical of the mainland and California material in terms of leaf and pubescence characteristics. This variation probably resulted from differences in the gene frequencies which would be expected to occur in small and relatively isolated island populations.

Eastwood (1903) recognized *Garrya veatchii* var. *palmeri* and *G. veatchii* var. *undulata*, basing her conclusions on the differences in leaf undulation, leaf size, pedicel length, and the internode length of the infructescences. Her treatment is not followed here since differences in the degree of marginal leaf undulation are common in *Garrya* with only a few taxa uniformly showing plane or undulate leaves. Moreover the variation in leaf size is dependent on fluctuations in soil moisture and other environmental influences which may cause considerable infraspecific variation. Also, the pedicel length, as with undulate leaf margins, is a highly plastic character showing extensive variation throughout *Garrya*. In fact, the pedicel length differs not only between populations but also on the same inflorescences or infructescences. Since no meaningful and stable pattern to this type of variation has been found, no infraspecific taxa within *G. veatchii* have been recognized in the present treatment.

### 3. *Garrya fremontii* Torrey

*Garrya fremontii* Torr., Pac. R. Rep. 4:136. 1857. HOLOTYPE: upper Sacramento above the canyon, California, 1846, *Fremont* 369 (NY). ISOTYPES: GH, CAS.

*Garrya fremontii* var. *laxa* Eastw., Bot. Gaz. 36:461. 1903. HOLOTYPE: Twin Lakes, Canyon Cr., Trinity Co., California, 1901, *Eastwood* 555 (CAS).

*Garrya rigida* Eastw., Bot. Gaz. 36:461. 1903. HOLOTYPE: Mt. Tamalpais, Marin County, California, 1856, *Eastwood* 562 (CAS). ISOTYPE: CAS.

Low shrubs or bush-like trees, 3–18 feet high. Crown sprouts well-developed. Young stems glabrate or with whitish-gray, silky, appressed pubescence, becoming glabrate with age, green, gray, or reddish-brown. Branching decussate. Stipules absent. Leaves simple, petiolate, decussate, oblong to ovate, elliptical, coriaceous, and persistent. Petioles (0.5–)0.8–1.3(–1.6) cm. in length; opposite petioles connate at the base and adnate to the stem. Leaf blades (2.3–)4.0–8.0(–9.8) cm. long and (1.4–)2.0–3.5(–4.9) cm. wide; apices mucronate, acuminate or acute; bases attenuate to cuneate; margins entire, plane; upper surfaces bright green, glabrate; lower surfaces glabrate or when young with long, upwardly appressed trichomes; light green-yellow; papillae well-developed; midrib and reticulate venation prominent on lower surfaces. Staminate inflorescences catkin-like, unbranched, fasciculate, pendulous at tips of branchlets, sometimes axillary and solitary, lax, 5–15 cm. long, internodes prominent. Staminate floral bracts ovate, acuminate or carinate, mid-veins prominent with recurved apical extensions, covered with silky trichomes, sometimes glabrate or ciliate; opposite bracts



connate for half their lengths. Flowers ternate, borne in the bract axils. Pedicels short, not exceeding the bracts. Perianth segments four, linear, lanceolate, apices connate, silky on abaxial surface. Stamens free, short, alternating with the perianth segments. Anthers oval-oblong, 2-3 mm. long, basifixed, introrse, opening by longitudinal slits. Filaments minute, 1-2 mm. long. Pollen tricolporate, reticulate, yellow-green. Pistillate inflorescences catkin-like, unbranched, fasciculate at ends of branchlets, sometimes axillary and solitary, pendulous or suberect, rigid, 3-10 cm. long with visible internodes when young. Pistillate floral bracts ovate, acuminate, carinate, prominent mid-veins form recurved apical extension, coriaceous, rigid, or foliaceous; opposite bracts connate for half their lengths. Flowers ternate in bract axils. Pedicels minute. Ovaries bicarpellate, rarely tricarpetate, unilocular, ovoid, subsessile, inferior, sometimes with paired perianth remnants alternating with and near the base of the styles, glabrate or when young sparsely pubescent. Styles two, rarely three, persistent, terete, subulate, longer than the ovary when young, divergent and undulate. Fruit a berry, subglobose, 6-7 mm. in diameter, glabrous, smooth, green or red, dark blue and brittle at maturity. Dehiscence irregular. Seeds two or rarely three, globose to oval, subterminal, parietal placentas, dark blue or black.

Flowering from late January to April at elevations ranging from approximately 3000-8000 feet from southern Washington to central California (Map 4).

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REPRESENTATIVE SPECIMENS. **California.** **Alpine Co.:** Silver Mt., Markleeville, *Embree* 207 (UC); mt. slope above Douglas Station, *Hoover* 4162 (NY,UC); S fork of Carson River, 10 mi. S of Markleeville, *McKinn* 5071 (UC). **Butte Co.:** Jonesville, *Copeland* 667 (GH,POM,ORE,WTC); slope above Sable Power House, Chico, *Sowder* 121 (UC). **Calaveras Co.:** 1-1/2 mi. SSW of Onion Valley, *Sowder* 129 (UC). **Del Norte Co.:** along I199 near the Smith River, ca. 15-20 mi. NE of Gasquet, *Dahling* 1310 (GH); about 21-1/2 mi. SW of Cave Junction, *Dahling* 1270 (GH); Preston Peak, *St. John* 289 (UC). **El Dorado Co.:** Pyramid Peak, 1 mi. W of Gregory in Plum Canyon, *Gifford* 272 (UC). **Humboldt Co.:** 2-1/2 mi. SW of Siskiyou Line, Somesbar to Orleans, *Balls* 23952 (RSA,UC); Willow Creek, mostly in the Indian Reservation, *Moseley* 34 (RSA); Trinity Summit Ridge, W of Mud Springs, *Tracy* 18214 (UC,US); Trinity River Valley at Willow Creek, *Tracy* 16184b (WTC), 9773 (CAS,WTC); along Klamath River, 1 mi. above mouth of Slate Creek, *Wolf* 1762 (POM). **Marin Co.:** just below the summit of Mt. Tamalpais, *Dahling* 399 (GH); northside trail, Mt. Tamalpais, *Howell* 17864 (GH). **Mariposa Co.:** Yosemite, *Abrams* 4547 (GH); Yosemite National Park, 3 mi. below the beginning of Snow Creek Trail, *Dahling* 679 (GH); between Vernal and Nevada Falls, Yosemite, *Rodin* 876 (UC). **Mendocino Co.:** Bell Springs, *Abrams* 5956 (GH,NY); Bucks Creek Ranger Station, E of Goose Lake, *Balls* 14652 (CAS,RSA,WTC); Ukiah, *Eastwood* 3351 (GH,UC); Inspiration Point, Eden Valley, *Lewis* 131 (UC); Mendocino, *Spencer* 647 (GH). **Napa Co.:** Napa River Basin, *Jepson* 2/23/96 (GH). **Nevada Co.:** 4 mi. E of Freeman's Bridge, Smartsville, *Burke* 11 (UC); 4-1/2 mi. W of Nevada City, Smartsville, *Sowder* 71 (UC); American Ranch Hill, 6 mi. SW of Grass Valley on McCourtney Rd., *True* 303 (CAS). **Placer Co.:** Emigrant Gap, *Brewer* 1305 (UC); Emigrant Gap, *Jones* 3301 (GH,ORE,POM,UC). **Plumas Co.:** S of Jackson Creek, Public Camp E of Quincy, on Hwy. 24, *Balls* 15695 (ORE); 5 mi. SW of Blairsden, *Canby* 152 (POM); Greenville, *Clemens* 10/20/19 (GH); 2 mi. NW of Mt. Jackson, Downieville, *Roseberry* 2 (UC). **Shasta Co.:** near the Pit River Ferry, *Brown* 277 (NY); 6 mi. NE of Platina, *Cuff* 107 (UC); Kennet, *Eastwood* 1485 (GH); Trail Gulch, Weaverville, *Lewis* 28 (UC). **Sierra Co.:** N fork of Yuba River between Downieville and Sierra City, *Bacigalupi* 1614 (POM); Downieville, *Eastwood* 6759 (GH,UC). **Siskiyou Co.:** 6 mi. NW of Callahan, *Alexander* 138 (UC); hills near Yreka, *Butler* 1125 (POM,US); ridges and meadows near Marble Mt., *Chandler* 1635 (UC); near confluence with the Klamath River, Elk Creek, *Detling* 6092 (ORE); Cantara, *Eastwood* 1945 (GH,UC); Yreka, *Smith* 310 (GH); Cottonwood Creek, Siskiyou Mts., *Wheeler* 2764 (GH); 4 mi. above junction of McCloud Rd. with the Pacific Highway, *Wolf* 2392 (UC). **Sonoma Co.:** Hood Mt., *Baker* 3 (UC); Kenwood region, Hope Valley,

Chamberlain Place, *Baker* 11263 (UC). **Tehama Co.:** Summerville Place, Deer Creek Canyon, *Eggleston* 7340 (NY); 5 mi. E of Paynes Creek on Plum Creek Rd., *Manning* 2 (UC). **Tuolumne Co.:** Sonoma Pass, *Bell* 1189 (UC,US); near Long Barn and old ski recreation area, disturbed site, *Dahling* 1100 (GH); between Long Barn and Spring Gap, about 4 mi. before the Spring Gap exit on Rd. 108, about 8 mi. SW of Summit Ranger Station, *Dahling* 11600 (GH); Dardanelles, 1 mi. E of Baker Station, *Peterson* 16643 (UC). **Trinity Co.:** Chloride Mine Trail, Dedrick, *Alexander & Kellogg* 5563 (UC,WTC); between Coffee and Eagle Creeks, *Eastwood & Howell* 4957 (GH,NY,UC); Trinity River near Don Juan Point, *Tracy* 7260 (UC,WTC); N Coast Range, S forks Mt., Cold Spring Lookout, *Wolf* 9192 (CAS,NY,WTC). **Unknown Co.:** Fremont's expedition to California, *Thurber* 369 (GH). **Nevada. Washoe Co.:** 3-1/2 mi. W of Mt. Rose, Washoe, *Lee* 786 (UC). **Oregon. Curry Co.:** between Rocky Peak and Bald Mt., 12 mi. S of Port Oxford, *Peak* 8948 (GH,NY). **Douglas Co.:** summit of Coast Mts., Roseburg Quadrangle, *Cusick* 4383 (ORE); Stage Rd. Pass near Josephine Co. line, *Detling* 6178 (GH,ORE); Glendale, Cow Creek Mts., *Henderson* 87 (ORE); Canyonville, *Howell* 177 (US), 4/81 (NY,ORE). **Hood River Co.:** Cascade Mts., S of the Columbia River, *Engelmann & Sargent* 8/4/80 (GH); bluffs, Hood River, *Henderson* 348 (ORE). **Jackson Co.:** Siskiyou summit, *Abrams* 11517 (GH); Carberry Creek, lower end of Collings Mt. Trail, *Detling* 7928 (ORE); Little Applegate River, *Detling* 3988 (ORE); Rogue River, 5 mi. below Whiskey Creek, *Leach* 1595 (ORE); Table Rock near Medford, *Thompson* 10330 (WTC). **Josephine Co.:** near Caves, *Applegate* 10437 (UC); Applegate Divide Trail, *Detling* 8097 (ORE); along Savage Creek, 8 mi. from Grants Pass, *Henderson* 5718 (ORE); Mt. Grayback, Siskiyou Mts., *Thompson* 12473 (WTC). **Klamath Co.:** Tom's Creek, *Applegate* 2107 (US); Red Blanket Canyon, Crater Lake National Park, *Baker* 6983 (NY). **Lane Co.:** part way up Bohemia Mt., *Andereus* 6/27/35 (ORE); Gold Hill, *Detling* 3674 (ORE); Black Canyon, *Henderson & King* 15958 (ORE). **Linn Co.:** NW of Jump-off Joe, *Steward* 6010 (GH,US,WTC). **Multnomah Co.:** growing in Government Locks Garden, seed collected at Bonneville, S of the Columbia River, 1.5 mi. up the trail, *English* 1931 (WTC). **Washington. Klickitat Co.:** several km. NW of Bingen, *Suksdorf* 6462 (GH); near mouth of Larm River (Big White Salmon), *Suksdorf* 6426 (GH,NY,UC,WTC); between Gilmer and Laurel, *Suksdorf* 7434 (GH,UC,WTC). **Skamania Co.:** base of Wind Mt. along Columbia River, *Thompson* 11544 (GH,WTC); Bunker Hill, Columbia National Forest, *Weber* 2673 (NY,WTC); Carson, Hemlock Ranger Station, *Weber* 747027 (UC).

*Garrya fremontii* is mostly distinct from other *Garrya* taxa and usually shows a relatively narrow range of variation. However, in some areas, especially Lake, Monterey, and Sonoma Counties in California, it tends to intergrade with the closely related *G. flavescens* ssp. *pallida*. The suggested affinity between the two species is supported by both morphological and phytochemical data. For example, trichomes of both *G. fremontii* and *G. flavescens* ssp. *pallida*, in addition to the common counterclockwise orientation of ridges and grooves, show extensive structural twisting (Plates 2A and 3E). This results in a compound counterclockwise trichome orientation which is unusual in *Garrya*. Both species are also similar in regard to the number and position of trichome protuberances. Another point in common is that the stomatal apparatus in *G. fremontii* and *G. flavescens* ssp. *pallida* both show strongly undulate contours. Moreover, phytochemical data demonstrate a general similarity in their flavonoid content, as shown by paired affinity indexes (Fig. 4).

Hybridization and introgression probably best account for the populations which are intermediate between *Garrya fremontii* and

*G. flavescens* ssp. *pallida*. These intermediate populations have bright and glabrous leaves and fruits which are less pubescent than is typical for *G. flavescens*. Since morphologically they approach and are sometimes difficult to distinguish from *G. fremontii* it seems likely that they are of hybrid origin.

Although Eastwood (1903) described *Garrya rigida* as a species closely related to *G. fremontii*, several later authors (Bacigalupi, 1924; Wangerin, 1910), on the basis of morphology, have considered the two as synonymous. The latter view is also supported by a phytochemical analysis of flavonoids and is followed here. Populations of *G. fremontii* from northern California were compared chemically with *G. rigida* from the type location on Mt. Tamalpais. The results show that both taxa are similar in terms of their flavonoids. Therefore, the placing of *G. rigida* as a synonym of *G. fremontii* is well supported by both morphological and chemical lines of evidence.

*Garrya fremontii* var. *laxa* was described in the same publication (Eastwood, 1903) and was characterized as having lax or loose inflorescences. Because the variation in the internode length of flowering and fruiting aments is both variable and nearly continuous throughout *G. fremontii*, an infraspecific taxon is unjustified.

#### 4. *Garrya corvorum* Standley & Steyermark

*Garrya corvorum* Standl. & Steyerm., Publ. Field Museum Bot. 23:16. 1943. HOLOTYPE: Guatemala, Dept. Huehuetenango, dense rocky (limestone) *Juniperus* forest, along the road in the region of Chermal, Sierra de los Cuchumatanes, at km. 36, 1940. Standley 81651 (F). ISOTYPE: GH.

Shrubs to trees, 6-40 feet high. Crown sprouts present. Young stems with whitish-gray, hispid, or appressed trichomes, becoming less pubescent with age and dark red-brown; stems rough. Branching decussate. Stipules absent. Leaves simple, petiolate, decussate, oblong to oblong-elliptical, stiffly coriaceous, persistent. Petioles short, (0.2-)0.3-0.4(-0.5) cm. in length; opposite petioles connate at the base and adnate to the stem. Leaf blades (2.5-)2.9-3.7(-4.1) cm. long and (0.9-)1.0-1.3(-1.5) cm. wide; apices obtuse, acute, and apiculate; bases tapering, rounded; margins entire, plane; upper surfaces glabrate, lustrous, glossy, dark green or tinged with yellow; lower surfaces with dense sericeous upwardly appressed trichomes, green or white; papillae well-developed; midrib and major leaf veins impressed and conspicuous above, obscured below except for midrib. Staminate inflorescences catkin-like, unbranched, solitary, pendulous at ends of branchlets, lax, 3-5 cm. long, peduncles densely pubescent, internodes prominent. Pistillate floral bracts broadly ovate, cuspidate to acute, 4-9 mm. long, silky pubescent, gray-white; opposite bracts connate for over half their lengths. Flowers ternate within bract axils. Pedicels short, not exceeding the bracts. Perianth segments four, oblong, minute, connate at apices, with ascending silky pubescence, gray-white. Stamens free, short, alternating with the perianth segments. Anthers oval-oblong, ca. 2 mm. long, basifixed, introrse, opening by longitudinal slits. Filaments minute. Pollen tricolporate, reticulate, yellow-green or tan. Pistillate inflorescences catkin-like, unbranched, solitary, pendulous at ends of branchlets, densely flowered, 2.5-5.0 cm. long, compact, internodes obscured. Pistillate floral bracts ovate, 3-8 mm. long, with subappressed, ascending whitish-gray silky trichomes; opposite

bracts connate for over half their lengths. Flowers ternate in the bract axils. Pedicels minute. Ovaries bicarpellate, rarely tricarpetate, unilocular, subglobose, subsessile, with gray or white ascending subappressed pubescence. Styles two, rarely three, persistent, terete, subulate, as long as ovary when young, semierect. Fruit a berry, subglobose, 6–7 mm. in diameter, pubescent, becoming glabrate and brittle at maturity. Dehiscence irregular. Seeds two or rarely three, oval, subterminal parietal placentas, dark blue-black.

Flowering in December and January at elevations of 9000–11700 feet in the Sierra Cuchumatanes of Guatemala (Map 10).

REPRESENTATIVE SPECIMENS. *Guatemala*. *Huehuetenango*: between Tojiah and Chermal at Km. 318 on Ruta Nacional 9N, Sierra de los Cuchumatanes, *Beaman 3827* (GH, MSC, TEX, UC); Cuchumatanes, *Hunnewell 17196* (GH); between Paquix and Llanos San Miguel on rd. to San Juan Ixcay, Sierra Cuchumatanes, *Molina 21226* (F, NY); Cuchumatanes, *Molina, Berber & Wallenta 16488* (F, GH); Sierra Cuchumatanes, *Steyermark 50134* (F); rd. to San Juan Ixcay, Sierra Cuchumatanes, *Molina, Berber & Wallenta 16551* (NY); near Chermal, *Williams 22226* (F, NY); 3–15 km. N of Chermal, *Williams 22200* (F, NY).

Geographically and anatomically, *Garrya corvorum*, an isolated central Guatemalan endemic, is anomalous within subgenus *Garrya* and occurs over two thousand miles from its distributional center. *Garrya corvorum* is geographically well-isolated and does not intergrade or hybridize with other *Garrya* species. It is commonly found in limestone soils and is arboreal, frequently reaching heights of up to 40 feet. While sharing the basic floral and inflorescence features of subgenus *Garrya*, *G. corvorum* is distinct in many other characteristics including leaf size, stomatal apparatus, pubescence, trichome fine structure, and phytochemistry. Moreover, with regard to the latter three features, *G. corvorum* strongly resembles members of subgenus *Fadyenia*. This resemblance is definite and well-documented by both chemical and morphological data. For example, the stomatal apparatus of *G. corvorum* is small and lacks the customary wavy and undulate subsidiary cells of subgenus *Garrya*. Also, the trichomes lack the protuberances which are found within subgenus *Garrya* and appear similar to those of the southern *Garryas* of subgenus *Fadyenia*.

With *Garrya corvorum* as an exception, *Garrya* species form two chemical subgroups corresponding quite well to the morphologically based subgenera. *Garrya corvorum* shows an abundance of flavonoids common to both subgenera but lacks a strong chemical affinity with either as is reflected by the low and high values for the paired and group chemical affinity indices respectively (Fig. 4 and Table 11). This is unique since the other *Garrya* taxa are chemically well-defined and can be easily placed in one subgroup or the other. Therefore, *Garrya corvorum* appears both chemically and morphologically intermediate between subgenera *Garrya* and *Fadyenia*. This may indicate convergence or a relict from an early evolutionary stage of divergence

from ancestral *Garrya* representatives. The latter is the most probable because of the isolated geographical distribution, mixture of characteristics, and the general affinity of *G. corvorum* for members of both subgenera.

### 5. *Garrya buxifolia* Gray

*Garrya buxifolia* Gray, Proc. Amer. Acad. 7:349. 1868. HOLOTYPE: Geological Survey of California, 1867, *Bolander* 6579 (CH). ISOTYPES: CAS, UC.

*Garrya flavescens* var. *buxifolia* Jepson, Man. Fl. Pl. Calif. 732. 1925.

Low bushy shrubs, 1-8 feet tall. Crown sprouts developed. Young stems with long, appressed pubescence, becoming glabrate, yellow-green to reddish-brown with age. Decussate branching. Stipules absent. Leaves simple, shortly petiolate, decussate, oblong or broadly elliptical, stiff, coriaceous, persistent. Petioles short, (0.3-)0.5-0.7(-0.9) cm. long; opposite petioles connate at the base and adnate to the stem. Leaf blades (2.0-)3.0-5.0(-5.7) cm. long and (1.0-)1.5-2.5(-3.0) cm. wide; apices mucronate, acute or acuminate; bases obtuse to cuneate, or truncate; margins entire, plane, stiff; upper surface glabrous or with sparse pilose pubescence near the petiole, light green, lustrous, glossy; lower surface with upwardly appressed, silky, whitish-gray trichomes; papillae well-developed; midrib and reticulate venation visible above, hidden below except for midrib. Staminate inflorescences catkin-like, unbranched, fasciculate in groups of three to six, pendulous at tips of branchlets, densely flowered, 4-8 cm. long, internodes inconspicuous. Staminate floral bracts 3.5-8.0 mm. long, apex strongly acuminate, sparingly covered with soft, shaggy trichomes, margins ciliate; opposite bracts strongly connate. Flowers ternate in the bract axils. Pedicels short, not exceeding bracts. Perianth segments four, oblong-lanceolate, 2-4 mm. long, mid-vein prominent, apices connate, abaxial side with dense curly white trichomes, the adaxial side glabrous. Stamens free, short, and alternating with the perianth segments. Anthers oval to oblong, 1-2 mm. long, basifixed, introrse, opening by longitudinal slits. Filaments ca. 1 mm. long. Pollen tricolporate, reticulate, yellow-green to yellow-brown. Pistillate inflorescences catkin-like, unbranched, fasciculate at ends of branchlets, pendulous or semierect, lax, 4-10 cm. long, internodes prominent when young but becoming compact with age. Pistillate floral bracts 3-5 mm. long, truncate, apices acute, covered with soft appressed trichomes; opposite bracts connate. Flowers ternate in the bract axils. Pedicels minute. Ovaries bicarpellate, rarely tricarpellate, unilocular, subglobose, inferior, glabrous, sometimes with perianth remnants alternating with and near the base of the styles. Styles two, rarely three, persistent, terete, subulate, divergent or nearly erect. Fruit a berry, subglobose, 5-6 mm. in diameter, glabrous, compact on infructescences, green-red becoming dark blue and brittle at maturity. Dehiscence irregular. Seeds two or rarely three, globose to oval, subterminal, parietal placentas, dark blue to black.

Flowering from February to April at elevations ranging from 200-7000 feet in northern California and southern Oregon (Map 2).

REPRESENTATIVE SPECIMENS. **California.** Del Norte Co.: Crescent City to Grants Pass Rd., *Abrams* 8588 (DS,POM); Gasquet to Patricks, *Bacigalupi* 8530 (DS,POM); City Dump No. 3, Gasquet, *Dahling* 1290 (CH); along Special Land Use Area Rd., Gasquet, *Dahling* 1292 (CH); near Telephone Point, *Eastwood* 139 (CAS,GH,UC,WTC); Boundary Hill, *Eastwood* 2190 (CAS,GH); Gordon Mt., *Kildale* 9901 (DS,MS,POM); Smith River along trail from Knapp Lodge toward Rattlesnake Mt., *McMinn* 5263 (UC); Monumental, *Parks & Parks* 24044 (DS,GH,MS,POM); Smith River at 18 mi. Creek, Old Gasquet Toll

Rd., *Parks & Parks* 5650 (DS,GH,MSC,NY,ORE,UC,WTC); 18 mi. Creek, *Parks & Parks* 5266 (GH,WTC); Del Norte, *Tracy* 10888 (GH); State Line N of Monumental at head of Shelley Creek, *Tracy* 16784 (UC). **Humboldt Co.:** Brennan Mt., near Willow Creek, *Abrams* 109 (DS); Grouse Mt., *Kildale* 15361 (RSA); Humboldt, *Tracy* 17841 (UC); 9 mi. from Willow Creek, 2 mi. from summit, *Wolf* 1169 (DS). **Siskiyou Co.:** Siskiyou National Forest, *Baker* 304 (GH); Siskiyou Peak, *Kildale* 8836 (DS). **Mendocino Co.:** Red Mts., *Eastwood* 8/4/03 (NY), 5/21-28/02 (GH,ORE), *Gankin* 2698 (CAS), *McMurphy* 594 (DS); summit of Red Mt. on barren rocky point, *Tracy* 10324 (UC). **Oregon. Curry Co.:** Iron Mt., S slope, *Baker* 3541 (CAS,UC,WTC); near Horse Sign Butte, *Leach* 3179, 3343 (ORE); near Craggy Trail, *Leach* 3491 (ORE). **Lane Co.:** above Waldo, *Henderson* 5716 (ORE); Eugene, *Cusick* 7/02 (ORE); Waldo, *Howell* 1506 (UC,WTC); hills near Waldo, *Howell* 4/93 (ORE). **Josephine Co.:** lower portion of grade on Oregon Mt. Rd. about 1-1/2 mi. above and S of Whiskey Creek Crossing which is at the foot of the grade, *Bacigalupi* 6912 (UC); rd. to Chetco Pass, about 10 mi. (airline) W of Selma, *Steward, Dennis & Haines* 7428 (CAS,DS,GH,RSA,WTC); Oregon Mt., *Sweaton* 5/27/23 (ORE); along old rd. 10 mi. SW of Waldo, *Thompson* 2243 (WTC); Siskiyou Mts. near O'Brien, *Thompson* 10268 (DS,GH,NY,POM,WTC); Rough and Ready Creek, *Tracy* 229a (UC).

*Garrya buxifolia* is distinct and confined to a small area in extreme northern California and adjacent Oregon. Morphological variation in the taxon is not extensive although individuals with less than the characteristic dense pubescence can occasionally be found.

An examination of several lines of evidence reveals that a lowering of taxonomic rank, as had been advocated by Jepson (1925) when he combined *Garrya buxifolia* with *G. flavescens* as a variety, is not supported. For example, while leaf undersides in *G. buxifolia* are densely pubescent with upwardly appressed trichomes as in *G. flavescens*, the ovaries and mature fruits are quite different. In *G. buxifolia* the ovaries are small, glabrous, and dark blue while in *G. flavescens* they are densely pubescent, appearing whitish-gray at maturity. Moreover, analysis with the SEM has shown that their respective trichome structures are also quite different. Trichomes of *G. flavescens* have a compound counterclockwise orientation while those of *G. buxifolia* sometimes do not. In addition, differences between *G. buxifolia* and *G. flavescens* in leaf size and general habit are pronounced.

The flavonoid constituents of *Garrya buxifolia* and *G. flavescens* are substantially different. *Garrya buxifolia* shows only a low chemical affinity for this as well as other species of *Garrya* (Fig. 4). The high degree of chemical distinctness of *G. buxifolia* is maintained despite the opportunities for interspecific hybridization from the overlapping ranges of *G. elliptica*, *G. fremontii*, and rarely *G. flavescens*. Apparently strong breeding barriers developed within *G. buxifolia* during early evolutionary divergence allowing for an independent and unique development of flavonoid constituents. Since *G. buxifolia* appears both morphologically and chemically different, the close relationship with *G. flavescens* advocated by Jepson must be rejected.

6. *Garrya flavescens* Watson

Low shrubs or small trees, 5-15 feet high. Crown sprouts developed. Young stems with whitish-gray, silky, appressed pubescence, becoming glabrate with age; cinereous, yellow-green to dark reddish-brown. Branching decussate. Stipules absent. Leaves simple, petiolate, decussate, oblong, elliptical or oval, stiff, coriaceous, persistent. Petioles (0.3-)4.0-1.0(-1.7) cm. in length; opposite petioles connate to the base and adnate to the stem. Leaf blades (3.0-)4.0-5.6(-7.8) cm. long and (1.3-)2.0-4.0(-4.4) cm. wide; apices acute, obtuse, mucronate, tip slightly reflexed; bases attenuate; margins entire, plane; upper surfaces with sparse appressed whitish pubescence, usually yellow-gray, cinereous, or sometimes dull green; lower surface glabrate or with silky or wavy upwardly appressed trichomes, yellow-green, gray, or glaucous with age; papillae developed; midrib and major veins visible above, obscured below except for midrib in high relief. Staminate inflorescences catkin-like, unbranched, fasciculate, pendulous on branchlets, densely flowered, 3-6 cm. long, internodes not prominent. Staminate floral bracts ovate, acute or acuminate, often with recurved apical projections, 3-8 mm. long, gray or reddish-green, with silky or shaggy pubescence; opposite bracts connate for half their length. Flowers ternate in the bract axils. Pedicels shorter than the bracts. Perianth segments four, oblong-lanceolate, connate at apices; abaxial surface pilose, surfaces glabrate, frequently reddish with green or yellow. Stamens free, short, and alternating with the perianth segments. Anthers oval to oblong, about 3 mm. long, basifixed, introrse, opening by longitudinal slits. Filaments minute. Pollen tricolporate, reticulate, yellow-brown or tan. Pistillate inflorescences catkin-like, unbranched, fasciculate, pendulous on branchlets, densely flowered, 2-7 cm. long, extremely compact, imbricate. Pistillate floral bracts 3-8 mm. long, ovate to lanceolate, concave, truncate, acuminate or acute, typically covered with appressed or shaggy pubescence; opposite bracts connate for about half their lengths. Flowers ternate in bract axils. Pedicels minute. Ovaries bicarpellate, rarely tricarpellate, unilocular, subglobose, subsessile, inferior, sometimes with paired perianth remnants alternating with and near the base of the styles, with dense silky appressed pubescence. Styles two, rarely three, persistent, terete, subulate, as long as ovary when young, divergent or nearly erect. Fruit a berry, oval, about 6.3-7.6 mm. long and 4.8-6.5 mm. wide, densely pubescent, gray to whitish-brown, dry at maturity. Dehiscence irregular. Seeds two or rarely three, globose to oval, subterminal on parietal placentas, dark blue or black.

## KEY TO THE SUBSPECIES

- A. Lower leaf surfaces glabrate or sparsely to moderately covered with coarse, wavy, more or less appressed and ascending trichomes. Shrubs and small trees. . . . . 6b. *G. flavescens* ssp. *pallida*.  
 A. Lower leaf surfaces densely covered with fine, straight, long, upwardly appressed or dense, gently wavy, slightly intertwining and weakly ascending trichomes. . . . . B.  
 B. Lower leaf surfaces densely covered with fine, straight, long, appressed, and strongly ascending trichomes. Shrubs to small trees. . . . . 6a. *G. flavescens* ssp. *flavescens*.  
 B. Lower leaf surface densely covered with gently wavy, slightly intertwining and appressed, more or less ascending trichomes. Shrubs. . . . . 6c. *G. flavescens* ssp. *congdonii*.

6a. *Garrya flavescens* Watson ssp. *flavescens*

- Garrya flavescens* Wats., Am. Nat. 7:301. 1873. HOLOTYPE: Kanab, South Utah, Watson (GH).  
*Garrya veatchii* var. *flavescens* Coult. & Evans, Bot. Gaz. 15:96. 1890.  
*Garrya mollis* Greene, Leaflet. Bot. Obs. and Crit. 2:86. 1910. HOLOTYPE: Oak Creek, Arizona, 1901, Pearson 399 (US).

Shrubs to small trees, 5–12 feet high. Adaxial leaf surfaces sparsely covered with appressed more or less straight trichomes; yellow-gray, gray-green, or yellow-green. Abaxial leaf surfaces with dense, fine, silky, long, more or less straight upwardly appressed trichomes; light gray-green or silvery. Fruit with dense silky appressed trichomes, becoming less dense with age, gray or tan-brown.

Flowering from the middle of March to early May at altitudes of 2600–9000 feet in western Arizona and southern California (Map 4).

REPRESENTATIVE SPECIMENS. **Arizona.** **Coconino Co.:** Bright Angel Trail, 1 mi. above Indian Garden, *Bailey 1058* (UC); Mt. Trumbull, 6 mi. S of Nixon Spring, *Cottam 8703* (ARIZ); Virgin Mts., NW Arizona, *Crew 36* (ARIZ); Williams, Sand Gap, *Demaree 42562* (ARIZ); Kaibab trail to Roaring Spring, Grand Canyon, *Eastwood 1038* (GH,POM); Apache Trail, on way to Mercury Mine, *Eastwood 17259* (CAS); Timp Point along rim of Kaibab Plateau, *Goodding 503–48* (ARIZ); Reconnaissance Range, Long's Canyon, *Hill 402* (ARIZ). **Gila Co.:** Matatzal Mts., *Collom 279* (GH); Sierra Ancha, *Eastwood 17284* (CAS); Three Bar Game Management Unit, Tonto National Forest, *Pase 885* (ARIZ). **Maricopa Co.:** 4 mi. N of Sunflower, *Lehto 3782* (RSA). **Mohave Co.:** Conner Canyon, 1 mi. NW of Parker Creek, *Armer 24* (UC); Secret Pass W of Kingman, *Braem 3/13/27* (DS,GH); Mt. Delenbaugh, *Cottam 4147* (UT); summit of Mt. Trumbull, E slope above Sullivan's Ranch, *Cottam 13084* (UT); top of Mt. Emma, *Cottam 14047* (UT); N Saddle Horse Spring above Bath Tub, *Cottam 14817* (UT); Chloride, *Jones 4/15/03* (NY,POM); E slope of Providence Mts., Mojave Desert, *Munz 4062* (DS,POM,UC). **Yavapai Co.:** Oak Creek Canyon, *Benham 2718* (ARIZ); Oak Creek Canyon, near Sedona, *Dahling 870* (GH); Tonto Creek, near Pine, *McDougal 720* (NY); rd. to Sunflower Mine in Mazatzal Range, *McKelvey 843* (GH), *1135* (GH); between Payson and Pine, *Whitehead 2078* (ARIZ). **Yuma Co.:** Palm Canyon, Kofa Mts., *Mason 2493* (ARIZ), *Niles 485* (ARIZ), *Peebles 6781* (ARIZ); canyon, Harquahala Mts., *Wright 65–66* (ARIZ). **California.** **Inyo Co.:** Walker Creek, SW of Olancho, *Alexander 2949* (DS); Sage Flat to Olancho Pass, *Howell 26661* (CAS,NY); E side of Olancho Pass, S Sierra Nevada, *Munz 15413* (WTC). **Kern Co.:** Red Hill, Prieta Mts., near Badfish, *Abrams 5366* (DS); Oak Canyon region of Tehachapi Peak, *Dudley 400* (DS); ridge SW of Cottonwood Creek, *Twisselmann 8860* (RSA); County Park Hdqtrs. near Apache Saddle, *Twisselmann 12571* (CAS,RSA). **Los Angeles Co.:** Rock Creek Desert slopes of the San Gabriel Mts., *Abrams 568* (DS); Angeles Crest Hwy., near Charlton Flats, San Gabriel Mts., *Beeks 193* (RSA); Mt. Baldy Camp, San Antonio Canyon, *MacFadden 14741* (CAS); Strawberry Ridge, San Gabriel Mts., *Richter 108117* (DS). **Riverside Co.:** trail to Tahquitz Peak, San Jacinto Mts., *Hoffmann 168161* (CAS); ridge E of Toro Peak, Santa Rosa Mts., *Munz 15372* (POM,WTC); along side of Santa Rosa Mt., *Rowntree 296413* (CAS); San Jacinto Mt., *Spencer 318* (GH); above reservoir at Idria, *Thomas 6061* (DS). **San Bernardino Co.:** E end of Granite Mts., 25 mi. NE of Amboy, *Jaeger 172786* (POM); New York Mts., *Kellogg 1449* (GH); E slope of Kings Range, *Kellogg 2381* (UC); New York Mts., Keystone Canyon at Mines, *Wolf 9728* (UC,WTC). **San Diego Co.:** San Diego, *Julian 106058* (UC); Deer Flat NE slope, Palomar, *Gander 4581* (SD); above Laguna Camp, Laguna Mts., *Munz 8347* (POM); 1 mi. S of Inspiration Point, *Thorne 33270* (RSA); Vallecitos Creek Trail, *Wiggins 2834* (SD). **Santa Barbara Co.:** San Emigdio Canyon, *Davy 2126* (UC); San Rafael, *Hardham 4157* (CAS); Figueroa Mt. region, *Moseley 187* (RSA); Alamar Canyon, *Peterson 319* (RSA); Montecito, *Tucker 325* (UC). **Tulare Co.:** Salt Creek, *Eastwood 172612* (UC). **Ventura Co.:** El Vallecito de los Piños, *Moseley 103* (RSA), *106* (GH); Ortega Hill Trail, between Cherry Canyon summit and Piñon Ridge, *Pollard 2/2/46* (CAS,GH); N side of Mutau Flat and Mt. Piños, *Sowder 498* (RSA,UC). **Nevada.** **Clark Co.:** U.S. Atomic Energy Commission Test Site, *Beatley 10738* (RSA); Charleston Park, *Clokey 5550* (GH,WTC); canyon bed 1/2 mi. up canyon above Wilson's Ranch, *Clokey 3449* (ARIZ,GH,MEXU,UT,WTC); Mary Jane Falls Recreation Area, Charleston Mts. Recreation Area, *Dahling 1318* (GH); Virgin River Canyon, Bunkerville, *Goodding 735* (GH,NY); New York Mts. near California line, *Shields 10/12/35* (UT); E of Manse Ranch, W slope of Charleston Mts., *Train 2058* (ARIZ,GH). **Utah.** **Washington Co.:** Pine Valley,



*Cottam* 6780 (UT); between Leeds and Oak Grove, *Eastwood* 9164 (CH,NY,POM); Zion Canyon, *Hunnewell* 10854 (GH); in canyon N of Leeds, *Maguire & Richards* 5201 (GH,UC); near Toquerville, *McNulty* 12/2/70 (UT); Beaverdam Mts., *Tidestrom* 9336 (GH).

*Garrya flavescens* ssp. *flavescens* is characterized by fine and upwardly appressed trichomes on the leaves. The abaxial surfaces are covered with a whitish-gray pubescence and frequently appear shiny white in sunlight. While *G. flavescens* ssp. *flavescens* intergrades with *G. flavescens* ssp. *pallida* and *G. flavescens* ssp. *congdonii*, they are all sufficiently distinct to allow for their recognition.

A large-leaf form of *Garrya flavescens* found growing in semimesic canyons of Arizona was described as *G. mollis* by Greene in 1910. While the leaves of *G. mollis* are somewhat larger than those of typical *G. flavescens* ssp. *flavescens*, there are similarities between the two in pubescence, floral, and fruit characteristics. In addition, phytochemical investigation of the flavonoid constituents of *G. mollis* and *G. flavescens* showed a marked similarity and there is a general correspondence in flavonoid content. Furthermore, field observations repeatedly showed that environmental factors influence leaf size. Therefore, the larger leaves of *G. mollis* probably reflect the more mesic growth conditions of deep canyons rather than distinguishing genetic differences.

*Garrya flavescens* was combined with *G. veatchii* as a variety by Coulter and Evans (1890) but the many differences between the two taxa make such a combination untenable. In fact, *G. flavescens* and *G. veatchii* are so distinctive in leaf, trichome, floral, and fruit characteristics that they are rarely confused or misidentified.

#### 6b. *Garrya flavescens* ssp. *pallida* (Eastwood) Dahling, comb. nov.

*Garrya pallida* Eastw., Proc. Cal. Acad. III. Bot. 2:287. 1902. HOLOTYPE: Kings River Canyon, South Fork of Kings River, Fresno County, California, 1899, *Eastwood* 559 (CAS).

*Garrya flavescens* var. *pallida* Bacigalupi ex Ewan, Bull. Torrey Bot. Club 64:519. 1937.

Shrubs to small trees, 5-15 feet tall. Adaxial leaf surfaces glabrous or rarely with sparse wavy appressed trichomes; gray-green or yellowish. Abaxial leaf surfaces glabrous or with coarse, wavy appressed more or less ascending trichomes. Leaves dull green, yellow-green and glaucous. Fruits with coarse appressed pubescence, whitish-gray to gray-brown or tan-brown with age.

Flowering from late February to April at elevations ranging from 1500-7755 feet from central California to northern Baja California (Map 4).

REPRESENTATIVE SPECIMENS. ✓ **California.** Alameda Co.: Cedar Mt., *Abrams* 108132 (DS); summit of Cedar Mt. Ridge, *Bacigalupi* 1306 (DS,POM). **Contra Costa Co.:** Meridian

Peak summit, *Bowerman* 779 (UC); Mt. Diable, *Mason* 2711 (UC), *McMinn* 88 (DS), *Rose* 34041 (WTC). **Fresno Co.:** San Joaquin River, Sierra Nevada, *Blether* 216835 (DS); Kings Canyon National Park, *Dahling* 930 (GH); Copper Creek Canyon Trail, *Howell* 34206 (CAS); Boyden Cave, S fork of Kings River, *Munz* 15923 (POM,WTC). **Kern Co.:** Fort Tejon, *Abrams* 283 (DS); San Emigdio Canyon, *Davy* 173653 (UC); Mt. Breckinridge, *Grinnell* 146 (US); SW of Black Mt. Saddle, *Howell* 38528 (CAS); Piute Mts., E of Bald Eagle Peak, *Twisselmann* 5047 (CAS); Toogate Ridge Mts., W end, *Twisselmann* 12270 (CAS). **Lake Co.:** 1-3 mi. up W side of Bartlett Grade, *Abrams* 12392 (DS); between Kouocti and Lower Lake, *Baker* 4316b (UC); along Kelseyville to Lower Lake Hwy., 8.9 mi. S of Kelseyville, *Baker* 11299 (UC); N of Lower Lake along the main highway, *Dahling* 842 (GH); N of Lower Lake along Hwy. 29, *Dahling* 884 (GH); about 7 mi. W of Upper Lake on the road to Ukiah, *Dahling* 977 (GH); about 8 mi. SW of Hwy. 29 on the Lower Lake-Knoxville Rd., *Dahling* 1024 (GH); about 10 mi. E of Hopeland, *Dahling* 1279 (GH); 7 mi. NE of jct. of Hwy. 20 and the road to Bartlett Springs, *Thorne* 31649 (US). **Los Angeles Co.:** 1 mi. N of Warm Springs, Tejon, *Gifford* 459 (UC); Gold Creek, *Lewis* 296 (UC). **Marin Co.:** near summit of Mt. Tamalpais, *Dahling* 1230 (GH). **Mendocino Co.:** Ukiah, *McMurphy* 518835 (DS). **Monterey Co.:** Pine Ridge, Santa Lucia Mts., *Abrams* 7406 (DS); Cone Peak, Santa Lucia Mts., *Dudley* 28117 (DS); between Reliz and Bear Canyons, Santa Lucia Mts., *Howell* 30188 (ARIZ,DS,RSa); 2 mi. N of Escondido forest service camp on trail to Arroyo Seco, Santa Lucia Mts., *Wolf* 10998 (UC). **Napa Co.:** Mt. St. Helena, *Eastwood* 7946 (GH); Pope Valley Grade near Palisades, Napa River Basin, *Jepson* 21610 (UC). **Orange Co.:** Santiago Peak Trail, *Abrams* 1911 (DS); 1.1 mi. E of Silverado, *Balls* 22847 (UC); Bedford Peak, Corona, *Norton* 47 (UC); Harding Canyon, Santa Ana Mts., *Weatherby* 1023 (RSa); between Bedford Peak and Santiago Peak, Santa Ana Mts., *Wolf* 5583 (RSa,WTC). **Riverside Co.:** Hagador Canyon, Corona, *Lewis* 358 (UC); between Trabuco and Santiago Peaks, Santa Ana Mts., *Pequegnat* 261681 (POM). **San Benito Co.:** shoulder to San Carlos Peak above Aurora Mine, *Abrams* 13842 (DS,GH); Hernandez, *Lathrop* 212587 (DS). **San Bernardino Co.:** Cold Creek, San Bernardino Mts., *Abrams* 814 (DS); S slope of Clark Mt., *Alexander* 495 (UC); Fountain Canyon, Providence Mts., *Beal* 668 (WTC); Home Creek, San Bernardino Mts., *Everett* 19356 (RSa); middle fork of Lytle Creek, San Antonio Mts., *Johnston* 1579 (POM,UC); Clark Mt., *Munz* 12890 (GH,POM); Clark Grade, Santa Ana River Valley, San Bernardino Mts., *Wheeler* 2025 (UC); 1.5 m. above Pachalka Spring, Clark Mt., *Wolf* 7016 (ARIZ,RSa,WTC). **San Diego Co.:** Cuyamaca Mts., *Abrams* 3872 (GH,POM,UC); upper SW Indian Canyon, *Bastil* 44111 (SD); Warners Springs, *Eastwood* 43346 (DS); San Isidro, *Epling* 224326 (DS); Monument Peak, Laguna Mts., *Munz* 8443 (POM); San Felipe Valley, *Wolf* 869 (RSa). **San Luis Obispo Co.:** 4-1/2 mi. SSE of Pozo, *Hendrix* 9 (UC); Caliente Mt. along summit ridge, *Hoover* 8332 (UC). **Santa Barbara Co.:** Santa Barbara Canyons, *Eastwood* 713 (UC); saddle between Junipera and Pinyon Peaks, *Howell* 30187a (DS); S of Potrero Seco along the Matiliza-Agua-Caliente divide, *Pollard* 453356 (DS). **Santa Clara Co.:** on road to Livermore from the summit of Mt. Hamilton near the observatory, *Dahling* 1130 (GH); summit of Mt. Hamilton near the observatory, *Dahling* 1151 (GH); Sierra Azule Ridge near Loma Prieta, *Ferris* 2091 (WTC); Santa Clara, *Heller* 7507 (GH); vicinity of Mt. Umunhum, *Thomas* 3967 (DS). **Santa Cruz Co.:** Loma Prieta Peak, Santa Cruz Mts., *Mexia* 634640 (UC). **Solano Co.:** Pine along ridge N of Mt. Vaca, *Crompton* 7421 (UC). **Sonoma Co.:** 3.5 mi. NE of Pine Flat, *Bell* 1145 (UC); 1/2 mi. SW of Veeder Mt., *Spring* 98 (UC). **Tulare Co.:** Mineral King Rd. about 1/2 mi. below Slapiack Creek, *Bacigalupi* 1197 (DS,GH); Fairview and Durwood Camp, Lower Kern River Canyon, 1.5 mi. above the Fairview Ranger Station, *Bacigalupi & Ferris* 2447 (GH,UC,WTC); along Hwy. 190, near Soda Spring, after Wishon, *Dahling* 1238 (GH); trail to Needles, vicinity of Lloyd Mt., *Dudley* 785 (DS); Lamont Meadow, Kern Plateau, *Howell* 42397 (CAS); Sierra Nevada, Upper Tule River, 3 mi. below Camp Nelson, *Wolf* 4589 (GH,UC,WTC). **Ventura Co.:** Topatopa Mts., *Abrams* 104 (DS); Maricopa Rd. above Wheeler Gorge, *Pollard* 2267 (CAS).

*Garrya flavescens* ssp. *pallida* is characterized by wavy, coarse, and more or less upwardly appressed trichomes on the lower leaf

surfaces. As the name implies, the leaf color is pale and often tinged with gray or blue.

In describing *Garrya pallida* in 1902, Eastwood suggested a relationship with *G. fremontii* based on the similarity of their leaves. Most *G. pallida* populations have leaves with the typical coarse wavy trichomes but some populations are nearly glabrous and therefore closely approach *G. fremontii*. Bacigalupi (1924) rejected Eastwood's argument and combined *G. pallida* with *G. flavescens* as a variety on the basis of the ovary pubescence. This is well-justified since both taxa intergrade morphologically and are difficult to distinguish in overlapping areas.

Chemical investigation supports a relationship between *Garrya pallida* and *G. flavescens* since both share similar flavonoid constituents (Figs. 3 and 4). Although they bear some relationship to *G. fremontii*, *G. pallida* and *G. flavescens* appear most closely allied with each other and as such, represent infraspecific taxa. This position is also well-supported by morphological evidence as outlined by Bacigalupi (1924). With regard to the populations of *G. flavescens* ssp. *pallida* which intergrade with *G. fremontii*, it is the author's view that these are probably the result of hybridization and subsequent introgression.

6c. *Garrya flavescens* ssp. *congdonii* (Eastwood) Dahling,  
comb. nov.

*Garrya congdonii* Eastwood, Bot. Gaz. 36:459. 1903. HOLOTYPE: New Coulterville Road, Mariposa Co., California, 1898, *Congdon 556* (CAS). ISOTYPE: GH.  
*Garrya flavescens* var. *venosa* Jepson, Man. Fl. Pl. Calif. 732. 1925.

Shrubs, 5-10 feet high. Adaxial leaf surfaces glabrous or with wavy, crinkled trichomes, lustrous glossy, and yellow-green. Abaxial leaf surfaces with long, gently wavy, slightly appressed and intertwining, ascending trichomes, whitish-gray or dull yellow-brown. Fruits with shaggy gray-white ascending pubescence, with age becoming glabrate toward the base, yellow-brown with purple or dark blue.

Flowering February to May, mostly at elevations of 2000-6000 feet in California from Tehama to San Benito and Mariposa counties (Map 2).

REPRESENTATIVE SPECIMENS. **California.** Colusa Co.: along Hwy. 20, just E of the Lake-Colusa border, *Baker 11645* (CAS); between Leesville and Stonyford, 4 mi. from Stonyford, *Ferris 6456a* (DS); near Hwy. 16, 6 mi. NW of Rumsey, *Slayback 2* (DS). **El Dorado Co.:** bank of Sweetwater Creek, *Robbins 1927* (CAS,GH); Sweetwater Creek, near Salmon Falls, *Wolf 5484* (GH,TEX). **Glen Co.:** hills W of Willows, *Eastwood 11140* (CAS); along dry creek near Stonyford, *Ferris 6464* (DS); W of Stoney Creek, outside Mendocino National Forest, *Porto 4a* (UC). **Lake Co.:** Mt. St. Helena, 4 mi. below the toll house, *Bacigalupi 488* (DS); between Burus Valley and Borax Lake, *Baker 11655* (CAS); 2.5 mi. NE of Middletown, *Gould 1026* (GH,UC); W of Leesville, *Heller 13139* (CAS,GH); Lower Lake to Knoxville Rd., *Howell 14652* (GH); Knoxville grade

to Lower Lake, *Jepson 21598* (UC); 13 mi. N of Calistoga, *Wiggins 5772* (DS,GH); 7 mi. E of Hough's Mineral Springs on rd. to Williams, *Wolf 1054* (DS). **Mariposa Co.:** 6 mi. S of Coulterville toward Bagby, *Belshaw 21128* (DS); Mariposa, *Congdon 57896* (GH); new Coulterville Rd., *Congdon 1/98* (GH). **Mendocino Co.:** S fork of Eel River, *McMinn 383* (GH). **Napa Co.:** Pope Creek, 7 mi. from Monticello, *Baker 9105* (CAS); below Conn Dam, *Raven 2827* (CAS); 5 mi. S of Reiff, *Schreiber 2353* (UC). **San Benito Co.:** S San Benito County area, *Hall 9940* (GH). **Santa Barbara Co.:** Zaca Lake Forest Reserve, *Eastwood 713* (GH); Santa Ynez Mts., *Moseley 78* (GH), *93* (GH). **Stanislaus Co.:** Adobe Creek, Red Mts., Mt. Hamilton Range, *Sharsmith 3532* (DS). **Tehama Co.:** Paskenta Grade, along rd. from Paskenta to Covelo, *Bacigalupi 2411* (DS); S fork of Battle Canyon on Ponderosa Way, near the head of Darling Ravine, *Griffin 1165* (UC); grade between Mud Flat and Bennett Spring, *Heller 13000* (CAS,GH); 10 mi. W of Paskenta below logging rd., *Wagon 2611* (CAS).

*Garrya congdonii* is not a distinct species and should not be given that rank because of the variation and instability in the pubescence and leaf characteristics. The present combination with *G. flavescens* appears justified because they commonly intergrade and appear closely related morphologically. *Garrya flavescens* ssp. *congdonii* is recognizable because of its thick, gently wavy trichomes on the abaxial leaf surfaces. The trichomes are long and have the compound counter-clockwise orientation that typifies the other *G. flavescens* subspecies.

#### SUBGENUS FADYENIA (ENDL.) DAHLING, COMB. NOV.

Based on *Fadyenia* Endl., Gen. Supp. IV. 1847:38.

Inflorescences racemose with branching common or sometimes restricted to the base. Floral bracts connate at the base, usually foliaceous, sometimes as large as the foliage leaves but frequently smaller, typically bearing solitary flowers in the axils. Pistillate inflorescences lax, spreading and not imbricate; internodes prominent during flowering and fruiting. Ovaries sometimes bearing minute variably adnate bracts opposite the styles. Styles typically short, thick, fleshy, often divergent and reflexed, usually not erect. Shrubs and tall trees.

### 234 7. *Garrya glaberrima* Wangerin

*Garrya glaberrima* Wang., Das Pflanzenreich IV, 56a:12. 1910. HOLOTYPE: Mexico, Encarnacion, *Ehrenberg 1097* (B), not seen.

Shrubs to small trees, 4-16 feet tall. Crown sprouts numerous. Young stems glabrous, ridged, quadrangular, green, with age becoming dark reddish-brown. Decussate branching. Stipules absent. Leaves simple, petiolate, decussate, elliptic to oblong, thick, coriaceous, persistent. Petioles (0.8-)0.9-1.1(-1.2) cm. long; opposite petioles connate at the base, adnate to the stem. Leaf blades (5.2-)6.0-7.5(-8.6) cm. long, (2.2-)2.5-3.5(-4.0) cm. wide; apices mucronate, bases attenuate or subcunrate; margins plane; upper surface glabrous, bright green; lower surface glabrous, dull green; papillae developed. Reticulate venation prominent above, only the midrib and primary lateral veins prominent below. Staminate inflorescences racemose, branched, pendulous, fasciculate on branches, 2-5 cm. long, compact, densely flowered, internodes inconspicuous. Staminate floral bracts ovate to elliptical, acuminate, shorter than the flowers, green, rarely ciliate; opposite bracts connate at the base. Flowers solitary in the bract axils. Pedicels short. Perianth segments four, elliptical, connate at apices, glabrous. Stamens free, short, alternating with the perianth segments. Anthers oval to oblong, ca. 2 mm. long, basifixed, introrse, opening by longitudinal slits. Filaments minute. Pollen

tricolporate, reticulate, green. Pistillate inflorescences racemose, branched, pendulous, fasciculate on branchlets, lax, 3-6 cm. long, glabrous. Internodes prominent. Pistillate floral bracts foliaceous below, long elliptical above; opposite bracts connate at base. Flowers solitary in the bract axils. Pedicels short. Ovaries bicarpellate, rarely tricarpetate, unilocular, elliptical, rarely with paired bracts opposite the styles, glabrous. Styles two, rarely three, persistent, short, thick, fleshy, divergent. Fruit a berry, elliptical, 7-8 mm. in diameter, dark blue to black, sometimes on prominent pedicel, becoming dry at maturity. Dehiscence irregular. Seeds two or rarely three, oval, subterminal on parietal placentas, dark blue or black.

Flowering during the winter in northern Mexico at elevations ranging from 4880-9000 feet, depending on the rainfall (Map 5).

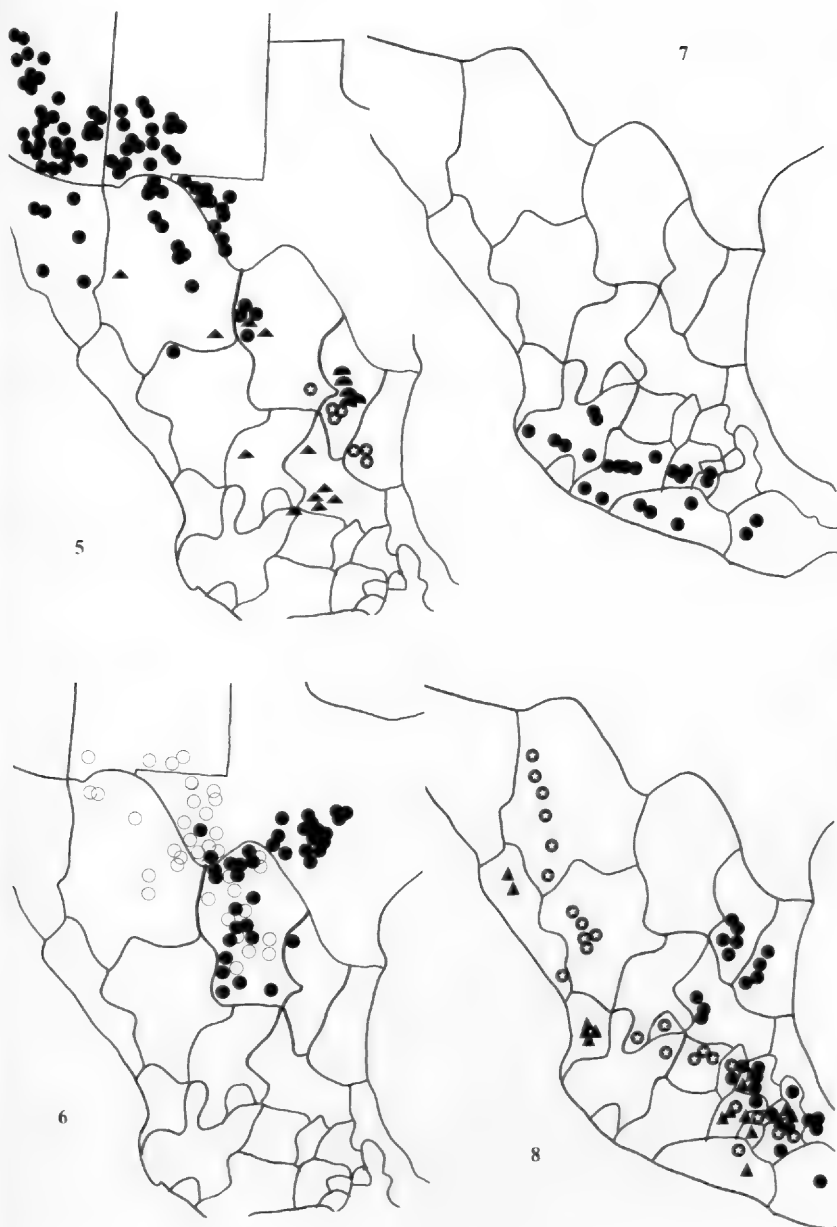
REPRESENTATIVE SPECIMENS. **Mexico.** **Coahuila:** Cañon de San Lorenzo, 5-6 mi. SE of Saltillo, *McVaugh 12346* (MEXU,MICH). **Nuevo Leon:** Cerro Potosi, *Chiang, Wendt & Johnston 8063* (TEX); Cerro Potosi, *Gilbert 86* (TEX); in the shrub zone of Potosi Mt., *Dahling 108* (CH); canyon below Las Canoas, Municipio Galeana, *Mueller 2220* (CH,MICH,MO,TEX); between San Francisco Cañon and Pabillito, 15 mi. SW of Galeana, Sierra Madre Oriental, *Mueller & Mueller 376* (CH,MICH,TEX,US). **Tamaulipas:** 5 km. SE of La Joya de Salas, top of Sierra Madre Oriental on trail to Gomez Farias, *Martin 125* (MICH); Dulces Nombres, just E of Nuevo Leon into Tamaulipas, *Meyer & Rogers 2829* (CH,MO); Sierra de Guatemala, *Webster & Webster 11* (TEX).

*Garrya glaberrima*, as the name implies, is completely glabrous and is the only member of *Garrya* lacking trichomes. It is easily distinguished from the other taxa, and shows nearly complete reproductive isolation. Frequently *G. glaberrima* is sympatric with *G. laurifolia* and *G. ovata*, but no intermediates or hybrids are produced. This is unusual in *Garrya* where reproductive flexibility is common and hybridization frequent.

With reference to flavonoids, *Garrya glaberrima* is chemically distinct and appears well-differentiated from other taxa of the genus. The independent development of flavonoids suggests the presence of strong breeding barriers which have effectively isolated *G. glaberrima* within *Garrya* over a long evolutionary period. Without such barriers, gene flow into *G. glaberrima*, due to interspecific hybridization, would have prevented this development.

*Garrya glaberrima* is morphologically the most similar to *G. ovata* and *G. laurifolia*. In exterior appearance, the staminate flowers and the yellow-green pollen are similar to *G. ovata*. The pistillate inflorescences resemble the condition found in *G. laurifolia* in that the bracts are somewhat foliaceous, especially at the base of the inflorescences. The fruits of *G. glaberrima* are elongated and contrast with the subglobose shape characteristic of most other taxa.

*Garrya glaberrima* occurs at high altitudes in scattered mountain localities where collecting is difficult, which explains why so little herbarium material is available.



MAPS 5-8. Distribution of *Garrya*: 5, *G. ovata* ssp. *ovata* (triangles); *G. ovata* ssp. *mexicana* (half circles); *G. wrightii* (dots); *G. glaberrima* (stars)—southwestern U.S. and Mexico. 6, *G. ovata* ssp. *lindheimeri* (dots); *G. ovata* ssp. *goldmanii* (circles)—southwestern U.S. and Mexico. 7, *G. longifolia*—Mexico. 8, *G. laurifolia* ssp. *laurifolia* (stars); *G. laurifolia* ssp. *macrophylla* (dots); *G. laurifolia* ssp. *racemosa* (triangles)—Mexico.

8. *Garrya ovata* Benth

Low shrubs or trees, 2-16 feet high. Crown sprouts numerous. Young stems tomentose, with age glabrate, dark gray or reddish-brown. Decussate branching. Stipules absent. Leaves simple, petiolate, decussate, narrowly ovate to elliptical, sometimes oblong or obovate, thick, coriaceous, persistent. Petioles (0.3-)0.7-1.9(-2.3) cm. long; opposite petioles connate at the base, adnate to the stem. Leaf blades (2.1)3.5-9.0(-10.8) cm. long, (1.0-)2.0-4.0(-4.9) cm. wide, ca. twice as long as broad; apices mucronate, acute or obtuse; bases obtuse or subcuneate; margins entire, plane, or strongly undulate. Upper surface crisp-hairy or sparsely tomentose, lustrous, glossy, bright green; lower surface densely crisp-hairy, tomentose or lanate, with age gray or yellow-green. Papillae developed; midrib and major leaf veins pronounced or inconspicuous above, midrib below in relief above the pubescence, secondary veins hidden. Staminate inflorescences racemose, branched, pendulous, fasciculate on branchlets, rarely solitary, 1-4 cm. long, clustered, internodes inconspicuous. Staminate floral bracts ovate to lanceolate, truncate to obtuse, small, shorter than the flower, green to red-brown, tomentose on abaxial surface; opposite bracts connate at base. Flowers solitary in the bract axils, pedicels short. Perianth segments four, connate at apices, pubescent near tips on abaxial side, glabrous on adaxial side. Stamens free, short, and alternating with the perianth segments. Anthers oval to oblong, 2-3 mm. long, basifixed, introrse, opening by longitudinal slits. Filaments minute. Pollen tricolporate, reticulate, yellow-green. Pistillate inflorescences racemose, branched, pendulous, fasciculate on branchlets, rarely solitary, lax, 4-8 cm. long, internodes conspicuous. Pistillate floral bracts ovate to lanceolate, foliaceous near inflorescence base, ca. 10 mm. long at inflorescence tip. Apices acute, acuminate, or obtuse, tomentose; opposite bracts connate only at base. Flowers solitary in the bract axils. Pedicels minute. Ovaries bicarpellate, rarely tricarpetate, unilocular, subglobose, subsessile, sometimes with bracts opposite the styles, glabrous. Styles two, or rarely three, persistent, short, thick, fleshy, divergent or nearly erect. Fruit a berry, subglobose, 6-7 mm. in diameter, glabrous, dark blue, becoming dry at maturity. Dehiscence irregular. Seeds two or rarely three, globose, subterminal, parietal placentas, dark blue or black.

## KEY TO THE SUBSPECIES

- A. Leaves strongly undulate, mature leaves with dense woolly, non-coiled pubescence . . . . . 8c. *G. ovata* ssp. *goldmanii*.
- A. Leaves mostly plane or slightly undulate, mature leaves sparsely villous, densely tomentose, or with strongly coiled trichomes forming a mat below and a slight covering above.
  - B. Mature leaves glabrate, sparingly tomentose or sometimes with villous pubescence. Leaves bright green below . . . . . 8d. *G. ovata* ssp. *mexicana*.
  - B. Mature leaves densely tomentose below, glabrous with conspicuous lateral veins above or densely crisp-hairy with strongly coiled trichomes below.
    - C. Mature leaves crisp-hairy. Trichomes strongly coiled, dense on the lower surface, less dense on top. Lateral veins not prominent above. Leaves often whitish-gray or gray-green below. . . . . 8b. *G. ovata* ssp. *lindheimeri*.
    - C. Mature leaves without coiled trichomes but densely tomentose on the lower surfaces. Upper surfaces glabrate with prominent lateral veins . . . . . 8a. *G. ovata* ssp. *ovata*.

8a. *Garrya ovata* Benth ssp. *ovata*

*Garrya ovata* Benth., Pl. Hartw: 14, 1839. HOLOTYPE: Gigante and on the Bufo Guanajuato, 1839, Hartweg 80 (x). ISOTYPE: CH.  
*Fadyenia ovata* Endl., Gen. Suppl. IV: 38, 1847. Based on *G. ovata* Benth.

Shrubs, 3–10 feet high. Adaxial leaf surfaces glabrous, rarely with sparse, separated trichomes, lustrous, major lateral and secondary veins conspicuous. Adaxial leaf surfaces tomentose, gray becoming brown with age. Leaves plane or weakly undulate. Ovary glabrous. Fruits dark blue-black at maturity.

Depending on the rainfall, flowering during the winter at elevations of 4800–8000 feet throughout central Mexico (Map 5).

REPRESENTATIVE SPECIMENS. **Mexico.** **Chihuahua:** SW Chihuahua, *Palmer 319* (GH,US); near Rio Conchos, N of Narancharic, *Pennington 538* (RSA,TEX). **Coahuila:** Sierra Mojada, just S of Esmeralda above Sociedad Cooperativa Mine, *Chiang, Wendt & Johnston 9086j* (RSA,TEX); Carneros Pass, *Pringle 2806* (GH,MEXU,US). **Jalisco:** mts. W of Hacienda Chinampas ca. 15 mi. WSW of Ojuelos, *McVaugh 17000* (MICH); Sierra de Laurel, near the Aguascalientes border, ca. 10 mi. SW of Calvillo, *McVaugh 18350* (MICH). **Nuevo Leon:** Rio Santa Rosa, *Quintero 3897* (MICH); road from Encinal to Pabillo ca. 15 mi. SW of Galeana, Sierra Madre Oriental, *Mueller & Mueller 461* (GH,MICH,TEX,US); El Fraile Peak, *Smith M654* (RSA,TEX). **San Luis Potosí:** region of San Luis Potosí, *Parry & Palmer 295* (MO,US); Bledos, Municipio Villa de Reyes, *Passini 862* (RSA); 5 km. E of the Station Maroma, Municipio Catorce, *Rzedowski 8155* (TEX); San Luis Potosí, *Schaffner 289* (US), *Schaffner 290* (MICH,US), *Schaffner 293* (US); ex convalli San Luis Potosí, *Schaffner 888* (GH,MEXU); San Rafael Mts., *Schaffner 889* (GH). **Zacatecas:** Puerto de la Paja, 20 km. al WSW de Valparaiso sobre el camino a Huejuquilla, *Rzedowski 17545* (MICH,TEX). **Unknown locality:** *Schumann 804* (US).

Because it grows in the high isolated mountains of central and northern Mexico, *Garrya ovata* ssp. *ovata* has been collected rarely and is poorly represented in herbaria. Consequently, little is known of its range of variability.

It appears morphologically closely related to *Garrya ovata* ssp. *lindheimeri*. Both are associated with limestone substrates and when in contact they frequently intergrade. Phytochemical data also support the idea of a close relationship. In fact, the flavonoid content of all *G. ovata* subspecies shows a general correspondence which is indicative of a tightly knit group.

#### 8b. *Garrya ovata* ssp. *lindheimeri* (Torrey) Dahling, comb. nov.

*Garrya lindheimeri* Torr., Pac. Rail. Rep. IV: 136. 1857. ISOTYPE: Western Texas to El Paso, New Mexico, 1849, *Wright 633* (GH).

Low shrubs or small trees, 3–12 feet high. Crown sprouts developed. Leaf margins plane, sometimes undulate. Upper leaf surface bright green, sparingly tomentose or with scattered coiled trichomes. Leaf undersides densely pubescent with tightly coiled trichomes, whitish-gray or gray-green. Ovaries glabrate, partially adnate bracts opposite the styles, conspicuous. Fruits dark blue at maturity.

Flowering from March through April at elevations of 200–6600 feet throughout southwestern Texas and northern Mexico (Map 6).

REPRESENTATIVE SPECIMENS. **Mexico.** **Coahuila:** Cañon del Mulato, Serranias del Burro, ca. 65 mi. NW of Sabinas, *Gould 10609* (MICH,TEX); 18 mi. S of Saltillo on Rt. 57, *Hess & Hall 520* (MICH); Cañon de Tinaja Blanca, Sierra de las Cruces, W of Santa



Elena Mines, *Johnston & Muller* 258 (GH,TEX); Sierra de Hechiceros, Cañon del Indio Felipe, *Johnston & Muller* 1332 (GH,TEX); Sierra de la Rata, *Johnston, Wendt & Chiang* 101611 (TEX); Sierra de la Madera, S side of the lower part of Cañon de la Hacienda, *Johnston, Wendt & Chiang* 10975 (TEX); Sierra de Jimulco, N side, *Johnston, Wendt & Chiang* 11502 (TEX); Mina El Aguirreno, N side of Sierra de la Paila, *Johnston, Wendt & Chiang* 11709a (TEX); Muzquiz, *Marsh* 375 (TEX); Santa Rosa Mt., *Marsh* 1430 (TEX); Cañon Espantosa, W slope of Sierra de San Vicente, central part of the state, *Schroeder* 98a (GH); Cañon de Milagro, Sierra de los Guajes, 12 km. W of Hacienda de la Encantada, *Stewart* 1517 (GH,TEX); Cañon de Ybarra, Sierra del Pino, *Stewart* 1823 (TEX); 8 km. W of Santa Elena, *Stewart* 2250 (TEX); vicinity of Santa Elena Mines, E foothills of Sierra de las Cruces, *Stewart* 2272 (GH,TEX); Muzquiz, near Puerto Santa Ana, *Wynd & Mueller* 276 (US); Rancho Agua Dulce, Sierra de San Manuel, Municipio de Muzquiz, *Wynd & Mueller* 382 (MICH,MS). **Nuevo Leon:** Rancho Resendez, Lampazos, *Edwards* 360 (MO,TEX,UC). **Texas. Bandera Co.:** along Seco Creek, W of Tarpley, *Correll* 29025 (TEX); 6-1/2 mi. N of Vanderpool, *Cory* 34706 (GH); ravine, 9 mi. W of Boerne, *Johnson & Webster* 539 (TEX,US); canyon of Can Creek, Lawless Ranch, 7 mi. N of Vanderpool, *McVaugh* 7056 (MICH,TEX). **Bexar Co.:** 15 mi. N of San Antonio, *Burr* 532 (TEX); N of Helotes, *Parks* 29441 (GH); vicinity of San Antonio, *von Schrenk* 4/19 (MO). **Blanco Co.:** *Reverchon* 1549 (MO); Rio Blanco, *Sargent* 5/29/85 (GH); Rio Blanco, *Sargent* 5/30/85 (GH). **Brewster Co.:** NE side of Casa Grande, Chisos Mts., Big Bend National Park, *Correll* 20674 (TEX); Juniper Canyon between Upper Juniper and Boot Spring, *Ferris & Duncan* 2776 (MO); S rim of Chisos Mts., Big Bend National Park, *Nelson & Nelson* 5103 (GH); Chisos Mts., Pulliam Canyon, *Sperry* 471 (US); Chisos Mts., *Warnock* 926 (US). **Comal Co.:** along Ranch Rd. 12, ca. 5 mi. E of Fischer in the Devil's Backbone Area, *Dahling* 804 (GH); 12 mi. W of San Marcos, *Ethridge* 3/16/64 (TEX); Comanche Spring, New Braunfels, *Lindheimer* 842, 843, 844 (GH,MO,TEX,US). **Edwards Co.:** Polecat Creek, *Cory* 41160 (GH,TEX), *Cory* 41162, 41163 (GH); Frio Water Hole, *Hill* 59 (US). **Gillespie Co.:** *Jermy* 128 (US). **Hays Co.:** Wimberley, *Fisher* 43056 (US); San Marcos, *Kiddler* 85 (GH). **Jeff Davis Co.:** along Limpia Creek near Fort Davis, *Palmer* 32183 (TEX). **Kendall Co.:** 6 mi. SW of Comfort, *Correll* 26948 (TEX); Spanish Pass, *Palmer* 9864 (GH,US); Sabina Creek, *Palmer* 13638 (GH,MO,US). **Kerr Co.:** along Lamb Creek, *Cory* 32419 (GH); on cliffs and ledges along Johnson Creek at Mountain Home, *Dahling* 417 (GH); above Turtle Creek, ca. 12-14 mi. SW of Kerrville, *Dahling* 716 (GH); Kerrville, bluffs of Guadalupe River, *Palmer* 33795 (GH,MO,US). **Kimble Co.:** bluffs overlooking Junction City above the storage tanks SE of the city, *Dahling* 562 (GH), *Sargent* 95 (GH). **Medina Co.:** Medina Dam bluffs, *Schulz* 2627 (MICH,TEX). **Real Co.:** E fork of Nueces River, *Correll* 13434 (TEX); 16 mi. N of Leaky, *Cory* 28008 (GH). **Travis Co.:** W branch of Onion Creek, 5 mi. S of Austin on old Lockheart Rd., *Barkely & Copeland* 68 (MO,TEX); Austin, *Bray* 1908 (MICH); Austin, *Buckley* 1881 (GH,US); near Austin, *Coville* 1831 (US); Lake Austin, near dam, *Crutchfield* 2426 (TEX); Austin, Mt. Burnell, *Hall* 1070021 (US); Austin, University of Texas, *Heimsch & Tharp* 398 (GH); Mount Bonnell, NW of Austin, *Warnock* 46030 (GH,TEX). **Uvalde Co.:** Montell Creek, *Cory* 8650, 23785 (GH); 6 mi. N of Montell, Montell Creek, *Cory* 42910 (TEX); Concan, Frio River, *Palmer* 10184 (MO,US). **Val Verde Co.:** Comstock, *Blair* 209 (US).

*Garrya ovata* ssp. *lindheimeri* is distributed throughout southwestern Texas and adjacent Mexico where it typically inhabits limestone mountainsides and also the edges and faces of cliffs. For example, throughout southwestern Texas, *G. ovata* ssp. *lindheimeri* is a common shrub of the limestone cliffs overlooking rivers and streams. While characteristically bushy on cliffs and ledges, it becomes arboreal in protected areas such as the moist, rocky ravines and gullies of steep, semiarid slopes.

*Garrya ovata* ssp. *lindheimeri* is distinct in Texas, but it tends to merge with both *G. ovata* ssp. *ovata* and *G. ovata* ssp. *goldmanii*

in northern Mexico. Apparently gene flow is frequent between these subspecies when they are sympatric.

73<sup>✓</sup>  
8c. *Garrya ovata* ssp. *goldmanii* (Wooton & Standley) Dahling,  
comb. nov.

37  
*Garrya goldmanii* Woot. & Standl., Contrib. U.S. Nat. Herb. 16:157. 1913. <sup>✓</sup>HOLOTYPE: limestone ledges, Queen, Eddy County, New Mexico, 1909, Wooton 562308 (US).

Small shrubs, 1-6 feet high. Crown sprouts developed. Leaves strongly undulate. Upper leaf surface glabrous or with sparse variably appressed pubescence, lustrous, major lateral veins inconspicuous. Lower leaf surface lanate, sometimes tomentose, whitish-gray or yellow-green. Ovary glabrous, bracts opposite the styles variably adnate and conspicuous. Fruits glabrous, dark blue at maturity.

Flowering from March to May at elevations ranging from 4550 to 7880 feet throughout southwestern Texas, southeastern New Mexico, and northern Mexico (Map 6).

REPRESENTATIVE SPECIMENS. **Mexico. Chihuahua:** Sierra de Chupaderes, extreme S end of Rancho Las Pampas, ENE of Jimenez, *Chiang, Wendt & Johnston* 8900 (TEX); cañon in N face of Sierra Rica, S of Rancho La Consolacion, *Johnston, Wendt & Chiang* 10756 (TEX); cañon in N face of Sierra Rica, S of Rancho La Consolacion, *Johnston, Wendt & Chiang* 10769 (TEX); Sierra Grande, ca. 3 km. E of Rancho El Muscielago, *Johnston, Wendt & Chiang* 11288A (TEX); Sierra de los Piños, *LeSeur* 1524 (MO,TEX); Santa Eulalia Mts., *Pringle* 131 (CH,MICH,RSA,US). **Coahuila:** 4 mi. W and 10 mi. S of Ocampo, *Graber* 173 (TEX); Sierra de la Madera, Cañon del Pajarito, *Huller* 3190 (MICH); Sierra de la Madera, vicinity of La Cueva, *Johnston* 8902 (TEX); Sierra del Piño, vicinity of La Noria, *Johnston & Muller* 524 (TEX); Sierra del Piño, W of camp at La Noria, *Johnston & Muller* 599 (CH,TEX); Del Carmen Mts., *Marsh, Jr.* 802 (CH,TEX); Puerto de San Lazaro, Sierra de San Lazaro, Municipio de Castanos, *Muller* 3088 (CH,MICH,MO,TEX); Cuatro Cienegas, *Muller* 3190 (CH,TEX); Cañon del Rayo, N end of Sierra del Diablo, *Stewart* 954 (CH,TEX); *Wynd & Mueller* 1936 (MO). **New Mexico.** **Eddy Co.:** Carlsbad Cave, *Bailey* 4/24 (US). **Hidalgo Co.:** Big Hatchet Mts., *Goldman* 1318 (US), *Goldman* 1319 (US). **Otero Co.:** San Andreas, Sheep Mts., *Gaut* 36 (US); Sacramento Mts., *Hershey* 301761 (CAS). **Texas. Brewster Co.:** Big Bend National Park, *Albers* 46217 (TEX); Chisos Mts., Big Bend National Park, *Correll* 29747 (TEX); Big Bend National Park, Chisos Mts. along trail to Lost Mine Ridge, *Dahling* 768 (GH); Santiago Mts., 8 mi. SW of Santiago Peak, *McVaugh* 7842 (CH,MICH,TEX); Honeysuckle Canyon, Glass Mts., *Warnock* W322 (CH,TEX). **Culberson Co.:** Guadalupe Mts., *Bailey* 452 (US); McKittrick Canyon, Guadalupe Mts., *Correll & Johnston* 18493 (TEX); Pine Spring, Guadalupe Mts., *Whitehouse* 8686 (TEX). **Jeff Davis Co.:** Mt. Livermore, *Hinckley* 10/13/34 (TEX); Fern Canyon, NW of Mitre Peak, 14 mi. NW of Alpine, *Muller* 8183 (CH,MICH,TEX); Davis Mts., *Palmer* 34340 (MO); Rose Canyon, N of Alpine, *Warnock* W881 (CH,TEX,UC); Davis Mts., *Young* 8/13/14 (TEX). **Pecos Co.:** Gap Tank, Glass Mts., 25 mi. N of Marathon, *Warnock* 5023 (TEX). **Presidio Co.:** near Vieja, Tierra Vieja Mts., *Hinckley* 20951 (US). **Real Co.:** *Harris* 14 (US).

*Garrya ovata* ssp. *goldmanii* is distinctive because of its small stature and short, narrow, very undulate leaf margins. When inhabiting the upper Sonoran zone, it commonly grows in the shade as a small shrub. However, sometimes it extends into the semiarid transition zone where, because of the exposure to the sun and general aridity,

it becomes nearly prostrate and forms a low-growing mat.

*Garrya ovata* ssp. *goldmanii* has very weak reproductive barriers and intergrades morphologically when in contact with other *G. ovata* subspecies. This is especially true in northern Mexico where the ranges of all *G. ovata* subspecies overlap. Also, like the other *G. ovata* subspecies, *G. ovata* ssp. *goldmanii* is often found in, but not restricted to, limestone areas.

8d. *Garrya ovata* Bentham ssp. *mexicana* Dahling, ssp. nov.

Arbores 3–4 m. altis. Folia late ellipticis vel ovatis, acuminatis vel acutis, obtusis, petioli (1.1–)1.2–1.8(–2.1) cm. longis; folia (5.4–)7.5–11.5(–13.1) cm. longis, (2.1–)3.0–4.0(–5.7) cm. latis, glabratiss vel parce villosis.

✓ HOLOTYPE: in the Gray Herbarium, collected on the mountain top above El Cercado, Nuevo Leon, Mexico, February, 1972, *Dahling 1180*. ISOTYPES: to be distributed.

Trees 3–5 m. tall. Leaves broadly elliptical or ovate, acuminate, acute or obtuse; petioles (1.1–)1.2–1.8(–2.1) cm. long; leaves (5.4–)7.5–11.5(–13.1) cm. long and (2.1–)3.0–4.0(–5.7) cm. wide, glabrate or sparsely villous.

Flowering from February to March at elevations of 4000–8400 feet throughout southern Nuevo Leon (Map 5).

REPRESENTATIVE SPECIMENS. ✓ Mexico. ✓ Nuevo Leon: Chipinque, *Calzado 2931* (MEMO); near the tops of the mts. surrounding Monterrey, about 1/2 days climb, *Dahling 118* (GH); Mesa de Chipinque, *Landaw 0935* (MEMO); Villa de Santiago, *Leavenworth 157* (MO); Cañon Guajuco, Rancho Vista Hermosa, Municipio Villa Santiago, *Mueller 2031* (GH, MICH, MO, TEX); near Monterrey, *Pringle 2104* (MEXU); Sierra Madre near Monterrey, *Pringle 2395* (MICH, MO, MSU, US), *11816* (GH, MICH, MO, MSC, TEX), *11817* (MICH, MO, MSC, TEX, US); at the point farthest E on the Chipinque Rd. in the thorn-oak ecotonal area, Monterrey, *Smith 450* (GH, TEX); Cerro de la Silla near Monterrey, *White 1484* (GH, MICH).

*Garrya ovata* ssp. *mexicana* is arboreal or shrubby and lacks the dense covering of trichomes common to other *G. ovata* subspecies. It appears most similar to *G. ovata* ssp. *lindheimeri* in leaf shape, dimension, and pollen exine structure. In addition, the fine structure of the trichomes is similar in its system of ridges, furrows, and prominent protuberances.

*Garrya ovata* ssp. *mexicana* inhabits the semiarid mountain summits near Monterrey, Nuevo Leon, Mexico. It is also found in the shrub zone on steep mountain slopes and on limestone near cliffs. It is easily distinguished from other members within *G. ovata* by the sparse pubescence and the more arboreal habit.

9. *Garrya wrightii* Torrey

*Garrya wrightii* Torr., Pac. R. Rep. 4:136. 1857. LECTOTYPE: on rocks at base of San Francisco Mt., New Mexico; common at Copper Mines (Santa Rita), New Mexico, 1851–52, *Wright 1789* (NY). ISOTYPE: GH.

Shrubs, 2–10 feet tall. Crown sprouts developed. Young stems with appressed, silky, long, whitish-gray pubescence; with age becoming glabrate, reddish-brown, or dark gray. Decussate branching. Stipules absent. Leaves simple, petiolate, decussate, elliptical or narrowly elliptical to obovate, thick, coriaceous, persistent. Petioles (0.3–)0.4–0.5(–1.0) cm. long; opposite petioles connate at the base, adnate to the stem. Leaf blades (1.9–)2.5–6.0(–6.6) cm. long, (0.8–)1.0–3.0(–3.7) cm. wide; apices tapering, mucronate, tips recurved or straight; bases tapering, attenuate or decurrent; margins entire, plane; upper surface glabrous or glabrate, green, yellow-green or gray; lower surface glabrate, or sparsely pilose when young, bright yellow or gray-green; papillae developed; midrib and major leaf veins prominent and yellow above, in relief below. Staminate inflorescences racemose, branched, pendulous, fasciculate on solitary branchlets, 2–5 cm. long, internodes short. Staminate floral bracts linear-lanceolate or oblong, apices acuminate, recurved, ca. 5 mm. long, green-red-brown, densely pilose with appressed trichomes on abaxial surfaces; opposite bracts connate only at the base. Flowers solitary, partially enveloped and in bract axils. Pedicels 1–2 mm. long. Perianth segments four, oblong-elliptical, connate at apices, pilose with appressed trichomes near tips on abaxial side, adaxial side glabrous. Stamens free, short, and alternating with the perianth segments. Anthers oval, 1–2 mm. long, basifixed, introrse, opening by longitudinal slits. Filaments minute. Pollen tricolporate, reticulate, yellow-green or dark orange-brown. Pistillate inflorescences racemose, branched, pendulous, solitary or fasciculate on branchlets, lax, 2–10 cm. long, internodes conspicuous. Pistillate floral bracts 3–9 mm. long, often foliaceous and 2–3 cm. long near inflorescence base, lanceolate or elliptical-ovate, apex acuminate and recurved, sparingly pilose; opposite bracts connate at the base. Flowers solitary in the bract axils. Pedicels minute. Ovaries bicarpellate, rarely tricarpetate, unilocular, subglobose, sessile, sometimes with paired bracts opposite the styles, glabrous or sparsely pilose. Styles two, rarely three, persistent, short, thick, fleshy, variously divergent. Fruit a berry, subglobose, 5.0–6.2 mm. in diameter, glabrous, dark blue-black or gray with age, becoming dry at maturity. Dehiscence irregular. Seeds two or rarely three, globose to oval, subterminal, parietal placentas, dark blue or black.

Flowering March to August at elevations of 3000–7000 feet, ranging from western Texas, northern Mexico to central and southern Arizona (Map 5).

REPRESENTATIVE SPECIMENS. **Mexico. Chihuahua:** Cañon de Santa Clara, 5 mi. N of Cerro Campana, *Christman* 259 (UC); canyon E of Majalca, *Correll & Johnston* 20295 (TEX); between Zaragosa and San Buenaventura, *Correll & Johnston* 21643 (TEX); Devil's Canyon, San Luis Mts., *Goldman* 1428 (US), 1436 (NY,US); 25 mi. SW of Chihuahua, *Muller* 3702 (GH,MICH,TEX,UC); near Lake Santa Maria, *Nelson* 6399 (GH,US); Cañon de Las Varas, Santa Clara Mts., *Shreve* 7944 (ARIZ,US); 15 rd. mi. NW of Colonia Juarez in "The Tinaja," *Wilson & Johnston* 8453 (TEX). **Coahuila:** Sierra de la Madera, 2 km. E of Picacho de Zozaya, *Johnston* 9033 (TEX); Sierra del Pino, W of camp at La Noria, *Johnston & Muller* 598 (TEX); near Chihuahua border, Sierra Almagre, above Rancho Almagre, *Johnston & Muller* 1148, 1195 (TEX). **Durango:** Cañon Cantero, Sierra Gamon, *Gentry* 8398 (GH,MEXU,MICH,NY,US). **Sonora:** Sierra de los Ajos, E of Cananea, *Marshall* 105 (ARIZ,USA); El Tigre Cañon and above El Tigre Mine, E of Esqueda and Lago Angostura, *Turner, Dodge & Mason* 2129 (ARIZ); Cañon de Santa Rosa, *White* 573 (ARIZ,GH,MICH); El Rancho de la Nacha, 25 mi. W of La Angostura, *White* 4096 (GH,MICH); El Rancho de Roble, NE of El Tigre, *White* 4378 (GH,MICH,TEX); Puerto del Cumarito, Sierra de la Cabellera, *White* 4640 (ARIZ,GH,MICH,TEX). **Arizona. Cochise Co.:** Saddle between Cave Creek and Turkey Creek, Chiricahua Mts., *Barr* 67–245 (ARIZ); Rhoda Riggs Ranch, Chiricahua Mts., *Blumer* 1295 (ARIZ,GH,MO,US); ca. 1/2 mi. NW of the tunnel beyond the summit at Bixbee Pass, *Dahling* 980 (GH); Guadalupe Lodge, Guadalupe Canyon, Guadalupe Mts., *Darrow, Haskell & Reynolds* 3750 (ARIZ); Bar fire station to Paradise, Chiricahua National Forest, *Eggleston* 10890 (GH,US); Bowie, *Jones* 4261 (ARIZ,GH,MS); Ramsey Canyon, Huachuca Mts., *Jones* 24866 (POM); near Bixbee, *McKelvey* 621, 626 (GH); Dragon Mts., near road into Cochise Stronghold

Area, S13, T17S, R23E, *Newsome* 69-148 (ARIZ); S fork of Cave Creek, Chiricahua Mts., *Ordway* 185 (ARIZ); near Fort Huachuca, *Wilcox* 9/94 (NY,US). **Coconino Co.:** San Francisco Mts., *Coville & Funston* 8 (NY,US); about 3 mi. W of Sedona, along highway 89A, *Dahling* 878 (GH); along highway 89A before the entrance to Oak Creek Canyon, *Dahling* 1076 (GH); Grand View Trail, Grand Canyon, *Thornber* 8432 (ARIZ). **Gila Co.:** San Carlos Indian Reservation, San Carlos to Cazador Spring, *Coville* 1924 (NY,US); along Rt. 60 ca. 8-1/2 mi. W of Miami, *Dahling* 843 (GH); Superior to Miami Hwy. near the E county line, *Gillespie* 8633 (GH,US); Calbecue Ridge Fort, Apache Indian Reservation, *Granfelt* 67-81b (ARIZ). **Graham Co.:** W slope of Gila Mts., *Goldman* 2355 (US); Mt. Graham, *Lemmon* 8/80 (GH,MO,US); Mt. Graham, *Peebles, Harrison & Kearney* 4487 (ARIZ,US). **Greenlee Co.:** Blue Range, *Goldman* 2410 (NY,US); Santa Rita Mts., *Greene* 1470 (GH,UC); Whitehouse Canyon in the Santa Rita Mts., *McKelvey* 506 (GH). **Maricopa Co.:** Four Peaks, *Stockwell* 1928 (ARIZ). **Navajo Co.:** 9 mi. W of Cibique, *Bohrer* 1609 (ARIZ); Apache Reservation, *Fish* 29 (UC). **Pima Co.:** Box Canyon, Santa Rita Mts., *Barr* 67-371 (ARIZ); below Lemmon Mts., road E of Tucson, 2.5 mi. below the Prison Camp, *Bell* 1202 (ARIZ); Sabino Canyon, Santa Catalina, *Benson* 6150 (ARIZ); Rincon Mts., *Goodding* 23 (ARIZ); Baboquivari Mts., *Goodding* 4578 (ARIZ); El Hambra region, Papago Indian Reservation, *Goodding* 418-45 (ARIZ); Quinlin Mts., *Goodding & Lusher* 174-45 (ARIZ). **Pinal Co.:** near the county line along the Superior to Miami Hwy., *Bell* 1207 (US); Belle Ridge, 0.75 of the distance between the gate and the top of the ridge, *Caldwell* 171 (ARIZ). **Santa Cruz Co.:** near Nogales, *Coville* 1620 (US), *Purpus* 106046 (UC). **Yavapai Co.:** S of Mt. Union, Prescott, *Benham* 7162 (ARIZ); ca. 1.2 mi. before the jct. of Hwy. 89 and 89A near Prescott, *Dahling* 1009 (GH); along Hwy. 89 ca. 2 mi. W of Sedona, *Dahling* 1020 (GH); ca. 4 mi. S of Prescott, *Dahling* 1171 (GH); N of Prescott, along Hwy. 89A, *Dahling* 1231 (GH); 14 mi. S of Prescott, *Gillespie* 8510 (GH,US); French Gulch, Senator Range, *Ruddock* 1915 (GH); 9.3 mi. NE of Wihoit, *Vasek* 328 (RSA). **New Mexico. Catron Co.:** Rio San Francisco near Glenwood, *Bailey* 1060 (NY,US); Mogollon Mts., *Wooton* 7/20/00 (GH). **Dona Ana Co.:** Dripping Springs, Boyd Ranch, W face of Organ Mts., *Dunn* 7285 (RSA); 3 mi. SE of Heuvas Rocks, 14 mi. E of Las Cruces, *Dunn* 7949 (RSA); Finley Canyon, Organ Mts., *Everett* 10/21/74 (ARIZ). **Grant Co.:** Fort Bayard Watershed, *Blumer* 152A (US), 152b (GH), 1905 (US); ca. 1/2 mi. W of Cental along Hwy. 80, *Dahling* 822 (GH); ca. 3-1/2 mi. E of Central on Hwy. 90, *Dahling* 1159 (GH); Silver City, *Demaree* 60806 (RSA); Burro Mts., 5 mi. SE of Leopold, *Goldman* 1518 (NY,US); Santa Rita Mt., end of the Black Range, *Metcalfe* 1470 (GH,US); Howell's Ridge, Little Hatchet Mts., *VanDevender & Spauling* 4/1/73 (ARIZ); Copper Mines, *Wright* 634 (GH,US). **Hidalgo Co.:** along Hwy. 90, just into Hidalgo Co. from the north, *Dahling* 830 (GH); N slope of Animas Peak, Animas Mts., *Goldman* 1347 (NY,US). **Lincoln Co.:** Godfrey Mts., *Humphrey* 6044 (ARIZ). **Luna Co.:** Florita Mts., *Goldman* 1487 (NY,US), *Jones* 9/7/03 (GH,MICH,MO,NY,US). **Otero Co.:** Fresnal Canyon, Sacramento Mts., 6 mi. NE of Alamogordo, *Bohrer* 1245 (ARIZ); Cloudcroft, *Jones* 26291 (MO). **Sierra Co.:** ca. 1/2-1 mi. E of Hillsboro, *Dahling* 560 (GH); 4 mi. W of Kingston, *Goldman* 1814 (NY,US); Hillsboro, *Nelson* 11285 (GH,MO). **Socorro Co.:** Madgalina Mts., *Goldman* 1657 (NY,US). **Texas. Culberson Co.:** Victoria Canyon, Sierra Diablo Mts., *Correll* 13763 (NY,TEX), *Beach* Mts., *Johnston* 3958 (TEX); N of Van Horn, *Waterfall* 5083 (GH). **El Paso Co.:** Van Horn, *Bailey* 483 (NY,US); Franklin Mts., *Barlow* 876039 (UC), Hueco Tanks, *Berkman, Lee & Tharp* 46231 (GH). **Hudspeth Co.:** Sierra Tinaja Pinja, Cornudas Range, *Correll & Correll* 24707 (GH,TEX); Black Mt. in the Cornudas Mts., *Correll & Flyr* 38381 (TEX,UC); along Hwy. 80, about 6-10 mi. W of Sierra Blanca, *Dahling* 450 (GH); head of Victoria Canyon, Sierra Diablos, *Warnock* 11488 (GH,TEX). **Jeff Davis Co.:** gorge, Madera Canyon, *Hinckley* 1266 (GH,NY); Little Aguja Canyon, Davis Mts., *Warnock* 8082 (TEX). **Presidio Co.:** Cottonwood Canyon, ZH Canyon, Miller Ranch, Sierra Tierra, *Hinckley* 1752 (ARIZ,NY,TEX,US).

*Garrya wrightii* is singular in its adaptation to harsh arid environments. This is particularly evident throughout western Texas where it is found amid rocks and boulders at the base and on the sides

of small mountains. Although growth conditions are harsh, the shrubby *G. wrightii* commonly thrives there, producing fruit and seed.

Leaves of *Garrya wrightii* are usually more or less glabrous although a few rather atypical populations in northern Mexico have leaves with upwardly appressed pubescence.

Within subgenus *Fadyenia*, only *Garrya wrightii*, *G. ovata*, and *G. grisea* have trichomes bearing protuberances. These are large, well-developed, and similar in *G. ovata* and *G. wrightii*, but appear as small swellings associated with the ridges in *G. grisea*. Whether these swellings represent reduced or incipient protuberances remains unsettled.

Phytochemical investigation of the flavonoids suggests a close chemical relationship between *Garrya wrightii* and *G. grisea*. While populations of *G. wrightii* and *G. grisea* show a high paired affinity index, populations of *G. wrightii* and *G. ovata* generally do not.

The variation in *Garrya wrightii* is within narrow limits, making the taxon distinct in most parts of its range. However, this is less the rule in Mexican populations toward the southern part of its range where larger leaved individuals, superficially resembling *G. laurifolia* ssp. *macrophylla*, can be found. Moreover, some of these individuals also have larger and somewhat foliaceous floral bracts which are more characteristic of *G. laurifolia* than of *G. wrightii*. It appears that the two taxa hybridize in their areas of contact, which would account for this convergence. Although *G. laurifolia* ssp. *macrophylla* occasionally shows glabrous leaves, it can be distinguished from the large-leaved *G. wrightii* forms or hybrids by its more arboreal habit.

### <sup>30</sup> 10. *Garrya grisea* Wiggins

*Garrya grisea* Wiggins, Contrib. Dudley Herb. of Stan. Univ. 1, no. 5: 172. 1933.

✓HOLOTYPE: collected in a small canyon at the upper end of the meadow at La Encantada, Sierra San Pedro Martir, 1930, Wiggins & Demaree 4988 (DS). ISOTYPES: GH, CAS.

Shrubs, 5–10 feet tall. Crown sprouts developed. Young stems covered with silvery strigose pubescence, becoming glabrate and gray with age. Branching decussate. Stipules absent. Leaves simple, petiolate, decussate, elliptical, or rarely narrowly ovate, coriaceous, persistent. Petioles (0.4–)0.5–0.6(–0.7) cm. long, opposite petioles connate at the base, adnate to the stem. Leaf blades (3.2–)3.5–4.0(–4.3) cm. long, (1.3–)1.4–1.7(–1.8) cm. wide; apices acuminate to acute; bases subcuneate; margins plane or slightly undulate; upper and lower surfaces covered with silvery strigose pubescence, yellow, gray-green, sometimes glaucous; papillae well-developed, midrib and major leaf veins conspicuous below. Staminate inflorescences branched at the base, pendulous, fasciculate or solitary on branchlets, 2–4 cm. long, internodes visible. Staminate floral bracts lanceolate, acuminate with recurved or straight apices, gray-green, appressed pilose on abaxial surfaces; opposite bracts connate only at the base. Flowers solitary, partially enveloped and borne in the bract axils. Pedicels 1 mm. long. Perianth segments four, oblong-elliptical, connate at the apices, pilose with appressed trichomes on the abaxial side, adaxial side glabrous. Stamens free, short, alternating with the perianth segments.

Anthers oval, minute, basi-fixed, introrse, opening by longitudinal slits. Filaments abbreviated. Pollen tricolporate, reticulate, yellow or orange-brown. Pistillate inflorescences branched at the base, pendulous, fasciculate or solitary on branchlets, lax, internodes conspicuous. Female floral bracts 5–10 mm. long, lanceolate to obovate; opposite bracts connate only at the base. Flowers solitary in bract axils. Pedicels minute. Ovaries bicarpellate, rarely tricarpellate, unilocular, oval, subsessile, sometimes with paired bracts opposite the styles, sparsely pilose, soon becoming glabrous. Styles two, rarely three, short, thick, fleshy, persistent. Fruit a subglobose berry, 5–6 mm. in diameter, glabrous or occasionally with appressed pubescence near the base, dark blue becoming dry at maturity. Dehiscence irregular. Seeds two, rarely three, oval to globose, subterminal, parietal placentas, dark blue or black.

Flowering February–April at elevations ranging from 4900–7950 feet in northern and central Baja California, Mexico (not mapped).

REPRESENTATIVE SPECIMENS. **Mexico. Baja California:** San Pedro Martir, *Brandegee 106054* (UC); Sierra San Pedro Martir, near Vallecitos, Municipio Ensenada, *Breedlove 16373* (CAS,MICH); Sierra La Encantada, E flank of Sierra San Pedro Martir, *Chambers 595* (DS,UC); Cerro Chato Summit, *Moran 11107* (DS,SD,UC); Cerro la Sandia, *Moran 11531* (DS,RSA,SD); Cerro Azufre, *Moran 11639* (DS,MEXU,RSA,UC); N slope of Cerro Azufre, *Moran 11644* (ARIZ); Volcan Las Tres Virgenes, *Moran 11665* (DS,RSA,SD,UC); Calbozo, 1/2 mi. SE of Rancho Calbozo, *Moran 13488-1/2* (RSA); head of Arroyo Copal, *Moran 15464* (SD); S of Cerro Venado Blanco, *Moran 15681* (SD); Cerro Prieto, *Moran 18122* (SD); Volcan Las Tres Virgenes, *Moran 20431* (SD); Cerro Matomi, *Moran 20781* (SD); Portezuelo de Jamau, *Moran 20957* (SD); above Yerba Buena, *Moran & Thorne 14203* (DS,SD,TEX); NE slope of Cerro Chato, 30° 35' N–115° 14' W, Sierra San Pedro Martir, *Thorne 31986* (MICH); NE slope of Cerro Chato, 30° 35' N–115° 14' W, Sierra San Pedro Martir, *Thorne 31996* (MICH); La Encantada, Sierra San Pedro Martir, *Wiggins & Demaree 4903* (MICH).

Herbarium material of *Garrya grisea* is not plentiful because it is endemic and confined to rugged northern and central Baja California. Conclusions are based on admittedly limited material and may require future modification when more material is available for study.

Wiggins (1933), in a note following his original description of the species, suggested a possible relationship with *Garrya wrightii*. Leaves of *G. grisea* are densely pubescent with upwardly appressed trichomes on both the upper and lower surfaces. This contrasts with *G. wrightii* in which the leaves are typically glabrate or with sparsely appressed pubescence when young. Some Mexican populations of *G. wrightii* are densely pubescent and are more or less covered on the lower side with ascending trichomes. While spatially separated from *G. grisea*, these pubescent forms of *G. wrightii* are more similar to *G. grisea* than other taxa of the genus. An investigation of the trichome structure, using the SEM, revealed several interesting features. The trichomes of *G. wrightii* have characteristic ridges and furrows with numerous well-developed protuberances restricted to the ridges. The trichomes of *G. grisea* also show a system of ridges and furrows but lack well-developed protuberances. Swelling can be seen periodically associated with the ridges but the question of their representing

incipient or reduced protuberances remains open. However, in either case the trichome structures of *G. wrightii* and *G. grisea* support the idea of a relationship between the taxa.

Although the fine structure of the exine is similar to *Garrya laurifolia*, pollen size in *G. grisea* is similar to that of *G. wrightii* and *G. ovata*. Phytochemical data also support the idea of a relationship with *G. wrightii* since the chemical paired affinity index is high. While an affinity, as suggested by Wiggins, is provisionally accepted, sufficient differences exist to warrant the recognition of *G. grisea* and *G. wrightii* as separate species. The inflorescences of *G. grisea* show reduced branching with typically smaller flowers than *G. wrightii*. In addition, the latter is adapted to extreme arid conditions and is generally found at lower elevations than *G. grisea*. A close relationship with other *Garrya* taxa is not indicated.

### 11. *Garrya salicifolia* Eastwood

*Garrya salicifolia* Eastw., Bot. Gaz. XXXVI:463. 1903. HOLOTYPE: Sierra de la Laguna, Baja California, Mexico, 1890, *Brandegee* 259 (CAS).

Shrubs to small trees, 6–15 feet tall. Crown sprouts developed. Young stems slender, slightly pubescent or glabrate, rough, lenticels prominent, becoming reddish-brown with age. Branching decussate. Stipules absent. Leaves simple, petiolate, decussate, lanceolate, thin, slightly coriaceous, persistent. Petioles pubescent, (0.6–)0.7–0.8(–0.9) cm. long; opposite petioles connate at the base, adnate to the stem. Leaf blades (4.0–)4.5–6.5(–7.1) cm. long, (1.3–)1.5–2.0(–2.5) cm. wide, apices tapering acuminate or subcuspidate; bases attenuate; margins entire, plane; upper surfaces glabrous, green, lustrous; lower surfaces glabrate or with appressed pubescence near the petiole, yellow-green; papillae well-developed. Midrib and major leaf veins prominent. Staminate inflorescences racemose, branched, pendulous, fasciculate or solitary on branchlets, slender, lax, internodes conspicuous. Staminate floral bracts small; opposite bracts connate at the base. Flowers solitary in the bract axils. Perianth segments four, pubescent on the abaxial side, connate at the apices. Stamens four, free, short, alternating with the perianth segments. Anthers minute, oblong, basifixed, introrse, opening by longitudinal slits. Filaments abbreviated, slightly longer than the anthers. Pollen tricolporate, reticulate, yellow, green, or orange-brown. Pistillate inflorescences racemose, branched, fasciculate or solitary on branchlets, lax, internodes conspicuous. Pistillate floral bracts 5–10 mm. long, lanceolate, attenuate; opposite bracts connate at the base. Flowers solitary in bract axils. Pedicels minute. Ovaries bicarpellate, unilocular, subglobose, subsessile, glabrous. Styles two, persistent, short, thick, fleshy, divergent. Fruit a globose berry, ca. 5.5 mm. in diameter, green becoming dark blue, brittle at maturity. Dehiscence irregular. Infructescences suberect. Seeds two, globose, subterminal, parietal placentas, dark blue or black.

Flowering August to December at elevations of 5100–6000 feet in southern Baja California, Mexico (not mapped).

REPRESENTATIVE SPECIMENS. Mexico. Baja California: La Laguna, Sierra de la Laguna, E of Todos Santos, *Alexander, Kellogg & Carter* 2305a (DS, CH, TEX, UC); La Chupanosa, *Brandegee* 259 (CH, UC); Sierra de la Laguna, *Brandegee* 1899 (CH); La Chupanosa, *Brandegee* 106049 (UC); La Laguna, *Gentry* 4423 (DS), *Jones* 522101 (DS, CH, POM), 9/22/30



(CH,DS,MO,POM), *Nelson & Goldman 7458* (CH); Laguna, Meadow Laguna, *Peters 249* (UC).

*Garrya salicifolia* is difficult to characterize because only limited collections are available. Because it is confined to the lower and until recently generally inaccessible regions of Baja California, few specimens have been collected and herbarium material consists of sterile or poorly preserved flowering specimens. Consequently, only tentative conclusions can be drawn about the diversity and variation within the taxon.

The trichome structure of *Garrya salicifolia* is interesting because both a counterclockwise orientation of ridges and furrows and a counterclockwise structural twisting are present. The occurrence of this compound trichome orientation is rare within *Garrya* and is found elsewhere only in *G. fremontii* and *G. flavescens* of subgenus *Garrya*. The trichomes of *G. salicifolia* lack protuberances and are therefore similar to *G. laurifolia* and other southern *Garryas* of subgenus *Fadyenia*. An SEM examination of pollen exines also shows a gross similarity with *G. laurifolia*. However, the leaves of *G. salicifolia* are not as coriaceous as are those of *G. laurifolia* and more closely resemble those of *G. longifolia*. This is also the case with the inflorescences which are conspicuously lax and have elongated internodes. While the flavonoid content of *G. salicifolia* suggests a relationship with *G. laurifolia*, the correspondence of flavonoids is not close enough to support a change in taxonomic rank.

Because of its complete geographical isolation, *Garrya salicifolia* does not hybridize with other members of the genus. However, the general morphological and chemical similarity suggests that *G. salicifolia* was evolutionarily derived from *G. laurifolia*-like ancestors.

## 12. *Garrya fadyenii* Hooker

*Garrya fadyenii* Hook., Icon. Pl. t. 333, 1840. HOLOTYPE: Jamaica, *Fadyen H1859/73-56* (K).

*Fadyenia Hookeri* Endl. Gen. Suppl. IV:38, 1847. Based on *Garrya fadyenii* Hook.

Shrubs or trees, 12-25 feet high. Crown sprouts present. Young stems pilose or densely tomentose, with age becoming glabrate and dark reddish-brown or black. Branching decussate. Stipules absent. Leaves simple, petiolate, decussate, narrowly elliptical, thick, coriaceous, persistent. Petioles (0.4-)0.6-1.0(-1.3) cm. long; opposite petioles connate at the base, adnate to the stem. Leaf blades (2.9-)4.0-9.0(-10.4) cm. long and (1.0-)1.5-3.5(-3.7) cm. wide; apices obtuse, acute or mucronate; bases attenuate, margins entire, plane; upper surfaces glabrous or with villous pubescence when young, lustrous, dark green; lower surface densely tomentose, gray, or silvery; papillae developed; midrib and major lateral veins conspicuous above, veins obscured by pubescence below. Staminate inflorescences racemose, branched, pendulous, fasciculate or solitary on branchlets, about 4 cm. long, compact, densely pubescent; internodes not conspicuous. Staminate floral bracts ovate to lanceolate, acute, acuminate, sometimes

concave, 3–6 mm. long, opposite bracts connate at the base. Flowers solitary in bract axils. Pedicels short. Perianth segments four, oblong, connate at the apices, with weakly ascending curly pubescence on the abaxial side. Stamens free, short, alternating with the perianth segments. Anthers oblong, minute, basifixed, introrse, opening by longitudinal slits. Filaments shorter than the anthers. Pollen tricolporate, reticulate, yellow-brown or orange. Pistillate inflorescences racemose, branched, pendulous, fasciculate or solitary on branchlets, ca. 6 cm. long, lax, tomentose, internodes prominent. Pistillate floral bracts linear-lanceolate, foliaceous, up to 2 cm. long, mucronate, pubescent; opposite bracts connate at the base, flowers solitary in the bract axils. Pedicels short. Ovaries bicarpellate, rarely tricarpetate, unilocular, oval, subsessile, sometimes with paired bracts opposite the styles, tomentose. Styles two, rarely three, persistent, short, thick, fleshy, nearly erect. Fruit a subglobose berry, dark blue or brown, becoming brittle at maturity. Dehiscence irregular. Seeds two or rarely three, globose, subterminal, parietal placentas, dark blue.

Flowering during the winter at elevations ranging from 2000–8130 feet throughout the Greater Antilles (Map 9).

REPRESENTATIVE SPECIMENS. **Cuba. Oriente:** Guantanamo, *Ekman* 10305 (US); Sierra Maestra, on top of Palmamocha, *Ekman* 14316 (NY); Pico Turquino, Sierra Maestra, *Leon* 10710 (GH,NY); Arroyo Frio, Sierra Jurias, S. Baracoa region, *Leon* 72197 (NY); Arroyo Peladero Arriba, Sierra Maestra, *Lopez-F.* 2174 (US); Farallon de la Perla Oriente, *Shafer* 8755 (GH), 8782 (US); Oriente, *Wright* 492 (GH,MO). **Las Villas:** summit of Pico *Shafer* 8755 (GH), 8782 (US); Oriente, *Wright* 492 (GH,MO). **San Blas:** mts. of Trinidad, Pico Potrerillo, *Ekman* 14019 (MICH); mts. of the Liguania Trinidad group, valley of Rio Hanabanilla, *Ekman* 18486 (US); San Blas-Buenos Aires, Trinidad Mts., *Gonzales* 637 (MICH); Las Vegas of Madagua above San Blas, *Jack* 5959 (F,GH,US); Santa Clara, *Jack* 6816 (GH); Las Lagunas, Buenos Aires, Santa Clara, *Jack* 6826 (US); Buenos Aires, Trinidad Mts., *Morton* 10373 (US); Santa Clara near reservoir, *Rehder* 1173 (GH); Trinidad Mts., *Webster, Dressler, Jones, Schubert & Wilson* 212 (GH). **Dominican Republic. Barahona:** Barahona, *Fuertes* 633 (US); Santo Domingo, *Fuertes* 1298 (F,MO,US); between Pedernales and Aceitunal, *Howard* 8193 (GH); between Palo and Montaease, *Howard* 12071 (GH); Rancho Viejo, S of Puerto Escondido, *Howard* 12172 (GH,MICH); Santo Domingo, *von Turckheim* 3010 (MO,US), 3292 (MO,US). **Benefactor:** N of Rio Arriba, *Howard* 9059 (GH,NY). **San Rafael:** Sierra de Neiba, near the crest of the range along the Haitian border between the provinces of San Rafael and Independencia, *Gastony, Jones & Norris* 454 (GH,US). **Santiago:** at base of la Cotorra, *Marciano & Marciano* 4868 (US). **Haiti. Ouest:** Massif de la Selle, Petionville between Fort Jacques and Cadets, *Ekman* 1813 (TEX); Massif de la Selle, Port au Prince, near Dufresnay, *Ekman* 1469581 (F); Plateau Pistache, Massif de la Selle, *Proctor* 10759 (US); Morne de Commissaires, *Holdridge* 1049 (MICH,US); Marmelade, Camp no. 4, *Nash & Taylor* 1255 (NY,US). **Jamaica. Portland:** below Portland Gap, *Crosby, Hespenehede & Anderson* 873 (DUKE,MICH,TEX); Gordon Town, *Hart* 585 (US); Portland Gap, *Hatch* 7/11/32 (NY); New Haven Gap Trail, *Johnson* 1393702 (F); vicinity of St. Helen's Gap, *Maxon & Killip* 1334 (GH,US). **St. Andrew:** Cinchona, *Adams* 8778 (DUKE); Craig Hill, *Adams* 11198 (DUKE,MO); Cinchona, *Anderson & Sternberg* 3166 (GH,MICH); ridge from Morces Gap to John Crow Peak, near the Portland border, *Anderson & Sternberg* 3460 (DUKE,GH,MICH); near Bellivue, *Eggers* 3773 (US); Blue Mts., leeward slopes, *Harris & Laurence* C15181 (US); near Cuichona, *Harris* 12414 (GH,MO,NY); Green River between Pleasant Hill and Green Valley below Cinchona, *Maxon & Killip* 1035 (F,US); Blue Mts., *Perkins* 1476 (GH); Blue Mts., Cinchona, *Phillipson* 908 (MO); between Guava Ridge and Bellevue, Port Royal Mts., *Proctor* 23561 (MICH,NY,TEX); Blue Mts. near Morces Gap, *Rehder* 2/10/03 (GH); between Gordon Town and Guava Ridge, *Walker* 323 (GH,US); Morces Gap to Cinchona, *Weaver* (DUKE). **St. Thomas:** Blue Mts., between Portland Gap and Blue Mt. Peak, *Webster & Wilson* 5444 (GH,MICH,US).

*Garrya fadyenii* is restricted to the Greater Antilles and is completely isolated from other *Garrya* taxa. Except for the smaller floral bracts



MAPS 9-10. Distribution of *Garrya*: 9, *G. fadyenii*—West Indies. 10, *G. corvorum* (dots); *G. laurifolia* ssp. *quichensis* (triangles)—Central America.

and the tomentose leaf pubescence, *G. fadyenii* morphologically resembles *G. laurifolia*. The trichomes of *G. fadyenii* appear similar to those of *G. longifolia*, *G. laurifolia*, and *G. salicifolia*, showing a counterclockwise orientation of very coarse and widely spaced ridges and furrows. Protuberances, as with the other southern Garryas, are absent. The size, shape, and fine structure of *G. fadyenii* pollen is quite similar to that of *G. laurifolia*. An examination of the flavonoid constituents within *G. fadyenii* reveals a high number of unique compounds. These probably developed in response to environmental influences and geographical isolation which allowed for their independent development unimpaired by the effects of hybridization and gene flow.

*Garrya fadyenii* is a tree species commonly associated with limestone soils at high elevations. While approaching *G. laurifolia* in some respects, it is sufficiently distinct to warrant specific status.

### 13. *Garrya longifolia* Rose

*Garrya longifolia* Rose, Contrib. U.S. Nat. Herb. VIII: 55. 1903-05.

HOLOTYPE: Mexico, Morelos, Sierra de Tepoxtlán, 1899, *Pringle 6998* (US). ISOTYPE: GH.

*Garrya gracilis* Wang., Das Pflanzenreich IV, 56a: 16. 1910. LECTOTYPE: Mexico, Morelos, Sierra de Tepoxtlán, 2500 meters, *Pringle 8363* (B), not seen. ISOTYPES: F, GH, MICH, MO, US.

Shrubs to trees, 10-25 feet high. Crown sprouts well-developed. Young stems pubescent, glabrate with age, silver-gray, green, reddish-brown or dark gray. Branching decussate and ascending. Stipules absent. Leaves simple, petiolate, decussate, oblong-elliptical or lanceolate, delicate, subcoriaceous, persistent. Petioles (0.5-)0.8-1.4(-1.6) cm. long; opposite petioles connate at the base, adnate to the stem. Leaf blades (4.5-)7.0-16.0(-18.0) cm. long, (1.5-)2.5-5.5(-6.5) cm. wide; apices acute, apiculate or obtuse; margins entire, plane, or weakly undulate. Upper surface glabrous, yellow-green or bright green, reticulate with impressed yellow veins; lower surfaces woolly when young, villous or glabrate with age, yellow-green or bright green, midrib and major lateral veins prominent; papillae well-developed. Staminate inflorescences racemose, branched, pendulous, fasciculate or solitary on branchlets, 6-12 cm. long, sparsely flowered; internodes elongated, pubescent. Staminate floral bracts narrowly ovate-lanceolate, 3-10 mm. long, recurved; opposite bracts wide and connate at the base. Flowers solitary in bract axils. Pedicels short. Perianth segments four, oblong-elliptical, apices connate, pubescent on the abaxial side, the adaxial side glabrous. Stamens free, short, alternating with the perianth segments. Anthers oval-oblong, 2-3 mm. long, basifixed, introrse, opening by longitudinal slits. Filaments about the same length as anthers. Pollen tricolporate, reticulate, yellow-green or orange-brown. Pistillate inflorescences racemose, branched, pendulous, fasciculate or solitary on branchlets, lax, sparsely flowered, 8-20 cm. long, graceful with conspicuous pubescent internodes. Pistillate floral bracts linear-lanceolate, 0.5-2.0 cm. long, petiolate or subsessile, sometimes foliaceous but smaller than the foliage leaves, abaxial side sericeous. Opposite bracts connate at the base. Flowers solitary, often sessile in the bract axils. Pedicels minute. Ovaries bicarpellate, rarely tricarpetate, unilocular, pubescent when young. Styles two, rarely three, persistent, short, thick, fleshy, semierect. Fruit a berry, subglobose-oval, green becoming glabrate, dark blue and brittle at maturity. Dehiscence irregular. Seeds two, rarely three, globose, subterminal on parietal placentas, dark blue or black.

Flowering from January through March at elevations ranging from 4200–8700 feet throughout central Mexico depending on the rainfall (Map 7).

REPRESENTATIVE SPECIMENS. **Mexico.** **Durango:** ca. 20 mi. SE of El Salto along Hwy. 40, *Dahling* 372 (GH); Cerro Huehueto, S of Huachichiles, ca. 75 mi. W of C. Durango, *Maysilles* 8015 (MICH). **Distrito Federal:** Pedregal, *Miranda* 1248 (MEXU). **Guerrero:** 23–24 km. E of Petatlan on road to Teapa at km. 123–124, *Anderson & Anderson* 5755, 5756 (MICH); Taxco, *Miranda* 3065 (MEXU); Tixtla Chilapa, *Miranda* 3980 (MEXU); trail from Taxco to Casahuates by small reservoir at head of waterfall above town, mts. W and above Taxco, *Moore* 5532 (GH, MICH); Cruz de Ocote, Municipio de Chihihualo sobre el camino de Xochipala al aserradero Agua Frio, approximately 43 km. W de Chilpancingo, *Rzedowski & McVaugh* 304 (MICH, MSC, TEX); shelf of bluff W of Chilpancingo, *Sharp* 441404 (MEXU, MO). **Jalisco:** Sierra de San Sebastian, 15–30 km. N of Mascota on the road to San Sebastian, *Anderson & Anderson* 5966 (MICH); 7–8 mi. NW of Los Volcanos along road between Ayutla and Mascota, *McVaugh* 12199 (MEXU, MICH); NE slopes of Nevado de Colima below Canoa de Leoncito, *McVaugh* 13478 (MEXU, MICH, TEX); Sierra de Cuale, SW of Talpa de Allende, SW of Pidra Rajada, *McVaugh* 14367 (MEXU, MICH, TEX), 14367A (MICH); N of La Cuesta below pass to Talpa de Allende, *McVaugh* 23344 (MICH); Sierra del Halo, near lumber road leaving the Colima Highway, 7 mi. SSW of Tecalitlan and extending SW to San Isidro, *McVaugh & Koelz* 1258 (MICH); San Sebastian, Segundo Arroyo, *Mexia* 1560 (GH, MICH, MO, US); trail from Real Alto to San Sebastian, *Mexia* 1633 (GH, MICH, MO, US); between San Sebastian and the summit of the Buffa de Mascota, *Nelson* 4114 (GH, US); San Juan Cosala, N of Lake Chapala, *Puga* 3/29/64 (MICH). **Mexico:** growing in Popo Park, about 3 mi. S of Amecameca along Hwy. 115, *Dahling* 520 (GH); along Hwy. 55, about 2 mi. N of Tenancingo, *Dahling* 714 (GH); along Hwy. 55 about 1 km. N of Villa Guerrero, *Dahling* 741 (GH); Cajones, Temascaltepec, *Hinton* 2385 (MO, US), 3201 (F, MO, US), 3666 (US). **Michoacan:** scattered along Hwy. 15, a few miles NW of Quiroga in view of the lake, *Dahling* 149 (GH); a few miles W of Patzcuaro in the hill-ravine area along the main highway, *Dahling* 670 (GH); Tancitaro, pedregal, *Hinton* 15641 (US), 15698 (GH, MEXU, MICH, US); between Jerdan and Uruapan, *Ikhagman* 3255 (MEXU); E of San Juan Nuevo about 8 km. S of Uruapan, *King & Soderstrom* 4755 (MEXU, MICH, TEX, US); between Rio de Salto and La Polvilla about 18 mi. E of Morelia, *King & Soderstrom* 5102 (MEXU, MICH, TEX, US); 2 mi. S of Tancitaro, pedregal, *Leavenworth* 571 (F, GH); Tancitaro, *Leavenworth & Hoogstraal* 1045 (MICH); 3 mi. S of Tancitaro, *Leavenworth & Hoogstraal* 6000 (GH, MO); NW of Aguillilla, about 6–7 km. S of Aserradero Dos Aguas, *McVaugh* 22714 (MICH); Sierra de San Joaquin, 11 km. al S de Talpujahua, *Moreno-G.* 191 (MICH); Patzcuaro, *Pringle* 3590 (GH); wet ravines near Patzcuaro, *Pringle* 3989 (GH, MO, MSC, US); between El Llano and Caleras, S of Zitacuaro, *Ramos* 612 (MEXU); near Uruapan, *Woronow* 701290 (F). **Morelos:** behind Amatlan on trail to San Jose Laurales, *Breedlove* 8045 (MICH); about 2–3 mi. W of Tepoxtlan along Hwy. 115D, *Dahling* 502 (GH); SW of Huitzilac, *Davis & Kincaid* 55–70 (TEX); Km. 53 on the Mexico-Cuernavaca Rd., pedregal, *Gomez-P.* 342 (MEXU); Valle de Tepeite, Valle de Cuernavaca, *Lyonnet* 730 (MO, US); Camino Real a Huitzilac, *Palacios* 11/24/64 (MICH, TEX); Sierra de Tepoxtlan, *Pringle* 6988 (F, MICH, MO, US); Sierra de Tepoxtlan, *Pringle* 8363 (F, MICH, MO, US); Sierra de Tepoxtlan, *Pringle* 9819 (F, MO, US); 10 km. NW de Tepoxtlan sobre la autopista Mexico-Cuernavaca, *Rzedowski* 26931 (MICH, MSC). **Oaxaca:** Oaxaca, *Bruff* 1276 (MEXU); Cerro San Blas Huanchilla, Santa de Nochiztan, *Conzatti* 3964 (MEXU, US); along Hwy. 190, NW of Huajuapán, *Dahling* 256 (GH); along Hwy. 190 near Huajuapán in the mountains, *Dahling* 260 (GH); about 27-1/2 mi. S of Oaxaca on Hwy. 190 near top of mt. chain in view of the Microwave Tower, *Dahling* 999 (GH).

*Garrya longifolia* is distinguished from other *Garrya* species by its long, branching, lax inflorescences. Both the male and female

inflorescences show elongated internodes and reduced floral bracts (Plate 8A). Although plants of this species are typically trees, shrubs are sometimes found in disturbed areas near roadways. The larger individuals usually are located in forested areas at elevations up to 9000 feet.

Over the years, the taxonomy of *Garrya longifolia* has become somewhat confused. The description of *G. longifolia* in Wangerin's monograph (1910) states "Flores masculi ignoti." They were unknown to Wangerin because he placed the male-flowered specimens in his new species, *G. gracilis*, which was described in the same work. This was curious, since the female elements of *G. gracilis*, although collected outside the *G. longifolia* type locality, were themselves typical members of *G. longifolia* as described by Rose (1903-05).

*Garrya longifolia* appears closely related to, and often intergrades morphologically with, *G. laurifolia* when they are in contact. SEM investigation shows that the trichomes of *G. longifolia*, *G. laurifolia*, *G. salicifolia*, and *G. fadyenii* are quite similar. The leaves of *G. longifolia* are subcoriaceous and therefore resemble leaves of *G. salicifolia* and *G. laurifolia* ssp. *racemosa*. The pistillate inflorescences are also quite similar to the lax inflorescences of *G. salicifolia*. Although the size of the *G. longifolia* pollen is similar to that of *G. laurifolia*, the fine structure of the exine is quite different and can be readily distinguished from the pollen of other *Garrya* taxa.

While complete reproductive isolation has not been achieved, and although hybridization with *Garrya laurifolia* does occur, *G. longifolia* is sufficiently distinct in most areas to justify its retention at specific rank. Moreover, this is also suggested by phytochemical data showing that the flavonoids of *G. longifolia* are rather different from those of other members of *Garrya*.

#### 14. *Garrya laurifolia* Benth

Shrubs to tall trees, 10-35 feet tall. Crown sprouts numerous. Young stems tomentose, with age reddish-brown and glabrate. Decussate, sometimes weakly ascending branching. Stipules absent. Leaves simple, petiolate, decussate, lanceolate to elliptical or oblanceolate, thick, coriaceous, persistent. Petioles (0.7-)1.0-2.5(-3.0) cm. long; opposite petioles connate at the base, adnate to the stem. Leaf blades (5.5-)8.0-16.5(-19.5) cm. long, (2.2-)3.0-7.5(-8.6) cm. wide; apices apiculate, mucronate; bases subobtusate or tapering. Margins entire, plane or weakly undulate; upper surfaces glabrous, lustrous, dark green; lower surface villous or lanate, becoming glabrate with age, green or grayish-white and brown; midrib and venation prominent and impressed above, less conspicuous or obscured below. Staminate inflorescences racemose, branched, pendulous, fasciculate at the ends of the branchlets, compact, 3-6 cm. long, pilose internodes inconspicuous. Staminate floral bracts ovate to lanceolate, 3-6 or rarely 8 mm. long, apices acute or acuminate; opposite bracts connate at the base. Flowers solitary, partially enveloped and in the bract axils. Pedicels 2-3 mm. long or lacking. Perianth segments four, oblong to elliptical, connate at the apices, abaxial side variably pubescent, adaxial

side glabrous. Stamens four, free, short, alternating with the perianth segments. Anthers oblong, 2–4 mm., basifixed, introrse, opening by longitudinal slits. Filaments about the same length as the anthers. Pollen tricolporate, reticulate, yellow-green. Pistillate inflorescences racemose, branched, pendulous, fasciculate or solitary on branchlets, lax, tomentose, 5–12 cm. long, internodes conspicuous. Pistillate floral bracts foliaceous, often as large as foliage leaves, tomentose when young, glabrate or less pubescent with age; opposite bracts connate at the base. Flowers solitary in the bract axils. Pedicels minute, rarely 5 mm. or larger. Ovaries bicarpellate, rarely tricarpetate, unilocular, subglobose, sometimes with paired bracts opposite the styles, pilose, glabrate with age. Styles two, rarely three, persistent, short, thick, fleshy, divergent. Fruit a berry, glabrate, green, dark blue, rarely whitish-gray, brittle at maturity. Dehiscence irregular. Seeds two or rarely three, oval, subterminal, parietal placentas, dark blue or black.

## KEY TO THE SUBSPECIES

- A. Leaves broadly elliptical, 10–18 cm. long and 4.5–9.0 cm. wide. . . . . 14b. *G. laurifolia* ssp. *macrophylla*.  
 A. Leaves long elliptical sometimes oblanceolate, 6.0–19.0 cm. long and 2.0–5.5 cm. wide.  
 B. Mature leaves tomentose below . . . . . 14a. *G. laurifolia* ssp. *laurifolia*.  
 B. Mature leaves glabrate or slightly pubescent below.  
 C. Leaves oblanceolate-long elliptical. Some pistillate floral bracts distinctly leaf-like and as long as the foliage leaves. . . . . 14c. *G. laurifolia* ssp. *racemosa*.  
 C. Leaves elliptical or long elliptical. Pistillate floral bracts not expanded to the size of foliage leaves . . . . . 14d. *G. laurifolia* ssp. *quichensis*.

14a. *Garrya laurifolia* Benth. ssp. *laurifolia*

- Garrya laurifolia* Benth., Pl. Hartweg. 14. 1839. HOLOTYPE: Mexico, near Guanajuato, 1839, Hartweg 81 (K). ISOTYPES: K, GH.  
*Fadyenia laurifolia* Endl., Gen. Suppl. IV: 37. 7 Based on *Garrya laurifolia* Benth.  
*Garrya oblonga* Benth., Pl. Hartweg. 51. 1840. HOLOTYPE: Mexico, hills near Regla, 1839, Hartweg 385 (K).  
*Fadyenia oblonga* Endl., Gen. Suppl. IV: 38. 1847. Based on *Garrya oblonga* Benth.  
*Garrya laurifolia* var. *genuina* Wang., Das Pflanzenreich IV, 56a: 14. 1910. Based on *Garrya laurifolia* Benth.

Shrubs to trees, 6–20 feet high. Crown sprouts numerous. Young stems pubescent. Leaves elliptical-long elliptical, plane; upper surfaces glabrous, lustrous, reticulate-rugose; lower surfaces tomentose, whitish-gray or brown with age. Ovary pubescent, frequently with prominent adnate bracts opposite the styles. Fruit glabrate, dark blue at maturity.

Flowering February through March at elevations of 2000–9000 feet throughout central Mexico (Map 8).

REPRESENTATIVE SPECIMENS. **Mexico.** **Águascalientes:** Sierra de Laurel, ca. 10 mi. SE of Calvillo, *McVaugh & Koelz* 220 (MICH). **Chihuahua:** Arroyo Hondo, Sierra Charuco, *Gentry* 8065 (MEXU,MICH,US); Guayanopa Cañon, Sierra Madre Mts., *Jones* 1903 (US), *Jones* 77759 (POM); Mojarachic, *Knoblock* 5601 (F,MSC), *Knoblock* 5788 (MSC,UC), *Knoblock* 7053 (MSC,US); below Basaseachic, *LeSeur* 808 (TEX), *LeSeur* 824 (RSA,TEX), *LeSeur* 825 (MO,US); Chihuahua, *Lumholtz* 1022 (US); La Pulvosa, *Martin* 56035 (MICH); Lagotera, *Pennington* 86, 179 (TEX); near Chuichupa in Sierra Madres, *Townsend & Barber* 428 (F,GH,MEXU,MO,MSC,TEX,US). **Durango:** 31 mi. N of Estacion Coyotes, N of La Dieneguita, *Breedlove* 18839 (CAS,RSA); Tepehuanes, *Fisher* 44274 (GH,MO); 10–12 mi. W of La Ciudad,

38-40 mi. W of El Salto along the rd. to Mazatlan from C. Durango, *Gentry & Gilly 10613* (MEXU,MICH,TEX); San Luis, 51 rd. mi. NW of Coyotes, *Maysilles 7215* (MEXU,MICH,US), *Maysilles 7951* (MICH,TEX); Quebrada de San Juan, 26 mi. N of railroad at Coyotes on rd. to San Luis, *Maysilles 8299* (MEXU,MICH); 34 mi. N of railroad at Coyotes, Laguna de Progreso, *Maysilles 8384* (MICH); Llano Grande, 42 mi. WSW of C. Durango, *Maysilles 8479* (MEXU,MICH). **Distrito Federal:** Lomas de Mixcoac, *Lyonnet 2049* (US). **Guanajuato:** along Hwy. 110 between Santa Rosa and Guanajuato near the 88 km. post, *Dahling 294* (GH); 14.5 mi. from Guanajuato on rd. to Dolores Hidalgo, *Johnston 2643* (MEXU,MICH,TEX); mts. ESE of San Jose Iturbide and ca. 5 mi. W of Cerro Zamorano near Mesa de Gato, *McVaugh 10387* (MEXU,MICH). **Hidalgo:** Cerro Juarez, 8 km. N de Tasquillo, *Qunitero 2932* (MICH,TEX); Peñas Largas, cerca de Texoantla, municipio de Real del Monte, *Rzedowski 22194* (MICH,MSC,TEX). **Mexico:** Valley of Mexico, *Rose & Hay 5366* (US). **Michoacan:** Quincho Cascade, vicinity of Morelia, *Br. Arsené 5409* (GH,MO,US). **Nayarit:** Volcan Caboruco, *Paray 3407* (MICH). **Puebla:** Chipantla, *Liebmann 2785* (F); Puente del Emperador, *Lyonnet 1039* (US). **Oaxaca:** Loma del Gallo, 3.5 km. al S de Magdalen Jicotlan, *Cisneros 2257* (MICH,RSA); near Reyes, *Nelson 1730* (NY,US). **San Luis Potosi:** San Luis Potosi, *Schaffner 2gi* (US). **Veracruz:** near the Puebla border, *Martinez 81* (US). **Zacatecas:** 38 km. al W de Jalpa sobre la carretera a Tlaltenango, 30 km. del entranque con la carretera Jalpa-Juchipila, *Rzedowski & McVaugh 1032* (MICH).

*Garrya laurifolia* ssp. *laurifolia* is a common constituent of the shrub zone on high mountain slopes. Although it usually inhabits the transition region between the arid lowland and the moist highland forests, *G. laurifolia* ssp. *laurifolia* is not restricted to this zone but occasionally extends into the forests. Individuals at these higher elevations commonly have narrower and less coriaceous leaves than is typical for other members of the taxon. Of the other subspecies within *G. laurifolia*, ssp. *macrophylla* appears to be closest to ssp. *laurifolia* as shown by similarities in pollen, pubescence, and leaf shape. Moreover, the flavonoid content of all the subspecies is fairly uniform suggesting close infraspecific relationships.

14b. *Garrya laurifolia* ssp. *macrophylla* (Bentham) Dahling,  
comb. nov.

- <sup>243</sup> *Garrya macrophylla* Benth., Pl. Hartweg. 50. 1840. HOLOTYPE: Mexico, Barranca del Encarnacion, 1839, Hartweg 50 (K).  
<sup>244</sup> *Fadyenia macrophylla* Endl., Gen. Suppl. IV:38. 1847. Based on *Garrya macrophylla* Benth.

Shrubs to trees, 8-18 feet high. Crown sprouts developed. Young stems pubescent. Leaves large, somewhat revolute, broadly elliptical, up to 8 cm. long and 9 cm. wide; leaf upper surfaces glabrous, lustrous, reticulate; leaf undersides tomentose, gray or with age dark brown. Ovary pubescent. Fruit glabrate, dark blue, brittle at maturity.

Flowering March through April at elevations of 3500-8850 feet from northern to southern Mexico (Map 8).

REPRESENTATIVE SPECIMENS: **Mexico.** **Hidalgo:** 13 mi. NE of Zimapan, *Anderson & Laskowski 4028* (GH,MICH,US); along Hwy. 85, ca. 12 mi. N of Zimapan near the 57 km. post, *Dahling 318* (GH); ca. 11 mi. SW of Jacala, along Hwy. 85 near the 89 km.



post, *Dahling* 590 (GH); at second zinc mine site, 12 mi. up rd. W of Mexico 85, 2 mi. N of Zimapan, *Mears* 292A (TEX); NE of Jacala at km. 281, Puerto de la Zorro, *Moore* 3802 (MEXU); 7 km. NE of Jacala, *Quintero* 1331 (MICH, MSC); 12 km. from Alfajayucan, *Quintero* 2056 (DS); 3 km. N of Jacala, *Rzedowski* 27675 (DS). **Mexico:** E de Mexico, between Tultenango and Tulpetlac, *Villada* 5 (MEXU). **Nuevo Leon:** Potosi Mt., along the Communication Tower Rd., a few miles NW of Galeana, *Dahling* 100 (GH); Mt. Anahuac, Monterrey, *Kenoyer* C93 (TEX); 15 mi. W of Dulces Nombres, municipality of Zaragoza, Cerro del Viejo, *Meyer & Rogers* 3040 (MO); Sierra Madre Mts., Monterrey, *Mueller & Mueller* 210 (GH, MEXU, TEX); between San Francisco Cañon and Pablillo ca. 15 mi. SW of Galeana, *Mueller & Mueller* 373, 382, 392, 634 (GH, MICH, TEX); Guajuco Cañon, El Cercado, *Mueller & Mueller* 1313 (GH, MICH, TEX, US); Sierra Madre Oriental above the Puertos, El Cercado, *Mueller & Mueller* 1341 (GH, MEXU, MICH, TEX, US); Cerro Potosi, *Rzedowski & Hinton* 17281 (MICH); Cerca de Los Hoyos, Km. 53 of the San Luis Potosi-Rio Cerde Road, *Rojas, Rzedowski & Salazar, Pr-1177* (MEMO, MEXU). **Oaxaca:** Cerro Zempoaltepetl, E slope, *Schultes* 547 (GH, US). **Puebla:** San Luis Tultitlanapa, near Oaxaca border, *Purpus* 3370 (GH, MO, US), *Purpus* 3371 (MO, US); 25 km. al N de Tehuacan cerca del Puerto Olivo, *Rzedowski* 18850 (MEXU, MICH, TEX). **San Luis Potosi:** 20-35 mi. W of San Luis Potosi along the road to Rio Verde, *Gentry, Barclay & Arguelles* 20166 (US); Km. 55 carretera San Luis-Rioverde, *Rzedowski* 4471 (TEX); 8 km. al NW de Guadalcazar, *Rzedowski* 5985 (MICH). **Tamaulipas:** Cerro Carrizo, *Bartlett* 10507 (F, MICH, US); Cerro Carrizo, vicinity of San Jose, *Bartlett* 10509 (GH, MICH); Cerro Carrizo, *Bartlett* 10516 (F, MICH, US); Gomez Farias region, Sierra de Guatemala, above Rancho del Cielo Biological Station, *Johnston* 7407 (TEX); Laguna Zarca, SE of La Joya de Salas, *Martin* H12 (MICH); La Joya Prieta, 4 km. SE of Carabanchel on trail to Montechristo, *Martin* H13 (MICH); Villa Mainero, Arroyo La Oveja, 10 km. SW of Pueblo, *Martinez* 2920 (MEXU); 8 mi. E of Dulces Nombres, *Meyer & Rogers* 2587 (GH, MO); 4 km. al S de Miquihuana, *Quintero* 3813 (GH, MICH, MSC); El Cielo to Ojo de los Indios and the Parque above Gomez Farias, *Sharp* 52155 (MEXU); 3-5 km. S of Huisachal, *Stanford, Lauber & Taylor* 2111 (UC, US); Gomez Farias region between Rancho del Cielo and Charco de los Perros, *Webster* 157 (TEX); near Rancho del Cielo Mine Rd., *Webster & Webster* 112 (TEX). **Veracruz:** Orizaba, *Botteri* 1 (US); ca. 26 km. N of Tehuacan along Hwy. 150, *Dahling* 620 (GH); Maltrata, *Matuda & Standley* 1220 (GH, MEXU, MICH, MO, TEX); Coscomatepec, *Matuda & Standley* 1325 (GH, MEXU, MICH, MO, TEX); Cerro San Cristobal, Orizaba, *Miranda* 4861 (MEXU); El Esquilon, municipio de Jilotepec, *Ventura* 4727 (MICH, RSA, TEX); Acejete, *Ventura* 5308 (MICH, RSA, TEX).

*Garrya laurifolia* ssp. *macrophylla* can usually be distinguished from other *Garrya* taxa by the large and extremely wide leaves. While distinct in some areas, it intergrades extensively with the closely related ssp. *laurifolia*. Frequently, *G. laurifolia* ssp. *macrophylla* is a shrub in dry localities but it becomes arboreal in moist sites. Also, the leaf dimension varies and appears related to the degree of aridity since in drier semiarid sites the leaves are smaller and less wide. As with most *Garryas*, *G. laurifolia* ssp. *macrophylla* is well-adapted to aridity and can maintain a green color even during the dry season when other plants have long turned brown.

14c. *Garrya laurifolia* ssp. *racemosa* (Ramirez) Dahling, comb. nov.

*Garrya racemosa* Ramirez, Anal. Inst. Med. Nac. Mex. 1:298. 1895. HOLOTYPE: Mexico, Morelos, Cuernavaca, *Ramirez* 431366 (US).

*Garrya laurifolia* var. *lanceolata* Wangerin, Das Pflanzenreich IV, 56a:16. 1910. HOLOTYPE: Mexico, *Uhde* 34 (B), not seen. ISOTYPE: B.

Large shrubs and trees, 8-35 feet high. Crown sprouts developed. Young stems pubescent. Leaves long-elliptical or oblanceolate, up to 4 cm. wide and 18 cm. long; margins plane; upper leaf surfaces glabrous, bright green, reticulate; lower leaf surfaces glabrate, bright green or green-yellow, rarely with sparse trichomes. Floral bracts as large as the foliage leaves. Ovary pubescent, becoming glabrous at maturity. Fruit dark blue or black.

Flowering from December through March at elevations of 3600-10000 feet throughout central Mexico (Map 8).

REPRESENTATIVE SPECIMENS. **Mexico. Distrito Federal:** Desierto de los Leones, W of Mexico City, *Dahling* 567 (GH); Cañada de Contreras, *Espinosa* 505 (MICH,TEX), 603 (US), *Rzedowski* 18276 (MICH,NY,TEX,US); Cañada de Contreras, junto al acueducto, *Espinosa* 649 (MEXU,MICH,TEX); La Marquesa, Desierto de los Leones, *Hernandez* 529 (TEX); Cañada de Contreras, cerca del Cuarto Dinamo, *Hernandez* 3/21/65 (MSC); Mixoac, *Lyonnet* 1262, 2971 (US); Desierto de los Leones, *Lyonnet* 2592 (US). **Guerrero:** Omiltemi, 20 km. al W de Chilpancingo, *Rzedowski* 15964 (MICH). **Hidalgo:** Money Station, Trinidad, *Pringle* 9/9/06 (MICH); 45 km. al E de Real de Monte, *Quintero* 12/19/64 (MICH,MSC). **Jalisco:** Cerro de Tequila al S Tequila, *Diaz* 414 (MICH); NW slopes of Nevado de Colima above Jazmin, 2-3 km. above the settlement of El Isote, *McVaugh* 10045 (GH,MICH,NY,TEX); NW slopes of Nevado de Colima above Jazmin, 1 km. above El Isote, *McVaugh* 10123 (MICH); N slopes of Nevado de Colima above sawmill called Piedra Ancha, *McVaugh* 11658 (TEX); Sierra de Manantlan, 20-30 km. SW of Autlan, along lumber rd. E of crossing called La Cumbre between El Chante and Cuzalapa, *McVaugh* 23155 (MICH). **Mexico:** near Amecameca, Sacromote Hill, *Beauchamp* 1926 (MO); San Nicolas, *Bourgeau* 997 (US); Km. 26.5 de la autopista Mexico-Puebla, *Cisneros* 532 (MSC); Valle de Bravo National Park, rd. leading to Valle de Bravo, about 21 mi. from Hwy. 15, *Dahling* 650 (GH); Nanchititla, *Hinton* 3605 (MO); Nanchititla-Temasaltepec, *Hinton* 3606 (US); Cumbre Temascaltepec, *Hinton* 5922 (US); Cruces Temascaltepec, *Hinton* 6852 (MICH,US); Temascaltepec, *Hinton* 8948 (US); Ixtaccapul, *Purpus* 237 (MO,NY), 1695 (MO,US); Sarrania de Ajusco, *Pringle* 12363 (US); 3 km. al E de San Rafael, municipio de Tlalmanalco, *Rzedowski* 19344 (MICH,MSC,TEX); 4 km. al NW de Santiago Tlazala, *Rzedowski* 27108 (MICH,MSC,RS,TEX); Sierra de Guadalupe, 6 km. al S de Coacalco, *Rzedowski* 30775 (MICH). **Morelos:** along Hwy. 95 about 10 mi. N of Cuernavaca, *Dahling* 561 (GH); al E de las Lagunas de Zempoala, Km. 9 carretera Tres Cumbres-Zempoala, *Palacios* 5/3/65 (MICH). **Sinaloa:** below Buenas Juntas, 5 mi. NW of Los Ornos along rd. to Mocorito, municipio of Sinaloa and Vela, Sierra Surotato, *Breedlove & Thorne* 18264 (MICH,RS); 3 mi. N of Los Ornos along rd. to Ocurahui, municipio of Badiraguato, Sierra Surotato, *Breedlove & Thorne* 18309 (MO,RS); Ocurahui, Sierra Surotato, *Gentry* 6370 (F,GH,MICH,MO). **Unknown:** mts., near Cuapinalpa, *Gregg* 686 (MO).

*Garrya laurifolia* ssp. *racemosa* is a distinctive tree, reaching heights of over 35 feet. It is often an important constituent of the secondary communities within high altitude coniferous forests where it grows well in moist sites. Although occasionally *G. laurifolia* ssp. *laurifolia* and ssp. *macrophylla* extend to the forest edges and intergrade with ssp. *racemosa*, the latter is generally separated from the other subspecies by its intolerance for arid conditions. The most distinctive character of *G. laurifolia* ssp. *racemosa* is its large foliaceous bracts found on the pistillate inflorescences. They reach lengths of nearly 20 cm.

14d. *Garrya laurifolia* ssp. *quichensis* (Smith) Dahling, stat. nov.

*Garrya laurifolia* var. *quichensis* Smith, Bot. Gaz. 54:237. 1912. HOLOTYPE: Guatemala, Department Quiche, San Miguel, Uspantan, 1892, *Smith* 3175 (US).

Shrubs to small trees, 10–35 feet high. Young stems pubescent, becoming glabrous, reddish-brown, or dark-brown with age. Leaves elliptical-long elliptical; petioles (0.8–)1.0–1.4(–1.6) cm. long, leaf blades (6.0–)7.5–10.5(–12.5) long, (1.8–)2.0–4.0(–5.5) cm. wide; margins plane; upper leaf surfaces glabrous, lustrous, reticulate; lower leaf surfaces sparsely pubescent becoming glabrate. Pistillate floral bracts narrowly elliptical, not expanded as foliage leaves. Ovary sparsely pubescent, becoming glabrous. Fruits glabrous, dark blue or black at maturity.

Flowering December to March at elevations of 4500–11700 feet throughout central and eastern Guatemala (Map 10).

REPRESENTATIVE SPECIMENS. **Costa Rica.** *Cartago:* 24.5 km. N of San Rafael on Costa Rica Rd. 8 to Volcan Irazu, *Almeda* 684 (DUKE); Volcan Irazu, S slope, *Hatheway & Perez* 1476 (US); S slopes of Volcan de Turrialba, *Standley* 34968 (US); N of Irazu, Potrero on Bridle Path, *Stork* 1271 (MICH); 1 km. from Rio Birris, about 9 km. NE of Cartago, *Wilbur* 14297 (GH,MICH,MO); NW of Ascuncion of the Cerro de La Nuerte, about 16 km. NW of Ascuncion, *Wilbur* 14585 (DUKE); Volcan Turrialba, trail from Finca Quernada, *Wilbur* 14640 (DUKE); near San Jose border, about 2 mi. NW of La Ascuncion and El Empalme on Interamerican Hwy., *Wilbur* 17392 (DUKE); Volcan Irazu, *Wilbur & Teeri* 13634 (MICH); upper slopes of Volcan Irazu, *Wilbur & Teeri* 13734 (GH,MICH,MO,TEX). **San Jose:** along trail to Valle de los Leones and lower part of Valle de los Conejos along upper Rio Talari, *Burger & Gomez-Pompa* 8299 (DUKE,MO); Cerro de las Vueltas, *Standley & Valerio* 43976 (US). **Guatemala.** *Chimaltenango:* Chichavac, *Skutch* 493 (GH,MICH,US), 700 (US); Cerro de Tecpan, region of Santa Elena, *Standley* 58738 (GH); Barranca de La Sierra, SE of Patzun, *Standley* 61567 (GH); between Los Idolos and Chocoyos, *Wallenta* 6220 (NY). **Guatemala:** near Finca La Aurora, *Aguilar* 292 (GH); 20 mi. E of Guatemala City, *Molina* 13539 (NY); 20 km. N of Ciudad Guatemala, *Molina & Molina* 12394 (US); slopes of Volcan de Pecaya, between San Francisco Sales and the base of the active cone, *Standley* 80720 (GH); Jalapa, between Jalapa and Montana Miramundo, *Steyermark* 32879 (GH). **Huehuetenango:** 4 mi. E of San Mateo Ixtatan on rd. to Barillas, Municipio of San Mateo Ixtatan, *Breedlove* 87777 (GH,TEX); 5 mi. S of San Juan Ixcay, Sierra de los Cuchumatanes, *Breedlove* 11512 (MSC); NW of Palestina on old rd. to Ostuncalco, *Standley* 84208 (GH,US); Volcan Santa Maria, vicinity of Santa Maria of Jesus, *Steyermark* 34248 (GH). **Quiche:** Quiche, *Aguilar* 969 (GH); Nebaj, near village on Cotzal Rd., *Contreras* 4887 (TEX); 2 km. E of Nebaj, *Contreras* 4916 (TEX); Nebaj, *Contreras* 4992 (DS,TEX,US), 4947, 5104 (TEX), *Skutch* 1904 (US); Nebaj on Sacapulas Rd., *Contreras* 4969 (MICH,TEX); San Miguel Uspantan, *Heyde* 3175 (US); S of Nebaj, *Proctor* 25177 (TEX); San Miguel Uspantan, *Smith* 3175 (US). **Sacatepequez:** Volcan Acatenango, *Kellerman* 4805; Volcano Agua, *Kellerman* 7443 (NY,US), 7452 (GH,US); near San Luca, *Molina* 15341 (GH,NY); Volcan Agua between Santa Maria de Jesus and San Juan Obispo, *Molina & Molina* 24916 (GH,MO); Cerro de la Cruz above Antigua, *Standley* 63329 (GH); between slopes of Volcan Santa Clara and town of San Pedro, *Steyermark* 47135 (GH); slopes N of Volcan Agua, near Km. 7 on rd. from Antigua to Santa Maria de Jesus, *Webster, Miller & Miller* 12847 (MO). **San Marcos:** Volcan Tajumulco between Las Canoas and the top of the ridge, 7 mi. from San Sebastian, *Steyermark* 3583 (GH); along rd. between San Sebastian and San Marcos, at Km. 21 and Km. 8, 8–18 mi. NW of San Marcos, *Steyermark* 35590 (GH). **Mexico.** **Chiapas:** valle E of Las Casas, *Alexander* 1105 (MEXU,MICH); W of Tenejapa, along trail to Paraiso, municipio of Tenejapa, *Breedlove* 6887 (GH); along trail to Colonia San Antonio from Tenejapa, municipio of Tenejapa, *Breedlove* 7020 (MICH); along trail from Tenejapa center to Pokolum, Barrio of Ho'Ho'Ch'en, Paraje of Shishintonil, *Breedlove* 7357 (GH,MICH); Chabul Ch'en in the paraje of Siganiil Ha', municipio of Tenejapa, *Breedlove* 7524 (MICH); 5 mi. N of Chamula Center, along rd. to Chenalho, municipio of Chamula,

*Breedlove 8146* (GH); SW of Hwy. 190 near Rancho Nuevo, 9 mi. SW of San Cristobal Las Casas, *Breedlove 9230* (GH, MEXU, MICH, TEX); barrio of Chinkh Ha', paraje of Yashanal, municipio of Tenejapa, *Breedlove 9380* (TEX); 1 mi. W of Nabenchauk along Hwy. 190, municipio of Zinacantan, *Breedlove 9527* (MSC); near the NE border of Aguacatenango, municipio of Venustiano Cerranza, *Breedlove 9661* (MSC); above Tenejapa Center along trail to Kulak'tik, municipio of Tenejapa, *Breedlove 10936* (MSC); along creek near the center of Amatenango, *Breedlove 12170* (MEXU, MSC); Teopisca, *Goldman 975* (US); Zinacantan Center Valley floor, *Laughlin 397* (MEXU, MICH); Kampana Ch'en along Hwy. 190, 3 mi. W of Paraje Navenchauk, municipio of Zinacantan, *Laughlin 1263* (MEXU, MICH); between Teopisca and San Cristobal, *Miranda 2727* (MEXU); Paraje Pahaltón, municipio of Tenejapa, *Ton 614* (MEXU, TEX); S of the center of Amatenango del Valle, *Ton 1122* (MSC); near Colonia Choro, municipio of San Pedro Chenalho, *Ton 2464* (DUKE); 3 mi. NW of Comitán, *Webster, Miller & Miller 12945* (MEXU, MO). **Panama.** *Chiriqui*: E side of Volcan Baru, from 3000 m. to just below the summit, *Mori & Bolten 7433* (MO).

*Garrya laurifolia* ssp. *quichensis* is confined to Central America and grows as a large shrub or tree in high mountainous areas and on volcanoes. As is common with other *Garrya* taxa such as *G. corvorum*, *G. fadyenii*, and *G. ovata*, *G. laurifolia* ssp. *quichensis* is frequently associated with limestone soil and outcroppings. It is the most geographically isolated of the subspecies of *G. laurifolia* since the Isthmus of Tehuantepec cuts the range of *G. laurifolia* and isolates *G. laurifolia* ssp. *quichensis* to the south.

Study of flavonoid constituents shows that *Garrya laurifolia* ssp. *quichensis* has become chemically different since its paired affinity index is distinctly lower than that of the other subspecies. Since its range does not overlap with the other *G. laurifolia* subspecies, these distinguishing chemical differences most likely developed in response to the greater isolation maintained by *G. laurifolia* ssp. *quichensis* throughout its history. Nevertheless, other morphological characters such as habit, leaf, pollen, and trichome structure support the connection with *G. laurifolia* and justify an infraspecific rank.

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THE GENUS *PENNELIA* (CRUCIFERAE)  
IN NORTH AMERICA

*Armando T. Hunziker*

STUDIES ON SOLANACEAE. XII.  
ADDITIONS TO THE GENUS  
*CHAMAESARACHA*

*A. Linn Bogle*  
and

*C. Thomas Philbrick*

A GENERIC ATLAS OF  
HAMAMELIDACEOUS POLLENS

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BY Otto T. Solbrig  
Kathryn Rollins

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## ANOTHER CRUCIFEROUS WEED ESTABLISHES ITSELF IN NORTH AMERICA<sup>1</sup>

REED C. ROLLINS

The Cruciferae is one of the plant families that has contributed a disproportionate number of introduced weedy species to the flora of North America. Many of these are of European origin but others came from North Africa, the Middle East and parts of Asia. In fact, the exact origin of most weedy crucifers now established in our flora cannot be ascertained. But the extent to which members of this family occupy vast territories once the haven of only native species is a cause for concern and regret. That these weeds occur in old fields and waste places is one thing but the many square miles of open desert in Utah and Nevada covered by *Sisymbrium altissimum* L. or the thousands of acres of the eastern Mohave Desert of California to Arizona with nearly a continuous stand of *Sisymbrium irio* L. are unwanted sights. I remember my first encounter with *Malcolmia africana* (L.) R. Br. in western Colorado in the year 1938. At that time, the species was scarcely known outside of the Salt Lake Valley in Utah, but now it is everywhere on the sheep ranges of western United States. *Chorispora tenella* (Pall.) DC. is another introduction whose geographic range has burgeoned in the past twenty years. Although widespread elsewhere in the west, it has found the western plains a particularly hospitable region in which to proliferate. Nearly forty years ago (Rollins, Contrib. Dudl. Herb. 3: 183, 1941), I reported the first known North American station for *Alyssum desertorum* Stapf, a species now widespread in the Intermountain West. *Alyssum alyssoides* L. has been around a long time and is common in old fields and waste places (as well as range-lands) all across the United States and southern Canada. Relative newcomers in this genus, *Alyssum minus* (L.) Rothm. and *Alyssum szowitsianum* Fisch. & Meyer are presently more restricted in their distribution in North America but they are spreading rapidly.

Although some of the annual species of the Cruciferae are difficult to control, especially in grainfields, gardens, etc., the real noxious members of this family are the perennials. For example, such species as *Cardaria draba* (L.) Desv., *C. pubescens* (Meyer) Jarm., *Rorippa sylvestris* (L.) Bess., and *Lepidium latifolium* L. are nearly impossible to clear out of irrigated lands once they get well-established. Therefore, it is with some alarm that I report a recently introduced perennial member of the mustard family. The comparative newcomer is *Brassica elongata* Ehrh. This species has turned up in a number of sites in eastern Nevada, particularly along U.S. Highway 50. The danger is

<sup>1</sup>Research supported by National Science Foundation Grant DEB 78-08766.

that the species will spread into the open desert where it could displace some of the native vegetation. A list of the localities where it has been found is given below.

*Brassica elongata* was brought to my attention by a specimen sent for determination by Mr. Sherel Goodrich (no. 8387) collected along Highway 50 about 50 miles east of Austin, Eureka County, Nevada, July 7, 1977. A search in the Gray Herbarium turned up a specimen misidentified as *Thelypodium* which was collected 13 miles west of Pancake Summit between Eureka and Ely, White Pine County, Sept. 2, 1968, by John Thomas Howell and Gordon H. True, their no. 44609. This appears to be the first record for the infestation in eastern Nevada but older specimens collected on ballast at Linnton, near Portland, Oregon, Sept. 2 and Nov. 3, 1911, *Wilhelm N. Suksdorf* 1704 and 1749 (GH) shows that the species came to North America at least once at a much earlier time. It is probable, as with many plants introduced on ballast, that *B. elongata* did not persist where Suksdorf first found it. At least, the species has not been recognized as part of the adventive flora of northwestern United States (Hitchcock and Cronquist, Fl. Pac. NW. 156, 1973). It is doubtful whether there is any connection between the Oregon introduction and that of Nevada. However, the source of the latter is not determinable at this time.

Following is a listing of more recent collections of *Brassica elongata*, all from Nevada. Eureka County: 26.6 miles west of Eureka, June 12, 1979, *Reed C. and Kathryn W. Rollins* 79216 (GH, duplicates to be distributed). White Pine County: 2.5 miles south of junction of highways 50 and 93, roadcut near KOA campground, June 28, 1978, *Margaret J. Williams* 78-164 (GH); same locality, June 25, 1979, *Margaret J. Williams* 79-97, *Laurie Birdsey and Arnold Tiehm* (GH); 12.1 miles east of Eureka, June 12, 1979, *Reed C. and Kathryn W. Rollins* 79215 (GH, duplicates to be distributed); 36.6 miles east of Eureka, June 12, 1979, *Reed C. and Kathryn W. Rollins* 79214 (GH, duplicates to be distributed); 30.2 road miles east of Eureka on Highway 50, near turn to Belmont Mine, June 28, 1979, *Arnold Tiehm* 5348, *Laurie Birdsey and Margaret J. Williams* (GH).

*Brassica elongata* is a deep-rooted fleshy perennial with numerous branches beginning just above the base and extending to the top of individual plants. Usually several main stems arise from a single root. The branches diverge at a wide angle and each is divided into many smaller branches which ultimately bear inflorescences of many flowers with yellow buds and bright yellow to orange-yellow petals. As the fruits mature, the infructescences become elongated including numerous siliques on straight divaricately ascending pedicels. It is clear that the individual plants are heavy seed producers and the possibility for rapid and continued spread is a feature of the plant.

Many patches of *Brassica elongata* were seen by the roadside (sometimes extending away from the road into the open desert) at intervals both east and west of Eureka for a distance of more than 100 miles. The species is obviously well-established and unless it is eradicated soon, an infestation of much larger proportions could easily take place.

According to Flora Europaea (Tutin et al., Fl. Eur. 1: 336, 1964), there are two subspecies of *Brassica elongata* based primarily on leaf form. Plants with somewhat divided leaves are most common in the western portion of the species range which could be characterized as southeastern Europe. Subspecies *elongata* was originally described from Hungary. It is subspecies *integrifolia* (Boiss.) Breistr. which has entire or nearly entire leaves that has become weedy in Nevada. This subspecies is native to the eastern part of the range of the species as a whole and is found in southern Russia, the Ukraine and extends southward to include at least Turkey and Iran. Both subspecies have become weedy even in their native areas where they are often found in fields and waste places. Each has been introduced elsewhere, as wasteland, roadside or field weeds, particularly in the Eastern Hemisphere.





# THE GENUS *Pennellia* (CRUCIFERAE) IN NORTH AMERICA<sup>1</sup>

REED C. ROLLINS

The genus *Pennellia* had its origin in the recognition by Robinson of section *Heterothrix* of *Thelypodium* in his treatment for the *Synoptical Flora of North America* (Robinson in Gray, 1895). Two species were included, *Thelypodium longifolium* (Benth.) S. Wats. and *T. micrantha* (Gray) S. Wats. Subsequently Rydberg (1907) raised section *Heterothrix* to generic rank. Nieuwland (1918) pointed out that *Heterothrix* had been used previously (Mueller, 1860) for a genus in the family Apocynaceae, and therefore *Heterothrix* of Rydberg is illegitimate. He proposed *Pennellia* as a replacement for *Heterothrix* and transferred *H. micrantha* to it. Thus *Pennellia micrantha* became the type species of *Pennellia*. However, Schulz (1924) used Rydberg's illegitimate *Heterothrix* when treating the group for *Das Pflanzenreich* and expanded it to include six species, three from North America and three from South America. In the course of his study, he became convinced that the species formerly known as *Heterothrix longifolia* should not be associated in the same genus with *H. micrantha* and described *Lamprophragma* as a monotypic genus to include it. Although no specific points were made by Schulz to justify splitting *Heterothrix longifolia* away from *H. micrantha*, it is clear from the protologue of *Lamprophragma* that he was much impressed with the slight zygomorphy present in the flower of *H. longifolia*. However, as distinctive as this feature is in *Pennellia longifolia*, it breaks down completely in *P. hunnewellii* where there is little or no zygomorphy shown by the flowers; yet this species is so close to what is here called *P. longifolia* that the collections of it have been included there up to the present. Schulz (1936) later recognized *Pennellia*.

The first two species of *Pennellia* described, *P. longifolia* and *P. micrantha*, were placed in *Streptanthus* (Benthams, 1839; Gray, 1849) but most subsequent authors have agreed that they do not belong in that genus. In fact, *Pennellia* is not closely related to *Streptanthus*. An early different disposition of these species was that of Watson (1871, 1882) who referred them to *Thelypodium*. However, Al-Shehbaz (1973) has concluded that species presently included in *Pennellia* do not belong to *Thelypodium*.

As *Pennellia* is now known from North America, including Mexico and Central America, it consists of eight species. We have deliberately not attempted to treat the species of South America because there is so little material available for study. Even with the North American species, one (*P. juncea*) is known from only one collection, a second

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(*P. mcvaughii*) is known from but two collections, and a third species (*P. robinsonii*) from only three collections. The genus is primarily Mexican with only two species occurring northward into southwestern United States. These are the two most widespread and best known species, *P. longifolia* and *P. micrantha*.

One of the distinctive features of *Pennellia* is the very small flower. In most species, just prior to full anthesis, the flower is cup-like in appearance with the petals only slightly exceeding the sepals. In some, the flower is almost closed. But as flower growth continues, both sepals and petals not only increase in length but they are less tightly associated than in early stages. The largest flower, with petals nearly twice the length of the sepals when fully expanded, is found in *P. mcvaughii* and this is exceptional. However, the flower form is in almost exactly the same mold as the other species with the exception that the petals only slightly exceed the sepals in all other species. The siliques of *Pennellia* are terete to very slightly flattened, very narrow (often ca. 1 mm. wide) and elongated. The seeds are numerous, either in a single or partially double row, and are often very crowded so that the seeds themselves are distorted in shape. The cotyledons are incumbent.

*Pennellia* is most closely related to the genus *Halimolobos* which in turn has been considered very close to *Sisymbrium*. Many of the species now placed in *Halimolobos* have been treated as *Sisymbrium* at one time or another. *Halimolobos berlandieri* is very much like *Pennellia patens* in general appearance and these two species of different genera can easily be mistaken for each other if only superficially examined. However, technical characters readily separate them. Recent trends in the systematic treatment of the Cruciferae have demanded a closer unity among the species of a given genus than was formerly acceptable. In part, this reflects an increased knowledge of the species and a better understanding of the interrelationships within each species group. This is especially true of genera whose species are concentrated primarily in Mexico or South America where new collections are providing the basis for a completely new assessment of their taxonomy.

***Pennellia*** Nieuwland, Amer. Midl. Natur. 5: 224. 1918.

*Heterothrix* Rydberg, Bull. Torr. Bot. Club 34: 435, 1907; not *Heterothrix* Mueller, 1860.

*Lamprophragma* O. E. Schulz, Das Pflanzenreich IV. 105: 298. 1924.

Biennial or perennial herbs, densely pubescent with mostly branched trichomes to glabrous; stems usually single from base, erect, branched above, up to 1.5 m. tall; basal leaves oblanceolate to broadly oblong, entire or sinuate dentate to shallowly

lobed, petiolate, the petiole often short, usually densely pubescent with branched trichomes (except in *P. juncea* which is glabrous throughout); cauline leaves petiolate to cuneate at base, usually narrowed and sessile upward; inflorescences narrowly racemose, terminating each branch; buds globose to obovoid; flowers most often remote, cup-shaped; sepals erect, non-saccate or the outer pair slightly saccate, often purplish; petals lingulate to spatulate, erect, purple to white, in most species barely exceeding sepals; stamens subequal, paired erect, single often with filament curved toward base; infructescences narrow, secund in some species; pedicels erect to arched downward, usually slender; siliques narrowly linear, erect or pendant, terete to slightly flattened parallel to septum, usually straight or nearly so and one-nerved at least below, sessile or with a short gynophore; styles present or absent; seeds small, mostly 1 mm. or less long, wingless, plump, often misshapen from overcrowding in the silique; cotyledons most often incumbent. Type species: *Pennellia micrantha* (Gray) Nieuwl. Chromosome numbers are known for only two species: *P. longifolia* (Benth.) Roll.,  $2n = 16$ ; *P. mcvaughii* Roll.,  $n = 8$ ,  $2n = 16$ .

## KEY TO THE SPECIES

- A. Siliques pendant; pedicels arched downward; infructescences usually secund.
  - B. Petals 4.5–6.0 mm. long, barely exceeding sepals; paired stamens included or nearly so; other floral parts relatively small.
    - C. Lower stems hirsute with coarse spreading simple or forked trichomes; basal and lower cauline leaves pubescent with coarse simple or few-branched stalked trichomes; buds and sepals glabrous; flowers slightly zygomorphic; pedicel apices asymmetrical . . . . . 1. *P. longifolia*.
    - C. Lower stems pubescent with fine appressed many-branched trichomes; basal and lower cauline leaves pubescent with fine dendritically branched trichomes; buds and sepals sparsely pubescent; flowers regular; pedicel apices symmetrical or nearly so . . . . . 2. *P. hunnewellii*.
  - B. Petals 9–21 mm. long, exceeding sepals by nearly half their length; paired stamens exerted by about one-third their lengths; other floral parts relatively large . . . . . 3. *P. mcvaughii*.
- A. Siliques erect or ascending; pedicels erect or divaricately ascending; infructescences not secund.
  - D. Pedicels and siliques erect or nearly so, usually appressed to rachis; infructescence narrow, usually dense.
    - E. Buds and sepals glabrous; fruiting pedicels less than 8 mm. long, usually 4–7 mm.; siliques less than 4 cm. long.
      - F. Siliques pointed, slightly compressed, less than 2 cm. long; styles evident; sepals deep purple; petals purplish . . . . . 4. *P. robinsonii*.
      - F. Siliques blunt, terete, more than 2.5 cm. long; styles obsolete or nearly so; sepals usually greenish; petals white . . . . . 5. *P. micrantha*.
    - E. Buds and sepals pubescent; fruiting pedicels more than 1 cm. long, siliques 4–6 cm. long . . . . . 6. *P. lasiocalycina*.
  - D. Pedicels rigidly divaricate; siliques erect to divaricate; infructescences broader, loose, pedicels usually remote.
    - G. Lower stems and leaves pubescent; fruiting pedicels 1 cm. or less long . . . . . 7. *P. patens*.
    - G. Lower stems and leaves glabrous; fruiting pedicels 1.5–2.0 cm. long . . . . . 8. *P. juncea*.

1. *Pennellia longifolia* (Benth.) Rollins

*P. longifolia* (Benth.) Rollins, *Rhodora* **62**: 16. 1960, based on *Streptanthus longifolius* Benth., Pl. Hartweg. 10. 1839. Type collected "In pascris montosis, Aguacalientes," Mexico, 1837, Hartweg 52. Holotype not seen, photo of type at Kew (MICH); isotype GH.

*Thelypodium longifolium* (Benth.) S. Wats., U.S. Geol. Explor. Fortieth Parallel (Bot.) V: 25. 1871.

*Heterothrix longifolia* (Benth.) Rydberg, Bull. Torr. Bot. Club 34: 435. 1907.

*Lamprophragma longifolium* (Benth.) O.E. Schulz, Das Pflanzenreich, Heft. 86. IV. 105: 299, fig. 63. 1924.

*Thelypodium anisopetalum* Greene, Pittonia 3: 247. 1897. Type collected in the Valley of Mexico, Federal District, Mexico, Sept. 30, 1896, C. G. Pringle 6548. Holotype not seen; isotypes F; GH, 2 sheets; MO; MSC; NY; PH; UC; US, 2 sheets.

Biennial; stems erect, most often single from base, branched above, usually virgate, 5-15 dm. tall, pubescent with coarse simple or forked spreading trichomes toward base, glabrous above; basal leaves usually not persisting beyond first year, rarely present on flowering or fruiting specimens, those seen petiolate, oblanceolate, entire to slightly sinuate, sometimes dentate, obtuse and short-petioled, i.e., petiole shorter than blade, mid-veins prominent below, 4-8 cm. long, sparsely pubescent on both upper and lower surface with simple stalked and forked or few-branched trichomes; cauline leaves linear, few, entire or lower shallowly dentate, narrower upward, sessile or lower with a short petiole, lower pubescent with coarse simple, forked, or few-branched trichomes, upper usually glabrous or nearly so; inflorescences terminating each branch, narrow and elongated; flowers remote, slightly irregular, cup-shaped; buds obovoid, glabrous; sepals purplish, oblong, 4-5 mm. long, 1.5-2.0 mm. wide; lateral pair slightly saccate at base, lower sepal larger than upper, both upper and lower non-saccate; petals purplish, narrowly lingulate, narrowing only slightly toward base, 5-6 mm. long, 1.0-1.5 mm. wide; paired stamens strictly erect, single stamens curved toward base; anthers erect, 1.0-1.2 mm. long, filament attachment below middle; glandular tissue surrounding base of single stamen filaments, only subtending paired filaments; pedicels slender, slightly ascending then arched downward, glabrous, 8-11 mm. long, markedly expanded and asymmetrical at apex; infructescences usually secund, 2-4 dm. long; siliques pendant, straight or nearly so, terete, glabrous, 6-8 cm. long, ca. 1 mm. wide, one-nerved from base nearly to apex; styles slender, 1.0-1.2 mm. long; seeds small, crowded, irregularly shaped, often angled, plump, marginless, variable in size, 0.7-1.3 mm. long, 0.4-0.5 mm. wide; funiculi slender, less than 1 mm. long; cotyledons incumbent, oblique or accumbent.  $2n = 16$  (Rollins and Rüdberg, 1977).

DISTRIBUTION: Arizona, Colorado, New Mexico, western Texas, and Mexico south to the Federal District. Mostly at elevations above 6,000 ft.

One of the outstanding and distinctive features of *Pennellia longifolia* when seen growing is the virgate or wand-like branches that bear pendulous siliques in a secund raceme. The plants are often a meter or more in height and may be abundant in favorable sites. They are sometimes aggressive colonizers, then tending to become established in disturbed places near or in cultivated fields, particularly in the mountains of Mexico.

It is difficult to understand why Schulz set this species apart as a monotypic genus. The flowers are so similar to those of *Pennellia micrantha* that the two species, when in flower, are sometimes misidentified as one another. The siliques, seeds, and other features are also basically of the same type and there are no fundamental differences that would justify placing these species into separate genera. The siliques are differently disposed, those of *P. longifolia* being pendulous while those of *P. micrantha* are erect. Plants in flower can be distinguished by the trichomes which are long-stalked and coarse

on the leaves, and simple or forked and spreading on the lower stems in *P. longifolia* while in *P. micrantha*, the leaf and stem trichomes are fine, many-branched, and extend farther up the stems than in the former species.

There is some variation in the intensity of pigmentation of both sepals and petals taking the full geographic range of *Pennellia longifolia* into account. In some populations, the sepals are markedly dark purple-red, other populations show less dense or incomplete coloration, the margins becoming whitish. The petals are similarly colored except the intensity is not as great or the coverage as complete as in the sepals. In some populations, the petals are nearly white.

In the protologue of *Pennellia longifolia*, Bentham (1839) did not give the place of collection of Hartweg no. 52, but supplied it in a subsequent fascicle of the publication as given above. According to McVaugh (1970), Hartweg collected in Aguascalientes between July 13 and September 17, 1837. The isotype specimen in the Gray Herbarium gives only the year, Mexico, the name Hartweg and the number 52 which Bentham assigned to the collection for purposes of publication and distribution.

REPRESENTATIVE SPECIMENS. **Mexico. Chihuahua:** Sierra de Santa Barbara, about 4 miles southwest of Villa Matamoros, 6,300 ft., Oct. 4-5, 1959, *D. S. Correll & H. S. Gentry* 22795 (GH); valley of Gonogochic, east of Creel and San Ignacio, Mpio. de Bocoyna, 7,400 ft., Aug. 24, 1973, *Robert A. Bye, Jr.* 4778 (GH); near Colonia Garcia in the Sierra Madres, 7,500 ft., July 29, 1899, *C.H.T. Townsend & C.M. Barber* 187 (F, GH, MEXU, MO, NMC, NY, POM, RM, UC, US); Memclichi, Rio Mayo, 7,500 ft., Sept. 16, 1936, *H. S. Gentry* 2738 (ARIZ, F, GH, MEXU, MO, UC, US). **Coahuila:** near summit at Las Cumbres Pass, 12 miles east of San Antonio, Sept. 28, 1974, *Reed C. Rollins and K. W. Roby* 7479 (GH); Canyon de Centinela, Sierra del Carmen, July 31, 1973, *James Henriksson* 11692 (GH); 26 km. northwest of Fraile, 3550 m., July 16, 1941, *L. R. Stanford, K. L. Retherford & R. D. Northcraft* 439 (ARIZ, GH, MO, NY). **Durango:** Otinapa, July 25-Aug. 5, 1906, *Edward Palmer* 546 (GH, NY, US); about 48 miles west of Parral and 12.5 miles west of Ojito, Sept. 13, 1972, *James L. Reveal & William J. Hess* 3053 (GH, MSC); arroyo of Rio Chico, 17 miles west/southwest of C. Durango, Sept. 1, 1951, *James H. Maysilles* 7659 (GH, MICH). **Federal District:** cerca del Cerro Conejo, al ENE de Ajusco, 2750 m., 23-VII-1967, *Rzedowski* 24118 (ARIZ, F). **Guanajuato:** summit east of Guanajuato, 8,000 ft., July 16, 1963, *Stuart K. Harris* 25887 (GH). **Hidalgo:** Tezoantha, Sept. 1945, *Maximino Martinez s.n.* (US); Sierra de Pachuca, Sept. 1, 1903, *J. N. Rose & Jos. H. Painter* 6734 (US); Pachuca, July, 1905, *J. N. Rose, Jos. H. Painter & J. S. Rose* 8850 (GH, US); below Guerrero on road from Real de Monte to Omitlán, Atotonilco el Grande, 2,700 m., July 30, 1948, *H. E. Moore, Jr. & C. E. Wood, Jr.* 4141 (GH). **Jalisco:** cerro viejo, cerca de la cumbre, municipio de Tlajomulco, Aug. 15, 1970, *Rzedowski* 27547 (MICH). **México:** near Santa Fe, Aug. 22, 1903, *J. N. Rose & Jos. H. Painter* 6501 (US); Cumbre Gavia, Sultepec, Oct. 27, 1935, *Geo. B. Hinton et al.* 8389 (NA, NY, PH, TEX, US); rich ravines, Mt. Orizaba, Aug. 8, 1891, *Henry E. Seaton* 250 (US); 8 km. al E de Coatlinchán, municipio de Texcoco, July 20, 1967, *Rzedowski* 24023 (MICH, MSC). **Michoacán:** vicinity of Morelia, Sept. 1, 1909, *G. Arsène* 7262 (US). **Nuevo Leon:** cerro Potosí, near microwave tower, ca. 9,000 ft., July 8, 1963, *R. L. McGregor et al.* 323 (GH); about 15 miles southwest of Galeana, June 28, 1934, *C. H. & M. T. Mueller* 907 (F, GH, MICH, TEX); Peña Nevada, 26 miles northeast of Dr. Arroyo, July 4, 1959, *John H. Beaman* 2707 (MSC). **Puebla:** Las Derrumbadas, municipio de Buenos Aires, Aug. 24, 1972, *F. Ventura A.* 5934 (GH). **San Luis Potosí:** in montibus

San Miguelito, 1876, *J. G. Schaffer 156* in part (CA, GH, MEXU, PH); Sierra de San Miguelito, cerca de El Capulín, Sept. 5, 1954, *Rzedowski 3993* (GH); San Luis Posotí, 1879, *J. G. Schaffer 556* (US). **Sinaloa:** steep slopes of barranca, 3 km. northeast of El Palmito, 1950 m., Aug. 12, 1974, *D. E. Breedlove 36458* (CAS, GH); 3 miles north of Los Ornos along road to Ocurahui, Sierra Surutato, Municipio de Badiraguato, 6,500 ft., Oct. 2, 1970, *D. E. Breedlove & R. F. Thorne 18344* (CAS); Ocurahui, Sierra Surutato, 6-7,000 ft., Aug. 27-30, 1941, *H. S. Gentry 6203* (ARIZ, DS, GH, MICH, MO, NY, PH). **Tamaulipas:** on Peña Nevada, July 18, 1949, *Stanford, Lauber & Taylor 2512* (NY, US) and *2512A* (US). **USA. Arizona. Apache Co.:** 1.5 miles east of Sheep Spring, 24-mile Draw, Sept. 5, 1949, *W. S. & T. K. Phillips 3365* (ARIZ, CAS); Riverside Ranger Station, Greer, 2,700 m., Aug. 24, 1920, *W. W. Eggleston 17158* (F, GH); 8 miles E of Nutrioso, Aug. 24, 1951, *K. F. Parker & E. McClintock 7516* (ARIZ, CAS, US). **Cochise Co.:** Rustler's Park, Chiricahua Mts., 8,000 ft., Oct. 21, 1974, *Reed C. Rollins & K. W. Roby 74197* (GH); same locality, Nov. 22, 1974, *Reed C. Rollins, Charles T. Mason, Jr. & George B. Cummins 74202* (GH). **Coconino Co.:** 13 miles north of Flagstaff, San Francisco Mts., 9,400 ft., July 20, 1946, *K. F. Parker 5992* (ARIZ, CAS, RSA); 3.5 miles from Flagstaff on Schulz Pass road, San Francisco Mts., 7,300 ft., Sept. 11, 1968, *John Thomas Howell & Gordon H. True 45064* (CAS, GH); San Francisco Mt., October, Sitgreaves Expedition of 1861 (GH). **Pima Co.:** Spud Ranch, Rincon Mts., 7,400 ft., Aug. 31, 1909, *J. C. Blumer 3316* (ARIZ, F, GH, MO). **Pinal Co.:** Santa Catalina Mts., Aug. 23, 1931, *G. J. Harrison & T. H. Kearney 8115* (ARIZ, CAS, F). **Yavapai Co.:** hills of boulders near Prescott on road to Ash Fork, Nov. 7, 1928, *Alice Eastwood 16728* (CAS). **Colorado. La Plata Co.:** river bottom, Bayfield, Aug. 9, 1917, *E. B. Payson 1151* (RM). **New Mexico. Catron Co.:** Mogollon Mts., 18 mi. northeast of Mogollon, 7,500 ft., Aug. 1, 1938, *C. L. Hitchcock et al. 4442* (CAS, NA, RM, UC, UCLA, UTC, WS, WTU). **Colfax Co.:** vicinity of Ute Park, Aug. 24, 1916, *Paul C. Standley 13719* (US). **Grant Co.:** Fort Bayard watershed, Sept. 3, 1905, *J. C. Blumer 53* (GH, NY). **Lincoln Co.:** White Mts., 7,000 ft., Aug. 11, 1897, *E. O. Wootton 316* (GH, MO, NMC, NY, POM, RM, UC). **Mora Co.:** Morphy Lake, July 24, 1972, *Larry C. Higgins 5860* (NY). **Rio Arriba Co.:** vicinity of Brazos Canyon, Aug. 21, 1914, *P. C. Standley & H. C. Bollman 10695* (US). **Sandoval Co.:** Sandia Mts., Sept. 6, 1884, *Marcus E. Jones s.n.* (GH, NY). **Santa Fe Co.:** near Glorieta, Aug. 30, 1928, *Emma Viveash s.n.* (F). **Sierra Co.:** Mineral Creek, 7,000 ft., Sept. 26, 1904, *O. B. Metcalfe 1417* (F, NY). **Socorro Co.:** Mogollon Mts., 7,500 ft., Aug. 2, 1903, *O. B. Metcalfe 350* (ARIZ, MO, NMC, NY, RM, UC). **Texas. Jeff Davis Co.:** Madera Canyon, Mt. Livermore, Aug. 5, 1935, *L. C. Hinckley 288* (F, NY, TEX); Mt. Livermore, Davis Mts., ca. 2250 m., July, 1936, *L. C. Hinckley s.n.* (GH).

## 2. *Pennellia hunnewellii* Rollins, sp. nov.

Perennial; stems one or few from an elevated crown, 5-12 dm. tall, branched above, pubescent below with appressed several to many branched trichomes, glabrous or sparsely pubescent above; basal leaves petiolate, oblanceolate, sinuate dentate, obtuse, strongly 1-nerved, 4-8 cm. long, 8-15 mm. wide, evenly pubescent on both surfaces with minute many branched trichomes; lower cauline leaves similar to basal but smaller, more nearly entire and with shorter petioles; upper cauline leaves narrowly linear without a differentiated petiole, often subtending branches, less densely pubescent than lower leaves; flowering pedicels slender, at first erect then recurving as fruit development occurs, sparsely pubescent; buds globose to obovoid, sparsely pubescent; sepals greenish to dull purple, broadly oblong, scarious margined, 3-4 mm. long; petals lingulate, white to purplish, 4-5 mm. long, ca. 1 mm. wide; fruiting pedicels slender, arched downward, sparsely pubescent, to glabrous, 8-12 mm. long, apex symmetrical or nearly so; siliques widely spreading and pendulous, straight or nearly so, glabrous, slightly flattened parallel to septum to nearly terete, 5-8 cm. long, 1-nerved from base to apex, nearly sessile or with a short gynophore less than 1 mm. long; styles evident but less than 1 mm. long; seeds in an irregular row, plump, wingless, ca. 1 mm. long, ca. 0.5 mm. wide; cotyledons incumbent.

Herba perennis, caulibus erectis superne ramosis sparse pubescentibus vel glabris

inferne pubescentibus 5–12 dm. altis, foliis basalibus petiolatis oblanceolatis sinuato-dentatis obtusis 4–8 cm. longis, foliis caulinis linearis vel filiformibus sparse dentatis vel integris pubescentibus; floribus poculiformibus, sepalis plus minusve veridis vel purpureis late oblongis 3–4 mm. longis, petalis linguiformibus albis vel plus minusve purpureis 4–5 mm. longis, pedicellis fructiferis filiformibus recurvatis 8–12 mm. longis, siliquis pendulis plus minusve teretibus rectis glabris 5–8 cm. longis, seminibus immarginatis noncompressis ca. 1 mm. longis, cotyledonibus incumbentibus.

Holotype in the Gray Herbarium collected in Cumbre de Soledad, Volcán Acatenango, 8,500 ft., Dept. of Sacatepéquez, Guatemala, Feb. 16, 1937, *F. W. Hunnewell 1482*.

DISTRIBUTION: Hidalgo and Jalisco, Mexico to Guatemala.

This species is named for the collector, Mr. Francis Welles Hunnewell (1880–1964) who was Phanerogamic Curator of the New England Botanical Club from 1913 until 1958 and a Research Associate of the Gray Herbarium for most of his adult life. He was Comptroller of Harvard University and later Secretary to the Corporation of the University. In establishing the Fernald Fund in Harvard College for field research in systematic Botany, Mr. Hunnewell left an enduring commitment to botanical field work, which he so enthusiastically enjoyed.

Most of the material cited below has been considered to belong to *Pennellia longifolia*. Certainly the phenological aspects of the specimens are very similar to that species and it is assumed *P. hunnewellii* and *P. longifolia* are closely related. In general, the geographical range of *P. hunnewellii* is to the south of *P. longifolia* but there is a broad area of overlap in the highland region of Mexico. The two species may be distinguished from each other by carefully examining the trichomes, particularly on the leaf surfaces and toward the base of the stems. The trichomes of *P. hunnewellii* are fine and many-branched whereas those of *P. longifolia* are coarse and simple or forked. The latter are spreading and produce a hirsute condition, especially on the stems. On the other hand, the trichomes of *P. hunnewellii* are so small that they scarcely show any divergence from the stem or leaf surfaces.

The siliques of *Pennellia hunnewellii* are slightly compressed parallel to the septum while those of *P. longifolia* are strictly terete. The former species is a perennial with strong tendencies to produce a woody foot at the apex of which the lower leaves are clustered. The latter species is biennial and the lower leaves are infrequently present on fruiting specimens. A woody foot is not produced.

OTHER SPECIMENS STUDIED. **Guatemala.** Calderas, July 5, 1941, *J. R. Johnston 1914* (f). **Chimaltenango:** Volcán de Agua, July 22, 1937, *J. R. Johnston 902* (f). **Huehuetenango:** Sierra de los Cuchumatanes, between Tojiah and San Juan Ixcay at km. 323 on Ruta Nacional 9N, ca. 3200 m., Aug. 1, 1960, *John H. Beaman 3951* (MSC); small limestone ridge covered with *Juniperus standleyi*, Sierra de los Cuchumatanes, between Paquix and Chemel at km. 311 on Ruta Nacional 9N, ca. 3360 m., Aug. 2, 1959,



*John H. Beaman 2964* (GH, MSC). **Sacatepéquez:** above Santa María de Jesús, north-facing slopes of Volcán de Agua, by trail, Nov. 8, 1958, *J. G. Hawkes et al. 1911* (GH). **México. Hidalgo:** Cerro Alto, 3 km. al SE de Epazoyucan, July 19, 1963, *Rzedowski 16911* (GH). **Jalisco:** Nevado de Colima, a few miles south of Ciudad Guzman (Zapotlan), 2700–2800 m., July 2, 1956, *David P. Gregory & George Eiten 307* (MICH); Nevado de Colima, northeast side of mountain near Puerto de los Cruces, ca. 3600 m., Aug. 27, 1958, *John H. Beaman 2385* (MSC); northeastern slopes of Nevado de Colima, below Canoa de Leoncito, Sept. 10, 1952, *Rogers McVaugh 12836* (GH, MICH). **México:** 19 km. NE de Texcoco, sobre la carretera a Calpulalpan, Aug. 17, 1971, *Rzedowski 28498* (MICH); Crucero, Temascaltepec, 3400 m., Oct. 24, 1933, *Geo. B. Hinton 4920* (GH); 1 km. al N de Llano Grande, Chalco, en las faldas del Cerro Telapón, July 26, 1964, *Rzedowski 18420* (GH); near Contreras, D.F., Aug., 1944, *G. T. Goodman 3457* (F); same locality, Aug. 9, 1910, *C. R. Orcutt s.n.* (F); Alrededores de la Estación la Cima, Serranía del Ajusco, D.F., Aug. 14, 1960, *Rzedowski 12586* (CAS, MICH). **Oaxaca:** Sierra de San Filipe, 10,000 ft., Sept. 18, 1894, *C. G. Pringle 5622* (GH). **Queretaro:** near summit of Cerro Zamorano, 2950 m., Aug. 3, 1972, *Melinda F. Denton 1958* (MICH); parte más alta Cerro Zamorano, Colón, 3,200–3,270 m., Nov. 13, 1971, *Rzedowski & McVaugh 419* (MICH). **Veracruz:** faldas del Pico de Orizaba, 3220 m., Oct. 16, 1971, *R. Hernandez M. 1321* (GH).

### 3. *Pennellia mcvaughii* Rollins

*Pennellia mcvaughii* Rollins, Taxon **28**: 24. 1979.

Type collected near Mexican Highway 40, 26 miles east of El Salto, Sierra Madre Occidental, Durango, Mexico, Sept. 21, 1974, *Reed C. Rollins & K. W. Roby 7423* (holotype, GH). Isotypes to be distributed.

Biennial or perennial, 1.0–1.5 m. tall; stems single or occasionally more from base, branched above, sparsely pubescent with spreading simple or sometimes branched trichomes below, glabrous above; complete basal and lower cauline leaves not seen, remnants sparsely pubescent with coarse stalked dendritically-branched trichomes, middle and upper cauline leaves linear, 4–8 cm. long, 1–4 mm. wide, sparsely pubescent with simple or forked trichomes to glabrous, upper leaves very narrow; inflorescences narrow, greatly elongated, up to 3.5 dm. long; buds purple, obovoid; flowers slightly zygomorphic with an asymmetrical receptacle and the lower stamen pair curved upward; sepals purple, scarious toward apex, 7–9 mm. long, 3–4 mm. wide, outer pair saccate, inner pair plain; petals purple, narrowly oblong to narrowly lingulate, scarcely narrowed below except at point of insertion, straight, 9–12 mm. long, 2–3 mm. wide; filaments gradually broadened toward base, those of paired stamens 8–10 mm. long, stamens exerted, anthers oblong, 1.5–2.0 mm. long; ovary and style slightly curved upward; stigma entire, slightly exceeding style in diameter; infructescences usually secund; fruiting pedicels slender, ascending then arched downward, glabrous, 7–11 mm. long, markedly expanded at summit, expanded portion asymmetrical; siliques pendant, straight to very slightly bowed, slender, terete to slightly flattened parallel to septum, glabrous, strongly 1-nerved below, 6–9 cm. long, ca. 1 mm. wide, usually purplish; septum without a median nerve; gynophore evident but short, less than 0.5 mm. long; styles 1.0–1.5 mm. long; seeds crowded, marginless, ca. 1 mm. long, less than 1 mm. wide, somewhat angled, pendant on funiculi ca. 1 mm. long.  $n = 8$ ,  $2n = 16$  (Rollins and Rüdénberg, 1977).

Known only from the Sierra Madre Occidentale west of C. Durango, Mexico.

The lower cauline and basal leaves are missing in the 14 individual plants of the two collections I have studied. Thus it is not known at present exactly the nature of these features of the plants. At the site of the type collection an effort to locate basal rosettes of the

species was made but none were found. Notes made at the time of this collection suggested that *P. mcvaughii* is probably a perennial but there was no positive evidence available. The root is sufficiently thick and the leafscars cover a sufficient distance on the crown to suggest a perennial habit. However, the fact that all basal leaves have been shed suggests a biennial which produces a rosette the first year, then when flowering occurs, the basal leaves wither and are ultimately shed. In any case, it is certainly not an annual species.

It is clear that *Pennellia mcvaughii* is most closely related to *P. longifolia*. These species are very similar in habit and in general they occupy the same types of habitats. Mostly, they occur in open conifer or oak forest areas at relatively high elevations in the mountains. *Pennellia mcvaughii* was found in the pine zone at about 8,000 ft.

SPECIMEN CITED OTHER THAN TYPE. **Mexico. Durango:** frequent in moist sloping meadow, pine-forest zone, 3 miles north of Coyotes, Sierra Madre Occidentale, ca. 2400 m., about 80 km. west of C. Durango, Sept. 28, 1962, *Rogers McVaugh 21680* (MICH, NY).

#### 4. *Pennellia robinsonii* Rollins, sp. nov.

Perennial with a multicapital caudex; stems one to several, up to 1 m. tall, branched above, pubescent with fine dendritic trichomes below, glabrous above, old stems often persisting; basal leaves tufted at apex of caudex branches, oblanceolate, obtuse, sinuate dentate to entire, petiolate, with a strong central vein, densely pubescent with fine dendritic trichomes, 5–15 cm. long, 6–20 mm. wide; lower cauline leaves linear to linear-lanceolate, sessile and tapered toward base but scarcely petiolate, entire or nearly so, sparsely pubescent or glabrous; upper cauline leaves narrowly linear to filiform, glabrous; inflorescence narrow, greatly elongating in fruit; buds globose to obovoid; glabrous; flowers cup-shaped; sepals dark purple, broadly oblong to ovate, nonsaccate, 3.5–4.0 mm. long, ca. 2 mm. wide; petals tipped with light purple, whitish below, oblong, not tapering toward base, 4–5 mm. long, ca. 1.5 mm. wide, barely exceeding sepals; fruiting pedicels strictly erect, appressed to rachis, glabrous, 4–6 mm. long; stamens erect, paired and single nearly the same length; filaments stocky, gradually broadening toward base; 2.5–3.0 mm. long; anthers ca. 1 mm. long, ca. 1 mm. broad; glandular tissue well-developed, surrounding base of single stamen, subtending base of paired stamens; siliques erect or nearly so, acute at apex, glabrous, slightly compressed parallel to septum, indistinctly one-nerved below, 1.5–2.0 cm. long, obscurely gynophorate; styles ca. 0.5 mm. long; stigma elongated over valves; seeds numerous, crowded, marginless, plump, angled, ca. 1 mm. long, in two distinct rows in each loculus; funiculi filiform; cotyledons incumbent.

Herba perennis, caudicibus ramosis, caulibus erectis superne ramosis glabris inferne pubescentibus, foliis basalibus petiolatis oblanceolatis sinuato-dentatis vel integris, foliis caulinis linearis vel filiformis superne glabris, inflorescentiis angustis elongatis, floribus poculiformibus, sepalis purpureis late oblongis vel ovatis nonsaccatis 3.5–4.0 mm. longis, ca. 2 mm. latis, petalis oblongis 4–5 mm. longis, pedicellis fructiferis erectis glabris 4–6 mm. longis, siliquis erectis 1.5–2.0 cm. longis plus minusve teretibus, stylis ca. 0.5 mm. longis, seminibus noncompressis immarginatis ca. 1 mm. longis, cotyledonibus incumbendis.

Holotype in the Gray Herbarium, collected on a steep granitic rocky hillside, 21 miles south of Chihuahua City, Chihuahua, Mexico, Oct. 15, 1974, *Reed C. Rollins and Kathryn W. Roby 74182*. Named for the late Professor B. L. Robinson, former

curator of the Gray Herbarium who first recognized *Pennellia* as section *Heterothrix* of *Thelypodium* and who annotated the Pringle specimen in the Gray Herbarium calling attention to the elongated stigma which has the lobes over the valves.

Known only from the state of Chihuahua, Mexico.

*Pennellia robinsonii* is nearest related to *P. micrantha* and the specimens of it have been distributed under that name. One of the most striking features of *P. robinsonii* is the multicipital caudex found in older plants. The short acute fruits are also distinctive when compared to those of *P. micrantha*. The flowers of *P. robinsonii* are cup-shaped and barely open during anthesis. They are fully as large as those of *P. longifolia*. The sepals are dark purple instead of greenish as in *P. micrantha* and the petals are purple-tipped, oblong, and non-tapering toward the base in *P. robinsonii* as contrasted with white lingulate petals that taper toward their bases in *P. micrantha*.

The habit illustration given by Schulz (1924, p. 296, fig. 62) is that of *Pennellia robinsonii* and probably was made from *Pringle 636* which he cites under *Heterothrix micrantha*. Unfortunately, the source of the illustration is not given in the legend. The different petal shapes "D-E Petala speciminum diversorum" are of two species. D illustrates a petal of *Pennellia micrantha* and E shows a petal of *P. robinsonii*.

Our field notes made at the time the type of *Pennellia robinsonii* was collected indicate that plants of the species were infrequent in the area. There were granitic outcrops on a steep, otherwise grassy hillside and the plants were growing at the base of these outcrops.

OTHER SPECIMENS STUDIED. **Mexico. Chihuahua:** rocky hills near Chihuahua, Sept. 12, 1885, C. G. Pringle 636 (DS, F, GH, NA, NY, PH, RSA, US); same locality, Oct. 1885, C. G. Pringle 294 (US).

## 5. *Pennellia micrantha* (Gray) Nieuwl.

*Pennellia micrantha* (Gray) Nieuwland, Amer. Midl. Natur. 5: 224. 1918, based on *Streptanthus micranthus* Gray, Mem. Amer. Acad. Arts and Sci. IV: 7. 1849. Type collected near Santa Fe Creek, New Mexico, A. Fendler 23, July, 1847. Holotype GH; isotypes GH, MO.

*Thelypodium micranthum* (Gray) Wats., Proc. Amer. Acad. Arts and Sci. XVII: 321. 1882.

*T. longifolium* (Benth.) Wats. var. *catalinense* M. E. Jones, Contrib. West. Bot. 12:2. 1908. Type collected in Sabino Canyon, Catalina Mts., Arizona, 3000 ft., August 20, 1903, Marcus E. Jones s.n. Holotype POM; isotypes MO, UC, US.

*Heterothrix micrantha* (Gray) Rydberg, Bull. Torrey Bot. Club 34: 435. 1907.

Perennial or biennial, stems usually one, sometimes several, from base, 5-10 dm. tall, branched above, pubescent below with simple, forked or dendritic trichomes, glabrous above or with scattered dendritic trichomes; basal leaves oblanceolate, sinuate dentate to shallowly lobed, rarely nearly entire, obtuse, densely pubescent with dendritic trichomes, lower cauline leaves similar to basal, petiolate, up to 10 cm. long but usually shorter, upper cauline leaves much reduced, cuneate at base, sparsely pubescent to

glabrous, usually entire; inflorescences narrow, elongated; buds globular to obovoid, glabrous or with a few trichomes near apex, usually greenish; sepals broadly oblong, scarious margined above, 2.5–3.0 mm. long, 1.5–2.0 mm. wide, outer pairs slightly saccate, inner pair plain; petals white or rarely purplish, spatulate to narrowly lingulate, gradually narrowed toward base, 3.5–4.5 mm. long, 1.0–1.3 mm. wide; stamens included, nearly equal, paired stamens straight, single stamens curved, filaments 1.5–2.5 mm. long, anthers ca. 1 mm. long; glandular tissue surrounding base of single stamens, supporting paired stamens; ovary sessile, glabrous or sometimes sparsely pubescent, terete, stigma entire or nearly so; pedicels erect or ascending, glabrous, (3-)4–7(-8) mm. long; siliques erect or nearly so, terete, nerved to middle or above; glabrous or rarely sparsely pubescent when young, (2-)2.5–3.5(-4.5) cm. long; styles obsolete or nearly so; seeds numerous, crowded, plump, angled, marginless, 1.0–1.2 mm. long, ca. 0.5 mm. wide; cotyledons incumbent.

DISTRIBUTION: Colorado to southern Arizona, New Mexico, west Texas and the mountains of Mexico south to the state of San Luis Potosí.

This is the most variable species of the North American members of the genus. Silique length, pedicel length, density of the indument, style length and the number of flowers per raceme all vary considerably. In all but three specimens seen, the siliques are sessile or very nearly so. In one specimen at the Gray Herbarium, collected by Wright, presumably in the Fort Davis area of Texas, the siliques are on a gynophore 1–2 mm. long. Similarly, specimens of *Stephen S. White* 3494 from northeastern Sonora, Mexico, at the University of Michigan show a definite gynophore. The siliques of a specimen at the U.S. National Herbarium, *Standley* 40609 from the Guadalupe Mts., Texas, are not quite sessile. Here the gynophore is less than 0.5 mm. long. Usually in the Cruciferae, a definite gynophore is a significant distinction often correlated with other differences that set off separate taxa. However, in this instance I have not been able to discover any correlated distinctions from other specimens of *Pennellia micrantha* and it seems best to regard the presence of a gynophore as an unusual feature of erratic occurrence. It is in the Wright specimen collected in 1851 where the striking gynophore suggests a closer look at other material from the area. However, with the exceptions given above, in all Texas material as well as that from elsewhere in the species range, the siliques are sessile or very nearly so.

The holotype of *Pennellia micrantha* consists of two branches, one bearing flowers, the other having more or less mature siliques. The lower parts of the plants are missing. However, *Fendler* 22, collected at the "foot of mts. on Santa Fe Creek" is from the same area as the holotype and the specimen on one sheet (GH) is complete except for lower and basal leaves. In reviewing the application of the name, *P. micrantha*, I have taken into account both *Fendler* 23 and *Fendler* 22. But the latter is a mixed collection with specimens of both *P. micrantha* and *P. longifolia* present on one sheet at GH.

The two more northerly collections of *Pennellia micrantha* in

Colorado have unusually small flowers and the specimens differ in other minor ways from those collected further south. However, the material is inadequate to fully test the possibility that a distinct taxon is represented.

REPRESENTATIVE SPECIMENS. **Mexico. Chihuahua:** Gulebra Mts., Aug. 18, 1936, *Harde LeSueur* 749 and 643 (F, GH); 7 road miles north of Colonia Juarez in "The Tinaja," 1600 m., July 28, 1972, *M. & E. Wilson, L. A. & M. C. Johnston* 8431 (GH); Cañon de St. Diego, Sierra Madre Occidentale, Sept. 16, 1891, *C. V. Hartman* 804 (F, GH, NY, UC, US); same locality, 6,600 ft., Sept. 16, 1903, *Marcus E. Jones* s.n. (POM, 2 sheets). **Coahuila:** Sierra de Santa Rosa, south of Múzquiz, July 25, 1938, *Ernest G. Marsh* 1459 (F, GH, TEX); Cañon Hundido on N side of Pico de Centinela, Sierra del Jardín, 1500–2250 m., July 27, 1973, *M. C. Johnston et al.* 11799b (TEX-LL); Hidalgo Piedra Blanca, Villa Acuña, 1936, no. 6647 (no collector given MEXU); Cañon de Centinela just S and SW of Pico de Centinela, Sierra del Jardín, 1600–2225 m., July 31, 1973, *M. C. Johnston et al.* 11984 (GH). **San Luis Potosí:** San Miguelito Mts., 1876, *J. G. Schaffner* 156 in part (CAS, GH, MEXU, PH). **Sonora:** Cañon de Bavispe, NE Sonora, Aug. 11–14, 1940, *Stephen S. White* 3253 (GH, MICH); Arroyo de la Galera, NE Sonora, July 27, 1940, *Stephen S. White* 3053 (ARIZ, GH, MICH, US); Cañon de El Temblor, NE Sonora, Aug. 19, 1940, *Stephen S. White* 3367 (ARIZ, GH, MICH, US). **USA. Arizona. Apache County:** 4.8 miles south of junction on Green's Mountain road, July 26, 1973, *Lehto, McGill and Pinkava* 11505 (NY). **Cochise Co.:** Guadalupe Canyon, Guadalupe Mts., 4300 ft., Oct. 4, 1947, *Frank W. Gould & H. S. Haskell* 4532 (ARIZ); Cave Creek, Chiricahua Mts., Sept. 21, 1929, *G. J. Harrison & T. H. Kearney* 6166 (GH); Barefoot Park, Chiricahua Mts., Sept. 12, 1906, *J. C. Blumer* 1363 (ARIZ, GH); Garden Canyon, Huachuca Mts., Sept. 21, 1949, *Leslie N. Goodding* 550–49 (ARIZ); near Fort Huachuca, Huachuca Mts., 1882, *J. G. Lemmon* 2635 (GH). **Greenlee Co.:** Blue River, 4000 ft., Sept. 1902, *A. Davidson* 848 (GH). **Pima Co.:** White House Canyon, Santa Rita Mts., 5200 ft., Aug. 27, 1939, *Lyman Benson* 9722 (ARIZ, POM); South Canyon, Baboquivari Mts., 3600–4000 ft., Aug. 31, 1940, *T. H. Kearney & R. H. Peebles* 14948 (ARIZ, NY, US); Santa Catalina Mts., May 16, 1881, *C. G. Pringle* 281 (GH). **Santa Cruz Co.:** Santa Rita Mts., July 25, 1884, *C. G. Pringle* s.n. (CAS, F, GH, MICH, NY); Sycamore Canyon, Ruby, July 17, 1938, *R. Darrow* s.n. (ARIZ); Stone Cabin Canyon, Santa Rita Mts., July 6–10, 1903, *J. J. Thormber* s.n. (ARIZ). **Colorado. Mineral Co.:** near Pagosa Peak, Aug. 5, 1899, *C. F. Baker* 5509 (POM). **Park Co.:** granite slide under cliff, North Fork, South Platte River, east of Shawnee, 7950 ft., July 13, 1950, *H. D. Ripley and R. C. Barneby* 10457 (CAS). **Teller Co.:** rocky cliffs, Mountain View, Pikes Peak, July 1901, *F. Clements* s.n. (NY). **New Mexico. Santa Rita de Cobre,** Aug. & Oct., 1880, *Edward Lee Greene* s.n. (F, MO, NY, PH); Florita Mts., Sept. 7, 1903, alt. 5300 ft., *Marcus E. Jones* s.n. (POM). **Dona Ana Co.:** Filmore Canyon, Organ Mts., Aug. 4, 1895, *E. O. Wooton* s.n. (NMC, NY); Organ Mts., Aug. 16, 1895, *E. O. Wooton* s.n. (US). **Grant Co.:** mts. near copper mines (Santa Rita), Aug. 1851, *C. Wright* 844 (GH, NY, PH). **Lincoln Co.:** El Capitan Mts., July, 1900, *F. S. & E. S. Earle* 491 (MO). **San Miguel Co.:** Provenir Creek, Las Vegas, 6,919,26, *G. Arsène* 17750 (F). **Santa Fe Co.:** foot of mts., Santa Fe Creek, 1847, *A. Fendler* 22 (GH). **Sierra Co.:** Mineral Creek, south end of Black Range, Sept. 26, 1904, *O. B. Metcalfe* 1417 (ARIZ, ENCB, MO, NMC). **Socorro Co.:** Mogollon Creek, Mogollon Mts., July 18, 1903, *O. B. Metcalfe* 260 (ARIZ, GH, MO, NMC, UC); Mogollon Mts., Aug. 1887, *Henry H. Rusby* 25-1/2 (F, MO, NA, PH). **Texas. Brewster Co.:** Toronto Canyon, ca. 5 miles west of Alpine, June 26, 1941, *Omer T. Sperry* T1179 (US); Chisos Mts., *C. H. Mueller* 8004 (F, TEX). **Culbertson Co.:** Pine Canyon, Guadalupe Mts., Aug. 15–17, 1924, *Paul C. Standley* 40609 (US); vicinity of Frijole Post Office, Aug. 10, 1930, *Carl O. Grasel* 187 (MICH). **Hudspeth Co.:** Eagle Mts., ca. 35 miles southeast of Sierra Blanca, Aug. 22, 1946, *U. T. Waterfall* 6708 (GH). **Jeff Davis Co.:** Livermore Peak and spur ridges, Davis Mts., July 9–12, 1921, *Roxana S. Ferris and Carl D. Duncan* 2570 (CAS); Madera Canyon, Mt. Livermore, June, 1936, *L. C. Hinckley* s.n. (ARIZ); Fort Davis, 1883, *V. Havard* 214 (GH); Limpia

Canyon, 1889, *J. C. Nealley 11* (F); mountains and arroyos of the Limpia, July, 1852, *J. M. Bigelow 33* (NY). **Presidio Co.:** west branch of ZH Canyon, above mouth, July 16, 1941, *L. C. Hinckley 1003* (ARIZ, GH, TEX, US); head of Pinto Canyon, northwest of Chinati Peak on the Marfa-Ruidosa road, Sept. 10, 1961, *D. S. Correll and M. C. Johnston 24385* (GH, TEX-LL).

## 6. *Pennellia lasiocalycina* (Schulz) Rollins, comb. nov.

Based on *Heterothrix micrantha* (Gray) Rydberg var. *lasiocalycina* O. E. Schulz, Das Pflanzenreich IV. 105. Cruciferae-Sisymbrieae. 86: 296. 1924. Collected in the Sierra de Parras, Coahuila, Mexico, 8-9000 ft., July, 1910, *C. A. Purpus 4604* (holotype B, not seen; isotypes F, GH, MO, UC, US).

*Pennellia micrantha* (Gray) Nieuwl. var. *lasiocalycina* (Schulz) Rollins, Contrib. Gray Herb. no. 206: 8. 1976.

Perennial; stems one or few, branched above, 6-10 dm. tall, densely to sparsely pubescent with fine dendritically branched trichomes sometimes glabrous above; basal leaves petiolate, oblanceolate, sinuate dentate to entire, obtuse, densely pubescent with stalked dendritically branched trichomes, usually the indument matted on lowermost leaves, 2-4 cm. long, 6-10 mm. wide, lower cauline leaves similar to basal leaves but less densely pubescent, cauline leaves gradually reduced upward, short-petioled to cuneate at base, pubescence reduced upward on both stems and leaves; inflorescences terminating each branch, narrow, lax; buds nearly globose, pubescent with branched trichomes; flower pedicels slender, erect, usually pubescent; flowers cup-shaped, regular, petals barely exceeding sepals; sepals purplish, pubescent, broadly oblong, scarious-margined, 2.5-3.0 mm. long, 1.5-2.0 mm. wide; petals white to tinged with purple, narrowly oblong, not differentiated into blade and claw, not tapered below, 3.0-3.5 mm. long, ca. 1 mm. wide; stamens included; fruiting pedicels strictly erect, pubescent or glabrous, 1.0-1.5 cm. long; siliques glabrous, erect, slightly flattened parallel to septum to nearly terete, 4-6 cm. long, acute at apex; styles evident but less than 1 mm. long; seeds numerous, marginless, plump, often misshapen, slightly more than 1 mm. long, ca. 0.6 mm. wide, in an irregular combination of one and two rows; cotyledons obliquely incumbent.

DISTRIBUTION: Coahuila to Hidalgo and Nuevo Leon, Mexico.

Unfortunately, most of the specimens studied are in flower, sometimes with young fruit, but they do not give an adequate basis for determining the variation undoubtedly present in this species. The isotypes show relatively long siliques compared to those of *Pennellia micrantha* and in the one specimen with mature siliques, *Chiang et al. 9435*, the siliques are about 6 cm. long. The siliques and pedicels of *P. lasiocalycina* are strictly erect and closely appressed to the rachis of the infructescence. The flowers are relatively larger and broader than those of *P. micrantha* and in general, the plants are taller. If there is any confusion of identity, it would most likely be with *P. micrantha*. But the upper parts of the latter species, particularly pedicels and buds, are always glabrous whereas those structures, particularly the buds, are sparsely to densely pubescent in *P. lasiocalycina*. The presently known distribution, from Coahuila to Hidalgo, is only sparsely represented by collections in the herbaria consulted.

SPECIMENS EXAMINED. **Mexico. Coahuila:** Sierra de la Madera SE and SSE of Ranchero Cerro de la Madera, 1500-2900 m., Sept. 20, 1972, *F. Chiang, T. Wendt and M. C. Johnston 9435* (TEX); Sierra Madre, 40 miles south of Saltillo, July, 1880, *Edward Palmer 37* (GH); ca. 35 km. W of Cuatro Ciénegas, above Cañon de la Hacienda, in limestone, Sierra de la Madera, 8900 ft., August 5, 1973, *James Henrickson and T. Wendt 11947* (GH). **Hidalgo:** cerro alto, 3 km. al SE de Epazoyucan, 2500 m., July 19, 1963, *Rzedowski 16911* (MICH); cerro de Santa Monica, N of Santa Monica, 40 km. NW of Apam on Pachuca highway, 2650 to 2850 m., July 11, 1966, *Robert C. West P-11* (MICH). **Nuevo Leon:** wooded slope near Ojo de Agua at foot of Cerro de Potosí, 6600 ft., July 14, 1945, *A. J. Sharp 45732* (GH).

## 7. *Pennellia patens* (Schulz) Rollins

*Pennellia patens* (Schulz) Rollins, *Rhodora* **62**: 15, 1960; based on *Heterothrix patens* O. E. Schulz, *Pflanzenr.* IV. fam. 105: 296. 1924. Lectotype from District Comitán, Chiapas, Mexico, 18 Aug. 1898, *Caec. and Ed. Seler 3038* (holotype B, not seen; isotype GH).

Biennial; stems usually single from base, up to 1.3 m. tall, branched above, sparsely pubescent below with fine dendritically branched trichomes or glabrous, glabrous above; basal leaves usually not persisting beyond first year, rarely present on flowering or fruiting specimens; sinuate dentate, oblanceolate, petiolate, pubescent on both surfaces with minute dendritically branched trichomes; lower cauline leaves cuneate or short petioled, lanceolate, irregularly dentate, sparsely pubescent with fine dendritically branched trichomes, one-nerved nearly entire length, 3-6 cm. long, 4-15 mm. wide, acuminate toward apex, often apiculate, lowermost usually missing; upper cauline leaves linear to narrowly linear, sparsely pubescent to glabrous; inflorescences greatly elongated, terminating each branch; buds ovoid, with a few trichomes at apex or glabrous; flowers remote; sepals greenish to purplish, oblong, glabrous, 3-4 mm. long, ca. 1-3 mm. wide; petals white, scarcely differentiated into blade and claw, slightly narrowed toward base, ca. 4 mm. long, ca. 1 mm. wide; stamens erect, single only slightly shorter than paired; fruiting pedicels slender, divaricate, glabrous, stiff, nearly straight, (4-)5-9(-9) mm. long; siliques divaricately ascending, terete, 3-6 cm. long, less than 1 mm. wide; seeds numerous in a single row to densely packed in semi-double rows, marginless, oblong, slightly over 1 mm. to less than 1 mm. long, ca. 0.6 mm. wide; cotyledons incumbent.

DISTRIBUTION: Mexico from Durango to Chiapas.

There are some inconsistencies evident in the material I have referred to *Pennellia patens* and it is possible that when a greater knowledge of the populations is available, more than one taxon will be recognized. The problem centers on the lack of mature fruiting material so that the size of the seeds and their positioning in the siliques cannot be properly assessed throughout the taxon at the present time. Of the 16 sheets of specimens studied, only seven possessed siliques that have mature or nearly mature seeds. The rest of the specimens are in flower or have flowers and young fruits. The isotype has the seeds strictly in a single row and they are definitely oblong and relatively smooth. Other specimens have less elongated, angular seeds that are much more crowded in the silique and are in an imperfect single row or approach a double-rowed condition. These differences,

if ultimately correlated with other features, could provide for the recognition of more than one taxon. But such correlations are not possible from the material under study. There are some puzzling specimens from Durango and Aguascalientes that I have included under *P. patens*, but which have shorter pedicels and siliques than the usual material of this species from further south. These in particular may represent a distinct taxon.

Aside from the divaricate pedicels and longer siliques distinguishing *Pennellia patens* from *P. micrantha*, the long pedicels and narrow fruits are distinctive. As the siliques become mature, they tend to take on a purplish pigmentation.

**SPECIMENS STUDIED.** **Mexico. Aguascalientes:** ca. 20 km. east of Rincón de Romos, road to Asientos, between Cerro Altamire and Cerro de San Juan, 2200–2450 m., Sept. 4–8, 1967, *Rogers McVaugh 23754* (GH, MICH). **Distrito Federal:** pedregal (lava beds), Valley of Mexico, Aug. 21, 1896, *C. G. Pringle 6454* (CAS, DS, F, GH, MEXU, MICH, MO, MSC, NY, PH, POM, UC, US); Talpan, Aug. 16, 1910, *C. R. Orcutt 3644* (F, GH, MO, US); same locality, July, 1905, *J. N. Rose et al. 8489* (GH, NY, US); Vertiente E del Cerro de Santa Catarina, cerca de Sta. Catarina, deleg. Tláhuac, Aug. 13, 1968, *Rzedowski 26074* (MICH). **Durango:** along route 40, 5.3 miles west of Los Mimbres, July 26, 1972, *D. J. Pinkava et al. 9484* (ASU); Tejamén, Aug. 21–27, 1906, *Edward Palmer 503* (GH, NY, US); city of Durango and vicinity, April to November, 1896, *Edward Palmer 696* (US); north slope of Canyon of Rio Chico, 18 miles west of the city of Durango, route no. 40, July 24, 1958, *D. S. Correll and Ivan M. Johnston 20070* (GH). **Hidalgo:** Cerro Ventoso, entre Pachuca y Real del Monte, Aug. 29, 1965, *Rzedowski 20595* (GH, MICH); Sierra de Pachuca, July 20 and 24, 1905, *J. N. Rose et al. 7842* (US); 22 miles east of Pachuca (4 miles west of Tulancingo), Sept. 8, 1962, *Frank W. Gould 10170* (MICH). **Jalisco:** mts. west of Hacienda Chinampas, ca. 15 miles west southwest of Ajuelos, Aug. 16, 1957, *Rogers McVaugh 17009* (GH, MICH). **México:** Vertiente E del Cerro del Pino, cerca de Ayotla, July 13, 1967, *Rzedowski 23996* (MICH, RSA); Entre El Oro y Via Victoria, Jun. 19–20, 1954, *E. Matuda 30926* (MEXU); near San Bernabe, Amaxac de Guerrero, Tlaxcala, Aug. 20, 1944, *A. J. Sharp and Ephraim Hernandez Xolocotzi 44469* (GH); La Gavi, 35 km. f. Toluca, Toluca-Morelia highway, Aug. 9, 1944, *A. J. Sharp 44287* (GH); cerca de la Presa "El Capulin," Fraccionamiento La Herradura, mpio. Huixquilucan, July 7, 1968, *Rzedowski 25866* (MICH). **Michoacán:** vicinity of Morelia, north of Zapote, Aug. 4, 1910, *G. Arsène 6850* (GH, MO, US); vicinity of Morelia, Jarapeo, July 13, 1911, *G. Arsène 5598* (GH, MO). **Oaxaca:** 19 km. southwest of Sola de Bega along road to Puerto Escondido, Aug. 30, 1965, *D. E. Breedlove 12296* (GH, MICH, US). **Puebla:** vicinity of Puebla, *G. Arsène s.n.* (US); Chila-Zapotitlan, Jul. 15, 1932, *F. Miranda 2814* (MEXU). **San Luis Potosí:** alrededores de La Salitrera, municipio de Zaragoza, Aug. 2, 1959, *Rzedowski 11408* (ENCB).

## 8. *Pennellia juncea* (Schulz) Rollins, comb. nov.

Based on *Heterothrix juncea* O. E. Schulz, Das Pflanzenreich IV. 105. Cruciferae-Sisymbrieae 86: 297, 1924. Collected in San Luis, Puebla, Mexico, 1908, *C. A. Purpus 3486a* (holotype B), vicinity of San Luis, Tultitlanapa, Puebla, near Oaxaca, July, 1908, *C. A. Purpus 3486* (UC, probable isotype).

Biennial, or possibly perennial, glabrous throughout; stems stiffly erect, virgately branched above, 4–6 dm. tall, purplish especially above; basal leaves not present; lower cauline leaves petiolate, narrowly oblanceolate, entire to shallowly dentate, obtuse, 3–5 cm. long including petiole, 4–8 mm. wide; upper cauline leaves narrowly



linear, acute, entire; inflorescences terminating each branch, branches subtended by leaf-bracts; buds globose to slightly elongated; sepals erect at anthesis, non-saccate, narrowly oblong, 3-4 mm. long, ca. 1.2 mm. wide; petals white to faint lavender, spatulate, not differentiated into blade and claw, 5-6 mm. long, ca. 1.5 mm. wide; glandular tissue nearly surrounding base of single stamens, subtending paired stamens, poorly developed; anthers narrowly ovate, ca. 1 mm. long; fruiting pedicels widely spreading, rigid, remote, 12-18 mm. long; siliques terete, divaricately ascending, 3.0-3.5 cm. long, ca. 1.2 mm. wide; valves obscurely nerved toward base, purplish; styles obsolete to less than 0.5 mm. long; stigma entire; seeds oblong, in a single row, not crowded, somewhat embedded in tissue of septum, marginless, 1.0-1.2 mm. long, less than 1 mm. wide; radicle exceeding cotyledons; cotyledons incumbent.

Known only from the type collection from near Oaxaca, Mexico.

*Pennellia juncea* is most closely related to *Pennellia patens* with which it shares the distinctive feature of having smooth oblong seeds that occur in a single row in the silique. This feature apparently characterizes the more southerly populations of *P. patens* but in the northerly populations, the seeds are crowded and misshapen as in most species of *Pennellia*. From the specimens available, the impression of rigidity of stems, pedicels and siliques is a striking feature of *P. juncea*. This is the only North American species we have seen that is completely glabrous.

The holotype of *Pennellia juncea* at Berlin bears *Purpus* no. 3486a with slightly different data than *Purpus* no. 3486 at the University of California as indicated above. It is clear that these specimens are of the same species and it is quite likely that they are of the same gathering. If the latter is so, it makes the UC specimen an isotype even though the number of the holotype is modified by the addition of the letter *a*. The handwriting on the labels of the two specimens is the same and is presumably that of Purpus. The UC specimen is more complete than the Berlin specimen having both flowers and mature siliques. The Berlin specimen lacks flowers and the siliques are immature.

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# STUDIES ON SOLANACEAE. XII. ADDITIONS TO THE GENUS CHAMAESARACHA

ARMANDO T. HUNZIKER<sup>1</sup>

## SUMMARY

*Chamaesaracha rzedowskiana* A. T. Hunz. sp. nov. is described and illustrated. It is closely related to *Ch. potosina* Rob. et Greenm. (México: San Luis Potosí) and *Ch. cernua* (Donn. Smith) A. T. Hunz. comb. nov. (México: Sinaloa, Guerrero, Guatemala: Alta Verapaz, Petén, Belize: El Cayo). These three species differ from the seven others heretofore assigned to the genus by their habit (*Ch. rzedowskiana* is a prostrate herb rooting at stem nodes, while the other two are erect plants up to 1 m high; probably the three are annuals) and their southern range where they occur in different types of forest vegetation. An identification key is presented.

## RESUMEN

Se describe e ilustra *Chamaesaracha rzedowskiana* A. T. Hunz. sp. nov. (México: San Luis Potosí), afin con *Ch. potosina* Rob. et Greenm. (México: San Luis Potosí) y *Ch. cernua* (Donn. Smith) A. T. Hunz. comb. nov. (México: Sinaloa y Guerrero, Guatemala: Alta Verapaz y Petén, Belice: El Cayo). Estas tres entidades forman un grupo muy natural, tanto por su morfología como por su ecología; las otras 7 especies de *Chamaesaracha*, son principalmente xerófitas de regiones desérticas del suroeste de Estados Unidos de Norteamérica y del norte de México, cuyos órganos subterráneos (raíz principal leñosa) y las secundarias frecuentemente gemíferas les permiten ser perennes. Es probable que estudios ulteriores—con mejores y más abundantes materiales—permitan demostrar que este terceto deba ser considerado una sección dentro del género; al efecto, se trae a colación una referencia bibliográfica pertinente. Se incluye por fin una clave diferencial, para facilitar el reconocimiento de las especies tratadas.

## *Chamaesaracha rzedowskiana* A. T. Hunziker, sp. nov.

(FIGURE 1)

Herbae depressae (annuae?) ubique pubescens caulibus repentibus. Laminae concolores parvae, late ovatae, leviter cordatae, apice acutae, (0.48-)0.9-2.7(-4.6) cm longae et (0.45-)0.82-2.2(-3.0) cm latae; petioli 0.6-2.3 cm longi. Flores axillares solitarii; pedicelli (14-)18-23(-35) mm longi. Calyx campanulatus 5-lobatus, 1.5-2.0 mm longus extus piliferus (trichomata paucicellulares simplicia vel glandulosa capite unicellulari); lobi triangulares ca. 0.85 mm longi et (basi) 0.9-1.1 mm lati, quam pars connata aliquantum breviori. Corolla rotata 9-11 mm diam; lobuli 5 late triangulares acuti, extus praecipue apice et marginibus trichomatibus simplicibus et ramosis induti; corollae tubus ca. 0.95 mm longus intus in parte inferiore glaber, sed parte inferiore limbi corollae cum trichomatibus simplicibus et plerumque ramosis sparse obsita. Filamenta glabra interdum laeviter inaequalia; antherae oblongae filamentis breviores, ca. 1.2-1.4 mm longae et 0.75 mm latae. Stylus leviter obsubulatus; stigma capitatum, depressum. Pedicelli fructiferi leviter elongati usque ad 40 mm longi; calyx fructifer valde accrescens (3.1-3.3 mm longus) fere omnino baccae arcte accumbens; pericarpium tenue, in sicco translucens; granula sclerotica desunt. Semina pauca (14-25) epispermate tuberculato, ca. 0.95 mm longa, 0.9 mm lata et 0.45 mm crassa.

TYPE: México. San Luis Potosí: Municipio de Xilitla, Las Crucitas. 600 m alt., *Rzedowski 10103*, 1 Mar. 1959. "Ladera caliza con vegetación de bosque tropical secundario." (Holotype: ENCB; isotype: CORD).

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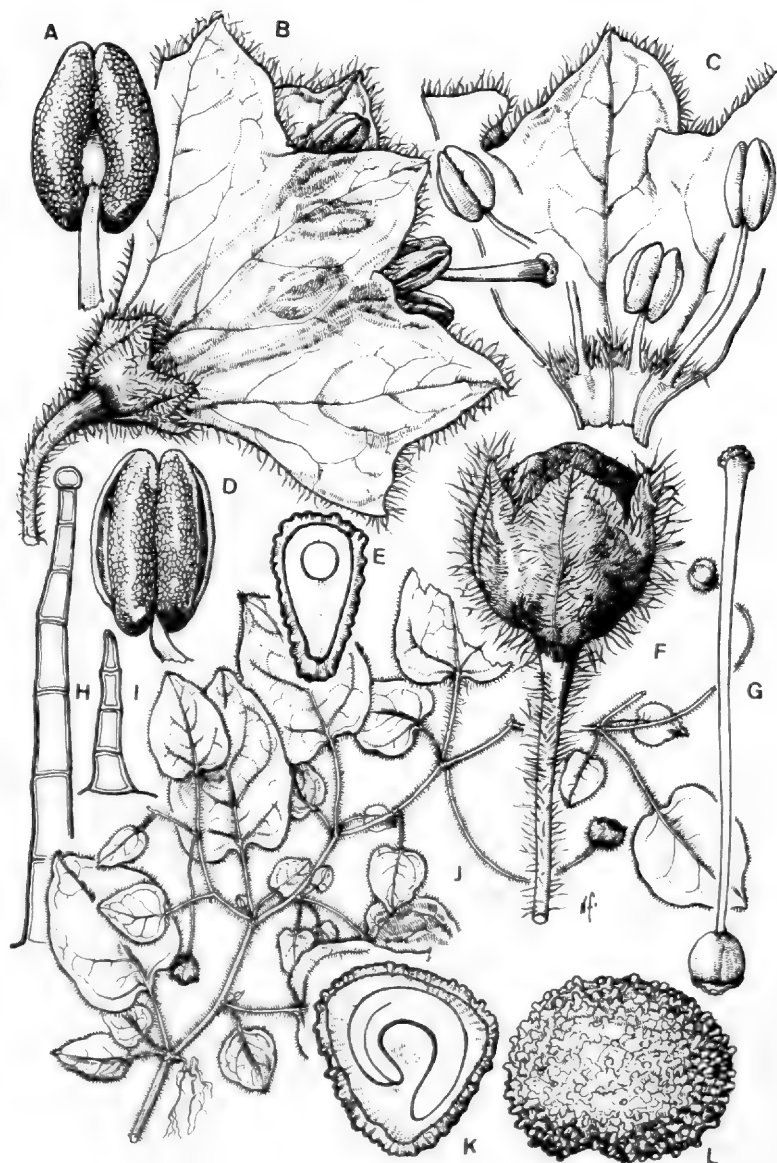


FIG. 1. *Chamaesaracha rzedowskiana*: A, D, anther (dorsal and ventral views),  $\times 16.5$ ; B, flower,  $\times 6.5$ ; C, sector of corolla (internal view) with two attached stamens,  $\times 6.5$ ; E, K, L, seed (transverse and longitudinal sections and lateral view),  $\times 25$ ; F, fruit,  $\times 6.5$ ; G, gynoecium,  $\times 8.5$ ; H, I, calyx trichomes,  $\times 83$ ; J, branch,  $\times 0.83$ .

Herbaceous pubescent plants (annual?) with prostrate stems rooting at the nodes. Leaves small, thin; blades concolorous (0.48–)0.9–2.7(–4.6) cm long and (0.45–)0.82–2.20(–3.0) cm wide; petioles 0.6–2.3 cm long. Flowers solitary; pedicels (14–)18–23(–35) mm long. Calyx campanulate, five-lobed almost to the middle, 1.5–2.0 mm long; external surface pubescent with few-celled simple and glandular trichomes (the latter with unicellular heads); lobes deltoid, somewhat shorter than the tube plus limb, ca. 0.85 mm long and 0.9–1.1 mm wide at the base. Corolla rotate 9–11 mm diam, with five small broadly triangular acute lobes, pubescent externally (particularly at the apex and margins) with simple and branched trichomes; tube ca. 0.95 mm long, interior glabrous; lower part of the limb with simple and branched trichomes. Filaments glabrous, sometimes slightly unequal in length; anthers oblong, shorter than the filaments, ca. 1.2–1.4 mm long and 0.75 mm wide. Style somewhat obsubulate; stigma capitate, depressed. Fruiting pedicels up to 40 mm long; the accrescent calyx (3.1–3.3 mm long) tightly enclosing the berry; pericarp thin, translucent when dry, lacking sclerotic nodules. Seeds few (14–25), tuberculate, ca. 0.95 mm long, 0.9 mm wide and 0.45 mm thick.

During a visit to the herbarium of the Escuela Nacional de Ciencias Biológicas (ENCB), I found *Chamaesaracha rzedowskiana* in the collections of the Solanaceae there. Although the materials do not allow definite conclusions about the underground organs and the persistence of individual plants, most probably they are annuals, lacking a woody tap root and secondary gemmiferous roots typical of the more northerly xerophytic species of the same genus.

*Chamaesaracha rzedowskiana* differs from the other species of the genus because of its thin leaves, with smaller and broader blades. The prostrate stems rooting at the nodes are another distinctive vegetative trait. The most closely related species are *Ch. potosina* Rob. and Greenm. and *Ch. cernua* (Donn. Smith) A. T. Hunz., which are considered below.

***Chamaesaracha cernua* (Donnell Smith) A. T. Hunziker, comb. nov.**

*Athenaea cernua* Donnell Smith, Bot. Gaz. 48: 297. 1909. TYPE COLLECTION: Guatemala, Dept. Alta Verapaz, Sasia, 900 m alt. *H. von Tuerckheim* II.2245, May 1908. HOLOTYPE: US; ISOTYPES: CORD, W.

*Physalis capsicoides* Bitter, Repert. Sp. Nov. 20: 371. 1924. TYPE COLLECTION: México, Veracruz, Papantla, *Schiede* 1191, Jan. 1829. I have not seen any representative of this collection, but the long and precise description by Bitter agrees in every detail with the plant under discussion.

*Physalis melanocystis* (Robins.) Bitter var. *cernua* (Donnell Smith) Waterfall, Rhodora 69: 99. 1967.

Herbaceous plant 1 m high. Flowers solitary, rarely geminate. Calyx 3.5–4.5 mm long, deeply cleft with slightly oblong lobes and with three types of trichomes (simple

multicellular, long-stalked with unicellular glandular heads, and short-stalked with multicellular glandular heads). Corolla rotate, 6–7 mm long. Anthers 1.3–1.8 mm long, on filaments exceeding them in length. Fruits orange-red with a thin and translucent pericarp, lacking sclerotic nodules; accrescent calyx 9–10 mm in length, tightly enclosing most of the pericarp. Seeds tuberculate, 1.2–1.4 mm long.

*Athenaea cernua* Donnell Smith is one of several species that have always perplexed taxonomists dealing with the Solanaceae of Mexico and Central America (Gentry & Standley, 1974). One of the reasons may be the scarcity of available materials, if one considers that up to the present it has been collected only seven times. Furthermore, the subtleties that characterize the reproductive structures of Solanaceae oblige one to make careful and time-consuming dissections. This is often not possible, especially on herbarium specimens if they are few and incomplete.

*Athenaea* Sendtner is a small Brazilian genus of about ten woody species (Hunziker, 1979). That *A. cernua* should be excluded from this genus is shown by the comparative data of Table 1. As Gentry (1973) pointed out, the transference of *A. cernua* to *Physalis* is unacceptable for this "very distinctive element in the Mexican and Central American floras;" its floral and fruit characters strongly advise against such an action. It should be added that for the same reason *Leucophysalis* Rydberg cannot be regarded as a sound choice to receive *A. cernua*. The genus where this problematic species fits adequately is *Chamaesaracha* (A. Gray) A. Gray. This is especially evident since the discovery of *Ch. rzadowskiana* described above.

ADDITIONAL SPECIMENS EXAMINED. MEXICO. GUERRERO: Distr. Galeana, Carrizo-El Rio, 800 m alt., *Hinton 14689*, 20 Oct. 1939, "by stream in mixed forest; 1 m high, fl. yellowish white, fr. shiny orange" (GH, US, NY); Distr. Montes de Oca, San Antonio, *Hinton 14034*, 21 Apr. 1938, "forest; 1 m high; fruit red" (GH, NY, US). SINALOA: Cañon de Tarahumare, Sierra Surotato, 3000–4000 ft, *H. Scott Gentry 7306*, 17/24 Mar. 1945, "Deep wooded canyon with mixed subtropical vegetation; shade. Wide spreading bush

TABLE 1. SOME REPRODUCTIVE STRUCTURES OF *ATHENAEA* AND *CHAMAESARACHA CERNUA*

<i>Athenaea</i>	<i>Chamaesaracha cernua</i>
Calyx cleft almost to its base, the lobes much longer than the tube.	Calyx with five lobes shorter than the tube.
Corolla aestivation valvate. Corolla lobes oblong, longer than the limb and the tube. Base of the corolla glabrous.	Corolla aestivation plicate; lobes broader than long, shorter than the tube and the limb; limb with a basal ring of scattered long trichomes.
Filaments short (usually shorter to slightly longer than anthers); basal part adnate to corolla tube, two lateral indentations present toward base.	Filaments longer than the anthers, lacking lateral indentations toward base.
Pericarp thick, coriaceous and opaque.	Pericarp thin, membranaceous and translucent.

1 m high" (US). GUATEMALA. DEPT. PETEN: Parque Nacional de Tikal, en camino del Templo no. 4, *Tun Ortiz* 998, 23 Apr. 1970, "Hierba en foresta alta; fruto colorado" (US, NY). BELIZE: El Cayo District, Arenal-Valentin road, *Lundell* 6181, Jun.-Aug. 1936, "Along roadside; herb; height 1 m" (GH, US, NY).

According to studies of Averett (1973), the genus *Chamaesaracha* comprises seven species, "largely restricted to the arid regions of southwestern United States and northern Mexico." The addition of *Ch. potosina*,<sup>2</sup> *Ch. cernua* and *Ch. rzedowskiana* increases the genus to ten species; also the geographical distribution is enlarged, with the inclusion of Belize, Guatemala, and regions of southern and western Mexico. The distinct geographical distribution of this meridional and not strictly desert inhabiting group of three species, coupled with some morphological characters (for example, the quality of the indument), may in the future permit the recognition of two sections in the genus. In case this position is adopted, the section *Capsicophysalis* Bitter (Repert, Sp. Nov. 20: 370, 1924) proposed to accomodate *Ch. cernua* (under the name *Physalis capsicoides* (Bitter) should be used. Chemical data, such as those of Averett (1973) for the xerophytic species, might be useful in elucidating this problem. For instance, it is not known whether these plants are perennials or annuals. The chances are in favor of them being annuals; the type collection of *Physalis capsicoides* (Schiede 1191) was considered annual by Schiede (Schlechtendal et Chamisso, 1831: 378). This is an important feature because it is a well-established fact that the seven northern xerophytic species are perennials, frequently with gemmiferous roots.

The following key is provided to facilitate the identification of the three species treated in this paper.

## KEY TO THE SPECIES

1. Stems prostrate, rooting at the nodes. Corollas 5-7 mm long; lobes broader than long, less than 1/2 as long as the rest of the corolla. Anthers oblong, 1.2-1.5 mm long . . . . . 1. *Ch. rzedowskiana*.
- 1'. Stems erect, up to 1 m high.
  2. Corolla 4.0-4.8 mm long, with lobes slightly shorter than the tube and the limb. Anthers ca. 0.6 mm in length (slightly less in breadth) . . . . . 2. *Ch. potosina*.
  - 2'. Corolla ca. 7 mm long, with lobes about 1/2 as long as the tube and the limb. Anthers oblong, 1.3-1.8 mm long . . . . . 3. *Ch. cernua*.

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Thanks to the generosity of Dr. J. Rzedowski, I had the opportunity to study at the Herbarium (ENCB) of the Escuela Nacional de Ciencias Biológicas (Instituto

<sup>2</sup> *Chamaesaracha potosina* Robinson & Greenman, Amer. J. Sci. **50**: 161. 1895. HOLOTYPE: México, San Luis Potosí, Tamasopo Cañon, *Pringle* 3654, 25 Nov. 1890 (GH). This very rare species, known only from the type collection, is closely related to the two other species discussed in this paper. The evidence makes wholly unacceptable its transference to *Saracha* (Averett, Ann. Mo. Bot. Gard. **57**(3): 380, 1970) which is quite a different genus indeed.



Politécnico Nacional, México, D. F.). I am also grateful to the staff of the Gray Herbarium and the Arnold Arboretum of Harvard University for the facilities made available including access to the Harvard University library and herbarium. Thanks are due as well to Prof. Reed C. Rollins for reviewing the manuscript and making valuable suggestions. The illustration was skillfully done by Mrs. N. M. de Flury.

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# A GENERIC ATLAS OF HAMAMELIDACEOUS POLLENS

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The Hamamelidaceae, when considered in the broad sense, i.e., including the subfamily Liquidambaroideae, which is often split off as a segregate family Altingiaceae, presently consists of 28 genera, or 29 if the poorly known segregate genus *Semiliquidambar* H. T. Chang (1962) is admitted.

Among angiosperms the Hamamelidaceae appear to be a relatively ancient family, with a very high proportion of small or monotypic genera having highly restricted or narrowly endemic distributions, and a high concentration of both genera and relatively primitive floral types in Southeast Asia. Concomitant with this phytogeographical evidence of antiquity is a fossil record which, in the form of the readily identifiable periporate pollen grains of *Liquidambar*, extends back at least as far as the Paleocene (Muller, 1970) or possibly even the Cretaceous on the basis of macrofossils of *Liquidambar* (Brown, 1933a, b). But the pollen of *Liquidambar* is relatively specialized within the family. If reliable identification of the more generalized and primitive tricolpate pollens which characterize the large majority of hamamelidaceous genera becomes possible, the microfossil record of the family may be found to extend considerably further back into the Cretaceous.

The pollen morphology of the family has been the subject of several investigations in recent years, but none of these has covered the entire family, and most have considered only a single genus or a few of the more common genera. Several of the more significant studies include the following:

Simpson (1936) categorized the pollen grains of 18 extant hamamelidaceous genera in six morphological groups which he considered convenient, and described fossil pollens of six genera which he attributes to the family from Tertiary lignitic coals of Argyllshire, western Scotland.

Erdtman (1943) provided descriptions of *Hamamelis* and *Liquidambar* as examples of Hamamelidaceae. He later (1946, 1952) provided brief descriptions of the pollen of 18 species from 15 genera, including *Distylium guatemalense* (= *Molinadendron guatemalense* (Radlk. ex Harms) Endress) as representative of the genus *Distylium*, and *Sycopsis dunnii* (= *Distyliopsis dunnii* (Hemsl.) Endress) as representative of the genus *Sycopsis*. In this respect a currently recognized species of *Distylium* is not included in his descriptions, but one of *Sycopsis*

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is by virtue of the fact that he added a description of *Sycopsis griffithiana* Oliv. in 1952. The 1946 descriptions apparently provided the basis for his general description of the pollen morphology of the family (1952).

Ikuse (1956) also provided brief descriptions of the pollen of ten species of six genera native or cultivated in Japan (*Liquidambar*, *Disanthus*, *Loropetalum*, *Hamamelis*, *Corylopsis*, *Distylium*).

Lee (1969), in a master's thesis (unpublished) written at the University of Pennsylvania, described the pollen of 22 species of ten genera, and recognized four pollen types: tricolpate, tricolporoidate, tricolporate, periporate.

Several authors have published detailed analyses of the pollen of *Liquidambar* and *Altingia* in relation to considerations of the taxonomic position and evolutionary history of these genera (e.g., C. T. Chang, 1958, 1959; Kuprianova, 1960; Makarova, 1957; Samorodova-Bianki, 1957; Sears, 1930).

The most extensive study to date has been that of C. T. Chang (1964), who examined and described (in Russian) 57 species of 21 genera of the family, including seven species of *Altingia* and *Liquidambar* which he separates in a family Altingiaceae, and 50 species of 19 genera of Hamamelidaceae. His descriptions are accompanied by 21 plates of photomicrographs. Several very rare genera were not included in this study for lack of material, and several new genera have since been recognized in the family.

Hesse (1978) describes the ultrastructural characteristics of the exine and "pollenkitt" of *Hamamelis vernalis*, *H. virginiana*, *Corylopsis platypetala*, and *Parrotia persica* in relation to their entomophilous (sticky pollen) or anemophilous (dry pollen) pollination ecology.

Most of these studies preceded the development and widespread use of the scanning electron microscope as a research tool in morphological studies, and were therefore conducted at the level of the light microscope, which is still the basic tool in pollen analysis. However, scanning electron micrographs of pollen grains, because of their three-dimensional appearance and great magnification, are much more useful for illustrating the surface details of grains than are light micrographs, and are increasingly being used in conjunction with light microscope analyses in palynological studies.

Scanning electron micrographs of hamamelidaceous pollen grains are infrequent in the literature, the largest assemblage that we know of being a group of eight photographs appearing in a recent review paper on evolutionary trends in the Hamamelidales-Fagales group (Endress, 1977). The SEM photographs presented here have resulted from a continuing effort to develop descriptions and illustrations of all 28 genera, in the hope that a broader base of data than has previously

been available will facilitate interpretations of intra- and inter-familial relationships and phylogenetic trends.

The genera illustrated here, and their distribution among the sub-families and tribes of the family, for purposes of this work, are as follows:

SUBFAMILY LIQUIDAMBAROIDEAE. *Liquidambar*, *Altingia*.

SUBFAMILY RHODOLEIOIDEAE. *Rhodoleia*.

SUBFAMILY EXBUCKLANDIOIDEAE. *Exbucklandia* (syn.: *Bucklandia*, *Sy-mingtonia*), *Mytilaria*, *Chunia*.

SUBFAMILY DISANTHOIDEAE. *Disanthus*.

SUBFAMILY HAMAMELIDOIDEAE.

Tribe Hamamelideae: *Maingaya*, *Ostrearia*, *Neostrearia*, *Trichocladus*, *Dicoryhe*, *Hamamelis*, *Tetrathyrium*, *Loropetalum*, *Embo-lanthera*.

Tribe Eustigmateae: *Eustigma*.

Tribe Corylopsideae: *Corylopsis*, *Fortunearia*, *Sinowilsonia*.

Tribe Fothergilleae: *Fothergilla*, *Parrotiopsis*, *Parrotia*.

Tribe Distylieae: *Sycopsis*, *Distyliopsis*, *Histylum*, *Molinadendron*, *Matudaea*.

#### MATERIALS AND METHODS

Pollen samples were taken from specimens collected in the field or in botanic gardens, or from specimens in or on loan from several major herbaria. Both pickled and dried materials were acetolyzed (Faegri and Iversen, 1975). For light microscope examination part of each sample was then mounted in glycerine jelly (Erdtman, 1952) and set aside for a period of at least two weeks to allow the grains to adjust to the mounting medium. Measurements were then made under oil immersion of at least thirty grains in each sample. The equatorial and polar axes were measured as seen in equatorial view. The ratio of the average dimensions of these axes (P/E) was then used to determine the shape classification according to the designations of Erdtman (1952). The magnification bars included in micrographs of whole grains represent lengths of approximately 10  $\mu\text{m}$ , while those in higher magnification pictures of surface details represent approximately 1  $\mu\text{m}$ .

For scanning electron microscopy, acetolyzed grains were washed in two successive distilled water washes, followed by two washes of 100 percent acetone, the first for ten minutes and the second for 30 minutes. The pollen was then transferred to aluminum stubs by means of Pasteur pipettes. The stubs had been previously coated with an acetone-tape adhesive (1 mm length of half-inch double-stick tape

partially dissolved in 10 ml of 100 percent acetone). The stubs were then coated with palladium-gold on a Technics Hummer 2 sputter coater and examined with an AMR 1000 scanning electron microscope at the Museum of Comparative Zoology of Harvard University.

#### OBSERVATIONS

*Size.* Pollen size in the family ranges from very small grains, averaging less than 20  $\mu\text{m}$  along the largest diameter, to large grains averaging close to 60  $\mu\text{m}$  along the largest diameter.

In general, the smallest grains among our samples are concentrated among the genera of the tribe Hamamelideae (subfamily Hamamelidoideae), in which flowers are complete, often contain staminodia and/or sterile disc lobes, and are presumably insect-pollinated. Conversely the largest grains appear among those genera which tend toward, or have advanced to, the naked-flowered, wind-pollinated state (Liquidambaroideae, *Chunia* among the Exbucklandioideae, members of tribe Distylieae in the Hamamelidoideae).

In contrast to the small grains of the Hamamelideae are the very large grains of the genus *Eustigma* (Eustigmateae, Hamamelidoideae), which is generally considered closely allied to the Hamamelideae. Although the flowers of *Eustigma* are complete, their petals are small and their styles greatly elongated, with broadly expanded sitgmatic surfaces, suggesting a specialized pollination mechanism which is, as yet, unreported.

Pollen size can also vary significantly among the species of a genus (e.g., *Fothergilla*, *Corylopsis*), or even among geographical races of the same species (C. T. Chang, 1964).

Among the most morphologically distinct pollen forms in the family are those of the large, nodding, red-flowered pseudanthia of *Rhodoleia* (Rhodoleioideae), which are reported to be bird-pollinated. These grains are small, with a very smooth surface marked only by minute perforations.

*Shape.* Pollen grain shapes among our samples ranged from oblate, through spheroidal, to prolate, with most of the taxa falling within the subspheroidal categories. Wind-pollinated genera with porate or polyporate grains, such as *Altingia*, *Liquidambar* and *Sycopsis*, exhibit large spheroidal grains. *Mytilaria* appears to be consistently oblate (C. T. Chang, 1964; Lee, 1969). However, shape designations are based on averages and may not reflect the full range of variation within a genus or species. Grains of the monotypic genus *Parrotiopsis*, for example, vary from oblate to prolate in shape, although the average form falls within the subspheroidal range. Furthermore, it is well-known that grain dimensions may be affected by the mounting medium

used, so one cannot be certain whether differing reports of grain shape are due to natural variation in the plant population, or to technique. For example, the general form of grains of *Loropetalum chinense* in our preparation (acetolysis, glycerine jelly) is subprolate, but C. T. Chang (1964, Methyl green/Glycerine jelly method of Wodehouse, 1935) reports grains of this species to be prolate, and Lee (1969, unacetolyzed grains in aceto-carmin, poly-vinyl alcohol, lactic-triacetin, or Calberla-basic fuchsin) reports them to be oblate-spheroidal. Consequently reports of pollen grain shape should be considered very carefully, and may be of little value from a taxonomic point of view. The general shape classification for our sample of each genus illustrated here is included in the plate caption.

**Apertures.** A large majority of hamamelid genera are tricolpate, with apertures varying in length, sharpness or bluntness of terminations, margin, and membrane characteristics among the genera. In general, apertures are long, with regular margins and pointed terminations approaching the poles in genera with complete flowers. Apertures become shorter, with blunt to round ends, and indistinct, irregular margins in those genera which tend toward incomplete or unisexual, wind-pollinated flowers. Rugate grains appear in *Chunia*, *Matudaea*, *Sycopsis*, and *Distylium*, and polyporate grains appear in *Altingia* and *Liquidambar*. Pore shaped apertures also appear rarely in *Chunia* (C. T. Chang, 1964), and with greater frequency (presumably through modifications of colpi or rugae) in *Distylium*, *Matudaea* and *Sycopsis*.

It thus appears that rugate to polyporate grains have arisen within three separate lineages within the family, in conjunction with a transition to naked, bisexual or unisexual, wind-pollinated flowers (Liquidambaroideae; *Chunia* among the Exbucklandioideae; *Distylium*, *Matudaea*, *Sycopsis* among the Distylieae in the Hamamelidoideae).

Tricolporate or tricolporoidate grains have been reported for a number of genera. Simpson (1936) described some degree of pore structure in the colpus membranes of twelve genera (*Exbucklandia*, *Corylopsis*, *Disanthus*, *Eustigma*, *Fortunaria*, *Fothergilla*, *Hamamelis*, *Loropetalum*, *Rhodoleia*, *Sinowilsonia*, *Tetrathyrum*, *Trichocladus*). Lee (1969) also reports tricolporate grains in *Exbucklandia*, and C. T. Chang (1964) for *Rhodoleia*. Tricolporoidate grains are described for *Mytilaria* and *Exbucklandia* by Erdtman (1952), *Chunia* and *Sycopsis* by C. T. Chang (1964) and *Fothergilla* by Lee (1969). Among the photographs included here there is the appearance of central pore-like protrusions in the colpi of *Fothergilla*. This aspect of aperture structure is in obvious need of detailed investigation.

Aperture margins are distinct in most genera and often differentiated as a pronounced margo with even or uneven edges, but margins become

indistinct in *Fortunearia*, *Sinowilsonia*, *Parrotia*, *Distylium*, *Sycopsis*, *Distyliopsis* and *Molinadendron*. In *Dicoryphe*, and to a lesser extent in *Embolanthera*, the margins of the apertures consist of the deep muri of the exine reticulum, which, on invagination of the colpus, close over and obscure the aperture.

Aperture membranes range from finely to coarsely granular. In some genera the granules appear to be concentrated in a longitudinal band in the center of the membrane, surrounded by a relatively smooth border. In this sense the membranes of *Disanthus* bear deeply sculptured opercula. In *Parrotia* the coarse granules of the membranes are fused in irregular ornate or vermiform patterns.

*Exine*. Sculpturing of the exine surfaces is generally reticulate in the family. The overall trend of modification is from a very coarsely reticulate pattern, with deep muri borne on pronounced bacula (e.g., *Dicoryphe*), through reduction of the meshes of the reticulum and depth of the muri, to very finely reticulate (*Chunia*, *Parrotiopsis*, *Distylium*), foveolate (*Altingia*, *Liquidambar*, *Matudaea*), or scrobiculate (*Rhodoleia*) patterns, with correspondingly shallower muri or a thinner tectum. In general this trend corresponds to the trends of floral modification from complete and presumably insect-pollinated types to incomplete, naked and/or unisexual forms, and is more or less evident among the three genera of Exbucklandioideae (*Exbucklandia*, *Mytilaria*, *Chunia*).

In a number of genera the exine reticulum is considerably finer in the polar than in the equatorial regions. This condition is well-developed in *Eustigma*, in which the polar areas may become scrobiculate or partially psilate. The very smooth, scrobiculate grains of *Rhodoleia* may also appear psilate in some cases.

The muri of a number of genera bear verrucae (*Altingia*, *Liquidambar*, *Fortunearia*, *Distylium*, *Distyliopsis*, *Sycopsis*, *Parrotia*). These are mostly wind-pollinated taxa but the significance of this structural feature in relation to the pollination mechanism is not known at present.

Unusually variable exine sculpturing, previously unreported, is evident in our samples of *Sinowilsonia* and *Molinadendron*, and is illustrated.

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PLATE 1. *Liquidambar* L. (Subfamily Liquidambaroideae)

VOUCHER MATERIAL: *Liquidambar orientalis* Mill.; Bogle 973: from cultivated tree in authors collection (NHA).

A. Somewhat angular, periporate grain with foveolate exine and numerous granules of irregular size and shape on the pore membranes. Note the minute supratectal verrucae scattered on the surface of the tectum,  $\times 2959$ . Shape: spheroidal. Size range: 32–55  $\mu\text{m}$ . (Bar = 10  $\mu\text{m}$ .)

B. Close up of grain surface showing a rounded aperture with a somewhat irregular margin, the supratectal verrucae, and the verrucate granules of the pore membrane,  $\times 10,000$ . (Bar = 10  $\mu\text{m}$ .)

A genus of three or four widely disjunct, wind-pollinated species distributed in Southeast Asia (*L. formosana* Hance), southeastern Asia Minor (*L. orientalis* Mill.) and southeastern North America and Central America (*L. styraciflua* L.). The Central American specimens are segregated by some authors as *L. macrophylla* Oerst. The genus has been the subject of several palynological investigations aimed at working out the evolutionary history and taxonomic relationships of the extant species (C. T. Chang, 1958, 1959, 1964; Kuprianova, 1960; Makarova, 1957).

Pore number, shape, diameter and margin characteristics appear to be somewhat variable within and among the species. Pores range from circular to elongate. Pore margins may be more or less even to fissured ("cracked").

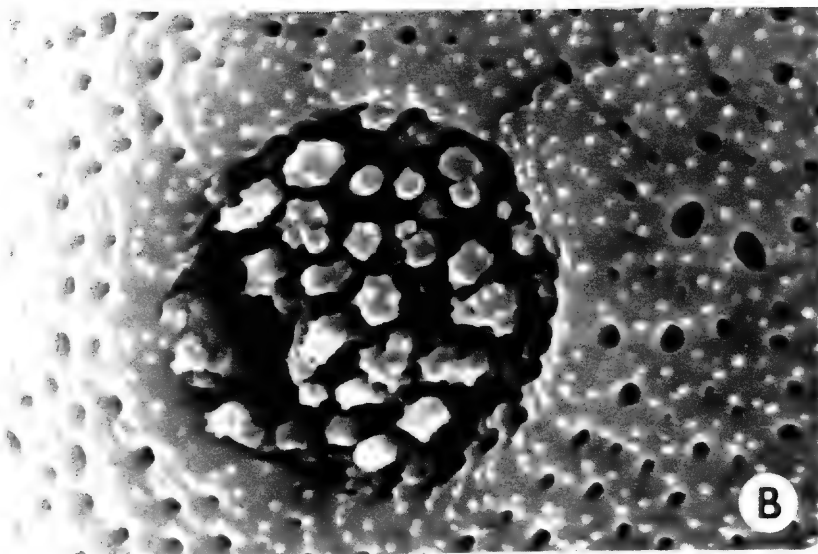
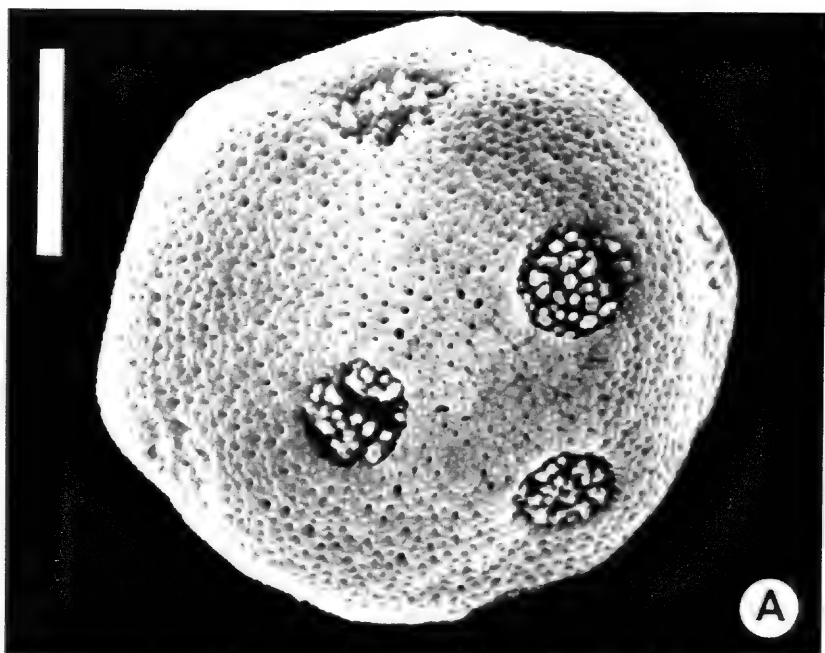


PLATE 2. *Altingia* Nor. (Subfamily Liquidambaroideae)

VOUCHER MATERIAL: *Altingia chinense* Oliver ex Hance; Bogle 583: Hong Kong Botanic Garden (NHA); *A. excelsa* Nor. Bogle 313: Mentigi Forest Reserve, Cameron Highlands, Malaya (NHA). *A. obovata* Merr. and Chun; H. Y. Liang 64734: Hainan, China (AA).

A. Periporate grain of *Altingia chinense* with foveolate exine; pore membranes bearing granules of varying size and shape. Note the small supratectal verrucae uniformly distributed over the surface of the tectum and on the membrane granules,  $\times 2780$ . Shape: spheroidal. Size range: 35–58  $\mu\text{m}$ . (Bar = 10  $\mu\text{m}$ .)

B–D. Close-ups of grains of three species to show sexine, pore margin, pore membrane and membrane granules (some of which bear verrucae). B, *A. excelsa*,  $\times 10,000$ ; C, *A. obovata*,  $\times 10,000$ ; D, *A. chinense*,  $\times 10,000$ . (Bar = 10  $\mu\text{m}$ .)

*Altingia* is a genus of one (Vink, 1957) to about 13 species (various authors; see Index Kewensis, H. T. Chang, 1973). The flowers and inflorescences of the genus are similar to those of *Liquidambar*. Pollination is anemophilous. The pollen grains of *Altingia* in our material have characteristically round pores which may vary slightly in diameter, and have a distinct margin which is very nearly regular or even. Figures B–D illustrate the variation, which is apparent also in light microscope observations, of perforation size in the reticulum of the tectum. In this respect *A. excelsa* (B) has many minute, rounded perforations; *A. obovata* (C) exhibits rounded perforations of larger diameter; and *A. chinense* (A, D) has perforations which may vary in shape from rounded to somewhat elongate or irregular. From a taxonomic point of view the significance of this variation is obscure.

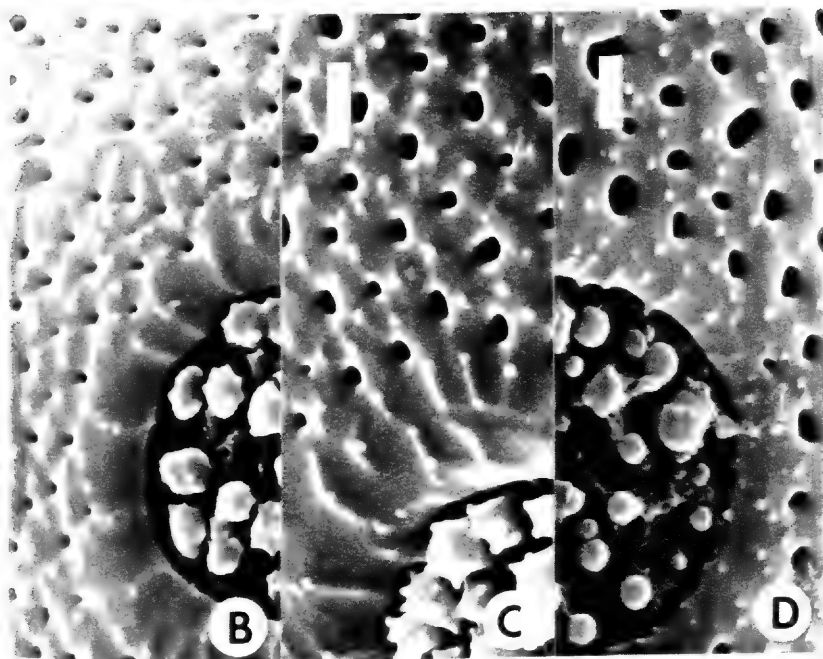
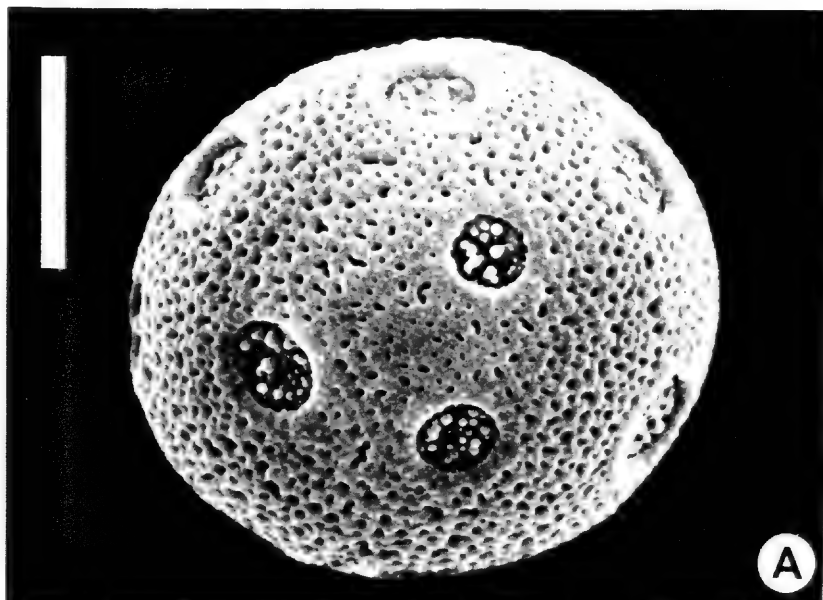


PLATE 3. *Rhodoleia* Champ. ex Hook. (Subfamily Rhodoleioideae)

VOUCHER MATERIAL: *Rhodoleia championi* Hook. f.; Bogle 276: Klang Gates, near Kuala Lumpur, Selangor, Malaya (NHA).

A. Oblique view showing relatively smooth, scrobiculate tectum and two invaginated colpi,  $\times 5800$ . Shape: subprolate. Size range in equatorial view: equatorial axis, 16–26  $\mu\text{m}$ ; polar axis, 20–29  $\mu\text{m}$ . (Bar = 10  $\mu\text{m}$ .)

B. Slightly oblique polar view showing very small perforations (lumina) of the tectum and granular sculpturing of invaginated colpus membranes,  $\times 5920$ . (Bar = 10  $\mu\text{m}$ .)

A genus of one variable species (Vink, 1957; Tardieu-Blot, 1965) or about 7–10 distinct species (see Exell, 1935; H. T. Chang, 1973; discussion in Tardieu-Blot, 1965) distributed from southern China southward through Indochina and Malaya to Sumatra. The pollen grains have been described as being "tricolpate-porate" by C. T. Chang (1964), but a pore is not evident in our scanning electron micrographs. *Rhodoleia* may be unique among hamamelids in being bird-pollinated or at least partially so (D. van Leeuwen, cited in Vink, 1957). The birds may be attracted to nectar reportedly secreted by a cycle of glands inserted between the stamens and the ovary, and the sticky, rather than powdery pollen may represent an adaptation toward ornithophily.

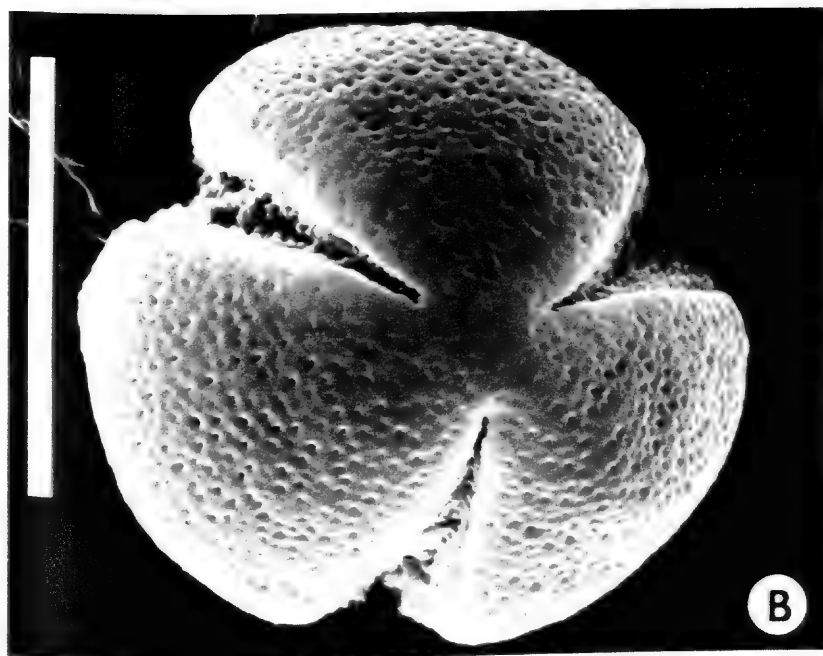
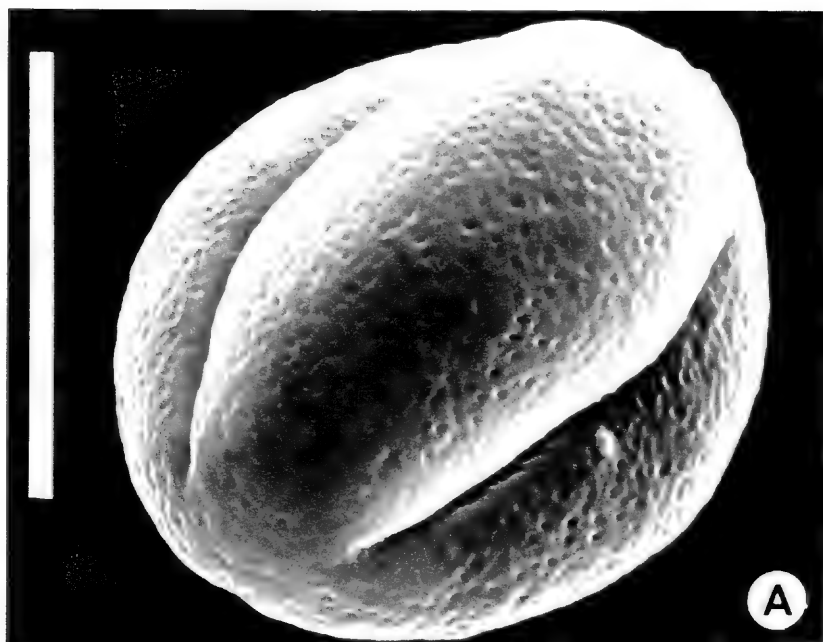


PLATE 4. *Exbucklandia* R. W. Brown. (Subfamily Exbucklandioideae)

VOUCHER MATERIAL: *Exbucklandia populnea* (R. Br. ex Griff.) R. W. Brown; Bogle 314; Tanah Rata Village, Cameron Highlands, Selangor, Malaya (NHA).

A. Equatorial view showing the coarse reticulum. Note the large lumina of fairly uniform size but somewhat irregular, angular shape; the margin of very small lumina bordering colpi; deep muri resting on distinct bacula; coarse granules on surface of the nexine; granular colpus membranes,  $\times 3520$ . Shape: prolate spheroidal. Size range in equatorial view: equatorial axis, 26–32  $\mu\text{m}$ ; polar axis, 23–37  $\mu\text{m}$ . (Bar = 10  $\mu\text{m}$ .)

B. Polar view showing coarsely reticulate exine with lumina not differing markedly in size from those of the mesocolpium. Note the colpi with acutely pointed ends reaching nearly to the poles; the distinct bacula subtending the muri; coarse granules on nexine surface,  $\times 3540$ . (Bar = 10  $\mu\text{m}$ .)

A genus of two (Vink, 1957; Tardieu-Blot, 1965) or three (H. T. Chang, 1973) species ranging from the Sikkim Himalaya to central China, and southward through Indochina and Malaya to Sumatra. The mature flowers of *Exbucklandia* are incomplete, lacking a calyx, and are rather inconspicuous. No published observations on the pollination mechanism are known to us. The pollen structure is similar in its coarsely reticulate exine and tricolpate condition to that of a number of other hamamelidaceous genera with complete and presumably insect-pollinated flowers, including those of *Dicoryphe* (Madagascar), and *Maingaya* (Malaya). The closely related genus *Mytilaria* (Indochina) has a finer reticulum. Simpson (1936) suggests the presence of a pore in a fossil grain he attributes to *Exbucklandia*, while Lee (1969) describes and illustrates (Pl. I, Fig. 6; Pl. III, Fig. 2) a pore in the colpus of *Exbucklandia*.

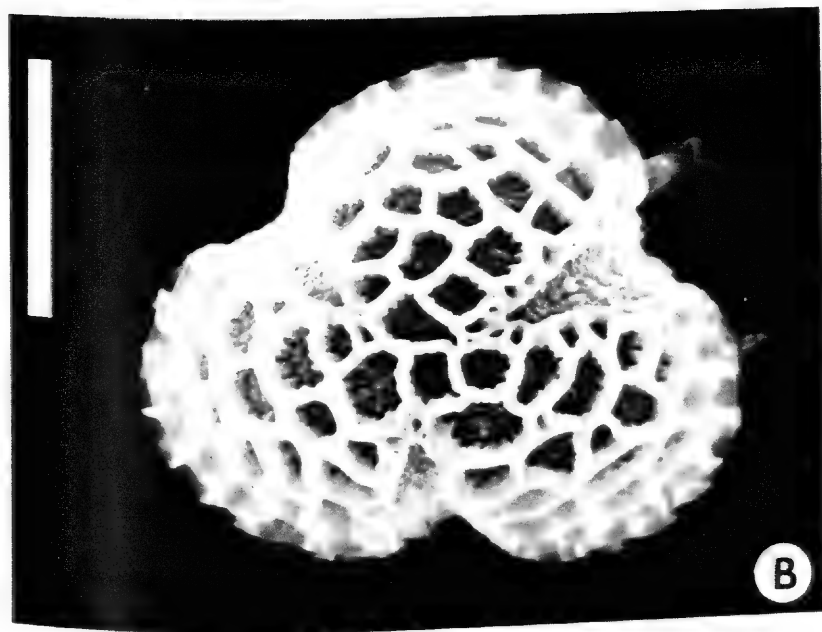
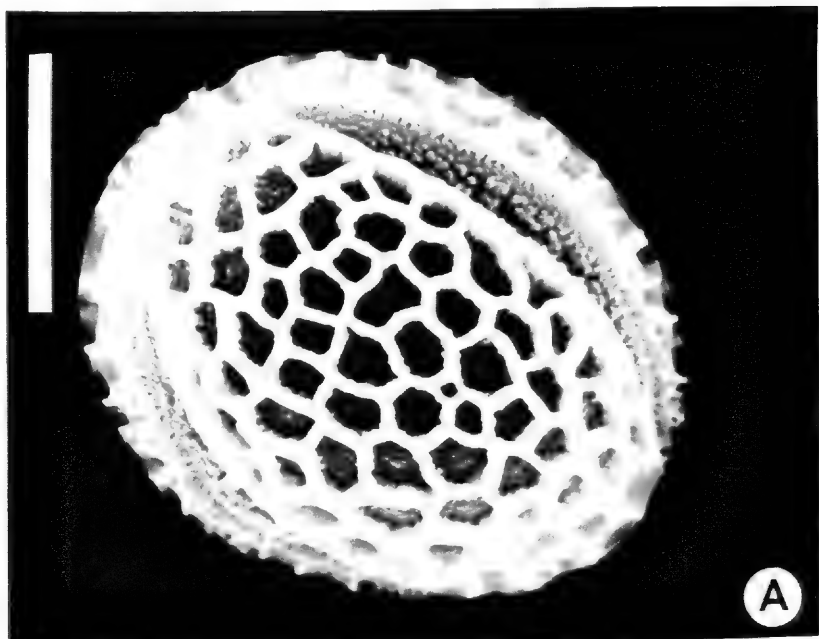




PLATE 5. *Mytilaria* Lecomte (Subfamily Exbucklandioideae)

VOUCHER MATERIAL: *Mytilaria laosensis* Lecomte; Ko 55988: Kwangsi, China (AA).

A. Slightly oblique equatorial view showing the coarsely reticulate exine, with deep muri borne on bacula. Lumina more or less isodiametric to elongate; angular in outline; varying in size, but on average smaller and more numerous per unit area than in the closely related *Exbucklandia*,  $\times 5550$ . Size range in equatorial view not available. (Bar = 10  $\mu\text{m}$ .)

B. Polar view of tricolpate grains. Note the less elongate lumina in the apocolpium as compared with *Exbucklandia*; margo distinct, with associated small lumina surrounding the colpi; colpus membranes appear to be relatively smooth in marginal areas, but finely granular towards the center,  $\times 5830$ . (Bar = 10  $\mu\text{m}$ .)

A little known monotypic genus found only in southern China and Indochina. It is almost indistinguishable from *Exbucklandia* and *Chunia* vegetatively, but differs strongly in floral morphology. The flowers are complete, with nearly inferior ovaries immersed in a fleshy spike. Ten stamens with horned filaments and hooded antlers are connivent in one cycle over minute styles and stigmas. Grains are oblate according to C. T. Chang (1964) and Lee (1969), or sub-oblate to oblate-spheroidal (Erdtman, 1946). There is no information on the pollination mechanism.

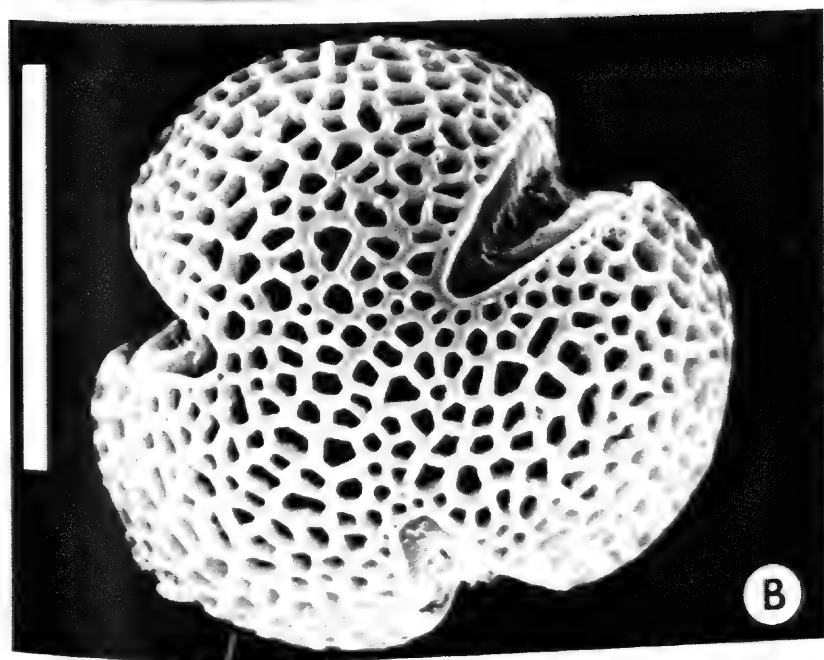
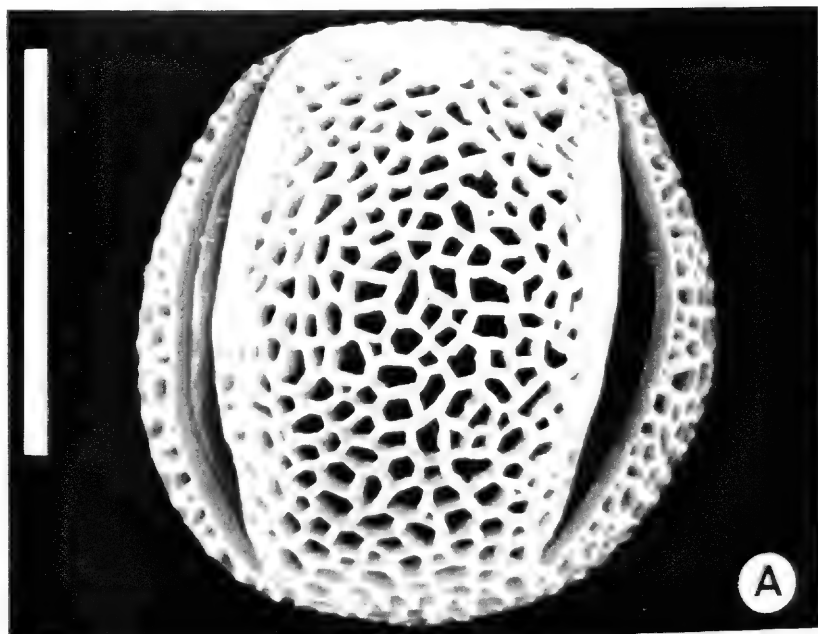


PLATE 6. *Chunia* H. T. Chang (Subfamily Exbucklandioideae)

VOUCHER MATERIAL: *Chunia bucklandioides* H. T. Chang; C. Wang 36075; Hainan, China (AA).

A. Slightly oblique equatorial view of a tricolpate grain, showing the microreticulate sexine with small lumina of variable size and shape, and granular membranes of the colpi. Note also the numerous small supratectal verrucae on the surfaces of the muri,  $\times 2840$ . Shape: prolate spheroidal. Size range in equatorial view: equatorial axis, 26–37  $\mu\text{m}$ ; polar axis, 29–38  $\mu\text{m}$ . (Bar = 10  $\mu\text{m}$ .)

B. Slightly oblique polar view of a tricolpate grain showing the foveolate exine of the apocolpium, with lumina of reduced size and regular shape. Note the distinct margo and bluntly rounded ends of the colpi, the coarse granules of the colpus membranes, and the verrucae of the tectum and margo,  $\times 3820$ . (Bar = 10  $\mu\text{m}$ .)

*Chunia* is another poorly known monotypic genus. It is endemic to the island of Hainan, off the southern coast of China. Although vegetatively similar to *Exbucklandia* and *Mytilaria*, its flowers differ by being naked and clustered in short, fleshy spikes that present a "ball" of stamens on elongate filaments at anthesis. The genus has apparently evolved toward wind-pollination. Further evidence of this tendency is the pronounced modification of the exine to a relatively smooth, foveolate condition, as opposed to the coarse reticula of *Exbucklandia* and *Mytilaria*, and a tendency toward an increase in the number of apertures. Grains in our sample range from 3- or 4-colpate to hexarugate (see Plate 7). C. T. Chang (1964) reports 15 per cent hexarugate grains and some polyporate grains in his material of *Chunia*. In our sample 81 per cent of the grains are tricolpate, while 19 per cent have more than three apertures.

These modifications (naked flowers; exerted anthers; increase in aperture number; relatively smooth, foveolate exine) run parallel to similar tendencies in other members of the family which have progressed independently toward anemophily (e.g., Liquidambaroideae; Distylieae of the Hamamelidoideae). However, the minute styles and stigmas of the ovaries in *Chunia* might seem to contradict this list of characteristics which often accompany anemophily.

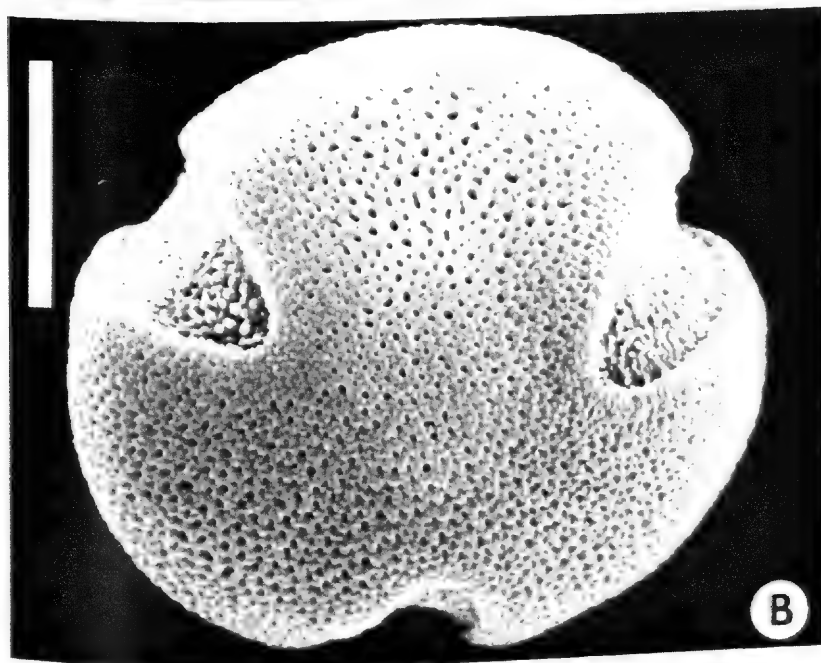
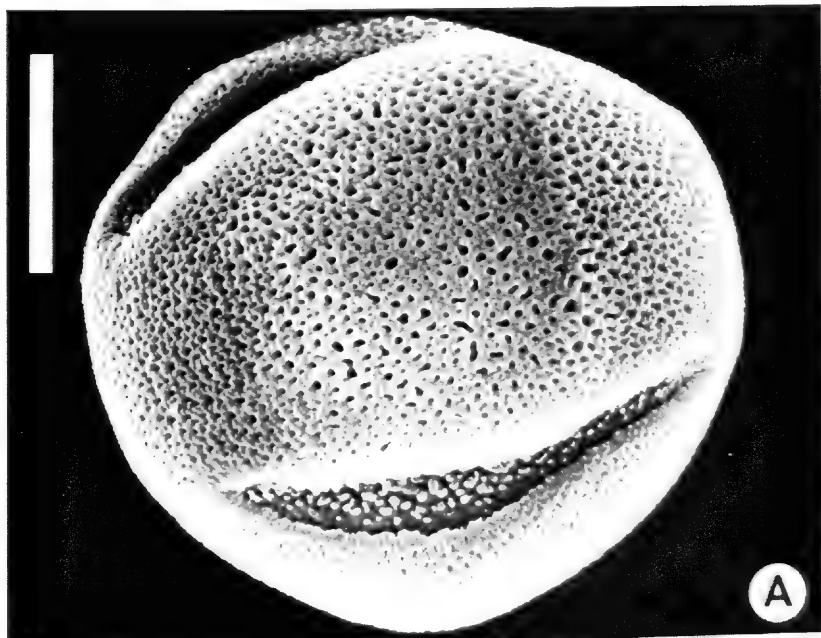


PLATE 7. *Chunia* H. T. Chang (Subfamily Exbucklandioideae)

VOUCHER MATERIAL: same as Plate 6.

A. View of hexarugate grain, showing three colpi of shortened length with coarsely granular membranes. Note the finely reticulate exine of the mesocolpium and the reduced size of lumina in the apocolpium,  $\times 3170$ . Size range for hexarugate grains, 32–43  $\mu\text{m}$ . (Bar = 10  $\mu\text{m}$ .)

B. Tricolpate grain (left) next to hexarugate grain. Note difference in length of the colpi,  $\times 2000$ . (Bar = 10  $\mu\text{m}$ .)

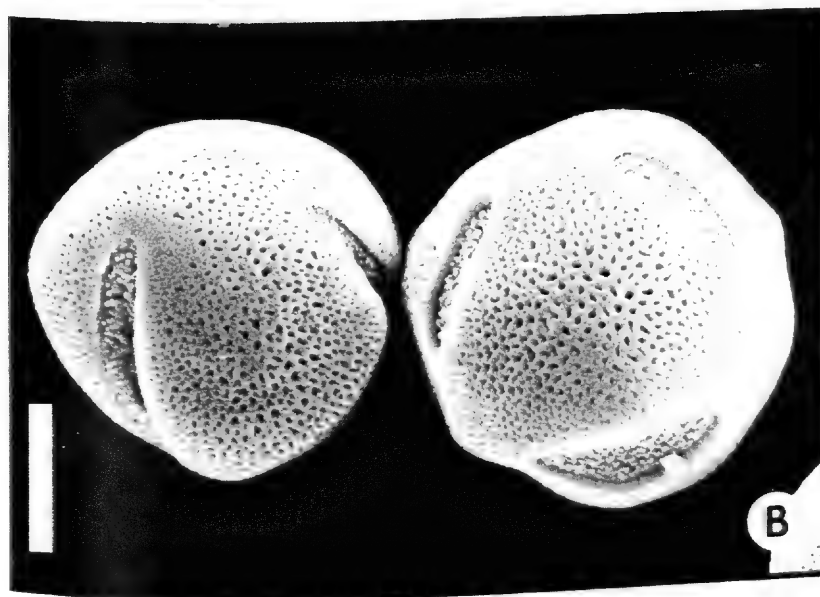
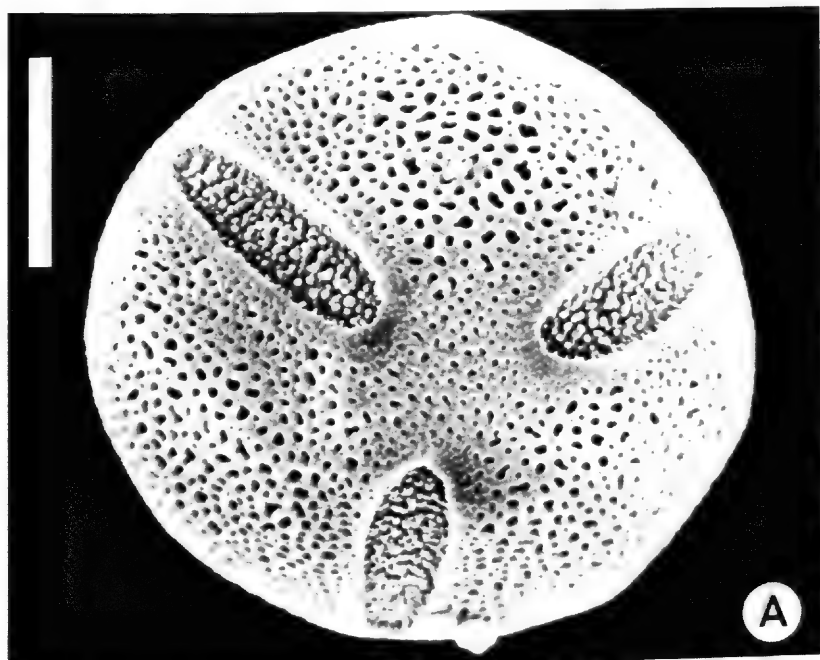


PLATE 8. *Disanthus* Maxim. (Subfamily Disanthoideae)

VOUCHER MATERIAL: *Dianthus cercidifolius* Maxim.; Bogle 1268, from M. Mizushima, s.n.: cultivated plant, Japan (NHA).

A. Equatorial view of tricolpate grain, showing reticulate exine, with relatively deep muri borne on short bacula. Note the generally uniform size and angular outline of the meshes, and the occasional small lumina scattered among the larger ones; the border of small lumina along margins of the colpi; the strongly sculptured exine of the colpus membrane,  $\times 4300$ . Shape: prolate spheroidal. Size range in equatorial view: equatorial axis 22–33  $\mu\text{m}$ ; polar axis, 22–33  $\mu\text{m}$ . (Bar = 10  $\mu\text{m}$ .)

B. Polar view showing reticulate exine with slight reduction in size of the lumina in the apocolpium; sharply pointed ends of colpi; operculum-like islands of deeply sculptured exine on colpus membranes. The exine frequently appears tectate along the margins of the opercula,  $\times 3900$ . (Bar = 10  $\mu\text{m}$ .)

A monotypic genus (and subfamily) distributed in the mountains of Japan and central China, but widespread in cultivation. The presence of opercula on the colpus membranes is distinctive among hamamelidaceous pollens. The pentamerous flowers of *Disanthus* are reported to bear nectaries on the inner face of the petals (Mizushima, 1968) which attract flies as pollinators.

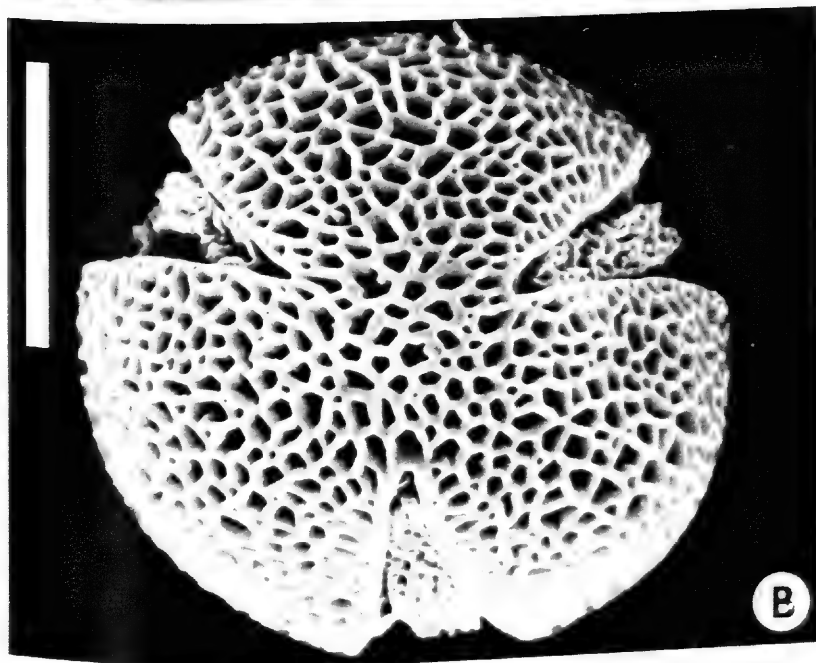
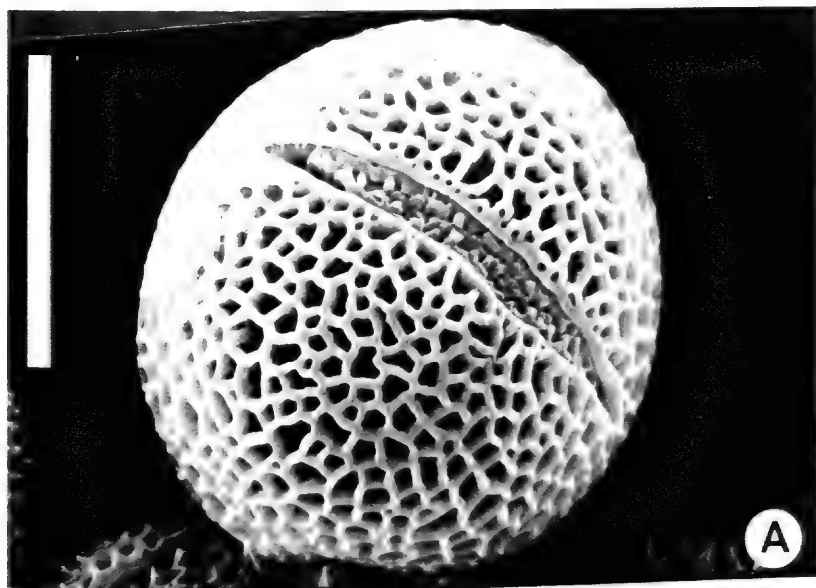




PLATE 9. *Maingaya* Oliver (Subfamily Hamamelidoideae; Tribe Hamamelideae)

VOUCHER MATERIAL: *Maingaya malayana* Oliv.; Burkill 7594; Penang, Malaya (AA).

A. Equatorial view of tricolpate grain, showing the coarsely reticulate sexine, with deep muri borne on relatively long bacula. Lumina of the sexine are irregular in shape and angular in outline. Note the very small lumina along the smooth margin of the colpus; occasional coarse granules on the nexine surface under the exine reticulum; coarsely granular central portion of the colpus membrane,  $\times 5960$ . Shape: oblate spheroidal. Size range in equatorial view: equatorial axis, 16–23  $\mu\text{m}$ ; polar axis, 13–21  $\mu\text{m}$ . (Bar = 10  $\mu\text{m}$ .)

B. Polar view, grain slightly indented at upper right. Lumina of the reticulum reduced slightly in size in the apocolpium. Ends of the colpi sharply pointed,  $\times 5910$ . (Bar = 10  $\mu\text{m}$ .)

*Maingaya* is a monotypic genus known only from a very few collections in Perak and Penang, Malaysia.

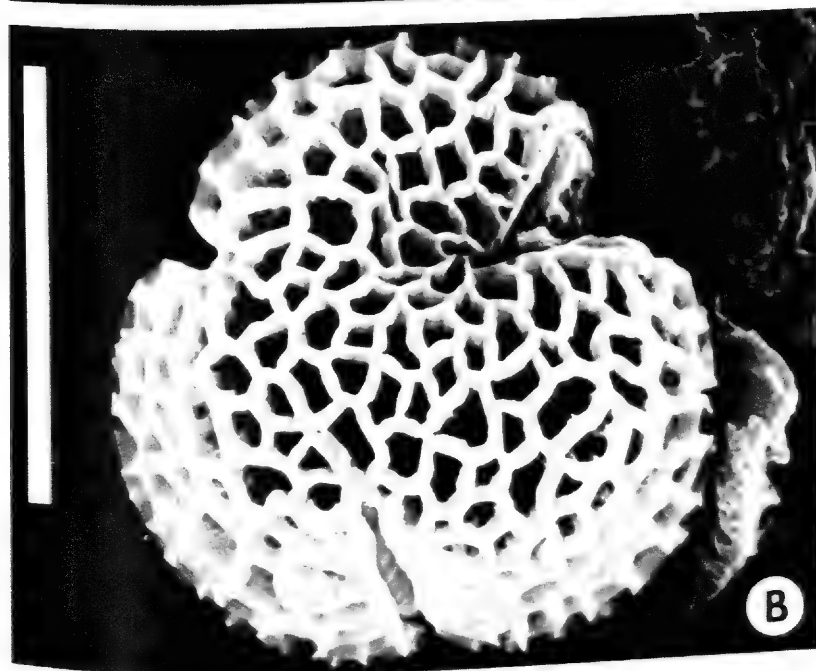
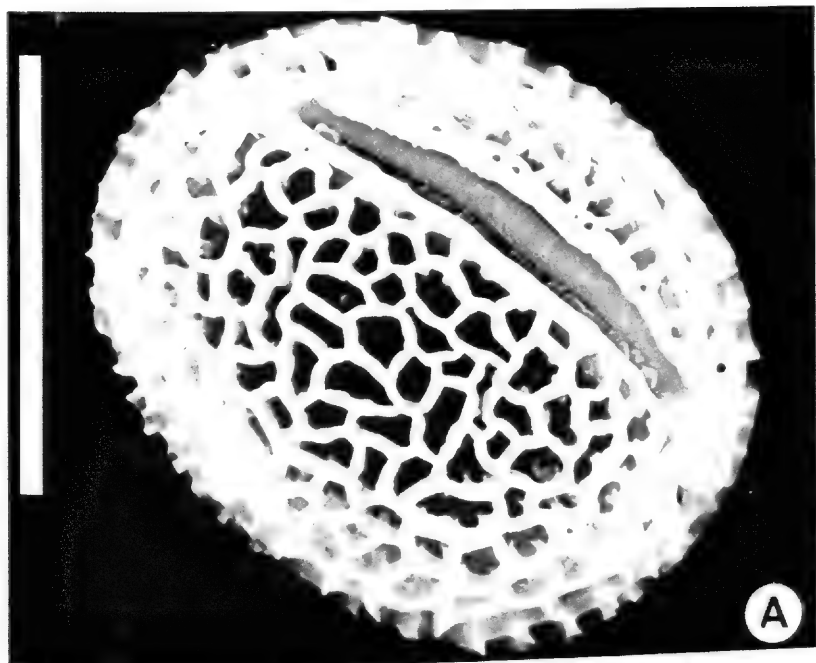


PLATE 10. *Ostrearia* Baill. (Subfamily Hamamelidoideae; Tribe Hamamelideae)

VOUCHER MATERIAL: *Ostrearia australiana* Baill.; Brass 20266: Queensland, Australia (AA).

A. Equatorial view of a tricolpate grain (partially collapsed), illustrating the moderately coarse reticulum of the sexine. The lumina vary widely in size and shape. The tectum is supported on short bacula. Note the elongate colpus, the distinct margo with numerous small perforations along the margins, and the granular colpus membrane,  $\times 5700$ . Shape: prolate spheroidal. Size range in equatorial view: equatorial axis, 17–20  $\mu\text{m}$ ; polar axis, 18–21  $\mu\text{m}$ . (Bar = 10  $\mu\text{m}$ .)

B. Oblique polar view. Reticulation of the apocolpium not differing significantly from that of the mesocolpium; short bacula supporting tectum visible in upper and lower left quadrants. Note acute ends of colpi, colpus margins and granular membranes,  $\times 5670$ . (Bar = 10  $\mu\text{m}$ .)

A monotypic genus endemic to the rain forests of northern Queensland, Australia, and together with *Neostrearia* the only members of the family presently known from that continent. The pollen morphology of the two genera is rather similar, the only obvious differences in our samples being the degree of coarseness of the reticulum, and in the distinctness and evenness of the colpus margins.

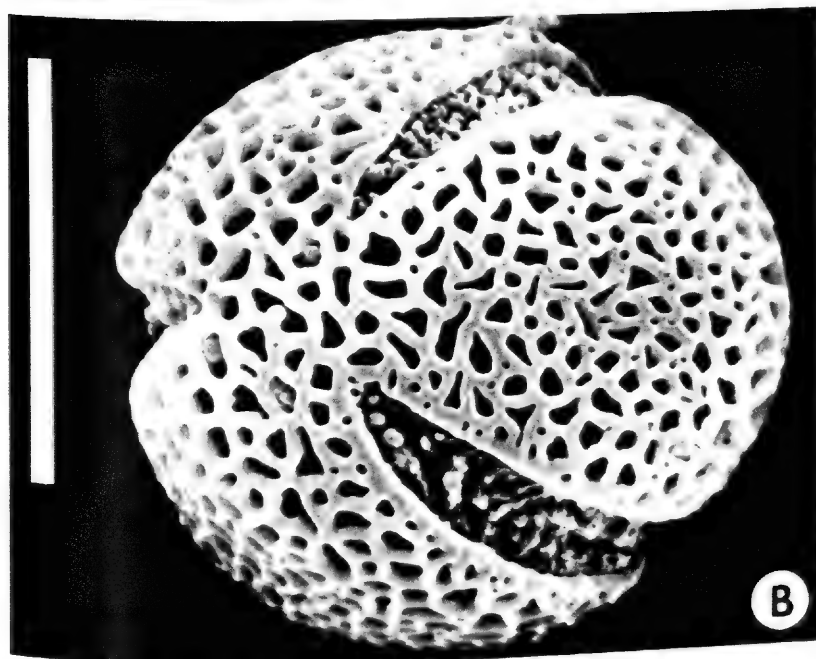
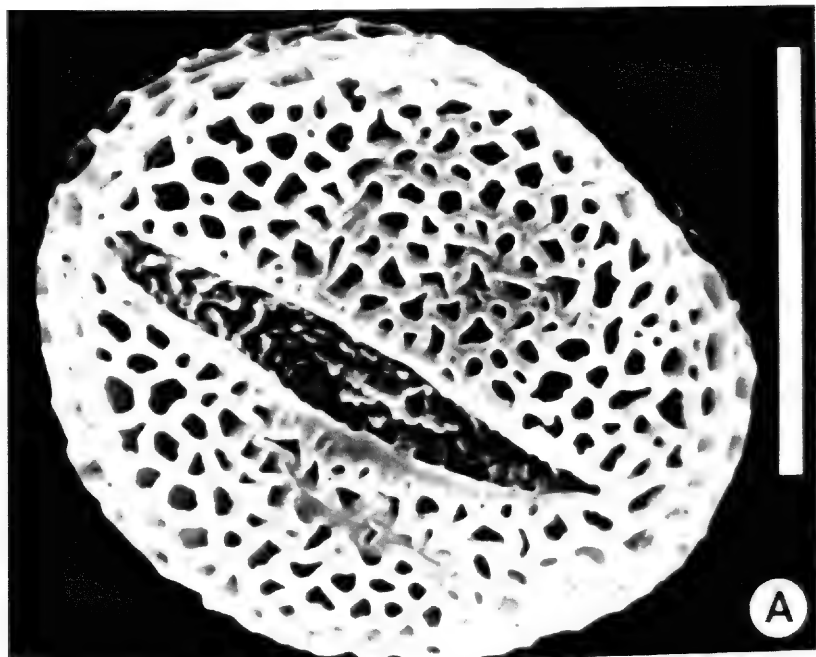


PLATE 11. *Neostrearia* L. S. Smith (Subfamily Hamamelidoideae; Tribe Hamamelideae)

VOUCHER MATERIAL: *Neostrearia fleckeri* L. S. Smith; Brass 2140: Mossman River Gorge, Cook District, Queensland, Australia (AA).

A. Oblique equatorial view of a tricolpate grain showing the irregular and moderately coarse reticulum of the exine. Note the elongate colpi with blunt ends; the degree of irregularity in the size and shape of the lumina; the uneven to "cracked" colpus margins, and the granular colpus membranes,  $\times 5650$ . Shape: oblate spheroidal. Size range in equatorial view: equatorial axis, 22–25  $\mu\text{m}$ ; polar axis, 20–27  $\mu\text{m}$ . (Bar = 10  $\mu\text{m}$ .)

B. Slightly oblique polar view. Lumina of sexine in apocolpium not differing significantly in size from those of the mesocolpium. Note the margins and membranes of the colpi,  $\times 4830$ . (Bar = 10  $\mu\text{m}$ .)

A monotypic genus endemic to rain forests of northern Queensland, Australia. *Neostrearia* is apparently closely related to *Ostrearia*. The pollen in our sample of *Neostrearia* appears to differ from that of *Ostrearia* in having slightly larger lumina in the reticulum, no distinct margo, and more uneven margins along the colpi.

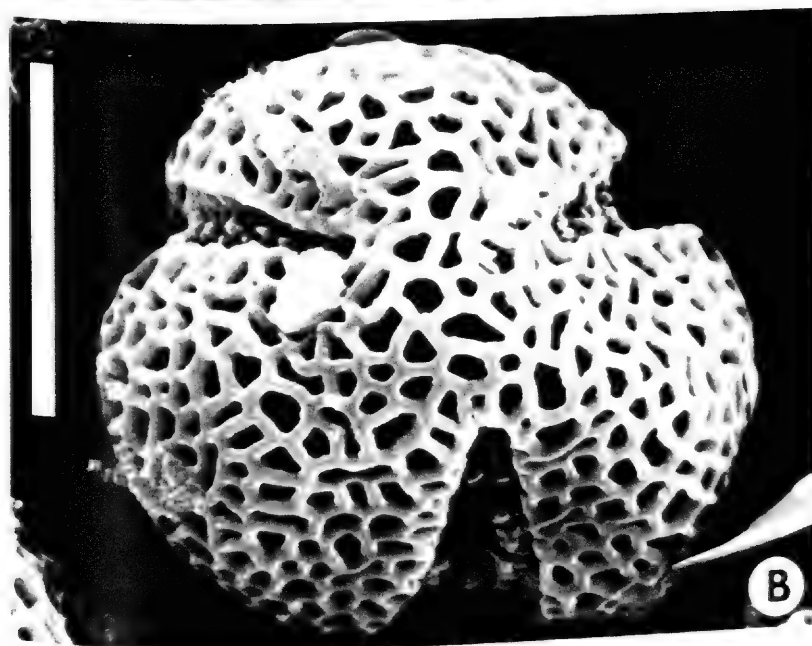
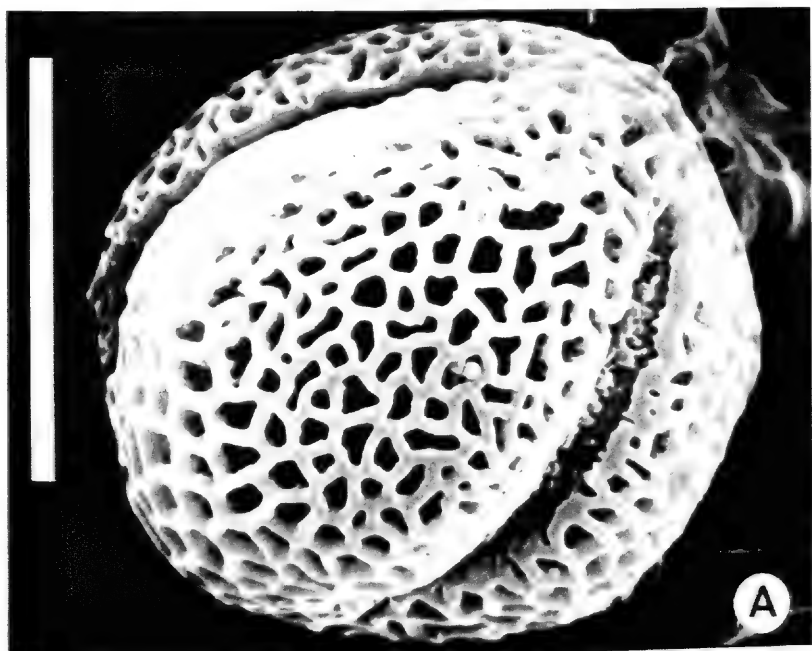


PLATE 12. *Trichocladus* Pers. (Subfamily Hamamelidoideae; Tribe Hamamelideae)

VOUCHER MATERIAL: *Trichocladus crinitus* Pers.; S. C. Troughton 180: Swaziland (NHA).

A. Equatorial view of a tricolpate grain showing elongate colpi and the moderately coarse reticulum of the exine. Note the numerous small, rounded lumina scattered among larger meshes of irregular shape; the outline of the lumina is not strongly polygonal or angular,  $\times 6000$ . Shape: prolate spheroidal to sub-prolate. Size range in equatorial view: equatorial axis, 15–22  $\mu\text{m}$ ; polar axis, 18–25  $\mu\text{m}$ . (Bar = 10  $\mu\text{m}$ .)

B. Polar view. The lumina of the apocolpium appear, on average, to be slightly smaller in diameter and more rounded than in the mesocolpium. In the distal portions of the mesocolpium the lumina appear to exhibit a tendency to become aligned in short, curving rows. Note the concentration of small lumina along the narrow margo of the colpi, the even edge of the margin, and the coarsely granular colpus membranes,  $\times 6000$ . (Bar = 10  $\mu\text{m}$ .)

*Trichocladus* consists of about five species distributed in eastern Africa, from Ethiopia southward to the Cape of Good Hope, in South Africa. Erdtman (1946) provides a brief description of the pollen of *T. crinitus*, while Bakker (1959) gives descriptions of *T. ellipticus* E. and Z. and *T. grandiflorus* Oliver.

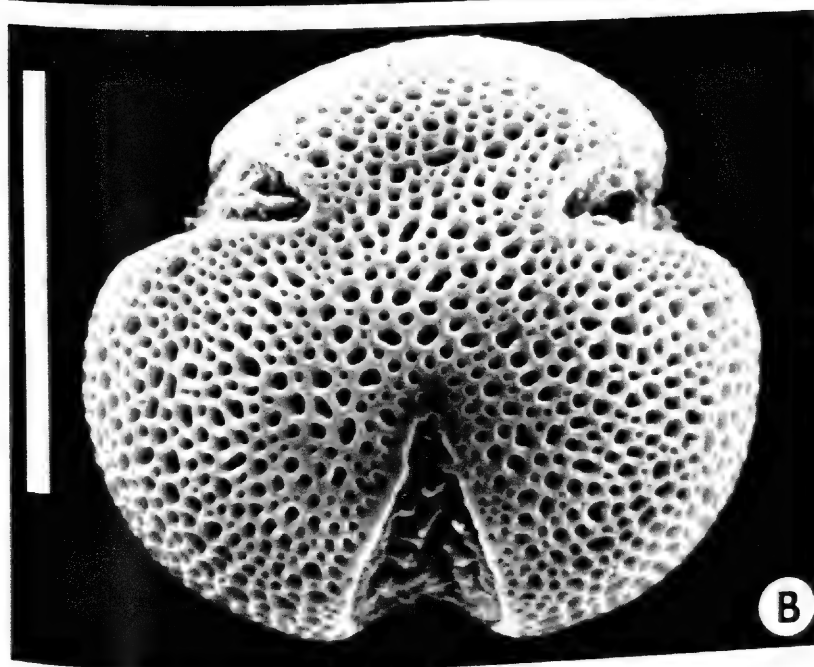
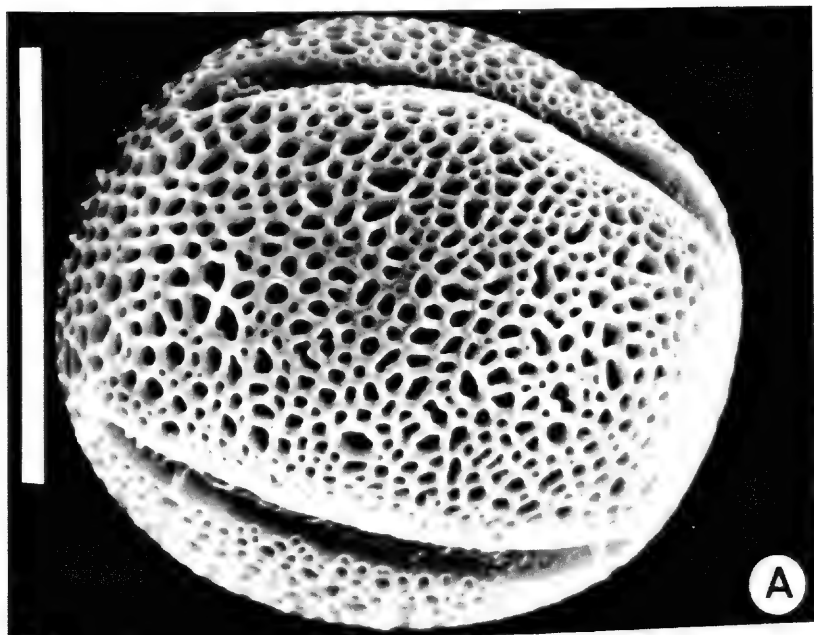




PLATE 13. *Dicoryphe* Thou. (Subfamily Hamamelidoideae; Tribe Hamamelideae)

VOUCHER MATERIAL: *Dicoryphe viticoides* Baker; Perrier de la Bathie 239; Ankaratin, Madagascar (P).

A. Slightly oblique view of a tricolpate grain showing the coarsely reticulate exine with deep muri resting on relatively long bacula. The lumina are angular, ranging in shape from regular pentagonal to mostly elongate or curving. Note the margin of the colpus; very small lumina or perforations occur only occasionally along the margins,  $\times 3030$ . Shape: oblate spheroidal. Size range in equatorial view: equatorial axis, 29–34  $\mu\text{m}$ ; polar axis, 27–35  $\mu\text{m}$ . (Bar = 10  $\mu\text{m}$ .)

B. Slightly oblique polar view. The lumina of the apocolpium do not appear to differ significantly in size from those of the mesocolpium. The colpi are slightly shortened. Note that the colpus margins (lower middle) consist of the undulating muri of adjacent large meshes. The projecting angles and indentations of the opposing margins appear to be complimentary, so that the colpi are obscured when invaginated,  $\times 2820$ . (Bar = 10  $\mu\text{m}$ .)

*Dicoryphe* is a genus of about 13 species endemic to the island of Madagascar. Little is known of this interesting group apart from the morphological descriptions of the species provided in various taxonomic accounts. Simpson (1936) attributed certain fossil grains in Scottish lignites to *Dicoryphe* on the basis of their coarse reticulum and colpus margin characteristics. Chang (1964) compares *Dicoryphe* with *Exbucklandia* on the basis of their coarse reticula.

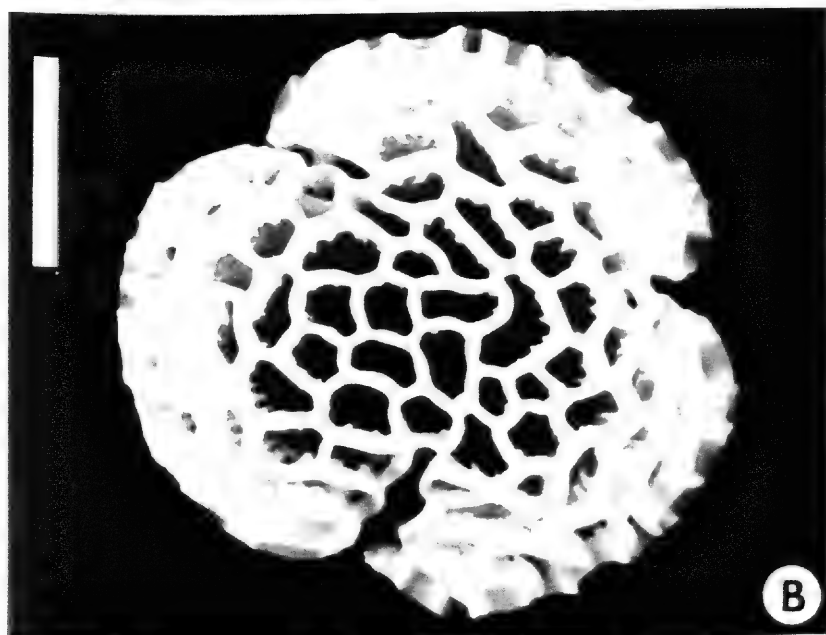
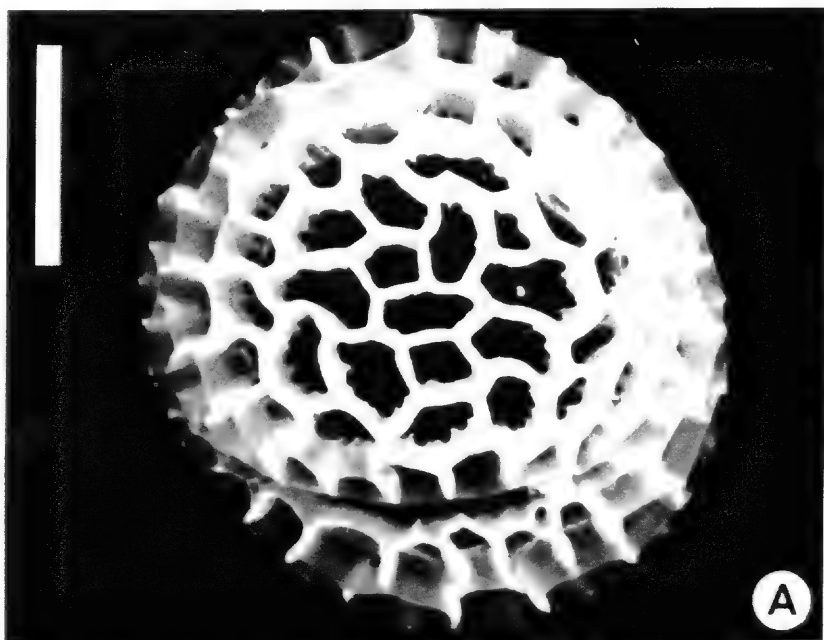


PLATE 14. *Hamamelis* L. (Subfamily Hamamelidoideae; Tribe Hamamelideae)

VOUCHER MATERIAL: *Hamamelis virginiana* L.; Bogle 771: Interstate Park, Polk Co., Wisconsin (NHA).

A. Equatorial view showing the moderately coarse reticulum and muri of moderate depth resting on short bacula, as shown in upper right of photograph. The lumina are polygonal, with pronounced angles. Note the occasional small, rounded perforations scattered among the polygonal meshes. The peripheral region of the colpus membrane appears unsculptured, the central portion granular,  $\times 5710$ . Shape: prolate spheroidal. Size range in equatorial view: equatorial axis, 15–19  $\mu\text{m}$ ; polar axis, 18–22  $\mu\text{m}$ . (Bar = 10  $\mu\text{m}$ .)

B. Slightly oblique polar view, showing the elongate colpi with acutely pointed ends. The reticulum of the apocolpium does not differ significantly from that of the mesocolpium. Note the narrow margo with associated small lumina, the even edge of the margin, and the central granular and peripheral unsculptured portions of the colpus membrane as shown in upper left of photograph,  $\times 6000$ . (Bar = 10  $\mu\text{m}$ .)

A genus of about nine species distributed in eastern North America, the mountains of Mexico, in Japan and China. The pollen of *Hamamelis* is similar to that of *Loropetalum*. The flowers of the two genera are similar in appearance and share a similar tetramerous floral plan. The two genera were once considered congeneric. Chang (1964) notes minor differences but basic similarity among the species of *Hamamelis* he examined, with the exception of *H. japonica* Sieb. et Zucc., which he reports to be larger in size and to have a thicker exine. Ikuse (1956) also provides brief descriptions of three species of *Hamamelis* (*H. japonica*, *H. mollis*, *H. virginiana*) in Japan. The pollen of *H. vernalis* and *H. virginiana* is "sticky," with "pollenkitt" deposited on the exine surface (Hesse, 1978). Small flies are the principal pollinators of *H. virginiana*.

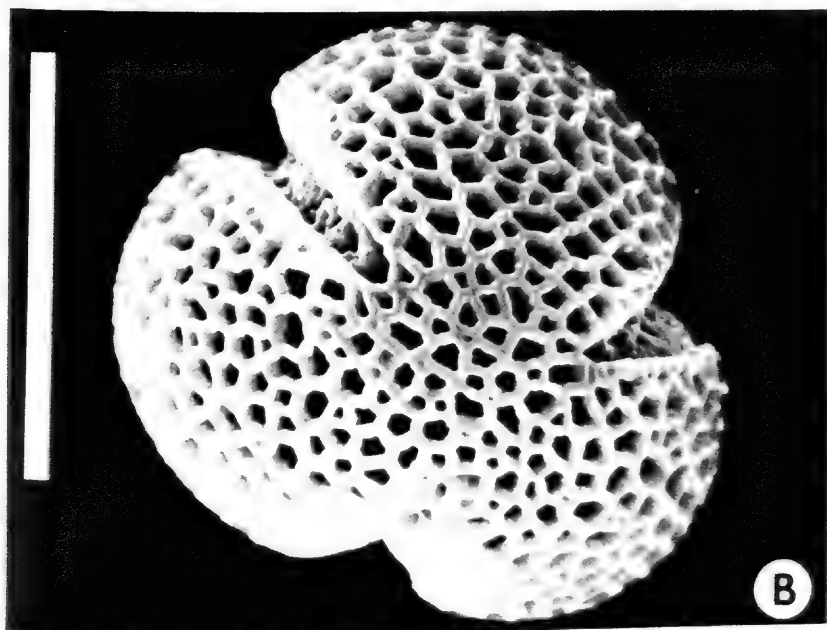
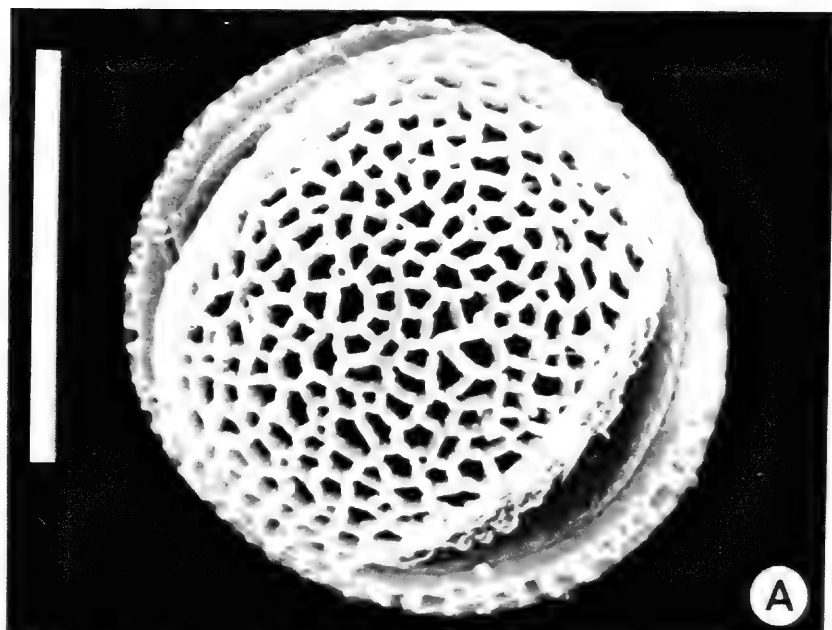


PLATE 15. *Tetrathyrium* Benth. (Subfamily Hamamelidoideae; Tribe Hamamelideae)

VOUCHER MATERIAL: *Tetrathyrium subcordatum* Benth.; Bogle 586: Bowen Road, Victoria, Hong Kong (NHA).

A. Equatorial view of a tricolpate grain showing a slightly expanded colpus with central zone of granular sculpturing and relatively smooth peripheral areas. Note the coarse reticulum of the mesocolpium with irregularly shaped, angular lumina, the relatively deep muri on short bacula, and the distinct but somewhat uneven margins of the colpus, with scattered small lumina along the margin and occasional breaks in the margo,  $\times 6350$ . Shape: oblate spheroidal. Size range in equatorial view: equatorial axis, 19–26  $\mu\text{m}$ ; polar axis, 16–25  $\mu\text{m}$ . (Bar = 10  $\mu\text{m}$ .)

B. Slightly oblique polar view illustrating the reticulum of the apocolpium; the lumina of the reticulum not differing significantly in size from those of the mesocolpium,  $\times 5800$ . (Bar = 10  $\mu\text{m}$ .)

*Tetrathyrium* is a monotypic genus which is endemic to Hong Kong. It was once thought to include *Loropetalum*, from which it differs in its pentamerous rather than tetramerous floral plan, in its coarse reticulum, and deeper muri.

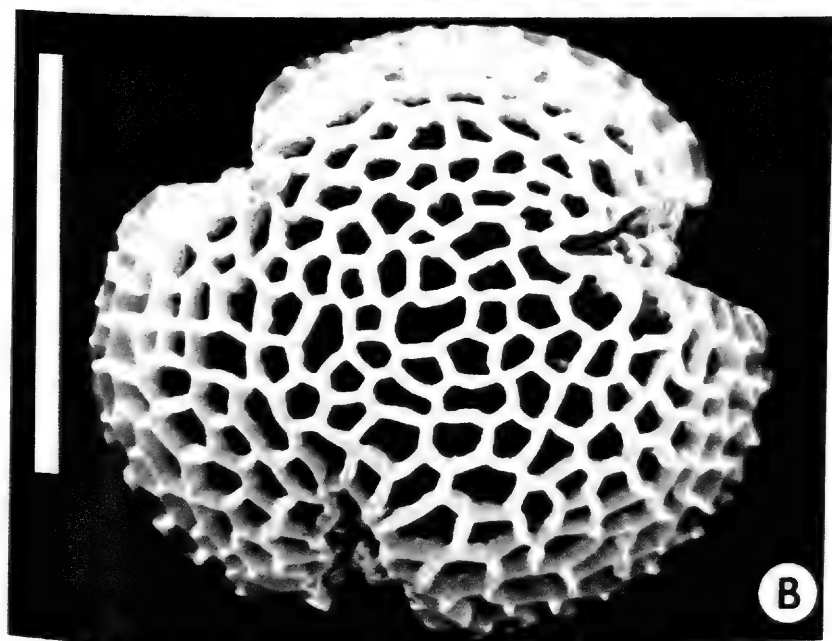
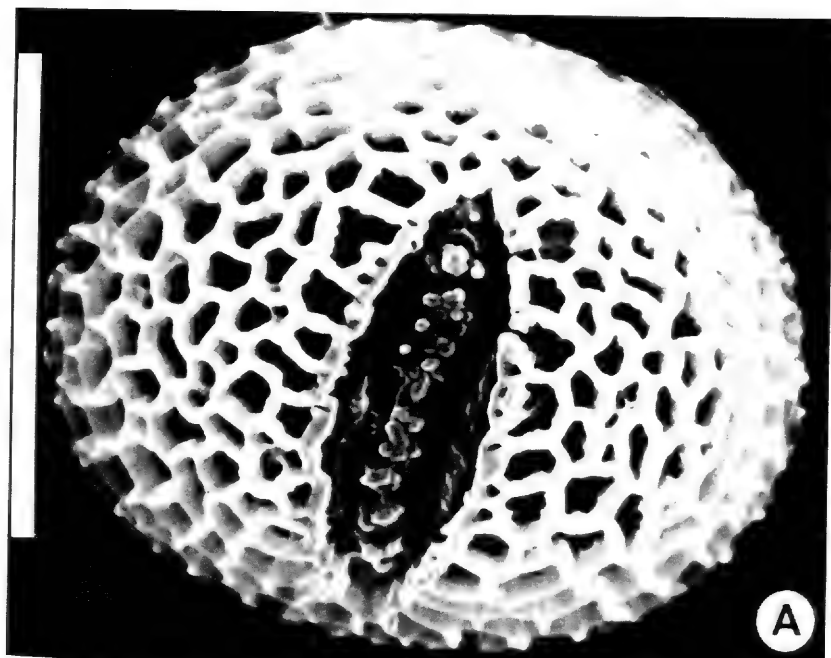


PLATE 16. *Loropetalum* R. Br. (Subfamily Hamamelidoideae; Tribe Hamamelideae)

VOUCHER MATERIAL: *Loropetalum chinense* Oliv.; Bogle 776: cultivated plant, U.S.D.A., Plant Introduction Station, Glenn Dale, Maryland (NHA).

A. Slightly oblique equatorial view of a tricolpate grain showing the moderately coarse reticulum of the exine, with muri of moderate depth resting on short bacula, and two elongate colpi. Note the very small, round lumina scattered among the larger, angular meshes, and along the margin of the colpi,  $\times 6090$ . Shape: subprolate. Size range in equatorial view: equatorial axis, 16–27  $\mu\text{m}$ ; polar axis, 19–23  $\mu\text{m}$ . (Bar = 10  $\mu\text{m}$ .)

B. Slightly oblique polar view, showing general reduction in size of the lumina of the apocolpium. Note the acutely pointed ends of the elongate colpi, and the coarsely granular membrane of the colpus (upper right),  $\times 6000$ . (Bar = 10  $\mu\text{m}$ .)

*Loropetalum* is a genus of about four species (Index Kewensis; H. T. Chang, 1973) distributed in China, Hong Kong and westward to the mountains of eastern India (Assam). Its tetramerous flowers are similar in appearance to those of *Hamamelis*.

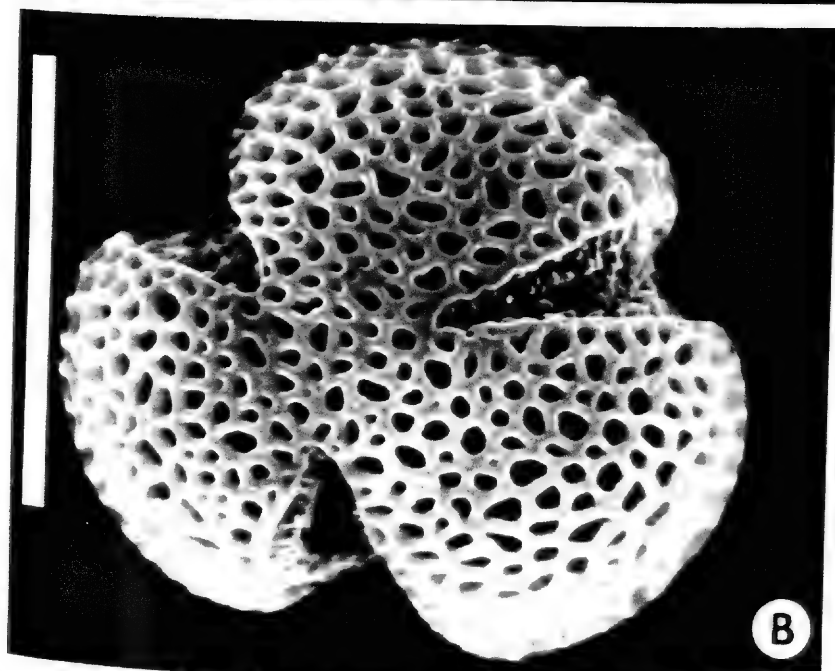
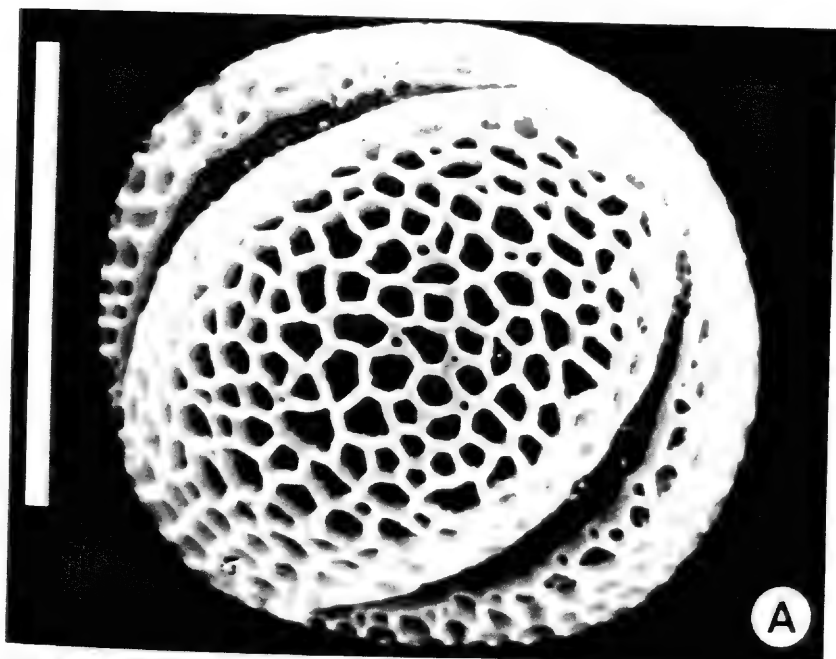




PLATE 17. *Embolanthera* Merr. (Subfamily Hamamelidoideae; Tribe Hamamelideae)

VOUCHER MATERIAL: *Embolanthera spicata* Merr.; Sulit 14791: Palawan, Philippine Islands (AA).

A. Equatorial view of a tricolpate grain, showing the coarse reticulum of the mesocolpium. Note the deep muri borne on short bacula; lumina are of fairly uniform dimensions and angular outline; margins of the colpi are distinct and even, containing a few very small, scattered lumina. The colpus membranes appear smooth peripherally, but bear a central zone of granular exine,  $\times 4140$ . Shape: prolate spheroidal. Size range in equatorial view: equatorial axis, 18–26  $\mu\text{m}$ ; polar axis, 17–25  $\mu\text{m}$ . (Bar = 10  $\mu\text{m}$ .)

B. Slightly oblique polar view. Lumina of the apocolpium appear slightly smaller than in the mesocolpium. Note the margins and membranes of the colpi,  $\times 5250$ . (Bar = 10  $\mu\text{m}$ .)

*Embolanthera* is a genus of only two species, one of which is known only from the island of Palawan, in the Philippines, the other from a single location in North Viet Nam (Lee, 1969; Merrill, 1909; Tardieu-Blot, 1965). The genus is considered closely related to *Main-gaya* and *Loropetalum*.

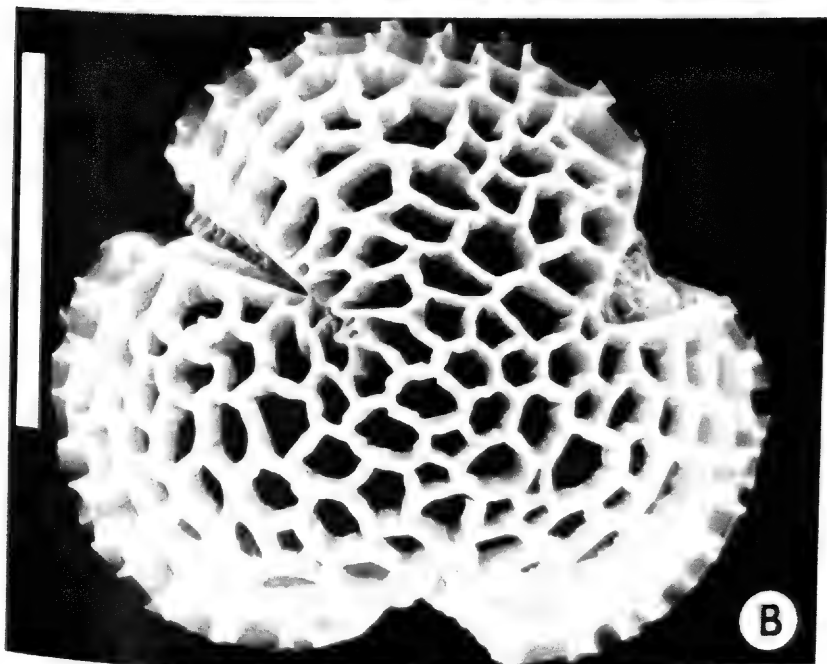
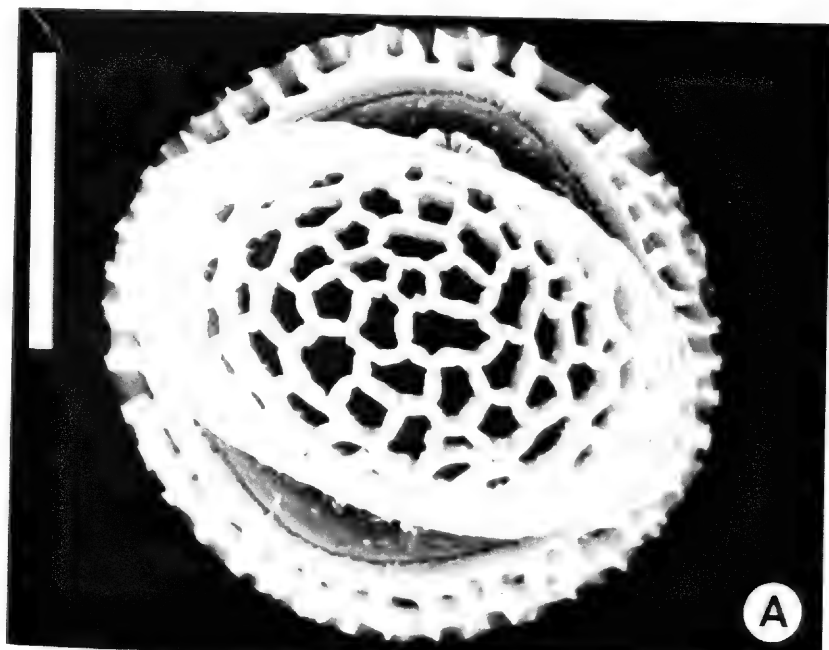


PLATE 18. *Eustigma* Gardn. and Champ. (Subfamily Hamamelidoideae; Tribe Eustigmateae)

VOUCHER MATERIAL: *Eustigma oblongifolium* Gardn. and Champ.; Bogle 584: Victoria Peak, Hong Kong (NHA).

A. Oblique view of an invaginated grain showing the irregular reticulum in the mesocolpium, with lumina varying from large and angular to very small and rounded, grading to a scrobiculate or fully tectate condition at the poles,  $\times 3830$ . Shape: subprolate. Size range in equatorial view: equatorial axis, 39–52  $\mu\text{m}$ ; polar axis, 45–61  $\mu\text{m}$ . (Bar = 10  $\mu\text{m}$ .)

B. Oblique polar view showing the reticulate mesocolpium and foveolate to scrobiculate apocolpium. Note the margo, rounded ends, even to slightly ragged margins, and granular membranes of the elongate colpi,  $\times 3440$ . (Bar = 10  $\mu\text{m}$ .)

A genus of two species distributed in China, Hong Kong, Taiwan (*Eustigma oblongifolium*) and Vietnam (*E. balansae* Oliver). Although it shares many basic similarities in floral morphology with members of the Hamamelideae, *Eustigma* is sufficiently different to merit recognition as the sole member of a separate tribe. Chang (1964) notes the basic similarity of the grains of the two species, but with *E. oblongifolium* he found that pollen grains from plants of Kwangtung, China, exhibit a thicker exine and a coarser reticulum than those from the island of Hainan, off the southern coast of China.

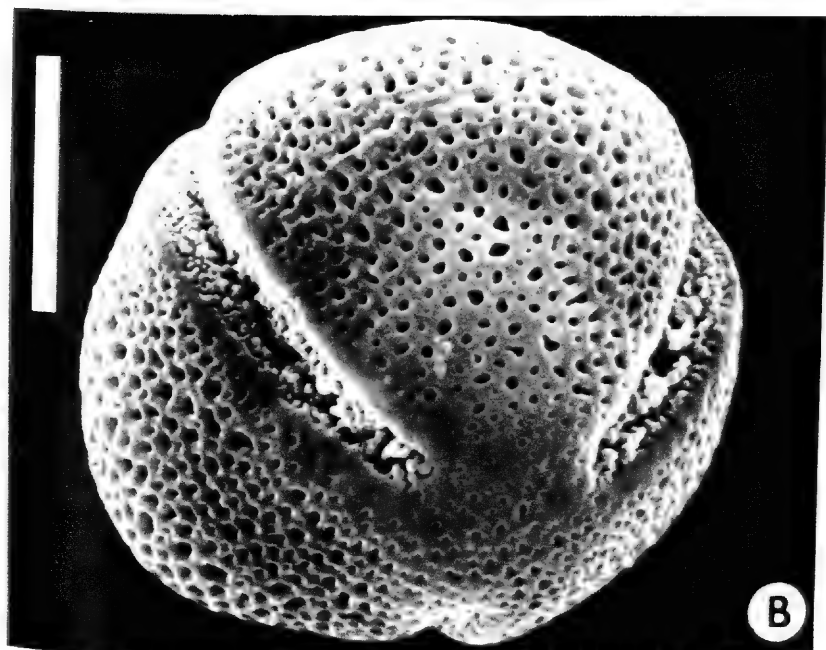
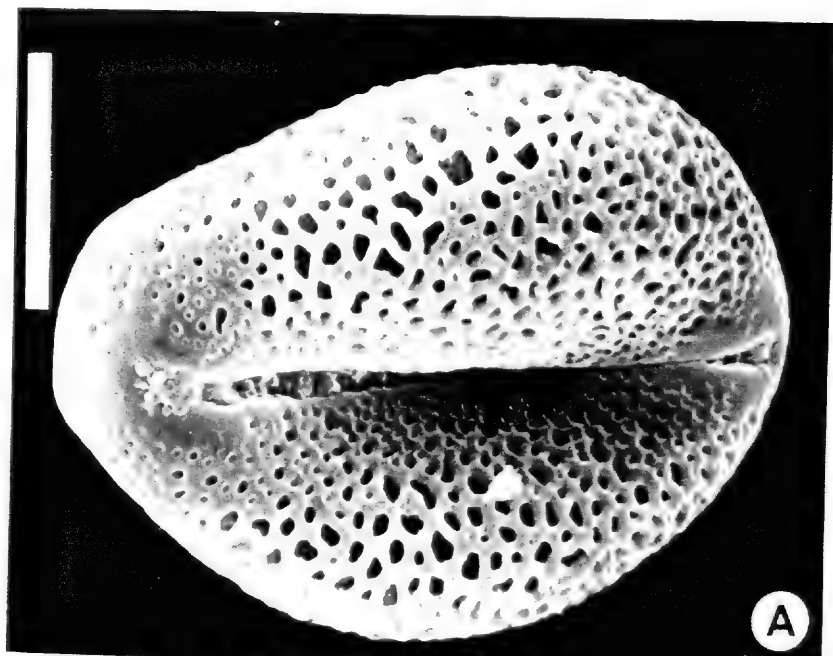


PLATE 19. *Corylopsis* Sieb. and Zucc. (Subfamily Hamamelidoideae; Tribe Corylopsideae)

VOUCHER MATERIAL: *Corylopsis platypeta* Rehd. and Wils.; Bogle 963: from a cultivated plant, Arnold Arboretum (NHA).

A. Oblique equatorial view of a tricolpate grain illustrating the coarsely reticulate exine with rather irregular, angular lumina, some of which are highly elongate and curved or constricted, the moderately deep muri borne on short bacula, the margo of the elongate colpus, and the finely granular colpus membrane,  $\times 5000$ . Shape: oblate spheroidal. Size range in equatorial view: equatorial axis, 19–24  $\mu\text{m}$ ; polar axis, 17–21  $\mu\text{m}$ . (Bar = 10  $\mu\text{m}$ .)

B. Oblique polar view, illustrating the reduction in size of the lumina in the apocolpium, and the minute lumina scattered along the margo of the sharply pointed ends of the colpi,  $\times 5640$ . (Bar = 10  $\mu\text{m}$ .)

*Corylopsis* is a large and poorly understood genus of at least 36 described species distributed in Korea, Japan, Taiwan, China, and the Himalayas of eastern India (see Index Kewensis; H. T. Chang, 1973). In a recent morphological survey of the genus Morley and Chao (1977) reduced the number of species to seven, while acknowledging that the genus needs intensive study. Lee (1969) reports occasional syncolpate grains in two of the six species he examined; he also failed to find pores in the colpi as reported by Simpson (1936). The flowers are insect-pollinated in cultivation (e.g., honey bees, blow flies, hover flies), but observations in nature are lacking (Morley and Chao, 1977). Hesse (1978) describes the ultrastructure of the sticky "pollenkitt" deposited on the exine surface.

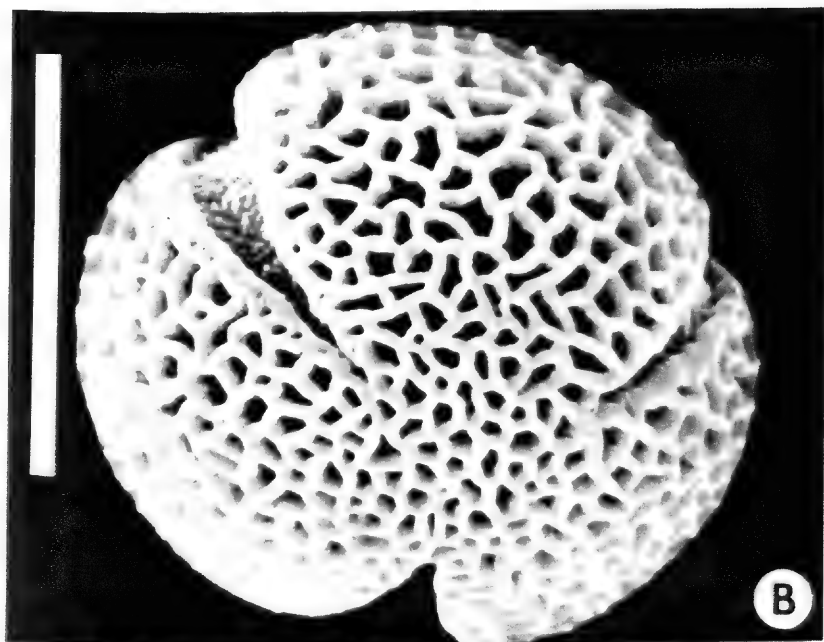
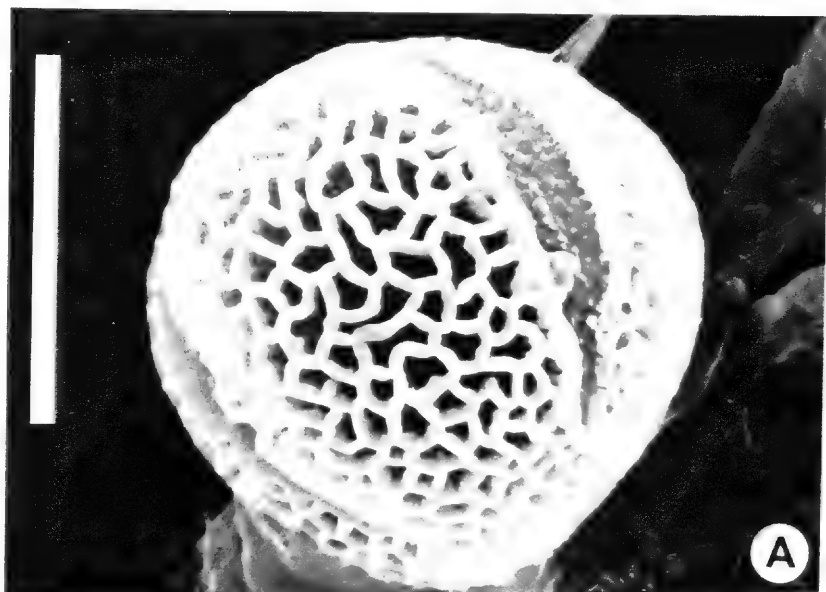


PLATE 20. *Fortunearia* Rehd. and Wils. (Subfamily Hamamelidoideae; Tribe Corylopsydeae)

VOUCHER MATERIAL: *Fortunearia sinensis* Rehd. and Wils.; Bogle 778: from a cultivated plant, grounds of U.S.D.A., Plant Introduction Station, Glenn Dale, Maryland (NHA).

A. Slightly oblique equatorial view of a tricolpate grain. The reticulum is moderately coarse, with very small, rounded lumina scattered among larger lumina which vary in outline from rounded to triangular or polygonal. The muri are verrucate. The colpi are relatively short, with rounded ends, indistinct margins, and finely granular membranes. The sexine appears here to become modified into a finely perforate and verrucate margo around the colpi,  $\times 3800$ . Shape: subprolate. Size range in equatorial view: equatorial axis, 18–34  $\mu\text{m}$ ; polar axis, 18–40  $\mu\text{m}$ . (Bar = 10  $\mu\text{m}$ .)

B. Oblique polar view. The reticulum of the apocolpium does not differ significantly from that of the mesocolpium. Note the finely perforate and verrucate margo of the colpus,  $\times 3900$ . (Bar = 10  $\mu\text{m}$ .)

*Fortunearia* is yet another monotypic genus which is endemic to China, with a very limited distribution in western Hupeh Province. It is vegetatively similar to *Sinowilsonia*, but its pollen is closer to that of *Parrotia*, differing in having a finer reticulum, broader muri, and less coarsely granular membranes. Several other genera, however, show basic similarities in having reticulate-verrucate exines (although with increasingly smaller lumina) and relatively indistinct colpi, rugae or pores with granular membranes, including *Molinadendron*, *Distylium*, *Sycopsis* and *Distyliopsis*.

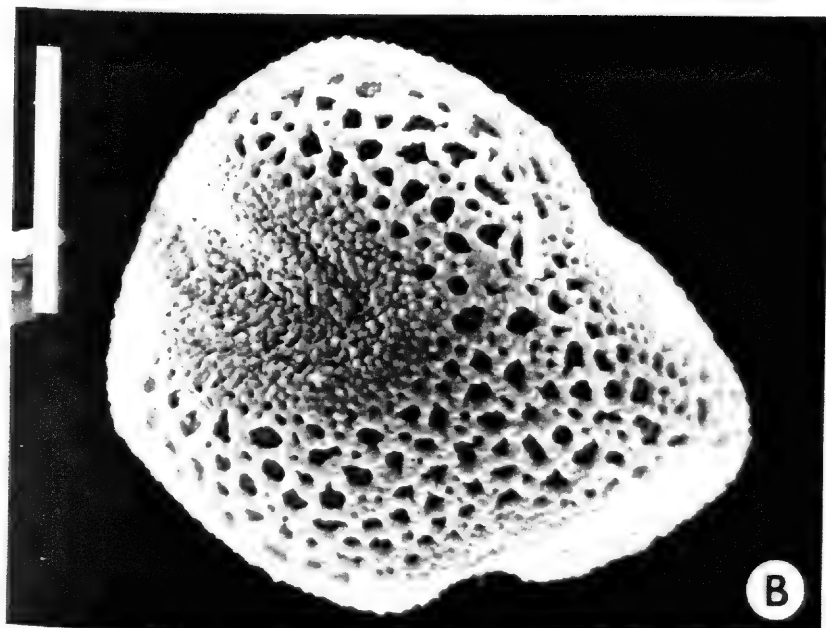
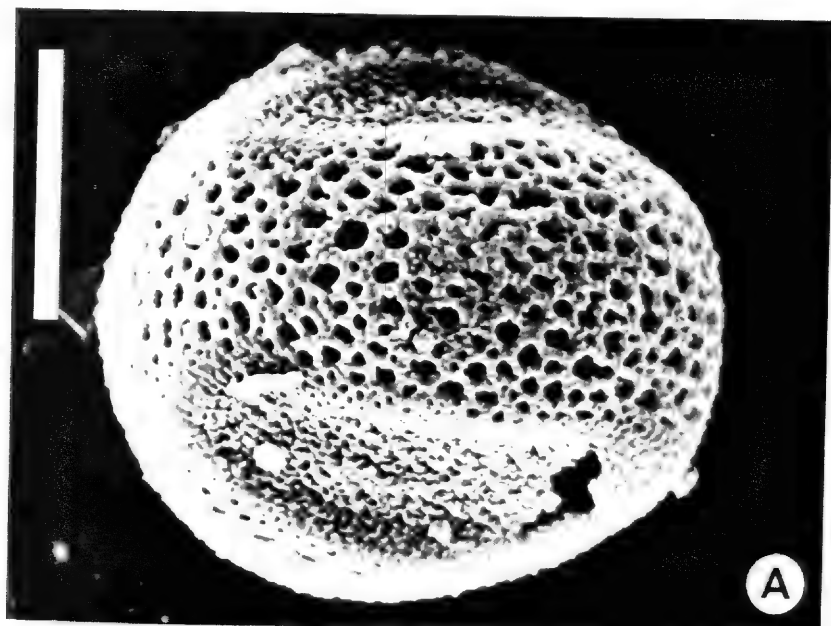




PLATE 21. *Sinowilsonia* Hemsl. (Subfamily Hamamelidoideae; Tribe Corylopsideae)

VOUCHER MATERIAL: *Sinowilsonia henryi* Hemsl.; Bogle 970: from a cultivated plant, Royal Botanic Garden, Kew (NHA).

A. Equatorial view of the interapertural area of a tricolpate grain with a moderately coarse reticulum. The lumina range from more or less isodiametric to angular, and show considerable variation in size, with numerous very small lumina occurring singly or in small clusters among the larger meshes. Absence of small segments of murus results in exceptionally large or erratically shaped lumina. The colpi are elongate, approaching the poles,  $\times 2800$ . Shape: prolate spheroidal. Size range in equatorial view: equatorial axis, 24–41  $\mu\text{m}$ ; polar axis, 28–43  $\mu\text{m}$ . (Bar = 10  $\mu\text{m}$ .)

B. Oblique polar view of another grain, illustrating a reduction in the size of the lumina in the polar area. The colpi exhibit a partial margo around their rounded ends, while the lateral margins tend to be less distinct, with numerous small lumina and a ragged to broken edge. The colpus membranes are coarsely granular,  $\times 2600$ . (Bar = 10  $\mu\text{m}$ .)

*Sinowilsonia* is a monotypic genus which, like *Fortunearia*, is endemic to Hupeh Province in central China. The two genera are somewhat similar vegetatively, but differ in their floral morphology, and to a certain extent in their pollen morphology. The flowers of *Sinowilsonia* are functionally unisexual, with the staminate and pistillate flowers in separate inflorescences, while the flowers of *Fortunearia* are functionally bisexual. Chang (1964) describes the exine of *Sinowilsonia* as coarsely reticulate. His photomicrographs (op. cit., Plate XII, Figs. 1–7) illustrate a reticulum that appears slightly finer than that illustrated here. However, we found extensive variation in the reticulum of grains taken from flowers of four mature male inflorescences in our material. The sculpturing ranged from relatively coarse to finely reticulate, foveolate, or scrobiculate. Some of this variation is shown in Plate 22. Still other grains exhibited coarsely granular to capillate sculpturing, suggesting an incomplete development of the exine.

In its various forms the reticulum in *Sinowilsonia* approaches that of *Fortunearia* and *Parrotia*, among others, but lacks the supratectal verrucae seen in these genera.

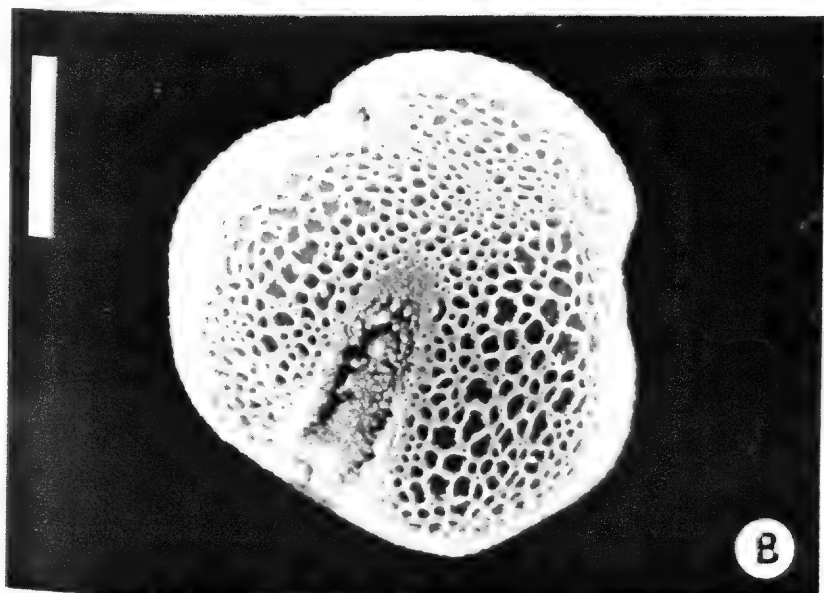
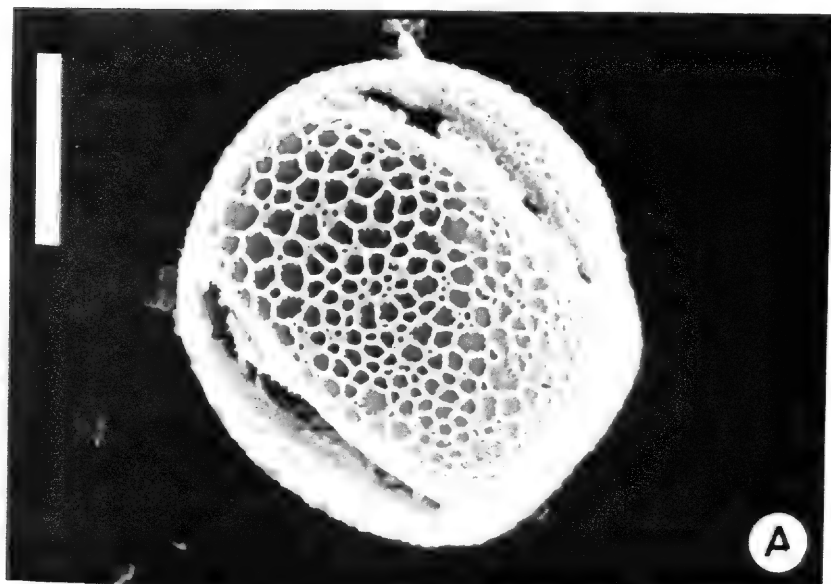


PLATE 22. *Sinowilsonia* Hemsl. (Subfamily Hamamiledoideae; Tribe Corylopsideae)

VOUCHER MATERIAL: Same as Plate 21.

A. Coarse reticulum and aperture margin of the grain illustrated in Plate 21B. Note the range of size in the lumina and the absence of supratectal verrucae,  $\times 10,000$ . (Bar = 1  $\mu\text{m}$ .)

B. Close-up view of the reticulum of a variant grain, the exine sculpturing varying from reticulate to vermiform. Note the ragged margin and granular membrane of the colpus,  $\times 10,000$ . (Bar = 1  $\mu\text{m}$ .)

C. Scrobiculate to vermiculate reticulum of another grain; the lumina varying from small, round perforations to much elongated and erratically curving and branching, surrounded by broad expanses of tectum. Note the erratic colpus margin and granular membrane,  $\times 10,000$ . (Bar = 1  $\mu\text{m}$ .)

Chang (1964) does not mention variability of this type in the exine of *Sinowilsonia*, but it is so prevalent in our sample that it seemed worthy of note. Further investigation is needed to explain the range of variation. Among the other genera included in this study only *Molinadendron* approaches *Sinowilsonia* in the variability of its sculpturing.

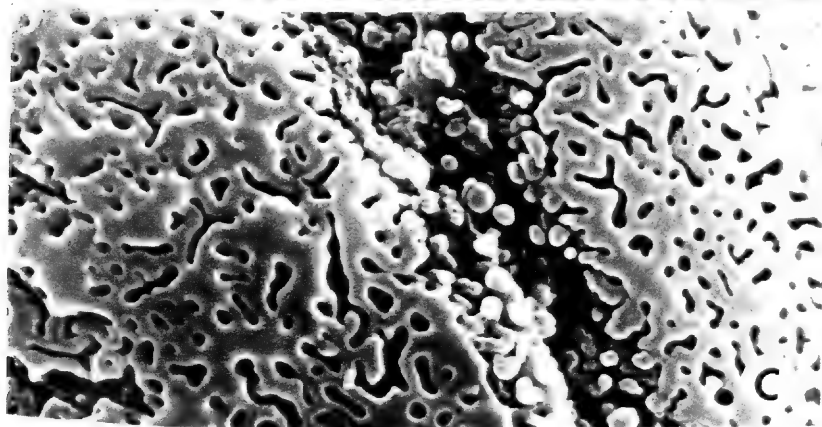
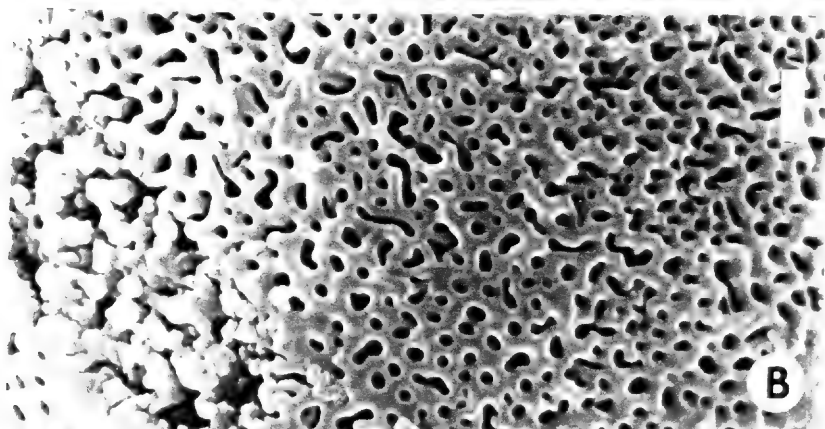
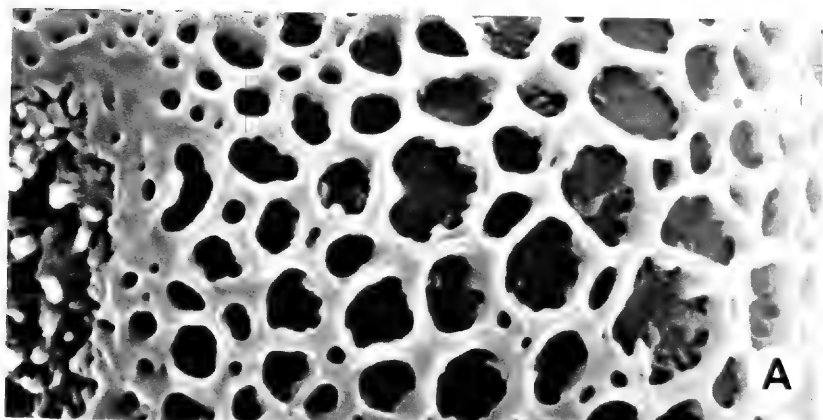


PLATE 23. *Fothergilla* Murr. (Subfamily Hamamelidoideae; Tribe Fothergilleae)

VOUCHER MATERIAL: *Fothergilla major* Lodd.; Bogle 929: cultivated plant in the author's collection (NHA).

A. Equatorial view of a tricolpate grain with elongate colpi. The moderately coarse reticulum contains lumina of highly variable size and shape, with numerous small round perforations scattered among larger lumina of erratic shape. The bacula supporting the tectum are visible to right and left. Note the concentration of small perforations in the margo of the colpus (upper left), the even margin and the sparsely and finely granular to almost smooth membrane. Note also the expanded central region (pore?) of the upper colpus membrane,  $\times 3540$ . Shape: subprolate. Size range in equatorial view: equatorial axis, 22–36  $\mu\text{m}$ ; polar axis, 25–50  $\mu\text{m}$ . (Bar = 10  $\mu\text{m}$ .)

B. View of a hexarugate grain. Note the reduced size of the lumina in the apocolpium,  $\times 2900$ . (Bar = 10  $\mu\text{m}$ .)

A genus of two (–3) species (Weaver, 1969) distributed in the coastal plains and mountains of southeastern United States. Rugate grains were not seen in our light microscope preparation of this species.

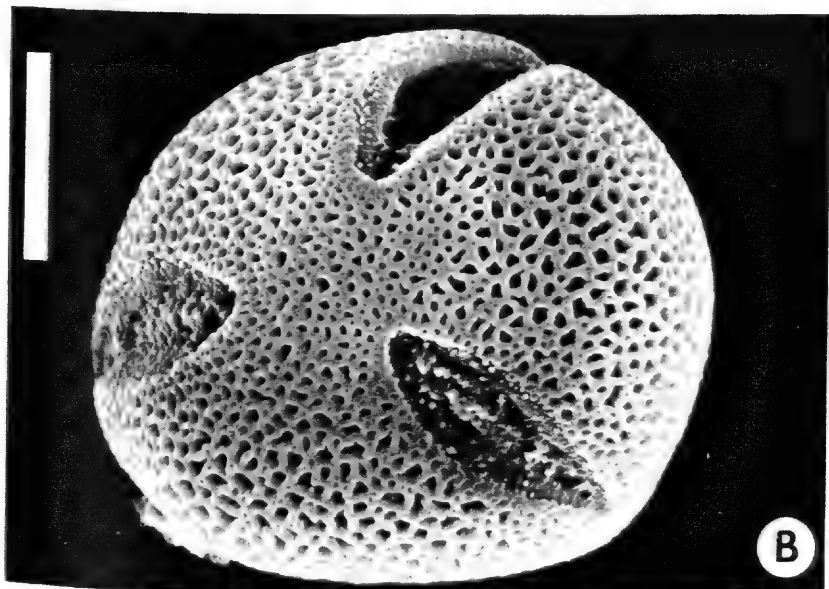
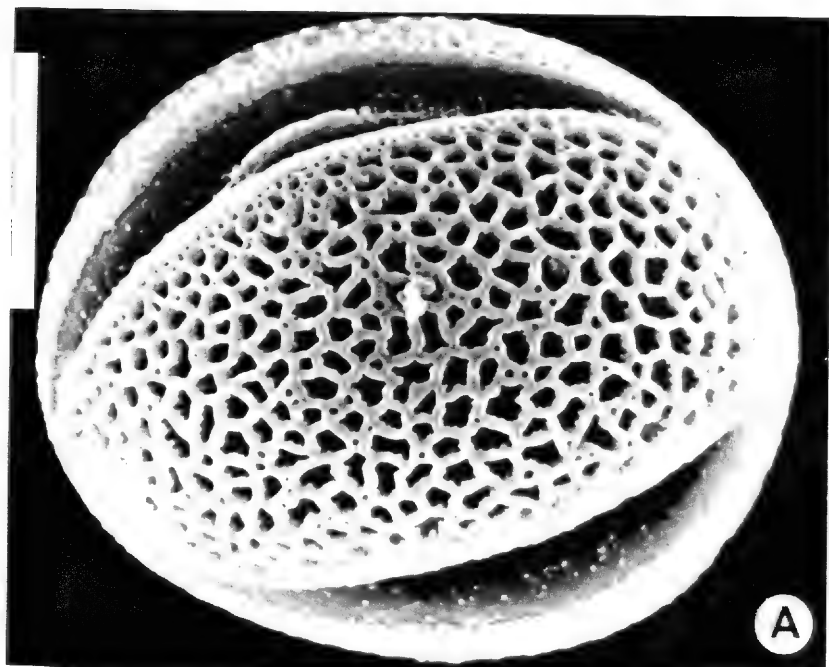


PLATE 24. *Fothergilla* Murr. (Subfamily Hamamelidoideae; Tribe Fothergilleae)

VOUCHER MATERIAL: *Fothergilla monticola* Ashe; Bogle 1270: cultivated plant, Arnold Arboretum (NHA).

A. Slightly oblique equatorial view of an invaginated tricolpate grain, with one intact and one ruptured colpus membrane apparent. Note the very small rounded perforations scattered among the larger lumina; the variable shape of the lumina, ranging from rounded to polygonal, elongate or stellate. The size of the lumina is strongly diminished toward the poles, as shown in the lower right. The colpi are long and acutely pointed at the ends, have a distinct margo containing many minute perforations, and finely granular membranes,  $\times 3280$ . Shape: prolate. Size range in equatorial view: equatorial axis, 27–36  $\mu\text{m}$ ; polar axis, 35–53  $\mu\text{m}$ . (Bar = 10  $\mu\text{m}$ .)

B. Slightly oblique polar view. Note the marked decrease in the size of the lumina in the apocolpium, the acutely pointed ends of the long colpi approaching the poles, the distinct and minutely perforated margo, and the granular colpus membranes. A central pore-like protrusion of the aperture membranes can be seen in the upper right and lower right colpi,  $\times 2800$ . (Bar = 10  $\mu\text{m}$ .)

*Fothergilla monticola* is considered either as a distinct species or as a variant of *F. major* (see Weaver, 1969, for a review of the genus). The grain figured in (A) exhibits more erratic shape in the lumina of the mesocolpium than is seen in *F. major* (Plate 23, A), through interruption of some muri, producing stubs of muri which project into lumina space. The "bottle brush" inflorescences of *Fothergilla* are very distinctive within the family. Pollinators are mainly bees and bumble-bees (Endress, 1977). Lee (1969) describes the grains of both *F. gardenii* and *F. major* as "tricolporoidate, pore-like appearance about 4  $\mu\text{m}$  in diameter." Chang (1964) does not describe pores in his analyses of the same species.

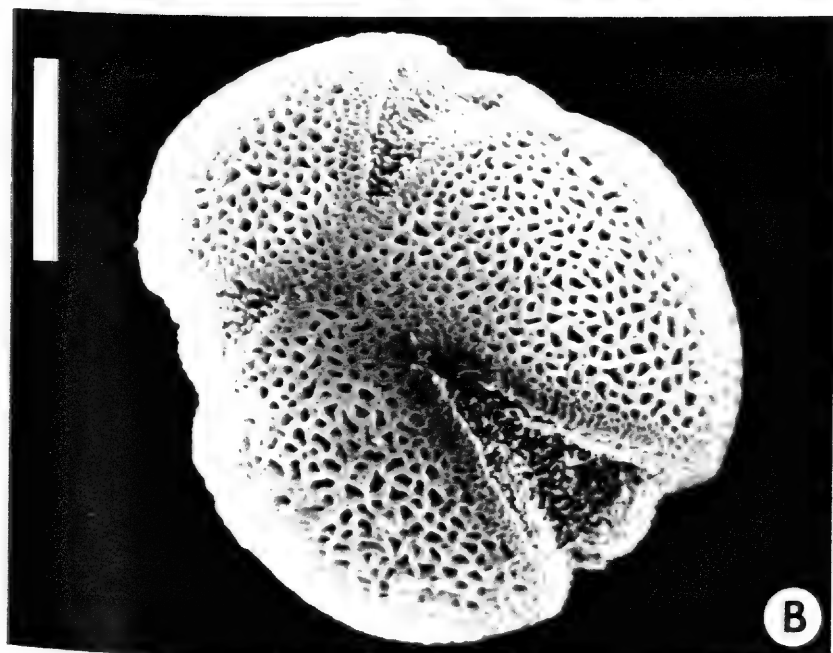
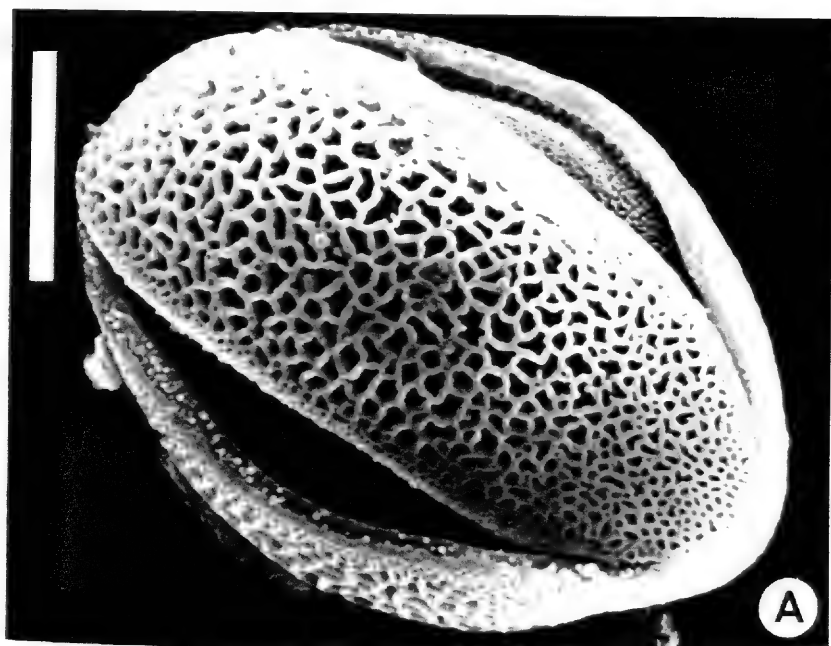




PLATE 25. *Parrotiopsis* (Niedenzu) Schneid. (Subfamily Hamamelidoideae; Tribe Fothergilleae)

VOUCHER MATERIAL: *Parrotiopsis jacquemontiana* (Decne.) Rehd.; Bogle 964: cultivated plant in garden of Dr. A. R. Kruckeberg, Seattle, Washington (NHA).

A. Slightly oblique equatorial view of a tricolpate grain. The reticulum of the exine is fine; with minute perforations scattered among larger lumina of irregular size and shape; the width of the larger lumina is about equal to or only slightly larger than the width of the adjacent muri. The surfaces of the muri are very weakly verrucate. The colpus membranes are finely and uniformly granular,  $\times 4840$ . Shape: subprolate. Size range in equatorial view: equatorial axis, 19–28  $\mu\text{m}$ ; polar axis, 26–35  $\mu\text{m}$ . (Bar = 10  $\mu\text{m}$ .)

B. Polar view. Note the reduction in size of the lumina in the distal portion of the mesocolpium and in the apocolpium. The colpi narrow to acutely pointed or rounded ends. A distinct but narrow margo with associated minute perforations and slightly rough margins borders the colpus. (Bar = 10  $\mu\text{m}$ .)

A monotypic genus restricted in distribution to the Himalayan mountains of northern Kashmir, northern West Pakistan, and north-eastern Afghanistan. *Parrotiopsis* is apparently closely related to *Parrotia* and *Fothergilla*, but the pollens of the three genera differ, and that of *Parrotiopsis* is closer to *Fothergilla* than to *Parrotia*. Chang (1964) notes pronounced similarities of *Parrotiopsis* with *Corylopsis cordata* Merr. ex Li.

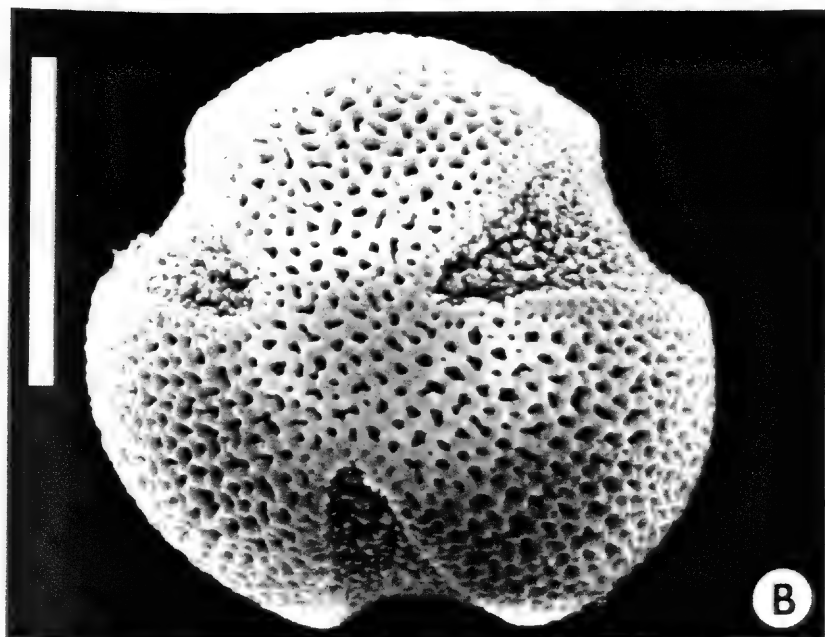
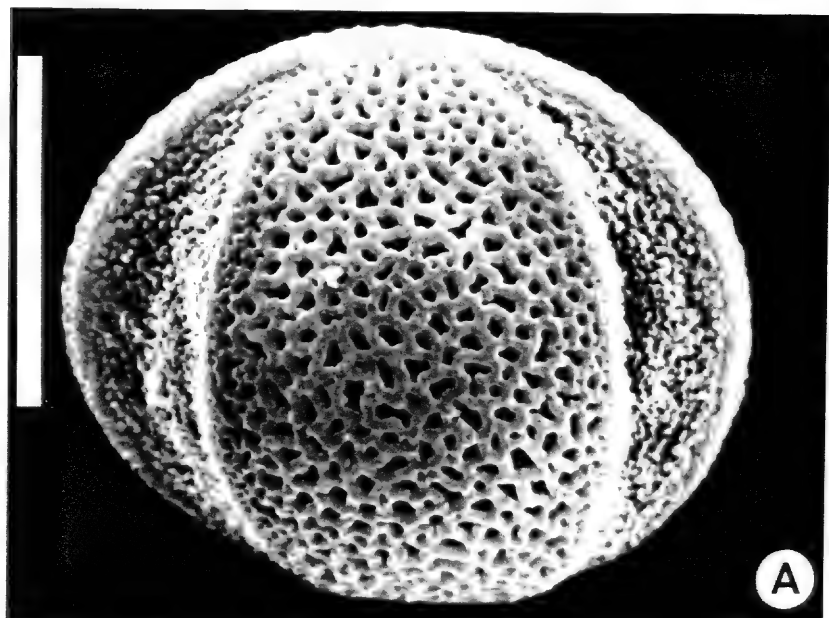


PLATE 26. *Parrotia* C. A. Meyer (Subfamily Hamamelidoideae; Tribe Fothergilleae)

VOUCHER MATERIAL: *Parrotia persica* (DC.) C. A. Mey.; Bogle 952: cultivated plant, Morris Arboretum, Philadelphia (NHA).

A. Equatorial view of a tricolpate grain with a moderately coarse reticulum and relatively thin exine. The lumina vary from scattered, small, round perforations to mostly large polygonal, elongate, or irregular meshes with intruding segments of murus. Numerous supratectal verrucae are borne on the muri. The colpi are of moderate length, with bluntly rounded ends, and indistinct, ragged to broken margins consisting of very finely reticulate or perforated exine. The colpus membranes are covered with very coarse, isolated to ornately fused, verrucate granules which in some areas become partially tectate,  $\times 2600$ . Shape: oblate to subspheroidal. Size range not available. (Bar = 10  $\mu\text{m}$ .)

B. Polar view. The lumina are slightly smaller in the apocolpium than in the mesocolpium. Note the concentration of very small lumina along the margins of the colpi, and the coarse sculpturing of the membranes,  $\times 2570$ . (Bar = 10  $\mu\text{m}$ .)

*Parrotia* is a monotypic genus which is narrowly distributed in forests on the southern shores of the Caspian Sea, in northern Iran and southern Russia (C. T. Chang, 1964). The verrucate reticulum and colpi of *Parrotia* in our sample are somewhat similar to, but coarser than, those of *Fortunearia*, *Molinadendron*, and *Distylium*. The similarity with *Sinowilsonia* cited by Chang (1964) is not apparent in our material. Lee (1969) reports the grains of *Parrotia* to be rarely dicolpate, tetracolpate, or syncolpate. Nair (1965) states that "a lolongate endocolpium is clearly noticed in some grains." Hesse (1978) describes and illustrates the ultra-structure of the pollen wall in *Parrotia* with regard to "pollenkitt" deposition, and the powdery form of the pollen in regard to its anemophilous pollination mechanism.

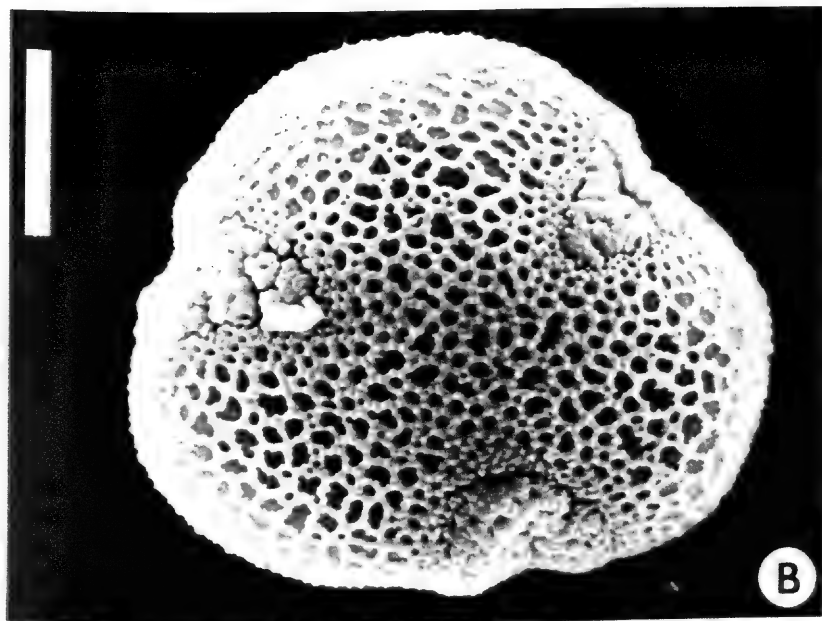
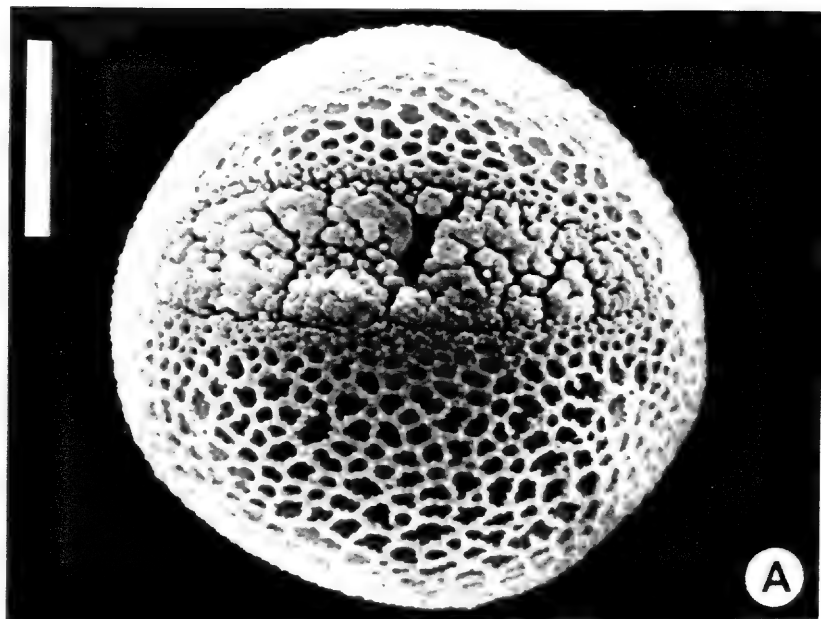


PLATE 27. *Sycopsis* Oliv. (Subfamily Hamamelidoideae; Tribe Distyliaceae)

VOUCHER MATERIAL: *Sycopsis sinensis* Oliv.; Bogle 949: cultivated plant, University of Washington Arboretum, Seattle, Washington (NHA).

A. Entire grain. The exine is finely reticulate, the lumina mostly rounded. Supratectal verrucae are numerous on the muri and on the coarse granules which cover the aperture membranes. The apertures range from more or less oblong rugae to rounded and pore-like. Aperture margins are indistinct, ragged to broken. The coarse granules of the aperture membranes appear to become fused and partially tectate in places,  $\times 2870$ . Shape: spheroidal. Size range: 34–55  $\mu\text{m}$ . (Bar = 10  $\mu\text{m}$ .)

B. Close-up view of the reticulum, pore margin, and heavily sculptured sexine on the membrane of the pore in middle-right of A (above),  $\times 12,000$ . (Bar = 10  $\mu\text{m}$ .)

*Sycopsis* consists of perhaps as many as nine species (cf. Index Kewensis; H. T. Chang, 1973), or 13 if the segregate genus *Distyliopsis* is included. The distribution of the genus (excluding *Distyliopsis*) stretches westward from Taiwan, through south-central China, across the tip of northern Burma into the mountains of Assam. In addition to *Distyliopsis*, the genus is closely related to *Distylium*, and to *Parrotia* of the Fothergilleae. The flowers are apparently wind-pollinated.

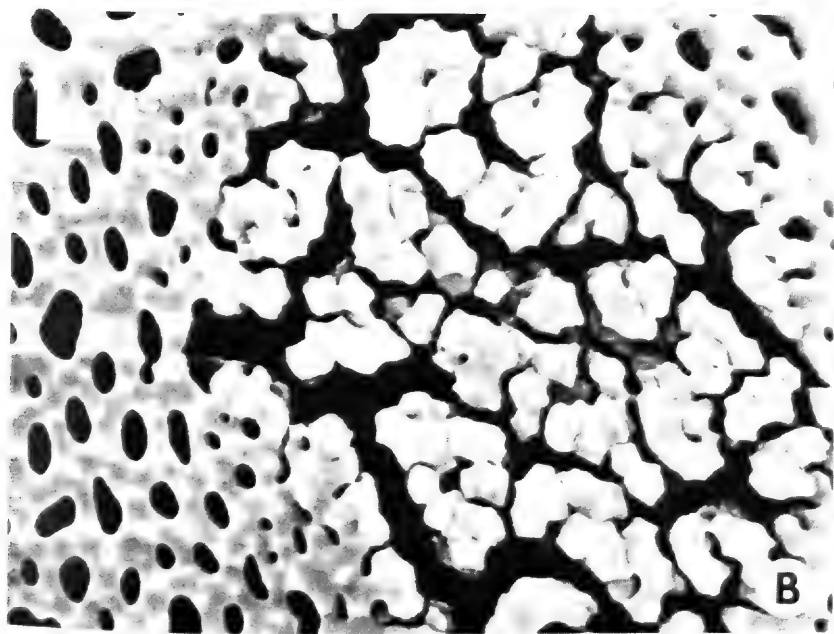
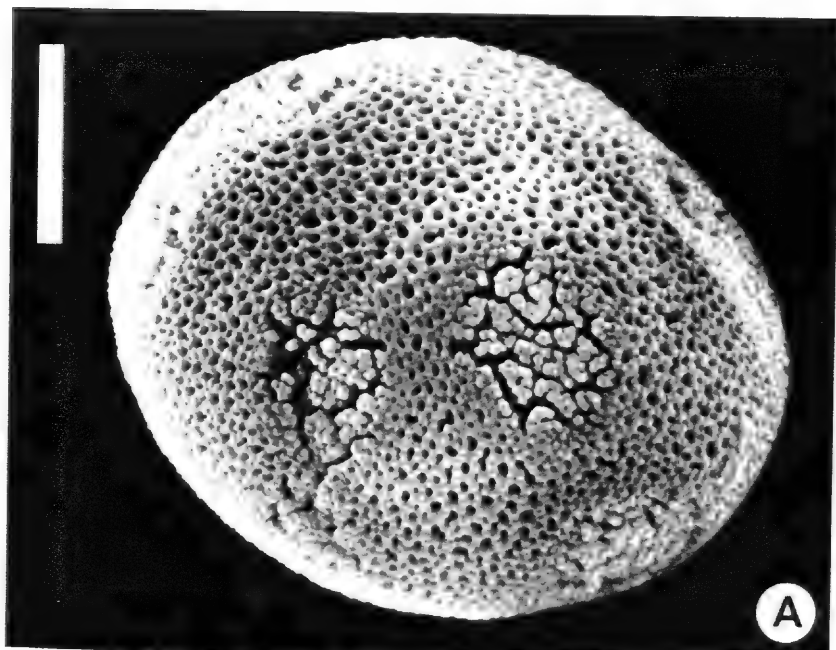


PLATE 28. *Distyliopsis* Endress (Subfamily Hamamelidoideae; Tribe Distylieae)

VOUCHER MATERIAL: *Distyliopsis dunnii* (Hemsl.) Endress; A. Kairo 44090; Yamap, Morobe District, New Guinea (AA).

A. Equatorial view of a tricolpate grain. The colpi are indistinct and of moderate length, with broadly rounded ends, little or no definition of the margins, and membranes covered with coarse verrucate granules. The exine is very finely reticulate, the lumina rounded to slightly elongate in outline, and of approximately the same width as the adjacent muri. Supratectal verrucae are borne on the muri,  $\times 3800$ . Shape: subprolate. Size range in equatorial view: equatorial axis, 25–36  $\mu\text{m}$ ; polar axis, 30–38  $\mu\text{m}$ . (Bar = 10  $\mu\text{m}$ .)

B. Polar view. The lumina of the reticulum are slightly reduced in size in the apocolpium. Note the terminal portions of the three colpi,  $\times 3440$ . (Bar = 10  $\mu\text{m}$ .)

*Distyliopsis* consists of about four species segregated from the genus *Sycopsis* (Endress, 1970). The distribution of the genus ranges from Taiwan and southeastern China westward in the mountains to Burma, southward in an arc through the Philippines and Sabah, possibly in Laos (see Tardieu-Blot, 1965), to Malaya and eastern Sumatra, and erratically eastward in Celebes and in the mountains of New Guinea (see map in Endress, 1970). The genus is closely related to *Distylium* and *Sycopsis*. Pollination is anemophilous. Vink (1957) and H. T. Chang (1973) reject *Distyliopsis*.

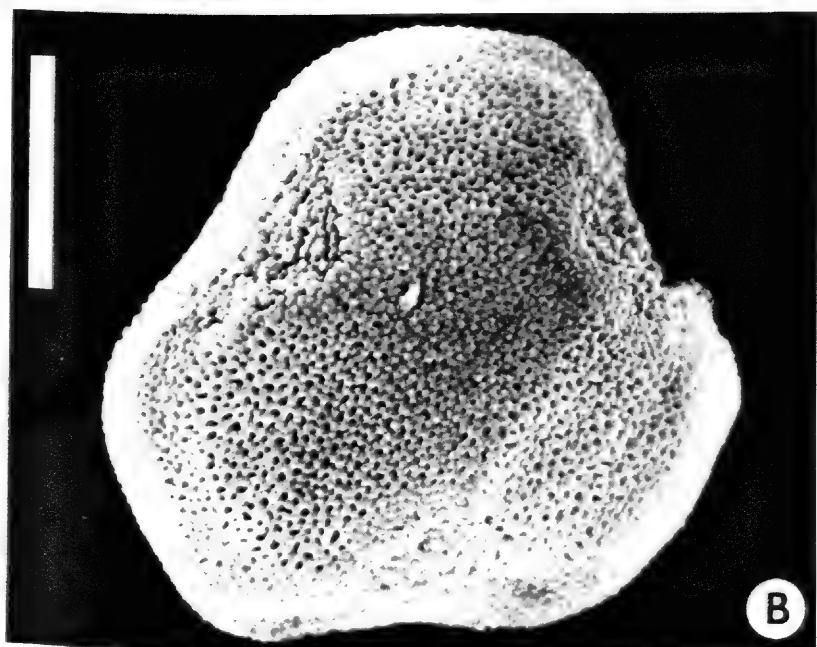
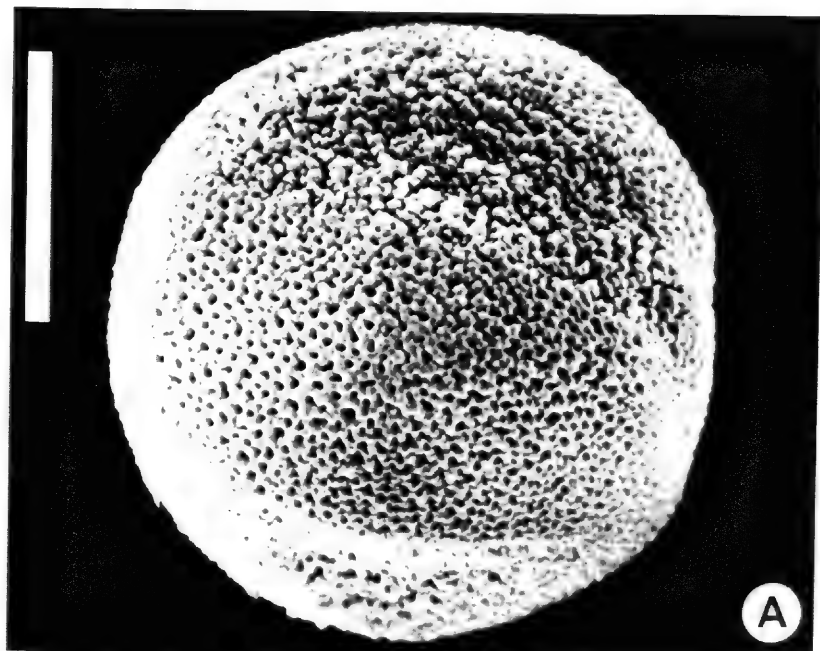




PLATE 29. *Distylium* Sieb. and Zucc. (Subfamily Hamamelidoideae; Tribe Distylieae)

VOUCHER MATERIAL: *Distylium racemosum* Sieb. and Zucc.; Bogle 740: cultivated plant, Dr. Graham's garden, Seattle, Washington (NHA).

A. Polar view of a tetracolpate grain, illustrating the finely reticulate exine. The lumina are rounded to slightly elongate or irregular in outline, and the muri are verrucate. The colpi are shortened, with broadly rounded ends, indistinct margins, and uniformly granular membranes,  $\times 3000$ . Shape: spheroidal to oblate spheroidal. Size range: 40–53  $\mu\text{m}$ . (Bar = 10  $\mu\text{m}$ .)

B. View of a grain with about ten apertures ranging in shape from rugae (right) to rounded and pore-like. Reticulum of the sexine finer than that in (A) (above), the lumina smaller and perhaps a little more irregular in outline. Aperture membranes coarsely granular, the granules also bearing verrucae,  $\times 3030$ . (Bar = 10  $\mu\text{m}$ .)

A genus of about 19 described species (see Index Kewensis; H. T. Chang, 1973) ranging from southern Japan and Korea southward and westward through central China to Assam, and southward through Indochina to Malaya, Sumatra, Java and eastward to Flores. The naked flowers are probably wind-pollinated.

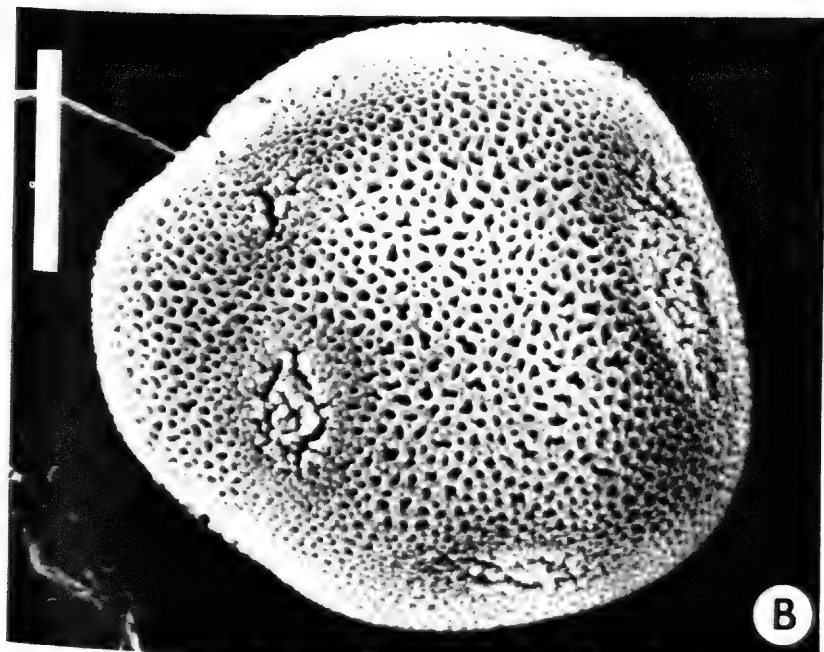
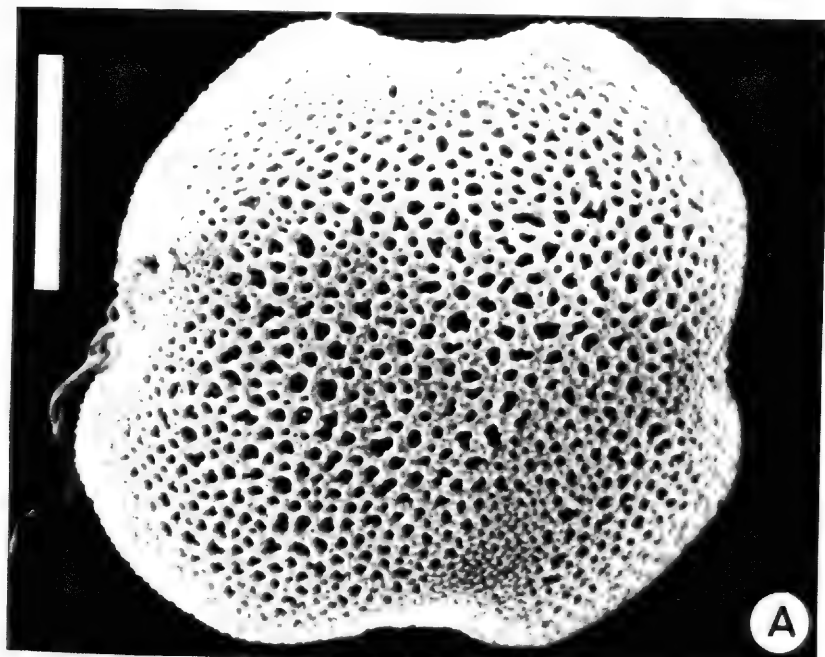


PLATE 30. *Molinadendron* Endress (Subfamily Hamamelidoideae; Tribe Distylieae)

VOUCHER MATERIAL: *Molinadendron sinaloense* (Standley and Gentry) Endress; Bogle 860; Sierra Surutato, Sinaloa, Mexico (NHA).

A. Equatorial view of a tricolpate grain. The reticulum is fine, consisting of numerous minute perforations interspersed among larger, rounded to elongate lumina. The muri are complex, often appearing multilayered; appearing to be made up of interwoven strands, some of which produce erect processes which project above the surface of the muri (compare enlargement in Plate 31, B-1), giving the outer surface a verrucate to papillate (as in this figure) appearance. The colpi are somewhat shortened, with bluntly rounded ends, indistinct margins, and coarsely granular membranes,  $\times 3630$ . Shape: subprolate. Size range in equatorial view: equatorial axis, 22–32  $\mu\text{m}$ ; polar axis, 26–41  $\mu\text{m}$ . (Bar = 10  $\mu\text{m}$ .)

B. Slightly oblique polar view of another grain, with processes of the exine more or less elaborated; the shape and variation of the lumina more apparent (compare close-up of exine in Plate 31, B-2),  $\times 3500$ . (Bar = 10  $\mu\text{m}$ .)

*Molinadendron* is a Central American genus consisting of three species distributed in the mountains of Mexico, Guatemala and Honduras. These taxa were originally described as species of *Distylium*, but anatomical and morphological evidence support their segregation as a separate genus (Bogle, 1970; Endress, 1969).

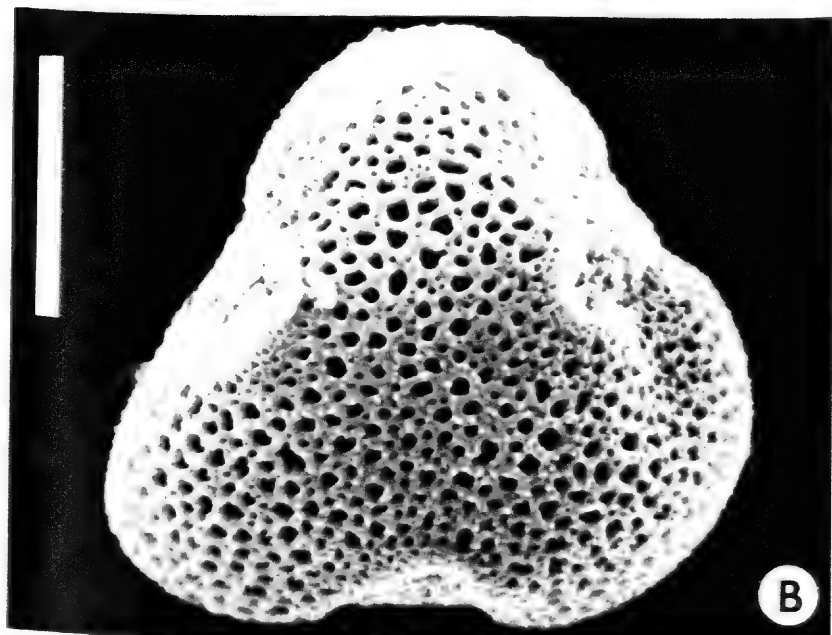
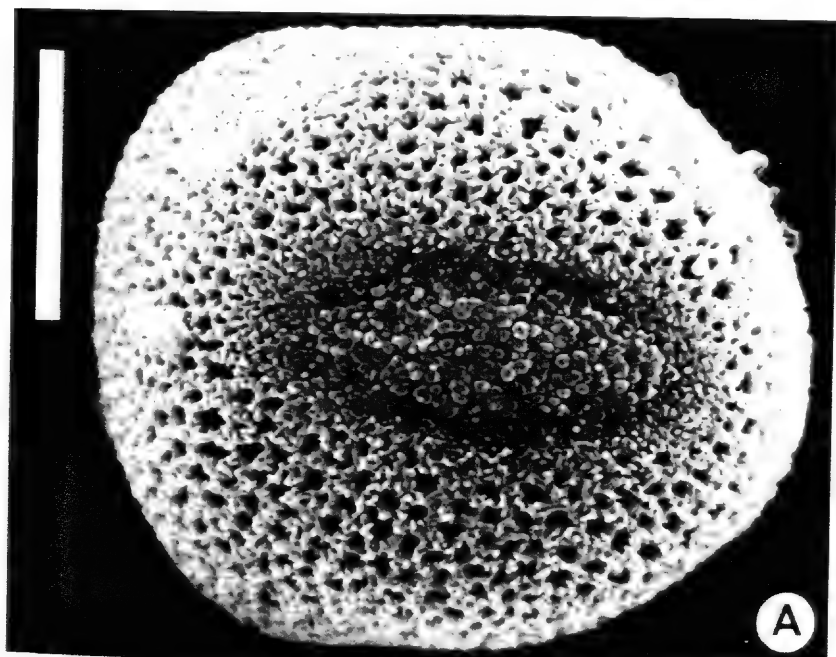


PLATE 31. *Molinadendron* Endress (Subfamily Hamamelidoideae; Tribe Distylieae)

VOUCHER MATERIAL: same as Plate 30.

A. A third variant form found in our sample. The lumina are much reduced and rather irregular in shape; the exine appears scrobiculate in some areas, particularly around the colpus, finely foveolate in other areas. The overall appearance is of a more extensive and smoother tectum than in the other grains of this species illustrated here,  $\times 3550$ . (Bar = 10  $\mu\text{m}$ .)

B. Close-ups of the exine sculpturing of the grains illustrated in Plate 30, (A) and (B). B-1: note the extensive intertwining of the exine strands in the muri, and elaboration of the supratectal processes. The muri often appear double (or even triple) banded in width. The exine grades into the granular pore membrane at left,  $\times 12,500$ . B-2: less extensive development of processes on the muri, and the more typical conditions seen in our sample. Note the interwoven, over-and-under appearance of the strands making up the muri, and in some areas strands lying side by side in the muri, giving the surface a channeled appearance. Processes less numerous and less protrusive,  $\times 12,780$ . (Bar = 1  $\mu\text{m}$ .)

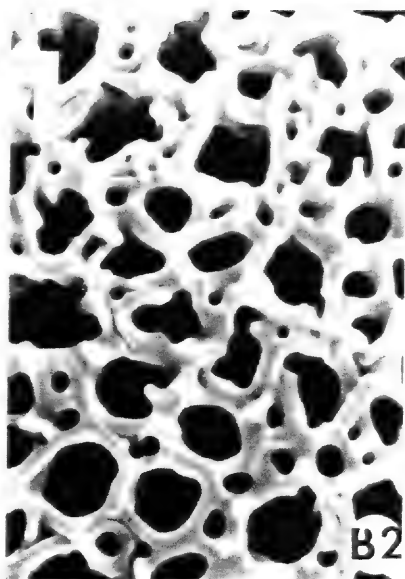
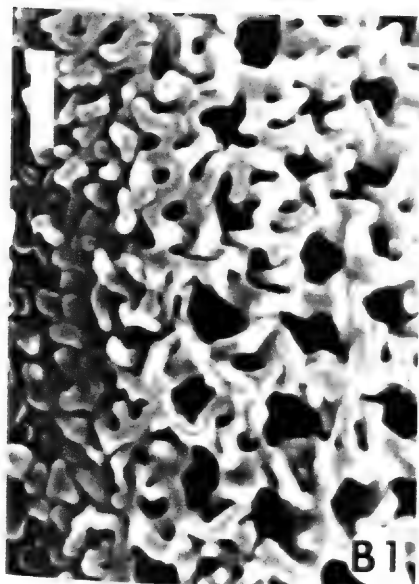
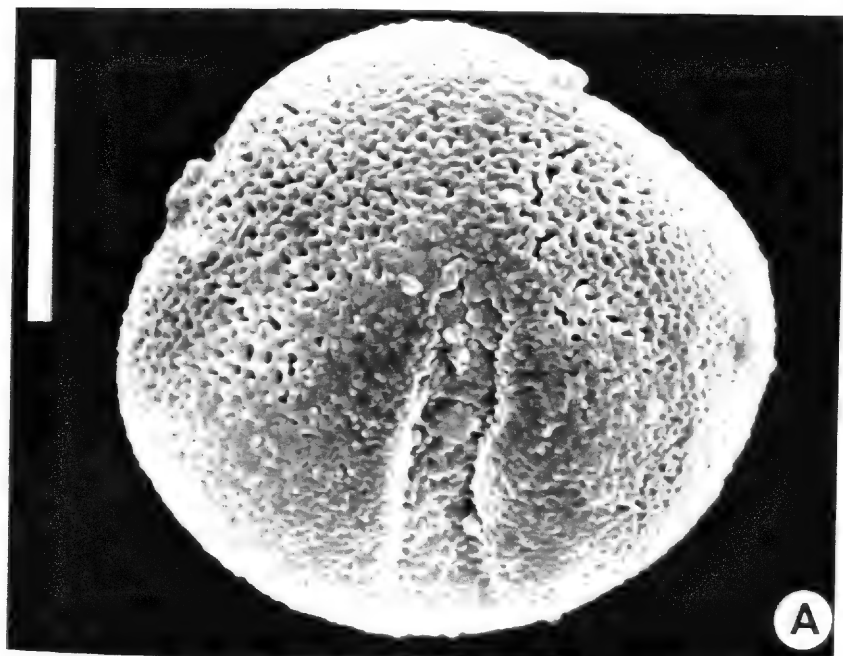


PLATE 32. *Matudaea* Lundell (Subfamily Hamamelidoideae; Tribe Distylieae)

VOUCHER MATERIAL: *Matudaea trinervia* Lundell; Bogle 848; Behucos, Nanchititla, Mexico, Mexico (NHA).

A. View of a rugate grain with six shortened colpi visible. The reticulum of the exine is very finely foveolate. The aperture margins are distinct but uneven, the aperture membranes are coarsely granular,  $\times 3000$ . Shape: spheroidal to subspheroidal. Size range: 32–45  $\mu\text{m}$ . (Bar = 10  $\mu\text{m}$ .)

B. Another grain with irregular apertures, ranging from shortened colpi to pores. The irregular pores at lower-middle and upper-middle may represent medianly constricted colpi (compare Plate 33, A and B, lower right grain),  $\times 2360$ . Size range: 32–45  $\mu\text{m}$ . (Bar = 10  $\mu\text{m}$ .)

*Matudaea*, like *Molinadendron*, is a Central American genus. It contains only two species distributed in mountain forests of Mexico, Guatemala, and Honduras. The number of apertures appears to vary from four (tetracolpate) to as many as 12-rugate. The genus is possibly allied with *Distylium* and *Distyliopsis*. Pollination is apparently anemophilous.

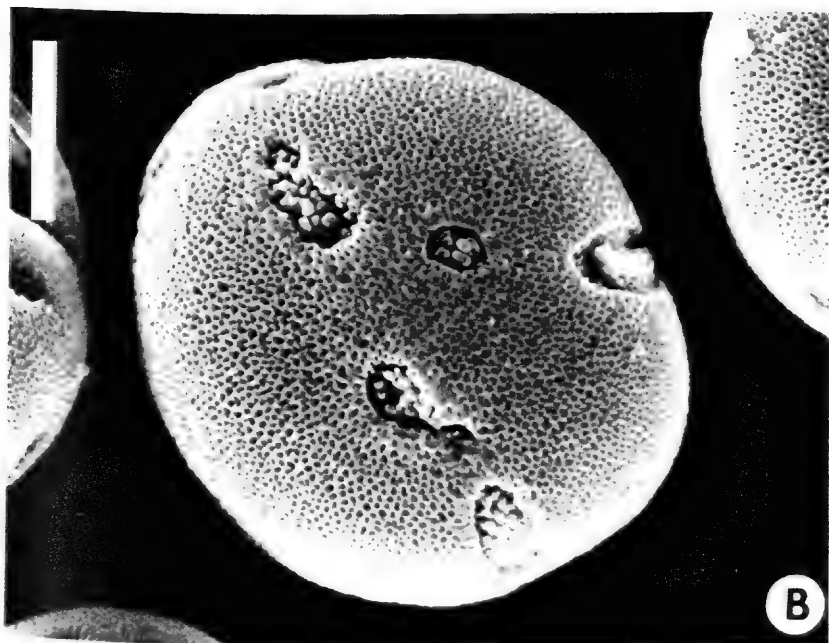


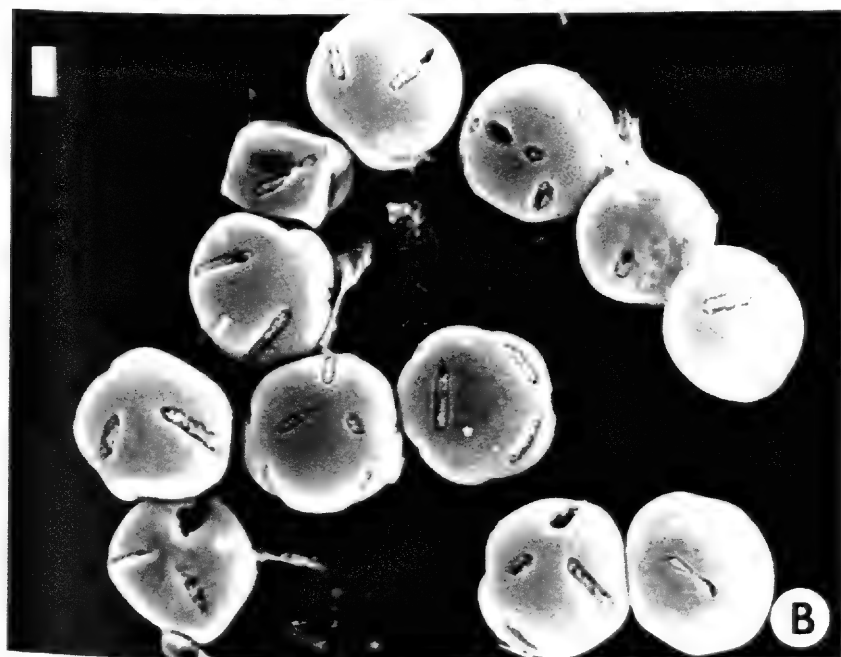
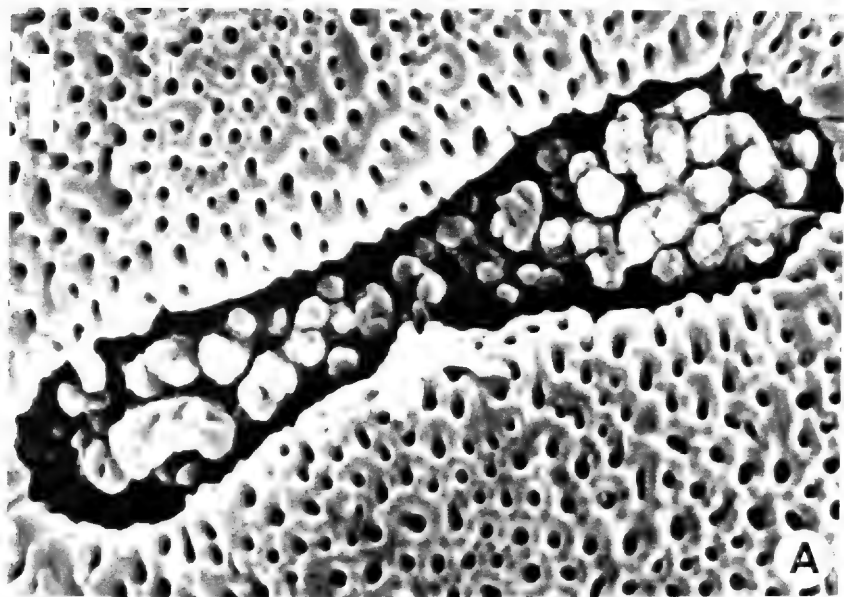


PLATE 33. *Matudaea* Lundell (Subfamily Hamamelidoideae; Tribe Distylieae)

VOUCHER MATERIAL: same as Plate 32.

A. Close-up view of the colpus of a rugate grain, showing an apparent early stage in the median constriction of a colpus which, when carried to the extreme, results in the formation of pore-like apertures. Note the foveolate exine, irregular margins and coarsely granular membranes of the colpus,  $\times 12,500$ . (Bar =  $1\ \mu\text{m}$ .)

B. A group of 12 grains, showing various aperture forms and configurations,  $\times 670$ . (Bar =  $10\ \mu\text{m}$ .)



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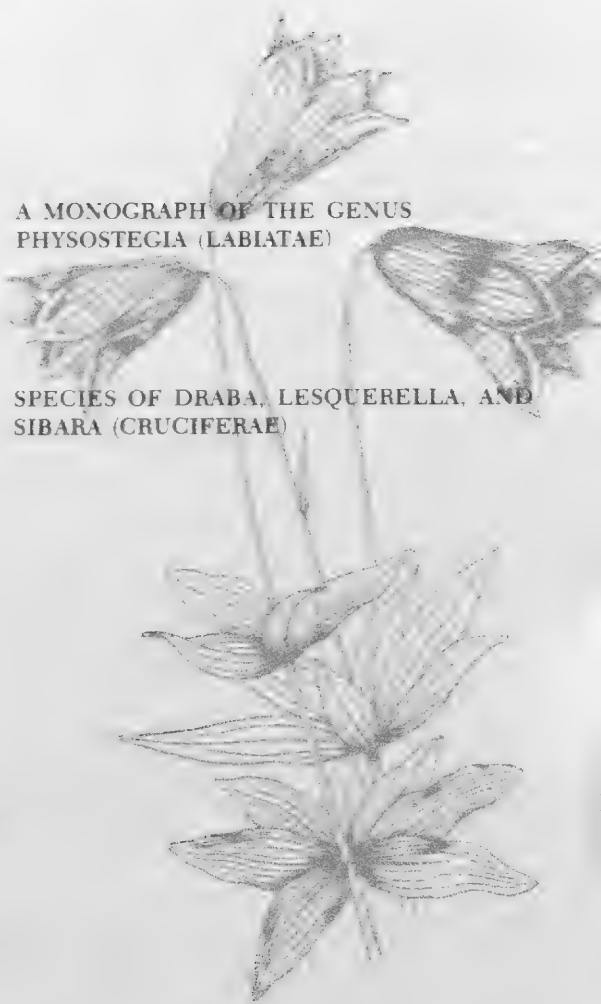
A MONOGRAPH OF THE GENUS  
PHYSOSTEGIA (LABIATAE)

SPECIES OF DRABA, LESQUERELLA, AND  
SIBARA (CRUCIFERAE)

EDITED BY Otto T. Solbrig  
Kathryn Rollins

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# A MONOGRAPH OF THE GENUS *PHYSOSTEGIA* (LABIATAE)

PHILIP D. CANTINO<sup>1</sup>

## INTRODUCTION

Species delimitation in *Physostegia* has long been a source of confusion. The genus has never been monographed, and its treatment in floristic works varies greatly. In *Gray's Manual* (Fernald, 1950), for example, seven species and two varieties are recognized, while Gleason and Cronquist (1963) accept only four species and do not recognize any infraspecific taxa in their manual covering approximately the same geographic area. Two of Fernald's species are neither accepted nor listed in synonymy by Gleason and Cronquist, and one species recognized by them is similarly absent from Fernald's treatment. Thus, even in the part of North America that is best known floristically, there is substantial disagreement about the taxonomy of *Physostegia*.

This derives in part from the lack of any thorough investigation of the morphological variation to be found in the genus as a whole; all previous studies of *Physostegia* have been restricted to a limited geographic area (e.g., Lundell, 1959, 1969; Mohlenbrock, 1963) or a single taxonomic subgroup (Boivin, 1966). As a consequence, there has been little recognition of the magnitude of the geographic variation found within some of the more widespread species. Accordingly, I have conducted an extensive survey of the morphological variation in the genus through the examination of some 5000 herbarium specimens from 51 institutions, supplemented by three summers of field study of natural populations. In addition, about 400 plants from 103 populations of eight species were grown together in the experimental garden, and many of these were transplanted into growth chambers where various environmental parameters could be manipulated. In this way it was possible to assess the plasticity of the morphological characters, and hence their taxonomic value.

In an effort to approach the systematics of the genus with an understanding of its biology, I have investigated the growth cycle, floral biology, habitat requirements, breeding system, and reproductive isolating mechanisms of various species. Cytological study of root tips has resulted in chromosome counts for 10 of the 12 species of *Physostegia*, many not previously reported. One product of these studies is the realization that the factors to which taxonomic complexity is most often attributed in the more difficult groups of vascular plants are not responsible for the taxonomic problems encountered in *Physostegia*. There is no evidence of apomictic seed production in the

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genus, very little evidence of natural interspecific hybridization, and few of the species are polyploid. Rather, the taxonomic complexity of *Physostegia* can be attributed to two aspects of its variation pattern—great interpopulational variability and a dearth of characters unique to a single species, the latter factor necessitating the recognition of species on the basis of combinations of characters.

In the classification presented herein I have employed a species concept that is primarily phenetic. I have relied heavily on morphology because it is easily studied and of no less adaptive significance than any of the other sorts of characters that could be used. Whenever possible I have considered ecological characters, and one physiological trait has proven to be of taxonomic value (i.e., photoperiodic requirements during inflorescence development). Its usefulness is noteworthy because differences in photoperiodic sensitivity have rarely if ever been employed for taxonomic purposes (Ornduff, 1978).

Although my species concept is primarily phenetic, it is not strictly so. I have attempted to maintain a reasonable degree of consistency in the magnitude of phenetic difference required, and in the amount of overlap permitted in key characters, between taxa that I have recognized as species. However, in certain borderline cases, I have ultimately based decisions on non-phenetic criteria, such as evidence concerning evolutionary history or isolating mechanisms. For example, the phenetic difference between *Physostegia ledinghamii* and *P. virginiana* is sufficiently low that, when compared to the interspecific phenetic differences elsewhere in the genus, it is unclear whether the two taxa should be treated as species or subspecies. However, the evidence that *P. ledinghamii* is a tetraploid derivative of a hybrid between *P. virginiana* and *P. parviflora* swings the balance in favor of treating it as a distinct species (Cantino, 1981a).

In the assignment of rank to infraspecific taxa, I have followed approximately the usage of Du Rietz (1930); i.e., a subspecies is a widespread segment of a species, while a variety is a local variant with a small but discrete distribution, and a form is a sporadic variant without a distinct distribution, usually distinguished by a single conspicuous character such as flower color. Many local variants are discernible within *Physostegia virginiana* and a lesser number within some of the other widespread species. Some of these have been described at the varietal level in the past and there are others that could be. Because these variants intergrade extensively, and many of them have likely arisen independently in more than one place, I see little purpose in giving them formal recognition. I have, however, recognized two wide-ranging subspecies of *P. virginiana*.

## ACKNOWLEDGMENTS

I would like to express my deep appreciation for the encouragement and guidance received throughout the course of this research from Professor Reed C. Rollins. Others who have offered helpful criticism and advice include Christopher S. Campbell, Michael J. Donoghue, Craig W. Greene, Walter S. Judd, Norton G. Miller, Otto T. Solbrig, Peter F. Stevens, Alice F. Tryon, and Carroll E. Wood, Jr.

Many other people have aided me in specific ways. Elizabeth A. Shaw edited my Latin description of *Physostegia longisepala*. Edward Seling provided essential technical assistance in the use of the scanning electron microscope of the Harvard University Museum of Comparative Zoology. Karen Stoutsenberger and Laurel Smith provided illustrations. I am grateful to Professor Wood for permitting my use of Ms. Stoutsenberger's work, carried out under his direction in connection with his Generic Flora of the Southeastern United States. John Lewis of the British Museum (Natural History) supplied me with photographs and descriptions of type specimens too valuable to send on loan. Bernd Heinrich, Karen S. Vinson, and Ronald J. McGinley identified my bee collections. William F. Mahler, Vernon L. Harms, and Joan Fryxell provided me with live plant material for cytological investigations. To all of these people I am deeply grateful.

My field studies were made possible through the support of the Fernald Fund, Harvard University. In the course of three summers of field work, I was aided in a variety of ways by people too numerous to name. However, I would like to extend my particular thanks to H. R. DeSelm for his hospitality and his invaluable aid in locating populations of *Physostegia* in eastern Tennessee.

I am grateful to Michael A. Canoso, Manager of Systematic Collections of the Harvard University Herbaria, for his help in obtaining specimen loans; I would also like to thank the curators and staff of the lending institutions.

## GENERIC AFFINITIES

Our understanding of intergeneric relationships in the Labiatae is heavily based on the work of Bentham (1832–36; 1848; 1876). Treatments of the family in modern floras are mostly patterned after the system of Briquet (1895–96), which does not differ greatly from Bentham's classification (El-Gazzar & Watson, 1970). In *Labiatarum Genera et Species* (1832–36), Bentham distributed the genera among eleven tribes but did not further subdivide the family. The Stachydeae, the tribe to which *Physostegia* was assigned, comprised a total of 26 genera. In Bentham's second major treatment of the family (1848), he reduced the number of tribes to eight but recognized subtribes within some of them. In this work, the subtribe Melitteae of the tribe Stachydeae comprised five genera—*Physostegia*, *Melittis*, *Brazoria*, *Macbridea*, and *Synandra*. In Bentham and Hooker's *Genera Plantarum* (1876), Bentham added the then recently described genus *Chelonopsis* to the subtribe Melitteae but transferred *Brazoria* to a different subtribe of the Stachydeae. Briquet (1895–96), in his treatment of the Labiatae in Engler and Prantl's *Die Natürlichen Pflanzenfamilien*, included within his subtribe Melittinae the same five

genera that composed Bentham's Melitteae in *Genera Plantarum*, namely *Physostegia*, *Chelonopsis*, *Macbridea*, *Synandra*, and *Melittis*. Following Bentham's lead, Briquet placed *Brazoria* in a different subtribe of the Stachydeae.

Primarily on the basis of pollen morphology, but considering other characters as well, Erdtman (1945) suggested that *Brazoria* belonged with the Melittinae. A numerical phenetic study of the Labiatae and Verbenaceae conducted by El-Gazzar and Watson (1970), while casting doubt on the naturalness of many of Bentham's and Briquet's groupings, confirmed the close relationship between *Brazoria* and three of the five genera of Bentham's subtribe Melitteae (*Physostegia*, *Synandra*, and *Melittis*); the other two genera were not included in their study. El-Gazzar and Watson suggested, however, that the Melitteae should be removed from the Stachydeae, the affinities of the subtribe lying rather with the tribes Ajugoideae and Prasieae.

In the absence of any published studies of the intergeneric relationships within the Melitteae, a preliminary morphological survey of the group has been carried out, based primarily on the collections of the Harvard University Herbaria but supplemented by published descriptions. The latter were necessarily relied upon heavily in the case of *Synandra*, of which there was but a single specimen available in the Harvard collections at the time of the study. The survey included the six genera that have, at one time or another, been placed in the Melitteae. Each genus was scored for 16 characters (Tables 1 & 2), which were selected for their diagnostic value in distinguishing *Physostegia* from at least one of the other five genera in the subtribe.

When the differences between the genera are totaled (Table 3), it is evident that *Physostegia* and *Brazoria* are much more similar to each other than either is to any of the other genera in the subtribe. *Brazoria* differs from *Physostegia* in its annual habit and strikingly bilabiate calyx. In addition, three of the four species of *Brazoria* (the exception being *B. scutellarioides*) have puberulent nutlets, bearded anthers, and pubescent stems, whereas *Physostegia* has glabrous nutlets, glabrous to sparsely pubescent anthers, and stems mostly to completely glabrous below the inflorescence.

Of the remaining four genera, *Macbridea* resembles *Physostegia* somewhat more closely than do *Synandra*, *Melittis*, and *Chelonopsis*. The foliage of *Macbridea*, *Physostegia*, and *Brazoria* is very similar in appearance and markedly different from that of *Melittis*, *Chelonopsis*, and *Synandra*. The leaves of the former group are firm in texture, usually glabrous or nearly so, and at least the upper (usually most or all of them) are sessile. In the latter group, the leaves are membranaceous, pubescent on both surfaces (often densely so), and

TABLE 1. CHARACTERS THAT DISTINGUISH *PHYSOSTEGIA* FROM RELATED GENERA.

1. Habit
  - a. Perennial
  - b. Annual
2. Stem Pubescence
  - a. Glabrous or nearly so below inflorescence
  - b. Pubescent throughout much of its length
3. Leaf Texture
  - a. Firm
  - b. Membranaceous
4. Leaves Conspicuously Glandular-punctate
  - a. Yes
  - b. No
5. Leaf Pubescence
  - a. Glabrous or at most ciliate on margins
  - b. Pubescent on both surfaces
6. Petioles
  - a. Only lower leaves petiolate
  - b. All leaves petiolate
7. Inflorescences
  - a. Flowers borne in bracteate racemes
  - b. Flowers borne in 1-3 tight capitula
  - c. Flowers borne individually in axils of upper foliage leaves
  - d. Flowers borne in bracteate cymose clusters in axils of upper foliage leaves
8. Floral Bracts
  - a. Narrow, not hiding calyx
  - b. Broad enough to hide much or all of calyx, but not leaf-like
  - c. Leaf-like, but somewhat reduced and different shape than foliage leaves
  - d. Absent (i.e., flowers borne in axils of normal foliage leaves)
9. Shape of Calyx
  - a. Campanulate to tubular-campanulate with 5 equal or subequal teeth
  - b. Bilabiate
  - c. 3-lobed
  - d. Shape irregular, with teeth of at least 3 different lengths
10. Venation of Calyx at Anthesis
  - a. Obscurely veined
  - b. Conspicuously veined
11. Flower Color
  - a. White to shades of pink and purple
  - b. Yellowish
12. Anthers Bearded
  - a. No (although may be slightly pubescent)
  - b. Yes
13. Anther Coherence
  - a. Anthers free from one another
  - b. Upper anthers coherent
14. Nutlet Shape
  - a. Trigonal
  - b. Oblanceolate to obovoid, not strongly compressed
  - c. Obovoid, strongly compressed
  - d. Subspherical, somewhat flattened on one side, convex on the other
15. Nutlet Pubescence
  - a. Glabrous
  - b. Puberulent
16. Nutlet Sculpturing
  - a. Smooth
  - b. With many irregular ribs running parallel to long axis of nutlet
  - c. Verrucose

all are petiolate. Although in the 16 characters considered in this study, *Macbridea* has a slightly greater overall resemblance to *Chelonopsis* than to *Physostegia* or *Brazoria* (Table 3), geographical considerations suggest that it is likely to be more closely related to the latter two. *Macbridea* and *Brazoria* are both endemic to the southern United States, the former to the Carolinas and Florida and the latter to Texas and Oklahoma, and the center of species diversity of *Physostegia* lies in the same region. *Chelonopsis*, on the other hand, is confined to eastern Asia. A cladistic analysis would help to determine whether *Physostegia*, *Brazoria*, and *Macbridea* form a monophyletic subgroup of the Melittea, as I suspect to be the case.

TABLE 2. DIAGNOSTIC TABLE: PHYSOSTEGIA AND RELATED GENERA (Use with Table 1).

Genus	Range	Number of Specimens Examined	Published Descriptions Used	Characters															
				1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>Physostegia</i>	N. Am.	5000		a	a	a	b,a	a	a	a	a	a	a	a	a	a	a	a	a,c
<i>Brazoria</i>	N. Am.	50	Correll & Johnston, 1970	b	b,a	a	b,a	a	a	a	a	b	a	a	b,a	a	a	b,a	a,c
<i>Macbridea</i>	N. Am.	11	Radford et al., 1964	a	a,b	a	a	a,b	a	b	b	c	b	a	b	a	b	a	b
<i>Melittis</i>	Europe	24	Ball, 1972	a	b	b	b	b	b	c	d	b	b	a	a	a	d	b	a
<i>Chelonopsis</i>	Asia	43	Ohwi, 1965	a	b	b	b,a	b	b	d	a	a,b	b	a,b	b	a	c	a	b
<i>Synandra</i>	N. Am.	1	Fernald, 1950; Gleason, 1952; Radford et al., 1964	?	b	b	b	b	b	a	c	d	b	b	b	b	?	?	?

TABLE 3. SUMMARY OF DIFFERENCES (Based on Table 2).

	<i>Brazoria</i>	<i>Macbridea</i>	<i>Melittis</i>	<i>Chelonopsis</i>	<i>Synandra</i>
<i>Physostegia</i>	2c; 3i	7c; 3i	10c; 1i	9c; 2i	10c; 1i
<i>Brazoria</i>	X	7c; 4i	8c; 5i	8c; 5i	8c; 3i
<i>Macbridea</i>	X	X	10c; 2i	6c; 4i	8c; 2i
<i>Melittis</i>	X	X	X	6c; 3i	6c; 0i
<i>Chelonopsis</i>	X	X	X	X	4c; 2i

c: a consistent difference between the two genera concerned.

i: an inconsistent difference—i.e., a character in which the state(s) that occur in one genus sometimes occur in the other.

In view of the kaleidoscopic interspecific variation pattern of *Physostegia* (species being distinguishable on the basis of combinations of characters; see p. 44), it is interesting to note that, similarly, there is no single character that will simultaneously distinguish *Physostegia* from all of the other genera of the Melittea; every character state that is found throughout *Physostegia* occurs in at least one of the other five genera. The trait that comes the closest to being unique to *Physostegia* is the shape of the calyx (character 9, Table 2), but some species of *Chelonopsis* have a similar calyx morphology. However, when the venation is taken into account, it is possible to distinguish *Physostegia* from the rest of the Melittea on the basis of the calyx alone; *Physostegia* is the only genus that has an obscurely veined tubular-campanulate calyx with five teeth of approximately equal length.

#### DISTRIBUTION AND HABITAT

*Physostegia* is endemic to North America (Fig. 14–17). The center of species diversity is in southeastern Texas and extreme southwestern Louisiana, where seven of the twelve species are found. Garden forms of *P. virginiana* have become widely naturalized in areas of the eastern United States where the genus is not native, as well as in at least one locality in Europe, near Turin, Italy (Tosco, 1954).

The genus occurs in a great diversity of habitats. Native populations range from sea level to at least 2300 meters in elevation. Most species occupy relatively moist sites and several are facultative aquatics, able to grow in up to a foot of water. In contrast, *Physostegia virginiana* may be found in limestone barrens which are very dry during the summer months when it is in bloom. *Physostegia* also appears to tolerate a broad range of soil acidity. *Physostegia virginiana* is capable of growing on nearly bare limestone, whereas the soils that support the pine forests frequented by *P. digitalis* are moderately to strongly acidic (Campbell, 1955). The distributions and habitats of the individual species are discussed in the taxonomic section.



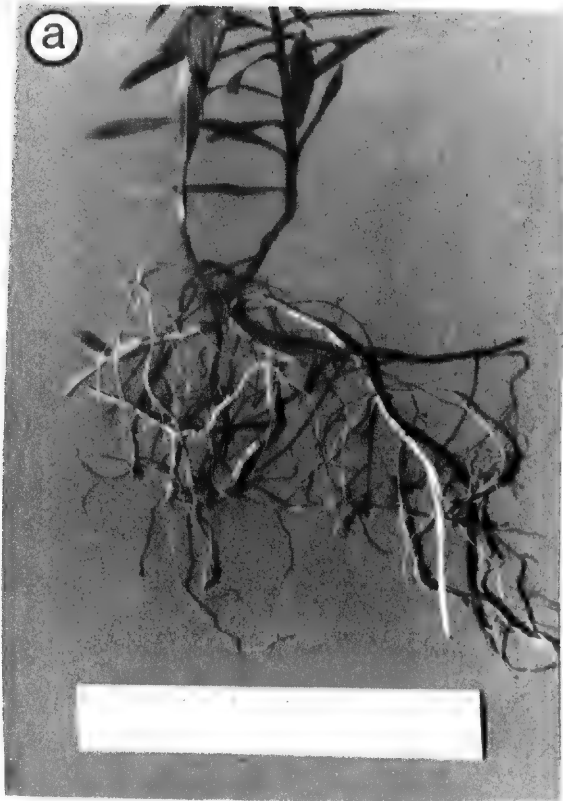


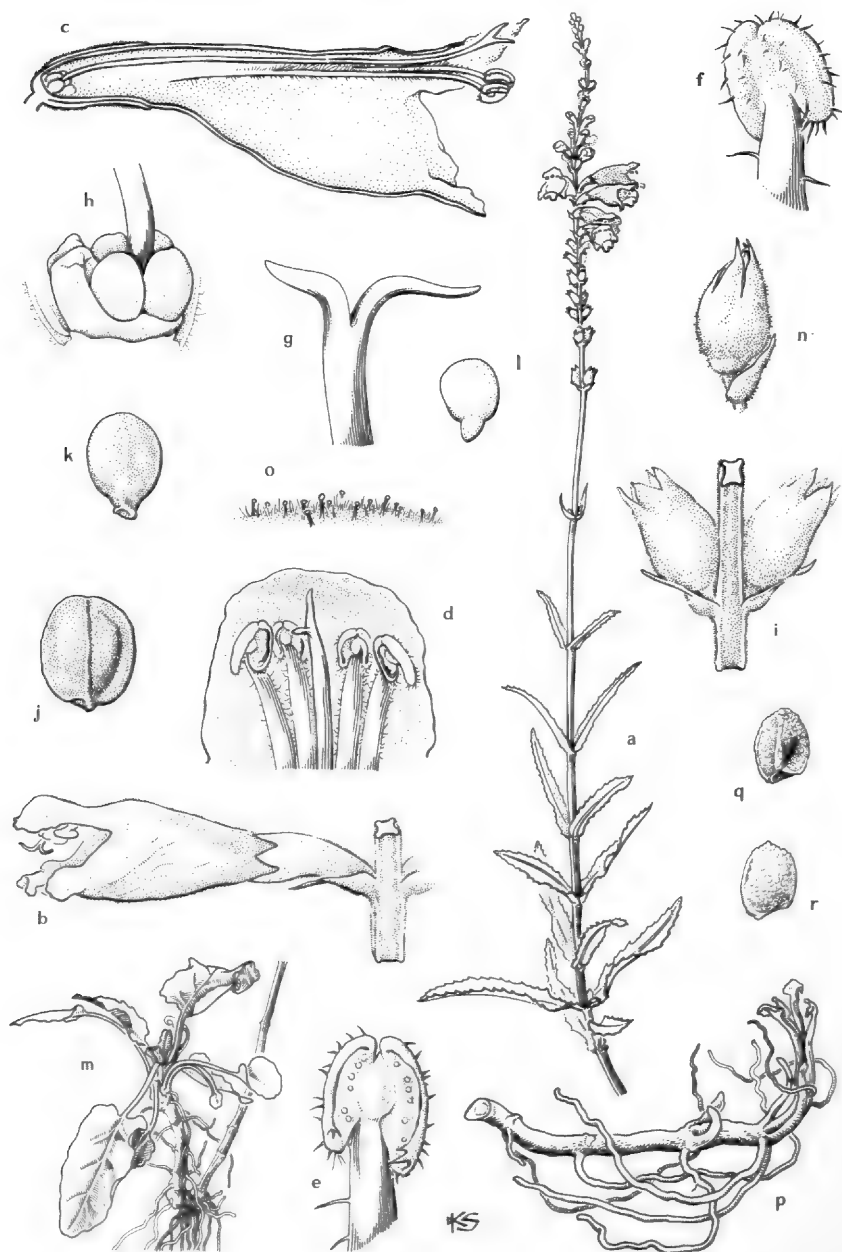
FIG. 1. Rhizome morphology of *Physostegia virginiana* ssp. *virginiana* (a) and ssp. *praemorsa* (b).

## MORPHOLOGY AND ANATOMY

**Rhizome and Root.** Two fundamentally different kinds of rhizomes are present in *Physostegia*. In *P. correllii*, *P. intermedia*, *P. ledinghamii*, *P. leptophylla*, *P. longisepala*, and *P. virginiana* ssp. *virginiana*, the primary rootstock gives rise to one or more elongate, horizontal secondary rhizomes (Fig. 1a), which may be simple or branched and up to 65 cm long. A perennating bud is borne at the apex of each horizontal rhizome (Fig. 2p). In *P. angustifolia*, *P. digitalis*, *P. pulchella*, and *P. virginiana* ssp. *praemorsa*, no horizontal rhizomes are produced. The perennating buds are borne directly on the primary rootstock (Fig. 1b) or, if it is deeply buried, at the ends of short, vertical secondary rhizomes (Fig. 2m). The fundamental difference between the two is in the directionality of the secondary rhizomes rather than the length. Although the horizontal rhizomes are usually much longer than the vertical ones, occasional plants have horizontal rhizomes as little as 2 cm long. The form of the rhizome is among the most taxonomically useful characters in *Physostegia*. Even in the four species in which both forms occur, there is rarely variation within populations. The single notable exception is *P. purpurea*, in which it is common to find, within a single population, plants with horizontal rhizomes and those with perennating buds borne directly on the rootstock. Except in very young seedlings, all roots are adventitious, arising from the nodes of the primary and secondary rhizomes (Fig. 2m,p).

**Stem.** The stem is quadrangular and slightly swollen at the nodes; the angles are composed of collenchymatous tissue. In most species of *Physostegia*, the base of the stem is only slightly thicker than the middle and upper sections, but in *P. intermedia* the base is often grossly enlarged and hollow. The same is very rarely true of *P. leptophylla* and is perhaps an adaptation related to the aquatic habit of these two species.

**Leaf.** The leaves of *Physostegia* are universally glabrous, with a prominent midrib and obscure secondary venation. Leaf shape and dentation are extremely variable. Leaf outline ranges from linear in *P. godfreyi* and *P. purpurea* to broadly elliptical, obovate, or ovate in *P. correllii*. The leaf base ranges from attenuate to rounded or auriculate and the apex from attenuate to obtuse. The margins may be sharply serrate, bluntly dentate, repand, or entire (Fig. 3). In most species the middle and/or upper leaves clasp the stem to some degree (Fig. 4b-d), but in *P. godfreyi* the leaves never clasp, and they rarely do in *P. virginiana*. Leaf shape and dentation vary little within populations, but *P. purpurea* exhibits a remarkable degree of variation in leaf shape both within and between populations (Fig. 13), and the



leaf margins in a few populations of *P. virginiana* and in one of *P. angustifolia* range from sharply serrate to entire.

The degree of reduction of the upper stem leaves is a useful taxonomic character. In some species (e.g., *Physostegia correllii*, *P. parviflora*), the uppermost leaves below the inflorescence are scarcely smaller than those borne on the middle of the stem, while in others (e.g., *P. angustifolia*, *P. purpurea*) the top few pairs of leaves are greatly reduced. The degree of reduction can be expressed quantitatively as a ratio of the length of the leaves of the second pair below the terminal raceme to the length of the internode above that pair. It is necessary to specify the terminal raceme as the reference point, rather than the inflorescence as a whole, so that plants with many racemes can be meaningfully compared with those bearing only a single raceme.

Both leaf surfaces are minutely pitted, the depressions occupied by microscopic glands of unknown function. Easily studied by means of longitudinal leaf sections and epidermal peels, these structures consist of a multicellular cap borne on top of a single basal cell. The cap is composed of from 4 (rarely 2 or 3) to about 25 cells, and its diameter ranges from 20 to 70  $\mu$ . When viewed from above, the basal cell is concealed by the larger cap, its circular outline faintly visible through the cap if the focus is properly adjusted (Fig. 5a,b).

In *Physostegia virginiana* and *P. angustifolia* the glands are of two distinct size classes. The smaller (20–45  $\mu$  dia.) has a cap composed of 4–8 cells, with the cell walls all situated perpendicular to the pe-

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FIG. 2. Selected morphological features of *Physostegia*. A–M: *P. angustifolia* (Cantino 1057). A, upper part of flowering plant,  $\times 0.3$ ; B, flower with bract,  $\times 1.8$ ; C, flower in longitudinal section,  $\times 2.7$ ; D, apex of upper lip with stamens and style, seen from below,  $\times 4.5$ ; E, anther from below,  $\times 10.8$ ; F, anther from above,  $\times 10.8$ ; G, stigmatic lobes,  $\times 10.8$ ; H, ovary and nectary,  $\times 10.8$ ; I, calyces in fruit,  $\times 1.8$ ; J, nutlet, adaxial surface,  $\times 5.4$ ; K, seed,  $\times 5.4$ ; L, embryo,  $\times 5.4$ ; M, developing winter rosette,  $\times 0.5$ . N–P: *P. correllii* (Cantino 1064). N, fruiting calyx,  $\times 1.8$ ; O, vestiture of calyx, showing stalked glands,  $\times 10.8$ ; P, horizontal rhizome, the terminal perennating bud starting to expand,  $\times 0.5$ . Q–R: *P. godfreyi* (Godfrey et al. 53473). Q, adaxial surface of nutlet,  $\times 5.4$  (note small size and verrucose surface); R, abaxial surface of nutlet,  $\times 5.4$ . The plants of *P. angustifolia* and *P. correllii* were grown in an experimental garden from rhizomes collected in the same natural populations as the voucher. Vouchers at GH.

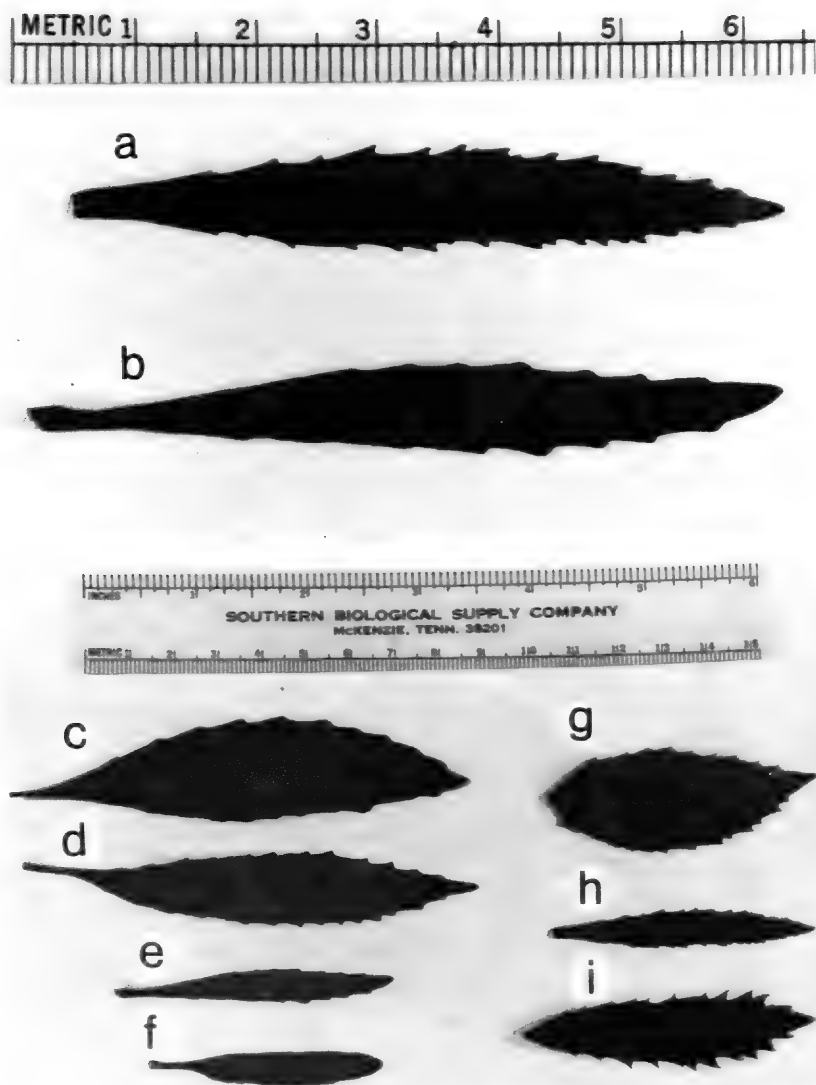


FIG. 3. Variation in leaf margin. A, *Physostegia virginiana* ssp. *praemorsa* (Cantino 918). B, *P. purpurea* (Cantino 1004). C and D, *P. leptophylla* (Cantino 973 and 970). E, *P. purpurea* (Cantino 1004). F, *P. intermedia* (Cantino 1065). G, *P. correllii* (Cantino 1064). H and I, *P. virginiana* ssp. *praemorsa* (Cantino 918 and 916).

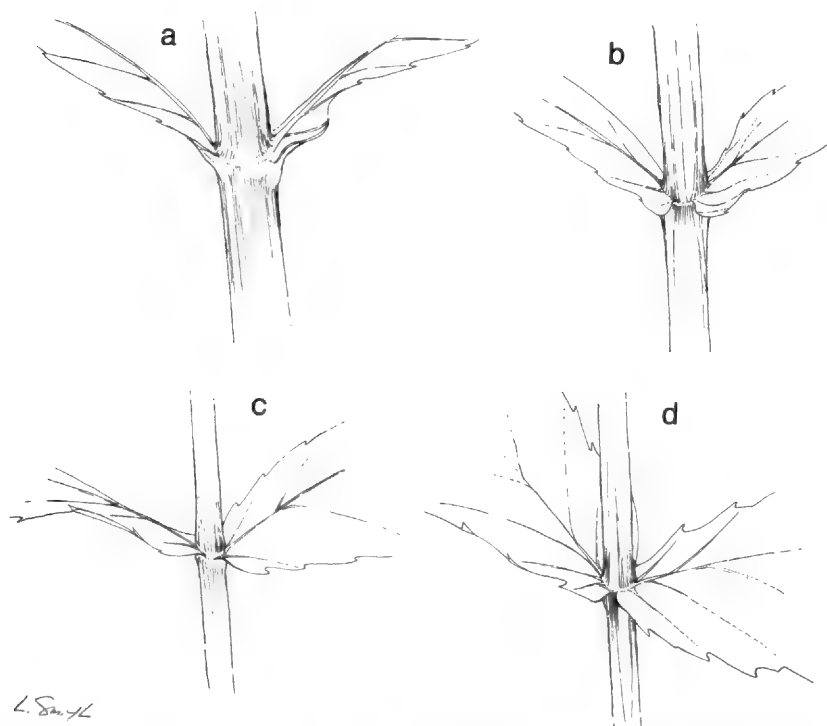


FIG. 4. Variation in leaf base morphology. A, *Physostegia virginiana* ssp. *virginiana* (Cantino 885). B, *P. angustifolia* (Cantino 874). C, *P. virginiana* ssp. *praemorsa* (Cantino 946). The subamplexicaulous leaves of this plant are atypical of *P. virginiana*, which nearly always has the non-clasping base illustrated in drawing A. D, *P. correllii* (Cantino 1064).

rimeter of the cap as seen from above (Fig. 5a,b). The larger type (50–70  $\mu$  dia.) has a cap composed of 15–20 cells, with many of the cell walls running parallel to the perimeter of the cap (Fig. 5c). In *P. purpurea* there is no such clear distinction between size classes. Here the cap is composed of 4–14 cells, often with a few cell walls running parallel to the perimeter when the number of cells is 8 or more; the diameter of the cap ranges from 20–45  $\mu$ , with no obvious correlation between the number of cells and the diameter of the cap.

The microscopic glands are present on all photosynthetic parts of the plant as well as on the corolla, and Junell (1937) has observed similar structures on the outside of the ovule in *Physostegia virginiana*. Statements in the descriptions and keys that the calyx is or is

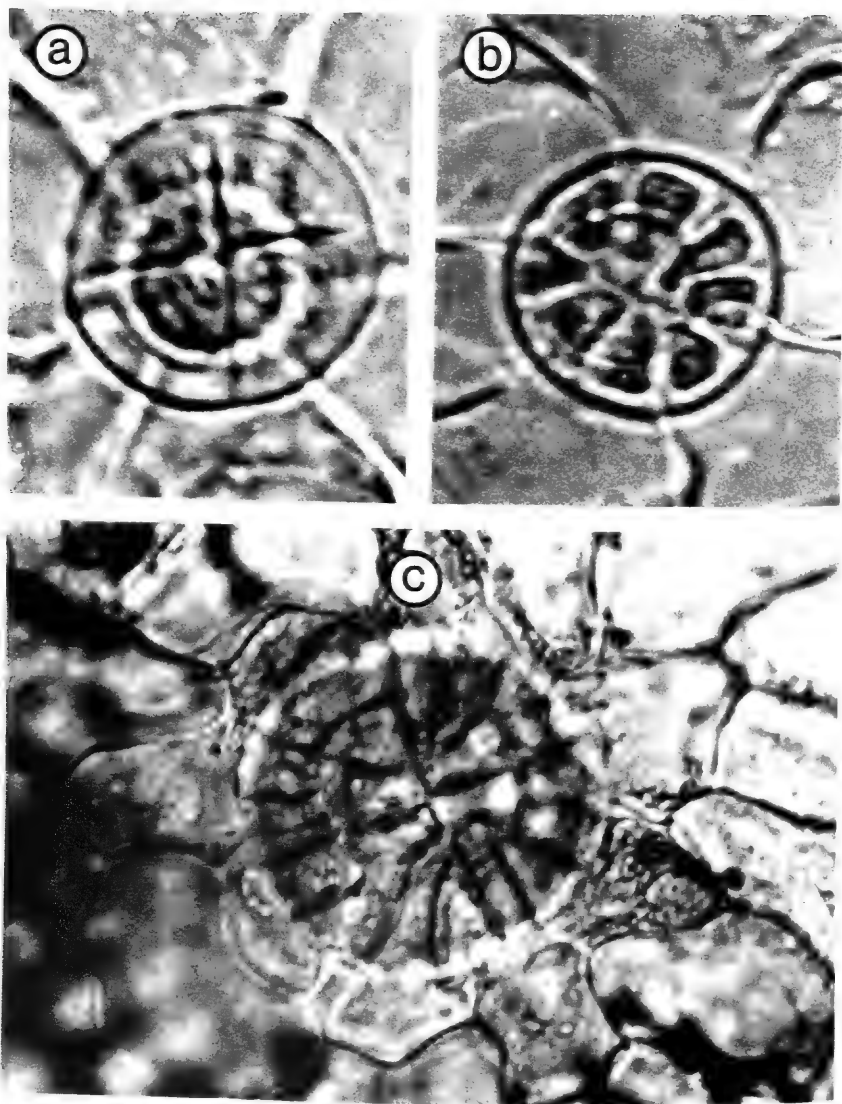


FIG. 5. Glands on leaf surface in *Physostegia virginiana*. A, small gland with four-celled cap,  $\times 1150$  (Cantino 944). Note circular outline of basal cell visible through cap. B, small gland with eight-celled cap,  $\times 850$  (Cantino 946). C, large gland,  $\times 700$  (Cantino 877). Note that some of the cell walls run parallel with the perimeter of the cap. Epidermal peels were obtained from greenhouse plants, grown from rhizomes collected from same natural population as voucher. Vouchers at GH.

not glandular-punctate, or that the leaf surface bears glandular dots, refer to the comparative conspicuousness of these structures, this perhaps being a function of the relative frequency of the larger-sized glands. The glands have a shiny, resinous appearance which is much more noticeable in dried material. However, even when they are particularly abundant and conspicuous, the surfaces they are borne upon are not sticky to the touch and have no distinctive odor.

Stomata are abundant on both leaf surfaces and are slightly elevated above the general level of the epidermis. They are amphidiacytic (terminology follows Dilcher, 1974), with three to four subsidiary cells of variable shape. Nearly the entire range of variation in both the number and shape of the subsidiary cells can be found on a single leaf.

**Inflorescence.** The flowers are borne in pairs (or aberrantly in whorls of four) in racemes, the uppermost terminating the shoot and the others situated in the axils of the upper leaves. Floral density varies greatly in the genus and shows a high degree of species-constancy.

In *Physostegia virginiana* ssp. *praemorsa*, there is commonly a row of empty bracts below those subtending flowers (Fig. 9a). The production of these sterile bracts is under photoperiodic control (see p. 25). The friction of the stiff bract against the pedicel and the base of the calyx is at least partially responsible for the phenomenon to which the common name "obedient-plant" alludes; i.e., when the flowers are rotated to the right or left in the raceme, they remain where they are placed. This phenomenon, termed "catalepsy," received considerable attention in the 19th century (Ventenat, 1801; Vilmorin-Andrieux & Co., 1866; Bailey, 1882; Coulter, 1882; Robertson, 1888; Meehan, 1897). Linsbauer (1940), who explored the mechanism in depth, concluded that it is not only the rigidity of the bract that prevents the flower from springing back to its original position, but also the friction between the trichomes on the bract and those on the calyx and pedicel. He aptly compared this phenomenon to the friction between a pair of brushes.

**Flower.** The flowers of *Physostegia* range from 1 to 4 cm in length. Although flower length is extremely variable within *P. purpurea*, its low variability in many other species (e.g., *P. intermedia*, *P. godfreyi*, *P. parviflora*) makes it a taxonomically valuable character. It must be used with caution, however, because adverse environmental conditions can lead to anther abortion accompanied by reduced flower size. The length measurements in the keys and descriptions are based on dried specimens; flowers on live plants average several millimeters longer.

The pedicels may be up to 2.5 cm long but are usually much shorter, the flowers appearing nearly sessile. The internal anatomy of



the pedicel of *Physostegia virginiana* has been studied by Müller (1933), who has documented the existence of a ring of specialized parenchymatous tissue at its base that, because of its unusual capacity for water absorption, provides the pedicel with the flexibility necessary to endure repeated rotation of the flowers in the inflorescence (i.e., the catalepsy mentioned above).

The calyx at anthesis is tubular-campanulate to campanulate, its five short lobes equal in length or nearly so. It becomes somewhat inflated as the nutlets develop (Fig. 2i,n). The corolla is illustrated in Figure 2 and described on p. 57. Although certain aspects of corolla morphology are quite variable in *Physostegia*, most characters that vary at all tend to vary a great deal within populations and are thus of little taxonomic value. The one character that has proven useful is coloration. Two species, *P. angustifolia* and *P. digitalis*, have consistently pale flowers, the color ranging from pure white to very pale lavender. In contrast, *P. pulchella* and *P. longisepala* have deep lavender to reddish violet corollas. Although flower color is constant or nearly so in the above four species, it is extremely variable in *P. virginiana*, ranging from pure white to deep lavender, occasionally even within a single population.

The four stamens ascend along the adaxial side of the corolla tube, the anthers lying side by side beneath the upper lip (Fig. 2b,d), or the outer pair of stamens slightly exceeding the inner. The stamens are epipetalous, the filaments of the inner pair becoming free of the corolla tube near its mouth, while the outer pair arises deeper within the tube (Fig. 2c). The filaments are densely villous, the tangle of trichomes causing the four stamens to cohere to one another and to hold the style in a position between them. The retention of the style in this position is an essential part of the pollination mechanism (Coulter, 1882; Cantino, 1980, pp. 97–98). The two equal to subequal anther sacs of each stamen are borne parallel to or slightly divergent from one another around a small connective (Fig. 2e). There is a scattering of multicellular glandlike structures of unknown function on the abaxial surface. The dehiscence is longitudinal, a few tiny teeth usually bordering the opening at its proximal end (Fig. 2e) and sometimes throughout its length. Delpino (1868) noted that these teeth facilitate the release of pollen when brushed by an insect.

The ovary is deeply cleft into four equal lobes (Fig. 2h), and the style is gynobasic. Lying adjacent to two of the ovary lobes and surpassing them in height is a single yellowish nectary (Fig. 2h). The development of the ovule, embryo sac, and seed in *Physostegia virginiana* has been studied by Billings (1909), Sharp (1911), and Junell (1937). The ovule is anatropous and has a single massive integument,

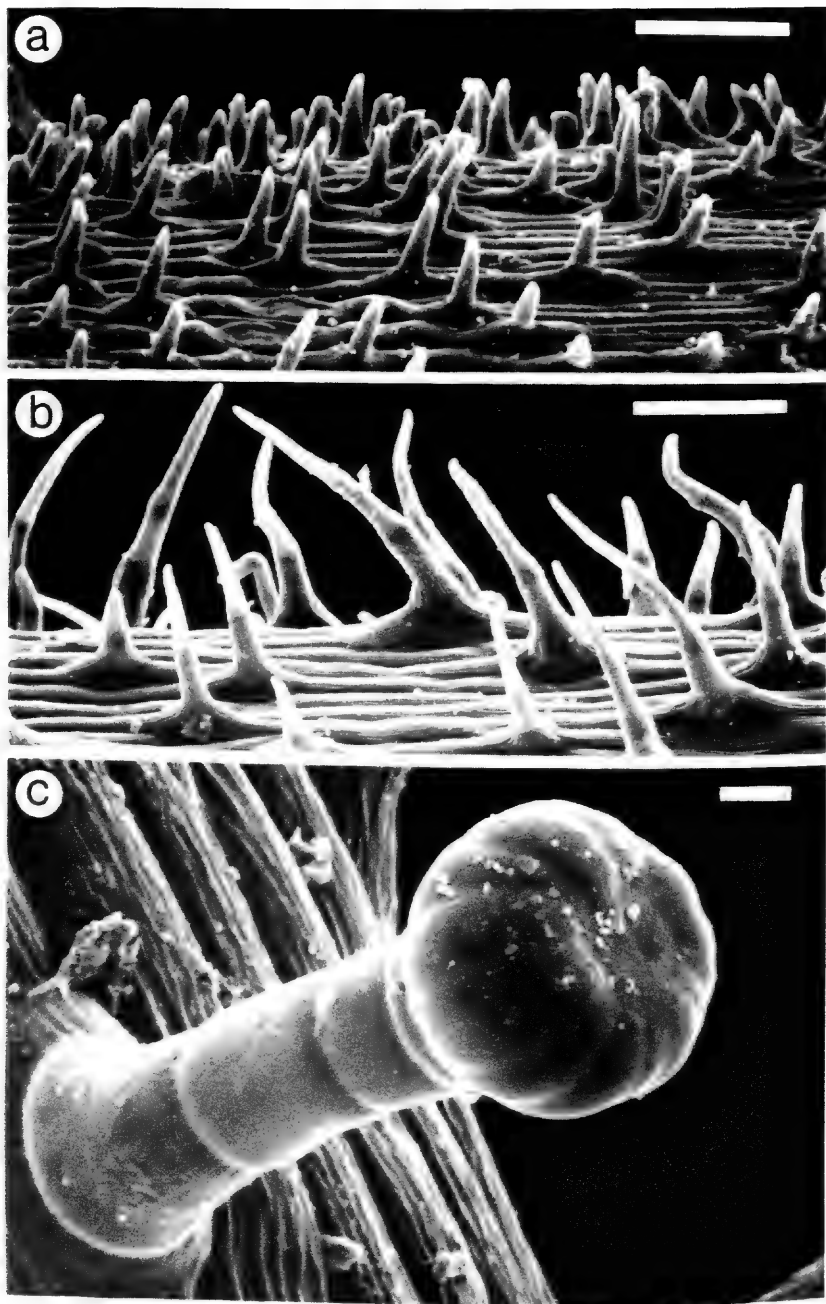
there being one ovule per ovary lobe. The embryo sac is unusual in shape, composed of two expanded regions, a downward-directed micropylar lobe and an upper lobe in which the endosperm later develops, with the two lobes separated by a constriction.

**Fruit and Seed.** Under optimal conditions, four nutlets are produced per flower. The nutlets are trigonal, the surfaces smooth in all but one species (Fig. 2j); the nutlets of *Physostegia godfreyi* are verrucose over part or all of their surface (Fig. 2q,r; also see Cantino, 1979, for SEM photomicrographs). The single seed inside each nutlet is obscurely trigonal (Fig. 2k), with a membranaceous seed coat. The mature seed is nearly filled by the ovoid-lenticular embryo, which has only a thin layer of endosperm surrounding it.

**Trichomes.** The vesture of *Physostegia* is composed of both glandular and nonglandular trichomes. It is largely confined to the inflorescence, the only exception being the sparse puberulence that is sometimes present in the nodal regions of the upper stem. The nonglandular trichomes are structurally similar throughout the genus but vary in length and density. They are simple, erect to slanting or somewhat curved (but never appressed), and composed of two to five cells in a single series. To obtain photomicrographs of the trichomes (Fig. 6), pieces of raceme axis from live plants were dehydrated by means of immersion in a series of progressively stronger acetone:water mixtures (50%, 70%, 90%, 95%, and 100% acetone), 30 minutes in each. The material was then mounted on aluminum stubs with double-stick tape, critical-point dried with carbon dioxide, sputter-coated with gold-palladium to a thickness of 200 Å, and examined with an AMR Model 1000 scanning electron microscope.

The striking difference in the length of the trichomes of *Physostegia angustifolia* and *P. virginiana* ssp. *praemorsa* (Fig. 6a,b) is the most reliable distinction between these two widespread and morphologically variable taxa. Although the absolute difference in length is small (in the order of 0.1 mm), the difference is significant in multiplicative terms; members of *P. angustifolia* generally bear at least a few trichomes twice as long as those of *P. virginiana* ssp. *praemorsa*. Trichome length is also useful in distinguishing *P. digitalis*, which has the longest trichomes in the genus, from *P. purpurea*. While trichome length shows a relatively high degree of species-constancy, the density of the vesture varies greatly within species, some rare individuals being nearly glabrous. One such variant was formally recognized by Fassett as *P. speciosa* var. *glabriflora*.

Stalked glands, both the cap and stalk of which are multicellular (Fig. 6c), can sometimes be found interspersed with the nonglandular trichomes in the inflorescence. When living material is examined, a



droplet of glandular exudate can be seen on top of the cap. The function of the liquid has not been explored. The presence or absence of these glands is among the most taxonomically useful characters in *Physostegia*, three species always producing them (*P. godfreyi*, *P. ledinghamii*, and *P. parviflora*) and six species always lacking them (*P. angustifolia*, *P. intermedia*, *P. leptophylla*, *P. longisepala*, *P. pulchella*, and *P. purpurea*). In the other three species that may or may not produce them, there is very rarely any variation within populations. The distribution of stalked glands on the plant is also of taxonomic value. Whenever they are produced, they are found on the calyx and the raceme axis and usually on the pedicel and floral bract, but in *P. parviflora* the glands are practically always present on the corolla as well, and in *P. ledinghamii* and *P. correllii* they are occasionally borne there; their presence on the corolla is extremely rare in the other three species that produce the glands.

**Pollen.** Erdtman (1945) has suggested that there are two major groups of genera in the Labiatae which can be defined on the basis of whether the pollen grains are (A) tricolpate and binucleate or (B) hexacolpate and trinucleate. The pollen of *Physostegia* is tricolpate and, according to Waterman (1960), binucleate; it is thus of type (A). Waterman published a photomicrograph of an acetylated pollen grain of *P. virginiana* and reported that grains obtained from three herbarium specimens were subprolate to prolate spheroidal with reticulate sculpturing. In equatorial view, the grains were 39–62  $\mu$  long and 29–59  $\mu$  wide; the polar diameter ranged from 38 to 58  $\mu$ .

The sculpturing of the pollen of *Physostegia* has been examined more closely by means of scanning electron microscopy (Fig. 7). Pollen from greenhouse plants and herbarium specimens was mounted on aluminum stubs with double-stick tape and sputter-coated with gold-palladium. The pollen was not acetylated or pretreated in any way. There was no striking difference in the sculpturing of the exine among the ten species examined; although a little variation could be observed in the size of the lumina of the reticulum, the differences were slight. The floor of the lumina of all species was found to be minutely pitted when examined at a high magnification (Fig. 7f). Length and width measurements in equatorial view (Table 4), ob-

FIG. 6. Trichomes and stalked glands on the raceme axis. A, *Physostegia virginiana* ssp. *praemorsa* (Cantino 883), white bar = 100  $\mu$ . B, *P. angustifolia* (Cantino 1057), white bar = 100  $\mu$ . C, *P. godfreyi* (Cantino 1054), white bar = 10  $\mu$ . Plants grown from rhizomes collected in same natural population as voucher. Vouchers at GH.

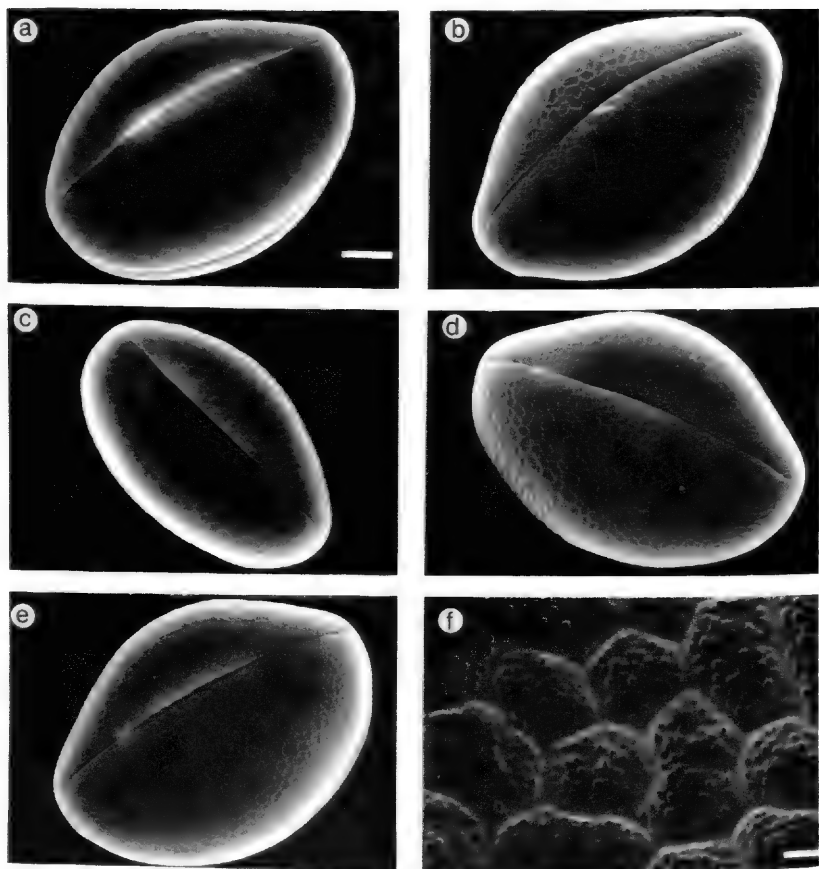


FIG. 7. Pollen grains of *Physostegia*. A, *P. virginiana* ssp. *prae-morsa* (Cantino 882). B, *P. correllii* (Cantino 1137). C, *P. parviflora* (Eastham s.n., DAO 16106). D, *P. digitalis* (Cantino 1068). E, *P. godfreyi* (Cantino 1054). A-E, white bar = 10 µ. F, *P. leptophylla* (Cantino 970), white bar = 1 µ. Pollen obtained from greenhouse plants grown from rhizomes collected in same natural population as voucher. Cantino vouchers at GH.

tained from SEM photomicrographs, were found to be roughly comparable to those obtained by Waterman. In Table 4, vouchers in the Cantino series do not represent the actual plant from which pollen was removed. In each case, pollen was taken from a greenhouse plant grown from a rhizome collected in the same natural population as the voucher. The vouchers in the collection series of other collectors rep-

TABLE 4. POLLEN MEASUREMENTS FROM SCANNING ELECTRON PHOTOMICROGRAPHS.

Taxon	Voucher	Equatorial View	
		Length ( $\mu$ )	Width ( $\mu$ )
<i>P. angustifolia</i>	Cantino 1132 (GH)	71	46
<i>P. correllii</i>	Cantino 1137 (GH)	70	46
<i>P. digitalis</i>	Cantino 1068 (GH)	70	50
<i>P. godfreyi</i>	Cantino 1054 (GH)	71	51
<i>P. intermedia</i>	Correll 20840 (LL)	51	41
<i>P. ledinghamii</i>	Frankton & Bibbey 384 (DAO)	70	48
<i>P. leptophylla</i>	Cantino 970 (GH)	68	48
<i>P. parviflora</i>	Eastham, s.n., 8-VIII-1947 (DAO 16106)	59	36
<i>P. purpurea</i>	Cantino 974 (GH)	64	49
<i>P. purpurea</i>	Cantino 1027 (GH)	57	35
<i>P. virginiana</i> ssp. <i>praemorsa</i>	Cantino 882 (GH)	69	49
<i>P. virginiana</i> ssp. <i>praemorsa</i>	Cantino 946 (GH)	65	37
<i>P. virginiana</i> ssp. <i>virginiana</i>	Cantino 910 (GH)	67	42

Measurements refer to single pollen grains, listed values do not represent means

resent the actual herbarium specimens from which pollen was removed.

### CHROMOSOME NUMBERS

The chromosome numbers of five species of *Physostegia* have been reported (Taylor & Brockman, 1966; Fedorov, 1969; Cantino, 1981a, 1981b). Three were found to have 19 pairs of chromosomes and the other two had 38 pairs. In agreement with the published reports, several specimens of *P. virginiana* in the herbarium of the Canadian Department of Agriculture (DAO) have been annotated with a diploid number of 38 by Wray M. Bowden (*Bowden Cyt. No. 3030-C1, 3175-C1, 3029*).

Using somatic tissues, I have determined the chromosome numbers of ten species of *Physostegia*. Root tips were obtained from greenhouse plants which had been raised from rhizomes collected previously in natural populations. The material was pretreated in 8-hydroxyquinoline and stained with aceto-orcein, according to a procedure (see Cantino, 1980 for further details) similar to that outlined by B. W. Smith (in Radford, et al., 1974: 251-252), originally adapted from Tijo and Levan (1950).

The results of this study have substantiated the earlier suggestion by Taylor and Brockman (1966) that the base number of *Physostegia* is 19. There are two tetraploid species with 76 chromosomes, and the other species investigated have a diploid number of 38. The chromosome numbers of eleven of the twelve species are listed in Table 5; the only species not examined is *P. longisepala*. All but two of the counts in Table 5 are my own; permanent slides have been retained and are available upon request. The chromosomes of selected species

TABLE 5. CHROMOSOME NUMBERS IN PHYSOSTEGIA.

Taxon	Chromosome Number (2n)	Location	Voucher and/or Reference
<i>P. angustifolia</i>	38	Louisiana: Tangipahoa Parish, 0.4 mi W of Loranger.	<i>Cantino 1132</i>
	38	Missouri: Newton Co., 2 mi N of Racine.	<i>Cantino 1133</i>
	38	Missouri: Newton Co., 3.5 mi SW of Neosho.	<i>Cantino 1134</i>
	38	Mississippi: Pearl River Co., 5.5 mi NW of Picayune.	<i>Cantino 1135</i>
	38	Oklahoma: McCurtain Co., ca. 6 mi S of Smithville.	<i>Cantino 1136</i>
<i>P. correllii</i>	38	Louisiana: Cameron Parish, ca. 9 mi E of Grand Lake.	<i>Cantino 1137</i>
<i>P. digitalis</i>	38	Louisiana: Vernon Parish, near Leander.	<i>Cantino 1071</i>
	38	Texas: Cass Co., N of Queen City.	<i>Cantino 1076</i>
<i>P. godfreyi</i>	38	Florida: Liberty Co., 10 mi S of Bristol.	<i>Cantino 1051</i>
	38	Florida: Gulf Co., 12.4 mi S of Wewahitchka.	<i>Cantino 1138</i>
<i>P. intermedia</i>	38	Texas: Orange Co., just W of Orange.	<i>Cantino 1139</i>
<i>P. ledinghamii</i>	76	Canada: Saskatchewan, ca. 8 mi S of Saskatoon.	<i>V. L. Harms 27623 (Cantino, 1981a)</i>
<i>P. leptophylla</i>	76	Five localities from Virginia to Florida.	<i>(Cantino, 1981b)</i>
<i>P. parviflora</i>	38	Canada: British Columbia, Lower Arrow Lake.	<i>J. A. Calder 37028 (DAO) (Taylor &amp; Brockman, 1966)</i>
<i>P. pulchella</i>	38	Texas: Navarro Co., 1 mi NE of Richland.	<i>W. F. Mahler 8520</i>
	38	Texas: Brazos Co., College Station.	<i>J. Fryxell 171</i>
	38	Texas: Brazos Co., just E of College Station.	<i>J. Fryxell 172</i>
	38	Texas: Brazos Co., ca. 7 mi E of College Station.	<i>J. Fryxell 173</i>
<i>P. purpurea</i>	38	Five localities from North Carolina to Florida.	<i>(Cantino, 1981b)</i>
<i>P. virginiana</i> (ssp. unknown)	38	Location unknown	<i>(Fedorov, 1969)</i>
<i>P. virginiana</i> ssp. <i>virginiana</i>	38	West Virginia: Raleigh Co., ca. 3 mi NW of Hinton.	<i>Cantino 915</i>
	38	Illinois: Macon Co., ca. 6 mi W of Decatur.	<i>Cantino 1144</i>
	38	Illinois: Piatt Co., 4 mi SE of Cisco.	<i>Cantino 1145</i>
<i>P. virginiana</i> ssp. <i>praemorsa</i>	38	Illinois: Vermilion Co., Ftian.	<i>Cantino 847</i>
	38	South Carolina: York Co., ca. 3 mi NW of Smiths.	<i>Cantino 1146</i>

TABLE 5. CONTINUED.

Taxon	Chromosome Number (2n)	Location	Voucher and/or Reference
	38	North Carolina: Transylvania Co., ca. 4 mi SW of Lake Toxaway.	<i>Cantino 1147</i>
	38	Arkansas: Craighead Co., Jonesboro.	<i>Cantino 1148</i>

have been photographed (Fig. 8). Unless otherwise stated, all vouchers listed in Table 5 have been deposited in the Gray Herbarium.

### GROWTH CYCLE

All species of *Physostegia* are perennial. The perennating buds may be present at the time of anthesis, but they are frequently not produced until after the blooming period has ended. Shinnery's (1956) erroneous assertion that some species of *Physostegia* are annuals was probably based on a misinterpretation of specimens collected before the perennating buds had developed.

These buds apparently always undergo a period of dormancy before bolting to produce the flowering shoot, but the duration of the dormant stage is enormously variable, even within species. Moreover, both vernalization and photoperiodism appear to be involved in the induction of bolting, the precise requirements being unknown. Generalization about this aspect of the growth cycle of *Physostegia* is therefore difficult. During their dormancy, the perennating buds may be located at or below the soil surface. If at the surface, and thus exposed to sunlight, a rosette of expanded photosynthetic leaves develops; if the bud is below the surface, only whitish scale-leaves are produced. It is common to find buds in both positions on a single plant.

The induction of bolting does not necessarily guarantee that flowering will occur. Experimental evidence indicates that in at least one species of *Physostegia* there are subsequent photoperiodic requirements for flowering (Table 6). Representatives of six species were grown from rhizome buds in Sherer Controlled Environment Chambers with photoperiods of 8, 12, and 16 hours. All plants were in the rosette stage when placed in the chambers, and all except *P. correllii* had received a previous cold treatment (1–4°C) to induce bolting (14 weeks for *P. angustifolia* and *P. virginiana*; 5 weeks for *P. intermedia*, *P. leptophylla*, and *P. digitalis*). Lighting was supplied by both incandescent bulbs and fluorescent tubes and was of similar intensity in all three chambers (ca. 3000 foot-candles). The temperature was gen-



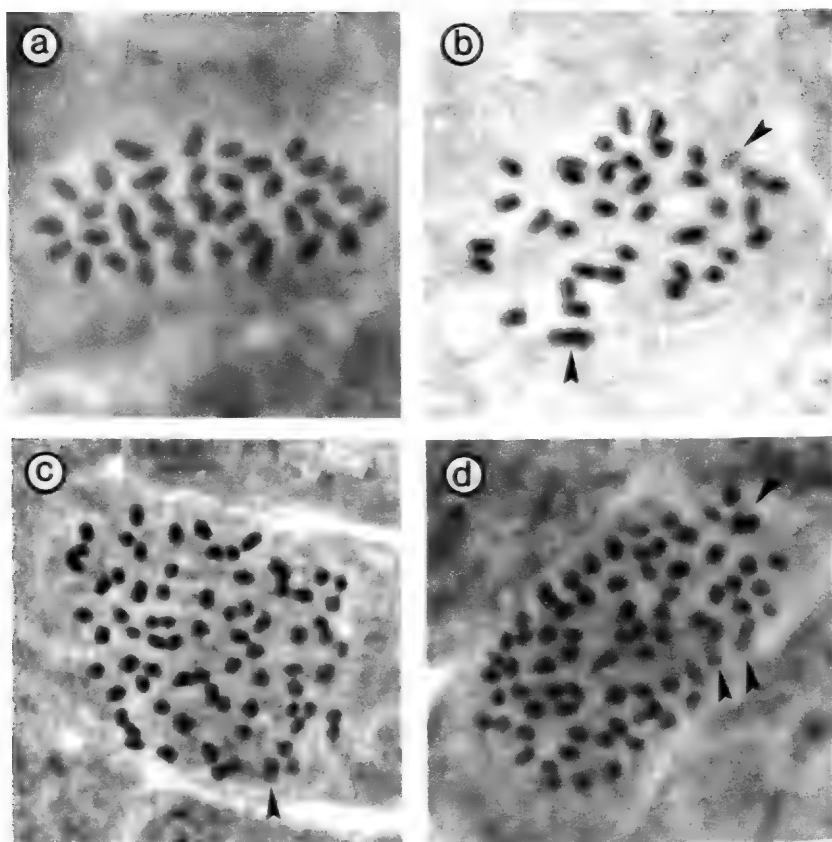


FIG. 8. Chromosomes of root tip cells. Magnifications are approximate. Vouchers at GH. A, *Physostegia godfreyi*,  $2n = 38$ ,  $\times 3250$  (Cantino 1138). B, *P. pulchella*,  $2n = 38$ ,  $\times 2700$  (Mahler 8520): upper arrow—chromosome lying partly outside the plane of focus; lower arrow—two overlapping chromosomes appearing as a single long one. C, *P. leptophylla*,  $2n = 76$ ,  $\times 1800$  (Cantino 1141): arrow—two overlapping chromosomes appearing as one. D, *P. ledinghamii*,  $2n = 76$ ,  $\times 2450$  (Harms 27623): upper arrow—two overlapping chromosomes; lower arrows—two chromosomes lying partly outside the plane of focus.

erally maintained at 21–25°C, but greater fluctuations were occasionally caused by malfunctioning of the equipment.

*Physostegia angustifolia*, *P. intermedia*, and *P. leptophylla* flowered normally in all three chambers and thus appear to be day-neutral. *Physostegia virginiana*, on the other hand, appears to be a long-day

species; when grown in an 8-hour or 12-hour photoperiod, most plants grew vigorously and produced an abnormal number of leaves, but no inflorescence was formed. They eventually grew too tall for the growth chambers and had to be removed, some with as many as 47 nodes; the species rarely produces more than 30 nodes in natural situations. It is not known whether inflorescences would eventually have developed if the plants had remained in the 8-hour and 12-hour chambers, but a longer daylength is clearly necessary if flowering is to occur at the normal time in the life of the shoot.

The photoperiodic requirements for flowering in *Physostegia virginiana* appear to be complex. In most plants of ssp. *praemorsa* and in one plant of ssp. *virginiana*, a variable number of empty floral bracts were produced below or intermixed with those subtending normal flowers when the plants were grown in a 16-hour photoperiod from the time of bolting to anthesis (Table 7). Normal flowering appears to require both an interval of long photoperiod and a subsequent interval of shorter daylength. Few or no empty bracts were produced when plants were transferred to a 12-hour photoperiod after four to eight weeks in a 16-hour photoperiod. Figure 9(a,b) illustrates the dramatic difference in inflorescence morphology that can be produced

TABLE 6. FLOWER PRODUCTION UNDER THREE PHOTOPERIODIC REGIMES.

Taxon	Sample Size	No. of plants producing flowers
<b>8-Hour Photoperiod</b>		
<i>P. angustifolia</i>	9 plants/3 populations	all
<i>P. digitalis</i>	1 plant	all
<i>P. intermedia</i>	2 plants/1 population	all
<i>P. leptophylla</i>	5 plants/3 populations	all
<i>P. virginiana</i> ssp. <i>virginiana</i>	27 plants/8 populations	none
<i>P. virginiana</i> ssp. <i>praemorsa</i>	25 plants/9 populations	2 (8%)
<b>12-Hour Photoperiod</b>		
<i>P. angustifolia</i>	9 plants/3 populations	all
<i>P. correllii</i>	1 plant (3 shoots/1 clone)	all
<i>P. digitalis</i>	1 plant	all
<i>P. intermedia</i>	4 plants/1 population	all
<i>P. leptophylla</i>	10 plants/3 populations	all
<i>P. virginiana</i> ssp. <i>virginiana</i>	30 plants/8 populations	4 (13.3%)
<i>P. virginiana</i> ssp. <i>praemorsa</i>	26 plants/10 populations	6 (23.1%)
<b>16-Hour Photoperiod</b>		
<i>P. angustifolia</i>	10 plants/4 populations	all
<i>P. correllii</i>	1 plant (3 shoots/1 clone)	all
<i>P. intermedia</i>	4 plants/1 population	all
<i>P. leptophylla</i>	7 plants/2 populations	all
<i>P. virginiana</i> ssp. <i>virginiana</i>	28 plants/8 populations	all
<i>P. virginiana</i> ssp. <i>praemorsa</i>	19 plants/9 populations	all

TABLE 7. PRODUCTION OF EMPTY FLORAL BRACTS IN 16-HOUR PHOTOPERIOD.

Taxon	Sample Size	No. of plants with empty bracts
<i>P. angustifolia</i>	10 plants/4 populations	None
<i>P. correllii</i>	3 shoots/1 clone	None
<i>P. intermedia</i>	4 plants/1 population	None
<i>P. leptophylla</i>	7 plants/2 populations	None
<i>P. purpurea</i>	2 plants/1 population	None
<i>P. virginiana</i> ssp. <i>virginiana</i>	28 plants/8 populations	1 (3.6%)
<i>P. virginiana</i> ssp. <i>praemorsa</i>	19 plants/9 populations	17 (89.5%)

in members of the same clone by growing them under different regimes. The shoot in Figure 9a was grown to flower in a 16-hour photoperiod (14 weeks); that in Figure 9b was grown for four weeks at 16 hours, followed by three weeks of a 12-hour photoperiod and six weeks at a daylength of about 15 hours. The taxonomic significance of empty bract production in *P. virginiana* is discussed on p. 92.

The early development of the inflorescence in plants that eventually produced a large number of empty bracts was strikingly different from that of plants that went on to flower normally. The newly formed racemes of the former had a squat, flat-topped appearance (Fig. 9c) which they generally retained for four to six weeks without any apparent growth, before elongating suddenly and rapidly. This contrasts with the usual pattern of inflorescence development in *Physostegia*, in which the raceme remains cylindrical at all times and elongates steadily without interruption (Fig. 9d).

Studies of seed germination in two species of *Physostegia* indicate that at least a low germination rate can be obtained without stratification or other pretreatment. Nutlets of *P. angustifolia* and *P. virginiana*, collected in natural populations six months previously, were planted in moist vermiculite, incubated in a growth chamber at 21–25°C, and watered daily with quarter-strength Hoagland's Solution. The study was continued for two months, but no seed germination occurred after 30 days. At least a few seeds from every population germinated, but the percentage varied widely (Table 8). Although the seeds in this study were six months old when tested, a single attempt

FIG. 9. Variation in inflorescence morphology of *Physostegia virginiana* ssp. *praemorsa* in response to different photoperiods. A, B, offshoots of same rhizome grown under different photoperiods (see text). C, early inflorescence development under 16-hour photoperiod. D, normal inflorescence development.

(a)



(b)



(c)



(d)



TABLE 8. SEED GERMINATION WITHOUT PRETREATMENT.

Taxon and Voucher*	No. of seeds	% germination after 30 days
<i>Physostegia angustifolia</i>		
Cantino 868 (Missouri)	113	4.4
Cantino 872 (Missouri)	80	10.0
Cantino 873 (Missouri)	150	0.7
<i>Physostegia virginiana</i> ssp. <i>praemorsa</i>		
Cantino 847 (Illinois)	55	1.8
Cantino 869 (Missouri)	49	22.4
Cantino 892 (Indiana)	150	60.0
<i>Physostegia virginiana</i> ssp. <i>virginiana</i>		
Cantino 852 (Indiana)	32	12.5

\*Each voucher represents population where seeds were obtained, but not the actual plant that supplied them. Vouchers are deposited in GH.

to germinate newly produced seeds of *P. angustifolia* was successful. The nutlets were collected as soon as mature and planted in vermiculite as just described. Of the 25 nutlets planted, the seeds inside 9 of them germinated within three weeks and those inside 3 others germinated within another month.

The early seedling development of *Physostegia angustifolia*, *P. purpurea*, and *P. virginiana* has been examined in the greenhouse. Germination is epigeal, the photosynthetic, leaflike cotyledons remaining on the seedling for four to eight weeks. The longest internode on the seedling is invariably that between the cotyledons and the first pair of foliage leaves; it is 3–8 mm long. The succeeding internodes are extremely short, the early foliage leaves forming a tight rosette resembling that of the perennating buds. The much branched primary root is the principal absorptive organ during the initial month, but it is soon dwarfed by the profusion of adventitious roots that arise from the lower nodes. The first adventitious roots develop from the cotyledonar node as little as three weeks after germination. Developing rapidly from the succeeding nodes, they generally form the bulk of the root system by the time the seedling is two months old. The primary root is eventually lost; the entire root system of the mature plant is adventitious.

As in the perennating buds, the rosette stage of the seedlings is of variable duration and can be shortened by vernalization. A few unvernallized seedlings of *Physostegia virginiana* grown in the greenhouse bolted as little as two months after germination, but most remained in the rosette stage at least four months, and many still had not bolted eight months after germination. The seeds used in this study were not subjected to any cold treatment previous to germi-

nation. It is unknown whether vernalization of the seeds of *Physostegia* will substitute for vernalization of the seedling, i.e., whether a seed that has overwintered will develop directly into a flowering shoot without an intervening rosette stage.

Because my study of natural populations of *Physostegia* was confined to the flowering season, the timing of germination and seedling development in nature is a matter of conjecture. In the garden, seeds reached maturity two to four weeks after fertilization, and newly produced seeds of *P. angustifolia* germinated without pretreatment in one to four weeks. It therefore seems likely that at least some seeds of *P. angustifolia*, and perhaps of other species that bloom in the spring or early summer, germinate late in the same season they were produced. Direct evidence from natural populations is lacking, but numerous seedlings of *P. angustifolia* and/or *P. virginiana* were observed in the experimental garden in early September, 1976. Because that was the first year *Physostegia* was grown in the garden, the seedlings had to have arisen from seeds produced earlier that summer. All seedlings were in the rosette state. In the species that bloom in the late summer and autumn, the seeds probably mature too late in the season for germination to occur until the following spring.

#### POLLINATION BIOLOGY AND BREEDING SYSTEM

At least 29 species of insects (Table 9) visit the flowers of *Physostegia*, and hummingbirds are occasionally observed as well. Of these, the primary effective pollinator is the bumblebee. Several of the other bees and wasps (i.e., *Apis*, *Anthophora*, *Megachile*, *Polistes*, *Vespula*) plus the soldier beetle (*Chauliognathus*) are large enough to effect pollination on a regular basis and may be locally important in populations of *Physostegia* where bumblebees are infrequent. Halictid bees frequently visit the flowers of *Physostegia*, but they are so much smaller than the mouth of the corolla that they are very ineffective pollinators. They generally enter along the lower lip of the corolla, feed on the nectar at the base of the flower, and then depart by the same route without ever touching the anthers or stigma. However, they do occasionally gather pollen and may contribute in a minor way to pollination.

*Physostegia* suffers a considerable loss of nectar to carpenter bees (*Xylocopa virginica*). They chew holes in the bases of the corollas through which they remove nectar without effecting pollination. Once a hole has been cut in the corolla, smaller insects such as syrphid flies and halictid bees use the opening as a means of withdrawing additional nectar as it is produced. Schneck (1891), who first noted

TABLE 9. INSECTS OBSERVED AT FLOWERS OF *PHYSOSTEGIA*.

HEMIPTERA	Unidentified member of subfamily Eumeninae
Pentatomidae	Colletidae
aff. <i>Cosmopepla</i>	<i>Hylaeus</i> sp.
Cydnidae (unidentified)	Halictidae
COLEOPTERA	<i>Agapostemon virescens</i>
Cantharidae	<i>Augochlora pura</i>
<i>Cantharis</i> sp.	<i>Augochlorella striata</i>
<i>Chauliognathus pennsylvanicus</i>	<i>Ceratina dupla</i>
Scarabaeidae	<i>Dialictus</i> sp.
<i>Popillia japonica</i>	Megachilidae
LEPIDOPTERA	<i>Megachile</i> sp.
Papilionidae (unidentified)	Anthophoridae
Hesperiidae (unidentified)	<i>Anthophora</i> sp.
Sphingidae	<i>Nomada</i> sp.
<i>Hemaris</i> sp.	Xylocopidae
DIPTERA	<i>Xylocopa virginica</i>
Syrphidae (unidentified)	Apidae
HYMENOPTERA	<i>Apis mellifera</i>
Formicidae (unidentified)	<i>Bombus fervidus</i>
Vespidae	<i>Bombus impatiens</i>
<i>Polistes fuscatus</i>	<i>Bombus</i> cf. <i>pennsylvanicus</i>
<i>Vespula</i> spp.	<i>Bombus terricola</i>
	<i>Bombus vagans</i>

this phenomenon in *Physostegia*, commented that honeybees prefer to take nectar through the holes left by carpenter bees and only enter the mouth of the corolla if no opening has been made at its base.

The flowers of *Physostegia* are practically odorless. Corolla color ranges from pure white to deep reddish violet. Although it is relatively invariable within most species, nearly the entire range of color can be found within some populations of *P. virginiana*. The movement of bumblebees foraging in these populations seems to be independent of flower color, and similar behavior was noted in the experimental garden, where many species of *Physostegia* were growing together.

The protandry of *Physostegia virginiana* (Fig. 10) has long been known (Delpino, 1868; Foerste, 1885). Although the genus is basically protandrous, there is a great deal of individual variation in the relative duration of the functionally carpellate and staminate stages, the relative lengths and positions of the stamens, style, and stigma lobes during both stages, and the rate at which the process progresses. The latter is also heavily influenced by weather conditions, all stages proceeding more rapidly at higher temperatures. For a generalized description of the flowering stages in *Physostegia*, including their timing, see Cantino (1980: 97). *Physostegia* is self-compatible. Members of the following taxa were self-pollinated with the aid of a pair of fine forceps and protected from external pollen contamination by enclosure



FIG 10. Stages of protandry in *Physostegia virginiana*. A, functionally staminate stage. B, functionally carpellate stage.

of the inflorescences in cheesecloth bags: *P. angustifolia* (8 plants/135 flowers); *P. correllii* (5 plants/75 flowers); *P. intermedia* (5 plants/63 flowers); *P. leptophylla* (6 plants/82 flowers); *P. purpurea* (6 plants/101 flowers); *P. virginiana* ssp. *virginiana* (11 plants/103 flowers); *P. virginiana* ssp. *praemorsa* (17 plants/208 flowers). After pollination, the stigma of each flower was examined to ascertain that pollen transfer had been effected. All plants produced seed, and in each species and subspecies the number of nutlets reaching maturity was comparable to or only slightly lower than that of intraspecific crosses involving the same taxa.

Observations of pollinator activity in natural populations suggest that the frequency of self-pollination may be quite high. Prolific asexual reproduction in *Physostegia* via rhizome offshoots results in a situation in which neighboring inflorescences are frequently members of a single clone. Foraging bumblebees are methodical and efficient; when



most or all of the flowers of a particular raceme have been visited, a bee will usually proceed to one of its nearest neighbors. Flights between clumps are much less frequent than between racemes in the same clump. Since the clumps are usually clones, the incidence of self-pollination (i.e., geitonogamy) is probably very high.

There is no evidence for agamospermy in *Physostegia*. Studies of *P. virginiana* indicate that, at least in that species, the embryo sac develops normally from one of the meiotic products of the megaspore mother cell (Sharp, 1911).

Anther sterility occurs sporadically in *Physostegia*. In some cases it is evidently induced by environmental conditions, as demonstrated by the growth of plants with fertile anthers from the rhizomes of pollen-sterile individuals. More frequently, anther sterility is a stable characteristic of an individual and is retained when the plant is grown under a variety of conditions. In Ohio, Indiana, and Illinois, the frequency and regularity of such apparently genetically fixed anther sterility is so great in *P. virginiana* ssp. *virginiana* that it qualifies as an example of gynodioecy. This breeding system is more common in the Labiatae than in any other angiosperm family (Darwin, 1897), so it is not surprising to find it in *Physostegia*.

Because casual observation suggested that the pollen-sterile plants in gynodioecious populations of *Physostegia virginiana* tend to have smaller flowers than the hermaphrodites, and that the separation of the stigma lobes to expose the receptive surface occurs earlier in the former, a quantitative study of these floral characters was undertaken. Four Ohio populations of *P. virginiana* were examined in August of 1977, three of them (A, B, & C) along the St. Mary's River in Auglaize and Mercer Counties, and one (D) on the banks of the Sandusky River in Seneca County, 4 miles north of Tiffin. The relative frequency of pollen-sterile shoots varied greatly among the four populations. Only 5% of the shoots in Population B were pollen-sterile, while the percentages in Populations A, C, and D were 49%, 53% and 18%, respectively. The relative frequency of pollen-sterile clones may be somewhat different than that of pollen-sterile shoots. The clones varied greatly in size, and it was not always possible to delimit them on the basis of the subtle differences in their morphology.

I attempted to sample from every clone at each site. Within each, one to four shoots were randomly selected for study; the number sampled was roughly proportional to the apparent size of the clone. The flower length was measured on each shoot, and the degree of separation of the stigma lobes in the most recently opened (i.e., the uppermost) flowers was recorded on a scale of zero to three, zero representing the stage shown in Figure 10a and three representing the stage shown in Figure 10b. Whenever either character varied among

the flowers of a given shoot, the midpoint of the range was recorded. Because the separation of the stigma lobes progressed through the day, I alternated between clones of the two sexual forms whenever possible; thus the observed difference in mean stigma lobe separation between hermaphrodites and pollen-sterile plants cannot be attributed to the timing of the sampling.

The results are shown in Table 10. The statistical significance was tested using a two-tailed t-test, unless the variances differed significantly, in which case the "approximate t-test" (Sokal & Rohlf, 1969) was used. In all four populations, the flowers of the pollen-sterile plants were 2–4 mm shorter than those of the hermaphrodites, and the separation of the stigma lobes occurred sooner after the opening of the flower in the former. These differences are highly significant.

Although the pollen-sterile flowers are smaller than those of the hermaphrodites, there is no obvious difference in the frequency of pollinator visits to the two sexual morphs. As suggested by Arroyo and Raven (1975) to explain a similar situation in *Fuchsia*, this may

TABLE 10. VARIATION IN FLOWER LENGTH AND STIGMA LOBE SEPARATION IN GYNODIOECIOUS POPULATIONS.

	Populations			
	A	B	C	D
FLOWER LENGTH				
Pollen-sterile Plants				
Sample Size	32	12	10	12
Mean (mm)	19.38	19.92	19.30	17.71
Variance	2.84	2.31	2.73	0.52
Hermaphrodites				
Sample Size	37	40	11	22
Mean (mm)	23.39	23.26	21.36	22.16
Variance	2.79	2.32	0.90	4.06
Difference of Means (mm)	4.01	3.34	2.06	4.45
Statistical Significance	p < .001	p < .001	p < .01	p < .001
STIGMA LOBE SEPARATION*				
Pollen-sterile Plants				
Sample Size	32	12	10	12
Mean	1.98	2.21	2.20	1.71
Variance	0.67	0.66	0.34	0.48
Hermaphrodites				
Sample Size	37	40	11	22
Mean	0.69	0.71	0.05	0.55
Variance	0.55	0.35	0.02	0.19
Difference of Means	1.29	1.50	2.15	1.16
Statistical Significance	p < .001	p < .001	p < .001	p < .001

\*On a scale of 0 to 3 (see text).

be due to the "flag effect"; i.e., pollinators are attracted by the showiness of the entire plant rather than by individual flowers.

At the time of the study, no mature nutlets had been produced, but fruit development had begun on many plants. The inception of fruit development was tallied by counting the number of ovary-lobes that had begun to enlarge (each flower produces four one-seeded nutlets corresponding to the four lobes of the ovary). The nutlet inception of the two sexual forms was compared in a percentage form based on the maximum possible, the latter figure being equal to four times the number of flowers that were developmentally advanced enough when sampled so that ovary enlargement would have been visible. As recommended by Sokal and Rohlf (1969), the percentages were converted to angles by means of the arcsine transformation. A two-tailed t-test was carried out on the angular values to determine whether the two sexual morphs differ in their mean nutlet inception.

There was no significant difference in the nutlet inception of the sexual morphs in the St. Mary's River populations (A, B & C). However, in the Sandusky River population (D), the nutlet inception of the hermaphrodites was significantly greater than that of the pollen-sterile plants (Table 11). These results appear to be in conflict with the expectation that the pollen-sterile plants should have a higher average seed yield than the hermaphrodites if the gynodioecious breeding system is to be maintained. However, inbreeding depression, which is thought to be a primary factor in the development and maintenance of gynodioecy (Valdeyron, et al., 1973; Lloyd, 1975; Arroyo and Raven, 1975), can be expected to reduce the viability of autogamously produced offspring at all stages of their development, including the period of seed maturation. Nutlet inception was scored relatively early in the development of the seed; it would not be surprising if, due to inbreeding depression, the eventual seed yield of the hermaphrodites were lower than that of the pollen-sterile plants, even though the amount of nutlet initiation is not.

TABLE 11. NUTLET INCEPTION IN GYNODIOECIOUS POPULATIONS.

	Populations			
	A	B	C	D
Pollen-sterile Plants				
Sample Size	28	10	7	11
Mean Nutlet Inception	49.5%	27.7%	38.0%	35.9%
Hermaphrodites				
Sample Size	32	28	7	20
Mean Nutlet Inception	50.9%	24.4%	49.2%	67.2%
Statistical Significance	n.s.	n.s.	n.s.	p < .01

The anther sterility in gynodioecious populations of *Physostegia virginiana* is variable in its expression. Flowers were collected from 17 pollen-sterile clones in the four Ohio populations, and the anthers were dissected in 1% acetocarmine. The anthers from a few plants were severely shriveled and completely empty, but variously abnormal pollen grains could be found in the anthers of most plants. In some of these the grains were very small and irregular in shape, while in others they were only a little smaller than normal but did not stain normally. This variation in the nature of the sterile anthers and their contents suggests that the normal course of pollen development is interrupted at different points in different plants, in turn suggesting that the genetic control of the phenomenon may not be simple. It is complicated still further by the existence of partial anther sterility. Although an infrequent occurrence, I have noted a few clones in gynodioecious populations of *P. virginiana* in which a variable amount of normal pollen is produced. The anthers of eight flowers from one such clone were dissected in 1% acetocarmine, and the percentage of stainable pollen was found to vary from 30% to 75%.

#### DISPERSAL

The nutlets of *Physostegia* are dry, 2–4 mm long, and lack projections that might facilitate their dispersal by wind or animals. They remain inside the calyx until knocked out by raindrops or by the swaying of the racemes in the wind. Because of their size and weight, they are unlikely to be carried far by normal winds. Endozoochory is unlikely to play a role in dispersal; the thin pericarp would be easily broken and the seed almost certainly destroyed by a mammal's teeth or a bird's gizzard.

Those species that grow along rivers are probably spread by floodwaters. The abundance of *Physostegia virginiana* along certain rivers, coupled with its complete absence from other apparently similar rivers nearby, strongly suggests that these waterways are serving as dispersal corridors. Most of the species of riverside habitats produce horizontal rhizomes, often in great quantity, which are easily broken from the plant and will float.

Man has played an important part in the spread of *Physostegia virginiana*, cultivated forms of which often escape and persist in disturbed sites. The entire northeastern segment of the modern range of this species owes its existence to naturalization following escape from cultivation (see p. 94). In addition, the native species that frequent roadsides and railroad right-of-ways (e.g., *P. purpurea* and *P. angustifolia*) are probably dispersed by mowers and other maintenance equipment.

## ISOLATING MECHANISMS

Other than the very existence of *Physostegia ledinghamii*, which appears to have had a hybrid origin (Cantino, 1981a), there is little evidence of natural interspecific hybridization in the genus. This being the case, it is pertinent to ask how hybridization is prevented. The following discussion is organized according to Levin's (1978) scheme for the classification of isolating mechanisms.

In Table 12, I have summarized what appear to be the principal factors that restrict interspecific gene flow in *Physostegia*. Above the diagonal, I have recorded the degree of distributional overlap for each pair of species. For those pairs of species that are sympatric or parapatric, and thus could potentially hybridize, I have summarized below the diagonal my present knowledge of the mechanisms by which gene flow is restricted. Of the 66 species pairs, 40 of them are allopatric. Of the 26 pairs that are not strictly allopatric, 12 of them have parapatric ranges; i.e., their distributions border one another (H. M. Smith, 1965). Although not parapatric by the strictest definition, I have included in this category those species whose ranges overlap very narrowly, as well as those that fall just short of meeting.

Of the isolating mechanisms recognized by Levin (1978), it is ecological and temporal isolation that principally restrict gene flow in *Physostegia*. The importance of habitat difference as an isolating mechanism may be far greater than is indicated in Table 12, where it is recorded in only the most dramatic cases. Less obvious differences in ecological requirements may contribute greatly to the re-

TABLE 12. GEOGRAPHIC AND REPRODUCTIVE ISOLATION IN PHYSOSTEGIA.

	Ang	Cor	Dig	God	Int	Led	Lep	Lon	Par	Pul	Pur	Vir
Ang	XXX	P	P	A	S	A	A	A	A	P	A	S
Cor	t	XXX	P	A	S	A	A	P	A	S	A	S
Dig	T	H	XXX	A	S	A	A	P	A	P	A	P
God	—	—	—	XXX	A	A	S	A	A	A	P	A
Int	C	T	H,T	—	XXX	A	A	S	A	S	A	S
Led	—	—	—	—	—	XXX	A	A	S	A	A	P
Lep	—	—	—	H	—	—	XXX	A	A	A	S	A
Lon	—	T	H,t	—	?	—	—	XXX	A	A	A	S
Par	—	—	—	—	—	?	—	—	XXX	A	A	P
Pul	t	T	T,H?	—	?	—	—	—	—	XXX	A	S
Pur	—	—	—	?	—	—	H,C	—	—	—	XXX	P
Vir	T	T,H?	T	—	H,C,t	?	—	T	?	T	t	XXX

Ang—*P. angustifolia*; Cor—*P. correllii*; Dig—*P. digitalis*; God—*P. godfreyi*; Int—*P. intermedia*; Led—*P. ledinghamii*; Lep—*P. leptophylla*; Lon—*P. longisepala*; Par—*P. parviflora*; Pul—*P. pulchella*; Pur—*P. purpurea*; Vir—*P. virginiana* (native only).

A—Allopatric; P—Parapatric; S—Sympatric; C—Cross-incompatibility demonstrated in experimental garden; H—Habitat requirements mutually exclusive in zone of sympatry; T—Blooming periods do not overlap in zone of sympatry; t—Blooming periods barely overlap in zone of sympatry (see text).

striction of gene flow between the members of many other pairs. It is significant in this regard that in twenty weeks of field study conducted over a wide geographic area, I have only once observed two species of *Physostegia* growing together (*P. digitalis* and *P. angustifolia* in Bowie County, Texas). I am aware of one other instance of two species occurring at the same site—*P. pulchella* and *P. intermedia* in Denton County, Texas (Shinners 18830, 18831, SMU).

If the co-occurrence of two or more species of *Physostegia* is as infrequent as my observations suggest, then the role of other isolating mechanisms may be minimal. However, temporal isolation may be of importance in the rare instances of two species occurring together. Of the 26 sympatric and parapatric species pairs, the members of 16 of them have nonoverlapping or barely overlapping blooming periods in the area of sympatry or near-sympatry. (For this purpose I consider blooming periods to be "barely overlapping" if the period of overlap constitutes no more than a quarter of the blooming period of either species.) In a number of pairs, there is some overlap if the entire range of each species is considered, but none in the zone of sympatry. Temporal isolation appears to be the principal mechanism preventing hybridization between *P. digitalis* and *P. angustifolia* in Bowie County, Texas (Cantino, 1980: 125–127).

Of the postmating isolating mechanisms recognized by Levin, only one (cross-incompatibility) is included in Table 12. Several postmating mechanisms are clearly not operative in *Physostegia* (i.e., isolation by differing reproductive mode; hybrid floral isolation), while others have not been investigated adequately to draw any conclusions (i.e., hybrid inviability or weakness; hybrid sterility; hybrid breakdown).

A study of cross-compatibility among six species of *Physostegia* has been conducted in the experimental garden of the Gray Herbarium. Plants were grown from rhizomes collected during previous summers from 64 natural populations. At the onset of the crossing program, cheesecloth enclosures were constructed around each inflorescence (see Cantino, 1980, for design). The following morning, and each succeeding morning, the newly opened flowers were emasculated. The second and succeeding mornings, pollen was transferred from the paternal parent (its inflorescence also enclosed in cheesecloth) to the stigmas of those flowers emasculated the previous day. The flat side of an open pair of forceps was used to transfer the pollen. After each cross, the forceps were wiped with a cloth and dipped in 95% ethanol to avoid contamination. With its large, protandrous flowers, *Physostegia* is well suited for studies of this sort; the stigma lobes are usually barely if at all separated at the time of anther dehiscence. Accidental self-pollination in the process of emasculation is therefore unlikely. As an additional precaution, the stigma of each flower was

examined with a 14× hand lens before pollination to ascertain that there were no grains already present. The grains are easily visible at that magnification.

For each intertaxon cross, 2–13 trials were run, each utilizing a different set of parent plants (Table 13). An effort was made to use plants from many different populations in the trials of a given cross, but this was not always possible; all of the individuals of *Physostegia correllii* used were offshoots of a single clone, and those of *P. intermedia* originated from but two populations. The other five taxa in the crossing program were each represented by plants from 9–16 populations. The number of flowers pollinated per trial was usually 10 or more.

TABLE 13. CONTROLLED POLLINATION EXPERIMENTS: SUMMARY OF RESULTS.

Cross*	Number of Trials	Total Number of Flowers	% Nutlet Inception	% Seed Yield	% Loss in Maturation
Ang × Ang	4	54	87.1%	81.9%	5.9%
Ang × Int	8	76	63.5%	7.9%	87.6%
Ang × Lep	5	88	62.5%	1.1%	98.2%
Ang × Pra	4	87	73.6%	55.7%	24.3%
Ang × Pur	5	72	57.3%	39.2%	31.6%
Cor Selfed	5	75	82.0%	61.7%	24.8%
Cor × Ang	7	124	78.4%	53.2%	32.1%
Cor × Pra	5	110	74.1%	34.8%	53.1%
Cor × Pur	3	49	46.4%	34.7%	25.2%
Int × Int	4	47	77.1%	68.1%	11.7%
Lep × Lep	5	93	73.9%	54.8%	25.8%
Lep × Ang	6	68	51.1%	0.0%	100.0%
Lep × Int	7	72	63.9%	0.3%	99.7%
Lep × Pur	6	77	68.2%	0.0%	100.0%
Lep × Vir	7	119	64.1%	18.6%	69.6%
Pra × Pra	5	96	90.9%	84.9%	6.6%
Pra × Ang	4	60	90.2%	75.0%	7.4%
Pra × Cor	4	56	65.2%	40.2%	38.3%
Pra × Int	5	78	56.1%	0.0%	100.0%
Pra × Lep	4	46	78.8%	23.4%	70.3%
Pra × Pur	3	49	75.5%	55.6%	26.4%
Pra × Vir	13	254	85.2%	54.9%	35.6%
Pur × Pur	5	60	60.4%	41.3%	31.6%
Pur × Ang	5	76	74.3%	65.5%	11.8%
Pur × Int	6	68	51.1%	29.4%	42.5%
Pur × Lep	5	57	81.6%	0.0%	100.0%
Pur × Vir	4	54	71.8%	52.3%	27.1%
Vir × Vir	11	166	79.4%	63.1%	28.4%
Vir × Ang	3	46	73.4%	72.3%	1.5%
Vir × Lep	2	38	75.0%	0.0%	100.0%
Vir × Pra	6	112	75.4%	65.0%	13.8%
Vir × Pur	6	46	66.8%	34.8%	51.2%

\*First listed taxon was pollen parent.

Abbreviations: Ang—*P. angustifolia*; Cor—*P. correllii*; Int—*P. intermedia*; Lep—*P. leptophylla*; Pra—*P. virginiana* ssp. *praemorsa*; Pur—*P. purpurea*; Vir—*P. virginiana* ssp. *virginiana*.

A few days after the termination of each trial, nutlet inception was scored by counting the number of ovary lobes that had begun to enlarge. After a maturation period of from two to four weeks, depending on species and weather conditions, the mature nutlets were collected. No attempt was made to record the number of nutlets initiated or matured in individual flowers; all flowers from a given trial were lumped.

Ten randomly selected nutlets from each trial were cut open and the seeds examined. If the seed was found to contain a large, white embryo, it was considered to be normal. In abnormal seeds, the embryo is dark and/or shriveled or missing entirely. Nutlets that were conspicuously smaller than their siblings usually lacked normal embryos, but many nutlets that were full-sized and appeared normal in every way also lacked good embryos, hence the need for dissection. If the ten nutlets examined were found to have apparently normal embryos, it was assumed that all other full-sized nutlets from that trial did so as well. (Noticeably small nutlets were always dissected.) However, if some of the ten randomly selected nutlets contained aborted embryos, then all the nutlets from the trial were cut open and the embryos examined. Only nutlets containing healthy-looking embryos were counted as "seed yield."

The raw data were used to calculate a set of percentages for nutlet inception and seed yield (Table 13). Since there are always four ovules per flower in *Physostegia*, the percentages were based on a maximum seed yield 4 times as great as the number of flowers used. Sokal and Rohlf (1969) recommend that when dealing with percentages, some of which are less than 30% or greater than 70%, they be converted to angles by means of the arcsine transformation before proceeding with the statistical analysis. This was done, and a one-tailed t-test was then used to test the hypothesis that the mean of the angular values calculated for the trials of a given cross is less than the mean of the angular values of the appropriate control. The control consisted of a set of intraspecific crosses between plants from different populations of the maternal taxon in the interspecific cross.

The results of the crossing program (Table 14, Fig. 11) indicate that interspecific fertility varies widely in the genus, although two species, *Physostegia leptophylla* and *P. intermedia*, stand out by showing a great reduction in seed yield in most of the crosses in which they were involved. Figure 11 leaves one with the impression that *P. purpurea* is highly fertile when used as the maternal parent in interspecific crosses. However, the absolute seed yield was usually rather low (Table 13). The seed yield in the set of control crosses (*P. purpurea* × *P. purpurea*) was so variable that only a complete failure to produce seed in the interspecific cross (as in *P. leptophylla* × *P. purpurea*)



constituted a statistically significant drop in fertility over the control.

A reduction or absence of seed yield in interspecific crosses may be the result of incompatibilities operating before or after fertilization. In this study, I have assumed nutlet inception to be an indication that fertilization has occurred, thus ignoring the unlikely possibility of parthenocarpy. With this assumption, it is possible to calculate the proportion of the fertilized ovules that abort before reaching maturity ( $[\text{number initiated} - \text{number matured}] / \text{number initiated}$ ). This parameter, converted to percentage form, is tabulated in the right-hand column of Table 13. The statistical significance of the difference in this parameter between the hybridizations and the controls (right-hand column of Table 14) provides a measure of the importance of post-zygotic incompatibility as a cause of low seed production. In 10 of the 17 crosses in which the seed yield was significantly lower than that of the control, the reduction in seed yield was due primarily to seed abortion after fertilization. In 4 others, seed abortion and a reduction in the frequency of fertilization were about equally responsible for the lowered seed yield. In only three crosses (Ang  $\times$  Pra, Pra  $\times$  Cor,

TABLE 14. CONTROLLED POLLINATION EXPERIMENTS: TESTS OF SIGNIFICANCE.

Cross*	Control	% Nutlet Inception Cross < Control	% Seed Yield Cross < Control	% Loss in Maturation Cross > Control
Ang $\times$ Int	Int $\times$ Int	Not signif.	$p < .0005$	$p < .0005$
Ang $\times$ Lep	Lep $\times$ Lep	Not signif.	$p < .0005$	$p < .0005$
Ang $\times$ Pra	Pra $\times$ Pra	$p \approx .04$	$p \approx .03$	Not signif.
Ang $\times$ Pur	Pur $\times$ Pur	Not signif.	Not signif.	Not signif.
Cor $\times$ Ang	Ang $\times$ Ang	Not signif.	$p \approx .03$	$p \approx .05$
Cor $\times$ Pra	Pra $\times$ Pra	$p \approx .03$	$p < .005$	$p \approx .01$
Cor $\times$ Pur	Pur $\times$ Pur	Not signif.	Not signif.	Not signif.
Lep $\times$ Ang	Ang $\times$ Ang	$p < .005$	$p < .0005$	$p < .0005$
Lep $\times$ Int	Int $\times$ Int	Not signif.	$p < .0005$	$p < .0005$
Lep $\times$ Pur	Pur $\times$ Pur	Not signif.	$p \approx .05$	$p \approx .01$
Lep $\times$ Vir	Vir $\times$ Vir	$p \approx .04$	$p < .005$	$p \approx .01$
Pra $\times$ Ang	Ang $\times$ Ang	Not signif.	Not signif.	Not signif.
Pra $\times$ Cor	Cor $\times$ Selfed	$p \approx .02$	$p \approx .05$	Not signif.
Pra $\times$ Int	Int $\times$ Int	$p \approx .04$	$p < .0005$	$p < .0005$
Pra $\times$ Lep	Lep $\times$ Lep	Not signif.	$p \approx .04$	$p \approx .03$
Pra $\times$ Pur	Pur $\times$ Pur	Not signif.	Not signif.	Not signif.
Pra $\times$ Vir	Vir $\times$ Vir	Not signif.	Not signif.	Not signif.
Pur $\times$ Ang	Ang $\times$ Ang	Not signif.	$p \approx .01$	Not signif.
Pur $\times$ Int	Int $\times$ Int	$p \approx .04$	$p \approx .005$	$p \approx .04$
Pur $\times$ Lep	Lep $\times$ Lep	Not signif.	$p < .0005$	$p < .0005$
Pur $\times$ Vir	Vir $\times$ Vir	Not signif.	Not signif.	Not signif.
Vir $\times$ Ang	Ang $\times$ Ang	Not signif.	Not signif.	Not signif.
Vir $\times$ Lep	Lep $\times$ Lep	Not signif.	$p < .005$	$p < .005$
Vir $\times$ Pra	Pra $\times$ Pra	$p \approx .04$	$p \approx .03$	Not signif.
Vir $\times$ Pur	Pur $\times$ Pur	Not signif.	Not signif.	Not signif.

\*First listed taxon was pollen parent. Abbreviations as in Table 13.

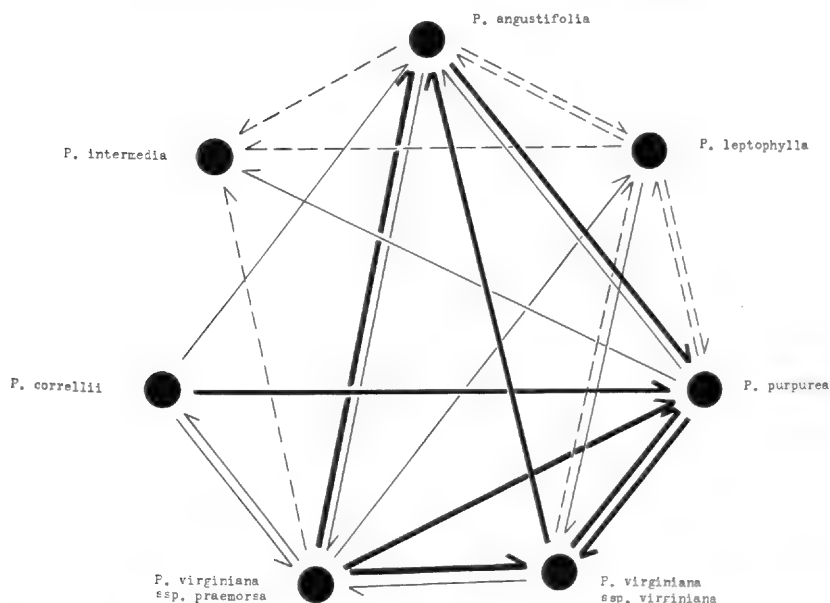


FIG. 11. Interfertility in *Physostegia*. Broken line—seed yield 10% or less of maximum possible. Thin solid line—seed yield greater than 10% but significantly less than control crosses. Heavy solid line—no significant difference between seed yield of experimental hybridizations and control crosses. No line signifies no cross attempted. Arrows indicate direction of pollen transfer.

and Vir  $\times$  Pra) was a reduced frequency of fertilization the principal cause of the reduced seed yield.

Seed-incompatibility (Valentine, 1954) is thus the primary form of cross-incompatibility in *Physostegia*. A very common phenomenon among angiosperms (e.g., Levin, 1978, p. 241), it results from a disharmonious interaction between embryo, endosperm, and maternal tissues and may be expressed in terms of abnormalities in the endosperm, the embryo, or both (Levin, 1978). Seed-incompatibility is particularly frequent in hybridizations between ploidal levels, even when the taxa involved are very closely related (Levin, 1978). It therefore cannot be assumed that the infertility of crosses between the tetraploid *P. leptophylla* and the diploid species, *P. purpurea* and *P. intermedia*, both of which show a degree of morphological overlap with *P. leptophylla*, indicates a lack of close affinities between the former and either of the latter. Morphology is a better indicator of affinities

than is interfertility in taxa that differ in ploidal level.

Although not as frequent a phenomenon in *Physostegia* as seed-incompatibility, prefertilization incompatibility appears to have been operating in eight of the experimental crosses (Table 14). This may only have been an artifact, however, in that nutlet inception was used as the sole indicator that fertilization had occurred; if seed-incompatibility were to cause seed abortion at a sufficiently early stage of development, the nutlet might never enlarge enough to be counted as fertilized. If, on the other hand, prezygotic incompatibility really does play a role in *Physostegia*, it is clearly a weak barrier to hybridization, inasmuch as at least 46% of the ovules were fertilized (i.e., nutlets began to enlarge) in every cross, when the data from all trials of the cross were combined (Table 13). The variation in nutlet inception between trials of a given cross was often great, and figures below 30% were fairly frequent, but in only 3 trials out of 172 conducted (over all crosses) were there no nutlets initiated whatsoever.

Germination tests were conducted with the seeds obtained in some of the experimental crosses. The nutlets were soaked in gibberellic acid (500 ppm) for 24 hours and then placed on filter paper moistened with distilled water. The statistical procedure described earlier in relation to seed yield was also used to test the hypothesis that seeds from interspecific and intersubspecific crosses have a significantly lower germination rate than those obtained in the appropriate control crosses (i.e., the set of crosses involving plants from different populations of the maternal taxon in the experimental cross). Seeds obtained from only two crosses were found to have a significantly lower germination rate than their respective controls (Table 15).

The seeds resulting from most crosses in which *Physostegia purpurea* served as the maternal parent had a low germination rate. This was true of the control cross (*P. purpurea*  $\times$  *P. purpurea*) as well as the interspecific crosses. Although the overall germination percentage of the former (all trials combined) was 40%, two of the four trials resulted in no germination. The variance of the control was therefore so high that the total failure of germination of the seeds resulting from the three trials of *P. virginiana* ssp. *praemorsa*  $\times$  *P. purpurea* was not a statistically significant reduction over the control. Whatever factors were responsible for the generally low and extremely variable seed yield when *P. purpurea* was used as the maternal parent may also have been responsible for the similarly low and variable germination rate.

Representatives of the  $F_1$  generation of the crosses listed in Table 15 were grown to anthesis. The incidence of grossly abnormal plants among the  $F_1$ s was extremely low, nearly all flowered, and the anthers

TABLE 15. GERMINATION EXPERIMENTS WITH HYBRID SEEDS\*.

Cross	Number of Trials	Total Number of Seeds	Percent Germination
Ang × Ang	4	159	86.2%
Ang × Pra	8	118	87.3%
Ang × Pur	7	98	13.3%
Ang × Vir	3	113	85.8%
Cor × Ang	4	100	35.0%**
Cor × Pra	4	78	59.0%**
Cor × Pur	4	39	48.7%
Pra × Pra	4	154	81.8%
Pra × Ang	6	110	62.7%
Pra × Pur	3	89	0.0%
Pra × Vir	8	171	62.0%
Pur × Pur	4	90	40.0%
Pur × Vir	5	120	68.3%
Vir × Vir	9	213	79.8%
Vir × Ang	3	117	83.8%
Vir × Pra	2	26	76.9%

\*Each trial involved seeds obtained from a different set of parents. \*\*Germination rate significantly lower than that of control (see text). Abbreviations as in Table 13.

contained pollen. However, no quantitative study of pollen viability was undertaken.

Because temporal and/or ecological differences form an effective barrier to hybridization between most sympatric species of *Physostegia*, the cross-incompatibility observed in the garden is probably of only occasional importance as an isolating mechanism in nature. It may reduce or prevent gene flow in the event of the breakdown of the usual premating isolating mechanism (for example, if the habitats to which two ecologically isolated species are confined were to occur closely enough together for an insect to carry pollen from one to the other), and it may serve as the principal form of reproductive isolation in a few cases in which premating isolation is lacking. The broadly sympatric species pair, *P. angustifolia* and *P. intermedia*, offers a possible example of the latter. These two species have overlapping blooming periods, and, although I know of no instance of the two actually growing together, I suspect there is some overlap in their habitat preferences as well. When the two species were crossed experimentally, seed yield ranged from 0 to 13% in seven trials and reached 25% in one trial. Seed abortion was the principal cause of the low seed yield.

There are six pairs of species whose members are sympatric or parapatric, not ecologically or temporally isolated, and have not been experimentally tested for cross-incompatibility (indicated by "?" in the lower portion of Table 12). It would seem that the members of these

pairs should be able to hybridize, yet apparently they rarely do. Three of the pairs are parapatric, their members probably coming into contact rarely if at all. The members of one of the remaining three pairs (*P. parviflora* and *P. ledinghamii*) differ in ploidal level. As pointed out earlier, this is often accompanied by a large reduction in cross-compatibility; those hybrid offspring that are produced in spite of this reproductive barrier will be triploid and hence largely sterile.

The remaining two pairs of sympatric species that theoretically should be able to hybridize comprise (a) *Physostegia intermedia* and *P. longisepala* and (b) *P. intermedia* and *P. pulchella*. Because *P. longisepala* is apparently quite rare, contact between it and *P. intermedia* is probably infrequent. However, the two species of pair "b" are broadly sympatric in eastern Texas and have been observed growing together at least once (Shinners 18830, 18831, SMU). *Physostegia intermedia* produced few seeds when crossed experimentally with a number of other species, including *P. angustifolia* (Fig. 11). On morphological grounds, I strongly suspect that *P. angustifolia*, *P. pulchella*, and *P. longisepala* are closely related. If true, it would not be surprising to find a similarly high degree of seed-incompatibility when either of the latter two is crossed with *P. intermedia*. This I suspect to be the principal barrier preventing gene flow between *P. pulchella* and *P. intermedia*, but proof will have to await experimental work. An additional isolating mechanism that may be involved in restricting gene flow between *P. pulchella* and *P. intermedia* is floral isolation. The two differ substantially in flower size (16–30 mm in the former vs. 9–19 mm in the latter), leaving open the possibility that ethological isolation may be operating to some degree.

#### VARIATION PATTERN

The interspecific variation pattern in *Physostegia* is best described as kaleidoscopic, and the species are polythetic groups. A polythetic group (Sneath & Sokal, 1973) is one in which the members share a large number of character states, but not every member possesses every one of the defining traits. A kaleidoscopic variation pattern (Cullen, 1968; Stevens, 1980a) is one in which the taxa are distinguishable on the basis of different combinations of a relatively few character states, none unique to a single taxon. The interspecific variation pattern of *Physostegia* is not entirely kaleidoscopic, in that there is one two-state character in which one state is unique to a single species (the verrucose nutlets of *P. godfreyi*) but lacking in a few members of that species. The extremes of some continuously varying characters are also confined to one species. There is, however, no character state that is both unique to a single species of *Physostegia*

and reliably present in every member of that species. There is also no character of value in distinguishing any pair of species that doesn't vary within some species in the genus.

A kaleidoscopic variation pattern can result from at least three sorts of evolutionary processes: (1) reticulate evolution involving hybridization and usually polyploidy, (2) the divergence of numerous daughter species from a variable and now extinct ancestral species in which all of the character states that distinguish each of the daughter species were present, and (3) parallel and reverse evolution within a collection of closely related species. It is unlikely that reticulate evolution has been a major cause of the kaleidoscopic variation pattern in *Physostegia*. Two of the twelve species are polyploids, but only one of them is clearly of hybrid origin. With this one exception, there is very little evidence of natural interspecific hybridization in the genus. The second process listed above, multiple divergence from a variable ancestor, may have contributed to the development of the kaleidoscopic pattern in *Physostegia*. There is no evidence either for or against this hypothesis. On the other hand, there is ample evidence (discussed below) that there has been parallelism and/or reversal in many of the taxonomically useful characters in *Physostegia* (i.e., those characters whose states are constant enough within at least a few species to be of diagnostic value). The third process listed above is therefore likely to have been a major cause of the kaleidoscopic variation pattern in the genus.

The absence of the clasping leaf base which is found in most species of *Physostegia* is a useful diagnostic characteristic of *P. virginiana*. However, in two widely separated localities (in Ohio and western North Carolina), a few specimens of *P. virginiana* have been collected in which the leaves do clasp the stem. Introgression is unlikely to be involved inasmuch as no other species of *Physostegia* occurs near either population. Nor is it likely that one of these variants evolved directly from the other; they lie 400 miles apart in very different habitats, and each resembles plants from nearby populations that lack clasping leaves much more closely than they resemble each other. This appears to be an example of parallel and/or reverse evolution. It is not possible to conclude which of the two processes has occurred without knowing the intraspecific phylogeny of the forms involved. There is no shortage of other examples. Indeed, there are probably few taxonomically useful characters in *Physostegia* in which parallel and/or reverse evolution have not occurred. A cladistic analysis based on a parsimony method has been carried out (see p. 46), in which only the diploid species of *Physostegia* were included (i.e., those species for which there is no evidence of a hybrid origin). The results indicate that at least half of the character changes involved in the evolution

of the diploid species from the common ancestor were parallel with, or reversals of, other character changes.

As an example of parallel evolution at a different taxonomic level, it is interesting to note that in *Brazoria* and *Macbridea*, the two genera that appear to be most closely related to *Physostegia*, the species are distinguished by many of the same characters as in *Physostegia*. The variation pattern of *Macbridea* is of particular interest because of the remarkable parallels that can be seen in the morphological and ecological differences between *Macbridea alba* and *M. caroliniana*, and between *Physostegia purpurea* and *P. leptophylla*. All four species occur on the Southeastern coastal plain. *Macbridea alba* and *Physostegia purpurea* grow in moist, open pine woods and pine savannas, while *Macbridea caroliniana* and *Physostegia leptophylla* are found in marshes and wooded river swamps (habitat data for *Macbridea* taken from Radford, et al., 1964; Ward, 1979). On the basis of a preliminary study of a small number of specimens of *Macbridea*, it appears that at least five of the six characters that help to distinguish *Physostegia purpurea* from *P. leptophylla* also distinguish *Macbridea alba* from *M. caroliniana*. The sixth character, form of the rhizome, remains uncertain because none of the immediately available specimens of *M. alba* include the underground parts. The pine flatwoods species, *Physostegia purpurea* and *Macbridea alba*, differ from the corresponding swamp species in having very much more reduced upper leaves, fewer petiolate lower stem leaves or none at all, leaves widest above the middle of the blade (vs. at to below the middle), leaves that tend to be obtuse to rounded at the apex (vs. acute), and paler colored corollas. In most of these characters, the interspecific difference is more marked in *Macbridea* than in *Physostegia*, suggesting that whatever environmental factors have provided the selective pressure behind this parallel evolution have been acting on *Macbridea* for a longer period of time. The rarity of *Macbridea*, and the confinement of its two species to limited and widely disjunct areas, are also suggestive of antiquity.

#### INTERSPECIFIC RELATIONSHIPS

There has been much recent interest in cladistic analysis as a means of generating phylogenetic hypotheses. The theoretical groundwork of Hennig (1950, 1966) and Wagner (1961, 1969, 1980) has provided the basis for a variety of techniques, many of them adaptable to the computer.

Several algorithms have been devised by Farris (1970, 1972) for the generation of what he has named "Wagner Trees" and "Wagner Networks," in reference to the initial development of the concept by W.

H. Wagner, Jr. Farris' "Wagner 78" program was used in this study. Wagner Trees are a subset of a more general category known as most-parsimonious trees; they differ from other such trees in permitting character reversal (Farris, 1970). A most-parsimonious tree is a cladogram requiring a minimum number of evolutionary steps (i.e., character changes) to derive all extant taxa from the ancestor of the group. A Wagner Network differs from a Wagner Tree in that it lacks evolutionary direction; related taxa are grouped together, but the hypothetical ancestor of the group is omitted.

A particularly critical and difficult step in any cladistic analysis that is intended to produce a rooted tree (as opposed to a network) is the determination of the evolutionary polarity of the character state transformations. In my original phylogenetic analysis of *Physostegia* (Cantino, 1980), I generated a Wagner Network using Farris' "Wagner 78" program and then rooted the network in the vicinity of the taxon that had the greatest number of presumed ancestral character states. This approach was patterned after that used by Anderson (1972) for *Crusea*. In the case of *Physostegia*, however, the determination of character polarity was based almost entirely on the ingroup criterion (i.e., the comparative frequency of occurrence of the alternative states of a character within the group under study). This "common equals primitive" criterion, although widely used, is based on faulty assumptions and can be very misleading (Stebbins, 1974; Stevens, 1980b; Wiley, 1980).

Unfortunately, the rejection of this criterion leaves no other basis for establishing the evolutionary polarity of most characters in *Physostegia*. Outgroup comparison, the most widely accepted criterion for determining ancestral condition, is of little use here. Of the five genera that are considered to be most closely related to *Physostegia* (see p. 3), three differ so greatly from *Physostegia* in their foliage, inflorescence structure, and calyx morphology that most of the characters pertaining to these structures in *Physostegia* have no true homologue in the related genera. Only in *Brazoria* and *Macbridea* is the foliage similar enough to that of *Physostegia* to permit a meaningful survey of the distribution in the outgroup of the leaf characters that distinguish the species of *Physostegia*, and only in *Brazoria* is the inflorescence similar enough to that of *Physostegia* to allow such a survey of inflorescence characters. *Brazoria* and *Macbridea* therefore constitute the only practical outgroup for the determination of character polarities. All but three of the characters used to construct the Wagner Network (see below) vary within or between *Brazoria* and *Macbridea* or have no homologue in either genus. In two or these three characters, the presumed apomorphic state (i.e., the state that does not occur in the outgroup) occurs in only one species or subspecies



of *Physostegia*. These two characters are therefore of no use in forming phylogenetic groupings. Thus outgroup comparison establishes the evolutionary polarity of but a single useful character, clearly an insufficient basis for constructing a phylogenetic tree. Because of this inadequacy of the data, only a network of relationships will be presented here, there being at this time no way to determine which portion of the network approaches the ancestral condition of the group.

Cladistic analysis assumes strictly divergent (i.e., non-reticulate) evolution. This is a serious drawback when one is dealing with angiosperms, a group in which a minimum of 30–35% of the species are polyploids (Stebbins, 1971) and many if not most of these are of hybrid origin (Grant, 1971). The best way to deal with this (Wagner, 1969, 1980) is to omit species from the data set used to construct the tree or network if they appear likely to be of hybrid origin. They may later be placed in the phylogenetic diagram with connections to both putative parents. This procedure was followed in the phylogenetic analysis of *Physostegia*. The two tetraploid species, *P. ledinghamii* and *P. leptophylla*, were omitted because of the likelihood that they are of hybrid origin. The evidence in support of this premise is far stronger in the case of the former, which almost certainly originated in a hybridization between *P. parviflora* and *P. virginiana* (Cantino, 1981a). The origin of *P. leptophylla* is uncertain. It is possible that it is an autotetraploid whose diploid ancestor is extinct or undiscovered, but autopolyploid species are thought to be rare among vascular plants (Grant, 1971); it is more likely that the ancestor of *P. leptophylla* was a hybrid. Morphology and distribution point to *P. virginiana* and *P. purpurea* as the most probable parents of such a hybrid (Cantino, 1980: 253–256).

Of the 32 morphological characters that are of taxonomic value in *Physostegia*, 16 of them are quantitative characters with more than two alternative states. They present a problem in *Physostegia* because of their frequently great intraspecific variability and the resulting interspecific overlap of the ranges of their character states. The problem is compounded because the standard statistical parameters, mean and standard deviation, cannot be used because the data were not collected in an unbiased manner (Cantino, 1980, p. 204). The continuously varying characters that could not reasonably be coded in a two-state form were therefore omitted from the analysis. The resultant loss of information is not as great as it might seem; most of the quantitative characters are of use in distinguishing but a few pairs of species or subspecies, the overlap between all other pairs of taxa being too great for the character to be of use. Characters of this kind, although sometimes useful in a key, are not likely to be significant indicators of phylogenetic relationship.

Of the 16 remaining characters which could be coded in a two-state form, 15 of them (Table 16) were used as the data base for the generation of an undirected network. The 16th character was omitted because it was not sufficiently independent of two other characters describing the same attribute (leaf shape). Even the coding of the two-state characters was problematical, because for every character there is at least one species or subspecies in which both states can be found. It is possible to circumvent this problem if one regards characters as being represented in taxa not by single states, of which a given taxon is capable of producing only one of the two alternatives, but rather by phenotypic tendencies. For any given character, some species will have a tendency closely approaching 100% for the possession of only one possible state, but others will have various tendencies to possess either character state. The tendency for a particular state can be roughly gauged by determining the proportion of specimens in which that state is present.

The use of character state frequency as an indicator of tendency within a taxon effectively converts a two-state character to a continuous character whose extremes are zero and unity. If, for example, 80% of the specimens of a given species possess state A of a particular character, while the other 20% possess state B, and if state A is arbitrarily assigned the value 1.0 and state B is given the contrasting value 0.0, then the species is scored with the value 0.8 for that character. The percentages were rounded to the nearest 10%. Thus the characters, as scored, are neither two-state nor continuously varying, but have 11 states ranging from 0.0 to 1.0 by intervals of 0.1.

TABLE 16. CHARACTERS USED IN CLADISTIC ANALYSIS.

Character	<ol style="list-style-type: none"> <li>1. One or more leaves widest below middle of blade: 0, no; 1, yes.</li> <li>2. At least one leaf widest near base of blade: 0, no; 1, yes.</li> <li>3. Majority of larger leaves bluntly toothed to entire, 0; sharply serrate, 1.</li> <li>4. One or more leaves clasp stem: 0, yes; 1, no.</li> <li>5. One or more petiolate leaves present at anthesis: 0, no; 1, yes.</li> <li>6. Empty bracts produced below flowers: 0, no; 1, yes.</li> <li>7. Base of stem conspicuously swollen: 0, no; 1, yes.</li> <li>8. Flowers crowded, adjacent calyces overlapping half or more of their lengths: 0, yes; 1, no.</li> <li>9. Horizontal rhizomes produced, 0; all rhizomes vertical, 1.</li> <li>10. Stalked glands present on calyx: 0, yes; 1, no.</li> <li>11. Stalked glands present on corolla: 0, no; 1, yes.</li> <li>12. Glandular dots on calyx inconspicuous, few, or absent, 0; abundant and conspicuous, 1.</li> <li>13. Calyx lobes all acute to attenuate, 0; some cuspidate, 1.</li> <li>14. One or more pairs of weak primary veins (besides midrib) at base of blade: 0, no; 1, yes.</li> <li>15. Nutlet surface smooth, 0; verrucose, 1.</li> </ol>
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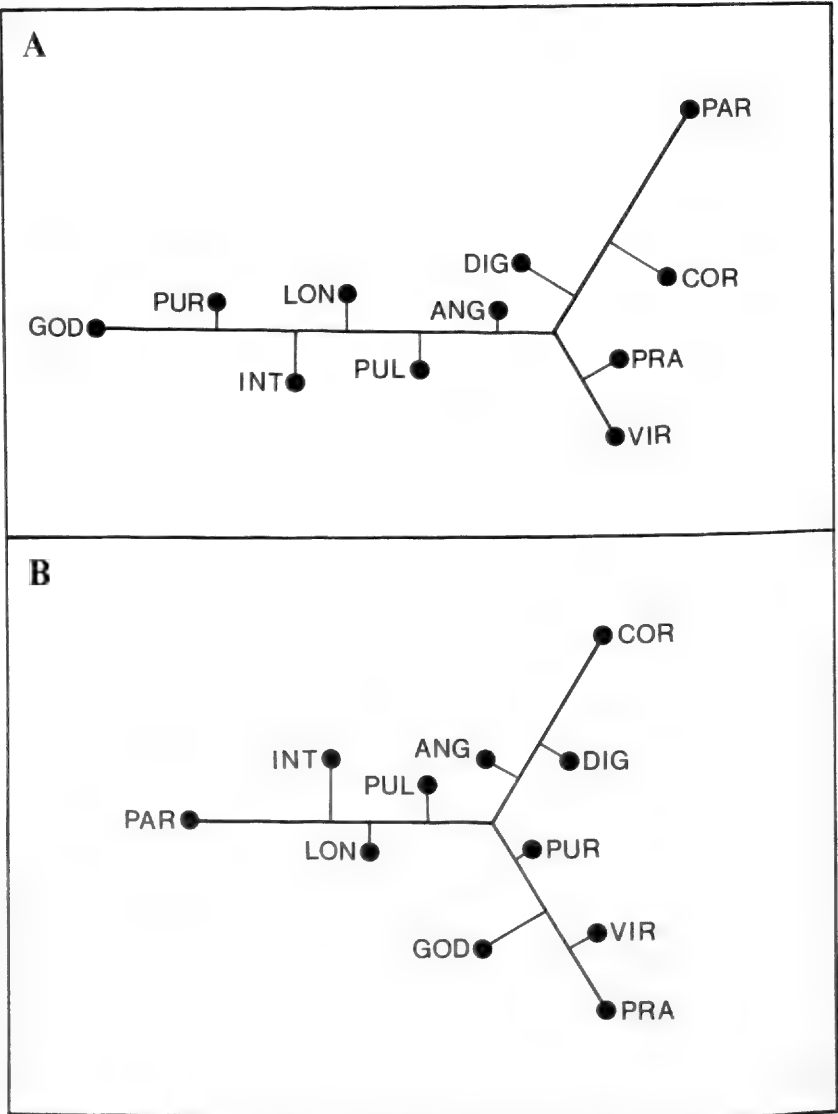


FIG. 12. Undirected networks for *Physostegia*. A, network based on entire 15-character data set. B, network based on data set lacking character no. 3. Taxon abbreviations as in Table 17.

The Wagner Network shown in Figure 12A was based on the data set in Table 17. The lengths of the branches are proportional to patristic distance, as defined by Farris (1967), i.e., the sum over all characters of the change from point to point on the phyletic line. To what extent are the relationships portrayed an accurate representation of the true situation? One criterion that can be used to evaluate the reliability of a network is its stability when characters are removed from the data set used to generate it. If the most parsimonious network produced when a single character is omitted is drastically different from that produced using all characters, it is probable that the inclusion of a new character, as additional data are collected, will also result in a different network.

As a simple test of the stability of the most parsimonious network, 15 additional networks were generated on the basis of data sets from which a single character had been omitted, each of the 15 characters being omitted once. Some of these networks were little different from that based on all characters, but others differed to various degrees. The network based on a data set lacking character 3 was among the most divergent (Fig. 12B). The degree to which the most parsimonious network can be altered by the omission of but a single character casts serious doubt on its reliability as an indicator of actual relationships. However, there are a number of elements in it that remain unchanged in most or all of the alternative networks generated through

TABLE 17. CHARACTER STATE DISTRIBUTION IN *PHYSOSTEGIA*\*

Character	Taxa**										
	ANG	COR	DIG	GOD	INT	LON	PAR	PRA	PUL	PUR	VIR
1	0.5	0.0	0.0	0.0	1.0	0.8	1.0	0.0	0.6	0.0	0.1
2	0.2	0.0	0.0	0.0	0.8	0.6	1.0	0.0	0.5	0.0	0.0
3	1.0	1.0	0.0	0.0	0.0	0.4	0.7	1.0	1.0	0.0	0.9
4	0.2	0.0	0.0	1.0	0.0	0.0	0.0	1.0	0.0	0.2	1.0
5	0.2	0.1	0.0	0.8	0.3	0.6	0.0	0.0	0.8	0.6	0.1
6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0
7	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0
8	0.0	0.1	0.0	1.0	1.0	0.4	0.0	0.1	0.6	0.8	0.3
9	1.0	0.0	1.0	0.5	0.0	0.0	0.0	1.0	1.0	0.4	0.0
10	1.0	0.3	0.9	0.0	1.0	1.0	0.0	0.5	1.0	1.0	0.5
11	0.0	0.2	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0
12	0.2	0.8	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.3	0.0
13	0.5	0.6	1.0	0.0	0.0	0.8	0.0	0.2	0.2	0.0	0.2
14	0.2	1.0	0.7	0.0	0.0	0.3	0.9	0.0	0.8	0.0	0.0
15	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0

\*Table 16 shows character definitions.

\*\*Abbreviations are: ANG, *P. angustifolia*; COR, *P. correllii*; DIG, *P. digitalis*; GOD, *P. godfreyi*; INT, *P. intermedia*; LON, *P. longisepala*; PAR, *P. parviflora*; PRA, *P. virginiana* ssp. *praemorsa*; PUL, *P. pulchella*; PUR, *P. purpurea*; VIR, *P. virginiana* ssp. *virginiana*.

the removal of characters. The two subspecies of *Physostegia virginiana*, not surprisingly, are grouped together in all 15 networks, and in 14 they terminate a line. In every network, *P. purpurea* and *P. godfreyi* are placed as nearest neighbors, and in 13 of them they terminate a line. In 11 networks, *P. purpurea*, *P. godfreyi*, *P. intermedia*, and *P. longisepala* are placed together in the cladistic configuration shown in Figure 12A, and in 9 of them, the cladistic relationship of *P. pulchella* to these four species is also as shown in Figure 12A. In 9 of the 15 networks, *P. parviflora* and *P. correllii* are nearest neighbors and terminate a line. There is less agreement as to the placement of *P. digitalis* and *P. angustifolia*. *Physostegia digitalis* is most often associated with *P. correllii*, but not necessarily in the configuration shown in Figure 12A. *Physostegia angustifolia* is always placed in a relatively central position, but its nearest neighbors vary, *P. pulchella* and *P. digitalis* being the most frequent ones.

In summary, this analysis suggests that the diploid species and subspecies of *Physostegia* fall into three groups: one consists of the two subspecies of *P. virginiana*; the second includes *P. parviflora*, *P. correllii*, and probably *P. digitalis*; and the third includes *P. purpurea*, *P. godfreyi*, *P. intermedia*, *P. longisepala*, and *P. pulchella*. The affinities of *P. angustifolia* within this scheme are uncertain.

A final point that can be made about the evolution of *Physostegia*, on the basis of the most parsimonious network, is that parallelism and character reversal have been extremely common in the genus. There is no guarantee, of course, that evolution has followed the most parsimonious pathway that would explain the distribution of character states over taxa, but even the most parsimonious network that could be devised by the Farris algorithm on the basis of the full 15-character data set required 52% of the character changes to be parallel with, or reversals of, other changes. This provides a measure of the *minimum* amount of homoplasy that has occurred during the phylogeny of *Physostegia*; the actual amount may be far greater.

#### TAXONOMIC TREATMENT

The specimen citations in this treatment are of two kinds. For the relatively rare species, *Physostegia correllii* and *P. longisepala*, every collection studied is listed. For the other species, only representative specimens are cited. For a more complete listing, see Cantino (1980). The first set of my own *Physostegia* collections has been deposited in the Gray Herbarium. Unless otherwise stated, all cited type specimens have been personally examined. Herbarium abbreviations follow the system used in *Index Herbariorum* (Holmgren & Keuken, 1974).

## NOMENCLATURAL HISTORY

A survey of North American floristic works published during the past 70 years testifies to the confusion and disagreement that has surrounded the application of the name *Dracocephalum* to the genus now correctly known as *Physostegia*. The situation has received considerable discussion (S. J. Smith, 1945; McClintock, 1949; Shinnars, 1949; Sealy, 1954; Hitchcock, et al., 1959; Mohlenbrock, 1963), the review by Sealy being the most thorough. With the conservation of a Eurasian species, *D. moldavica* L., as the type of *Dracocephalum* (1961 *International Code of Botanical Nomenclature*), permitting the application of the more recent name, *Physostegia*, to the North American genus, the controversy should finally have been resolved. However, the incorrect use of the name *Dracocephalum* in a number of relatively recent floras (e.g., Radford, Ahles & Bell, 1964; Welsh & Moore, 1973) suggests that the situation is still widely misunderstood.

The earliest published description of a representative of *Physostegia* is probably that of Morison (1669), who referred to it as "Galeata & verticillata, persicae foliis, digitalis aemula." Morison did not provide an illustration, but Boccone's (1674) "Pseudo-Digitalis persicae foliis," under which Morison's earlier name is listed in synonymy, is accompanied by an unmistakable picture of *Physostegia virginiana*.

The name *Dracocephalon* was first applied to the genus by Breynia (1680), in fanciful allusion to the shape of the flowers, and again by Tournefort (1700); it was modified to *Dracocephalum* by Linnaeus (1737) in the first edition of *Genera Plantarum*. Within his circumscription of *Dracocephalum*, Linnaeus included not only the American genus to which Breynia and Tournefort had applied the name *Dracocephalon*, but also the Eurasian genus referred to by Tournefort as *Moldavica*. After outlining the differences in calyx morphology by which Tournefort's two genera could be distinguished, Linnaeus dismissed these characters as too variable within the genera to be of diagnostic value; he finished by stating that the uniting feature of his *Dracocephalum* was the shape of the corolla. Of the 11 species included under *Dracocephalum* in *Species Plantarum* (1753), only the first one listed, *D. virginianum*, was a member of the genus now known as *Physostegia*.

Linnaeus' broad circumscription of the genus did not long stand unchallenged. Adanson (1763, Vol. 2: 187-194) distributed the species included under *Dracocephalum* by Linnaeus into three genera, *Dracocephalon* Tourn., *Moldavica* Tourn., and *Rhuyschiana* Amm., each assigned to a different section of the family. He did not indicate types for his genera, but, as pointed out by Sealy (1954), the type of *Dracocephalum* L. emend. Adanson must be the species that Linnaeus

named *D. virginianum*, because this species (under a different name) was the only one placed by Tournefort in his genus *Dracocephalon*, upon which Adanson based his *Dracocephalon*. Moench (1794) also subdivided *Dracocephalum* L., distributing the species Linnaeus had included within it among four genera, *Dracocephalum*, *Moldavica*, *Cedronella*, and *Zornia*. Under *Dracocephalum*, Moench placed only a single species, *D. lancifolium* Moench, a superfluous name for *D. virginianum* L. because the latter was listed in synonymy.

These treatments were not widely accepted. Jussieu, for instance, followed Linnaeus' broader circumscription of the genus in his *Genera Plantarum* (1789). It was not until Bentham's treatments of the Labiatae were published, first a synopsis of the family in the *Botanical Register* of 1829–1830 (sub t. 1282, 1289, 1292) followed by an exhaustive monograph of the family, *Labiatarum Genera et Species* (1832–36), that Linnaeus' view was finally rejected once and for all. Recognizing the disparate nature of the elements included by Linnaeus under *Dracocephalum*, Bentham erected a new genus, *Physostegia*, to comprise *D. virginianum* L. and its congeners, while distributing the remainder of Linnaeus' species among several other genera, the largest of which he called *Dracocephalum*. Thus Bentham agreed with Adanson and Moench that *D. virginianum* belonged in its own genus distinct from the Old World species of *Dracocephalum* L., but unlike these earlier authors he reserved the name *Dracocephalum* for the larger Eurasian genus and provided a new generic name for the American plants. Sealy (1954) has expressed the opinion that Bentham reversed the earlier approach of Adanson and Moench for the sake of convenience, choosing to rename the one American species as *Physostegia* rather than creating new combinations for more than 20 species that would have had to have been transferred to *Moldavica* if the name *Dracocephalum* had been reserved for *D. virginianum* L. The name *Physostegia* is derived from the Greek, *physis* (bladder) and *stegē* (covering), in allusion to the calyx, which becomes slightly inflated when the plant is in fruit (Fernald, 1950).

Bentham's treatment in *Labiatarum Genera et Species* was almost universally accepted for nearly 80 years. Endlicher (1838), Meisner (1839), Lindley (1846), Gray (1848, 1868), Bentham and Hooker (1876), Baillon (1891), Briquet (1895–96), Britton and Brown (1898), Britton (1901), and Small (1903) all applied the name *Physostegia* to the American genus. However, in 1913, when Britton and Brown published the second edition of their *Illustrated Flora of the Northern United States and Canada*, they reversed their earlier usage and applied the name *Dracocephalum* to the American genus and *Moldavica* to the primarily Eurasian genus, specifying *D. virginianum* L. as the type of the former and *D. moldavica* L. as the type of the latter. No

reason was given for the change. While Sealy (1954) suggested that Britton and Brown were simply following Adanson rather than Benth., a more likely explanation was hinted at by Shinnars (1949), although he incorrectly attributed the reversal of Benth.'s usage to Small rather than to Britton and Brown. The 1907 *American Code of Botanical Nomenclature* (cf. *Bull. Torrey Bot. Club* 34: 167–178) stipulated that the rule of priority in typification should apply to the precedence of names within a given publication as well as to the dates of different publications. Inasmuch as N. L. Britton was one of the foremost proponents of the American Code (Lawrence, 1951), it is likely that he chose *Dracocephalum virginianum* as the type of *Dracocephalum* because it was the first species listed by Linnaeus, rather than because Adanson had indirectly typified the genus in this way by reference to Tournefort's earlier usage.

McClintock's assertion (1949) that Epling (1929) selected *Dracocephalum virginianum* as the type of *Dracocephalum* is incorrect; he merely chose a lectotype for the species. However, Britton and Brown's typification of *Dracocephalum* with *D. virginianum* was supported by Hitchcock and Green (1929) in their list of proposed "standard-species" for Linnean genera. This list was incorporated as a supplement to the 1935 and unofficial 1947 editions of the *International Rules of Botanical Nomenclature*. Although the proposals contained in the list were not binding, they were undoubtedly influential, with the result that many floristic works published in the United States after 1930 used the names *Dracocephalum* and *Moldavica* rather than *Physostegia* and *Dracocephalum* for the American and Eurasian genera, respectively (e.g., Rydberg, 1932; Small, 1933; Kearney & Peebles, 1951; Davis, 1952; Hitchcock, Cronquist & Ownbey, 1959; Radford, Ahles & Bell, 1964). Other floras published during the same period retained Benth.'s usage, referring to the strictly American genus as *Physostegia* (e.g., Deam, 1940; Fassett, 1940; Bailey, 1949; Stevens, 1950; Fernald, 1950; Jones & Fuller, 1955; Steyermark, 1963). The publication of new taxa under both generic names compounded the confusion.

By the mid-1940's, dissatisfaction with the situation led to several informal proposals that one or another member of the Old World genus (i.e., *Moldavica* L. emend. Adanson or *Dracocephalum* L. emend. Benth.) be conserved over *D. virginianum* as the type of *Dracocephalum*, thus permitting the use of the name *Physostegia* for the American genus (Smith, 1945; Weatherby, 1947, as footnote 50a to Hitchcock & Green's supplement to the unofficial *International Rules of Botanical Nomenclature* [Brittonia 6:115]; McClintock, 1949). This culminated in a formal proposal by Sealy (1954) that the name *Dracocephalum* L. emend. Benth. (type: *D. moldavica* L.) be placed



on the list of *Nomina Generica Conservanda*. This proposal was referred to committee at the 8th International Botanical Congress in Paris. It was eventually endorsed but changed in form to agree with Article 48 of the International Rules (Rickett, 1960); i.e., it was recommended that *D. moldavica* L. be conserved as the type of *Dracocephalum*, rather than *Dracocephalum* L. emend. Benth. being conserved over earlier circumscriptions of the genus. The proposal was adopted as part of the 1961 *International Code of Botanical Nomenclature*, where *Dracocephalum* first appeared in the list of *Nomina generica conservanda et rejicienda*.

*Dracocephalum* has thus now been typified, but *Physostegia* has not. In connection with McClintock's (1949) proposal that *Dracocephalum ruyschiana* L. be selected as the type of *Dracocephalum*, she suggested that *D. virginianum* L. be treated as the type of *Physostegia*. The former was not a formal proposal and was never acted upon by an International Botanical Congress. However, now that *D. moldavica* L. has been conserved as the type of *Dracocephalum*, I propose that McClintock's informal typification of *Physostegia* be accepted. In the protologue of Bentham's original publication of the name *Physostegia* (Bot. Reg. sub t. 1289. 1829), he stated that the genus includes *Dracocephalum virginianum* L., *D. variegatum* Vent., *D. denticulatum* Ait., and probably *D. cordatum* Nutt. The first three he synonymized under *Physostegia virginianum* in *Labiatarum Genera et Species* (1832–36), and the lattermost he placed in a different genus, *Cedronella* (it is now known as *Meehania cordata*). If Bentham's inclusion of *D. variegatum* and *D. denticulatum* within *Physostegia virginiana* is accepted (and it is in this treatment), then the only species of *Physostegia* known to Bentham at the time he described the genus was *P. virginiana*.

**Physostegia** Bentham, Edward's Botanical Register 15: sub t. 1289. 1829.

Erect perennial herbs to 2 m high, normally unbranched below the inflorescence. Rhizome simple or branched, vertical or horizontal. Stem mostly glabrous below the inflorescence, the puberulence, if any, confined to the upper nodes. Leaves of the overwintering rosette usually deciduous before anthesis. Cauline leaves all sessile or the lower pairs petiolate; petiole up to 6.5 cm long; blade glabrous, broadly elliptical, ovate, or obovate to linear, serrate to entire. Inflorescence of 1–20 racemes, the raceme axis puberulent to tomentose throughout or glabrous towards the base, the vestiture sometimes including minute stalked glands; floral bracts lanceolate to ovate, acute to attenuate; pedicels 0.5–2.5 mm long, densely pubescent, sometimes bearing a few stalked glands. Calyx regular, campanulate to tubular-campanulate, very obscurely 10-nerved, the exterior densely puberulent to pubescent (very rarely subglabrous) and often glandular-punctate and/or stipitate-glandular, the interior glabrous or stipitate-glandular; the 5 lobes equal or nearly so, deltoid to lanceolate, acute to cuspidate,

0.6–4 mm long. Corolla bilabiate, the lips usually equal in length or nearly so and a fourth to two-thirds as long as the tube, the exterior puberulent or tomentulose to glabrous, the interior mostly glabrous to subglabrous except in the region of fusion with the filaments (where long trichomes may be present), the color ranging from pure white to deep reddish violet, usually with darker markings on the interior surface; tube narrow at the base and dilated in the apical half to two-thirds; upper lip flat to slightly galeate, horizontal or divergent; lower lip 3-lobed, the lobes divergent to reflexed. Androecium of 4 stamens, ascending parallel with or slightly divergent from each other beneath the upper lip of the corolla, protruding from the corolla tube but shorter than or barely reaching the end of the upper lip, the outer pair (of lateral origin) equaling to surpassing the inner pair (of adaxial origin); filaments densely villous and coherent due to the interlocking of the trichomes; anthers purple to white, 1–2 mm long at anthesis, glabrous or pubescent on the adaxial surface, with a few large multicellular glands on the abaxial surface, the dehiscence introrse and longitudinal. Pollen grains binucleate, tricolpate, subprolate to prolate spheroidal, the sexine reticulate, the lumina of the reticulum minutely pitted. Ovary deeply cleft into 4 equal lobes, the lobes trigonal and obovoid to ovoid, 0.8–1 mm long, shorter than the single large nectary that lies adjacent to 2 of the lobes; style ascending parallel with the stamens beneath the upper lip; stigma with 2 equal or subequal lobes, 0.8–3 mm long. Nutlets 1.7–4.2 mm long, trigonal; seed obscurely trigonal, usually not completely filling the nutlet, the seed coat brown and membranaceous, the endosperm forming a thin layer around the embryo. CHROMOSOME NUMBERS:  $2n = 38, 76$ . LECTOTYPE SPECIES: *Physostegia virginiana* (L.) Benth.

## ARTIFICIAL KEY TO THE SPECIES

The polythetic nature of the species in *Physostegia* (see p. 44) greatly complicates key construction. A choice must be made between a key with extremely complex couplets, in which each species appears only once, and one with simpler couplets but with some species keying out several times. I have elected to employ the latter because the lengthy couplets of the former are apt to strain the patience of the user to the point of carelessness. The statements in the couplets do not necessarily apply to all members of the species concerned, but only to the portion of the species that keys out under that statement.

Illustrations of the following key characters have been provided: elongate, horizontal rhizomes (Fig. 1a); perennating buds borne directly on rootstock (Fig. 1b); leaves sharply serrate (Fig. 3a, g–i), bluntly toothed (Fig. 3b–e), repand (Fig. 3f), clasping (Fig. 4b, d), inconspicuously clasping (Fig. 4c), not clasping (Fig. 4a); sterile bracts below flowers (Fig. 9a); nutlets smooth (Fig. 2j), warty (Fig. 2q, r); trichomes of *Physostegia angustifolia* (Fig. 6b), of *P. virginiana* (Fig. 6a); stalked glands on raceme axis (Fig. 6c). The stalked glands on the calyx and raceme axis are barely visible with a 10X hand lens. Those on the corolla in *P. parviflora* are smaller but clearly visible with a dissecting microscope. The latter are most easily seen on flower buds just before anthesis and near the tip of the upper lip in newly opened flowers.

- A. Calyx and rachis of inflorescence bearing minute stalked glands as well as non-glandular puberulence ..... B.
- A. Calyx and rachis of inflorescence puberulent but lacking glands ..... H.
- B. Leaves sessile or petiolate, but none clasping stem ..... C.
- B. One or more leaves clasping stem, sometimes narrowly so ..... D.
- C. Nutlets 1.7–2 mm long, usually warty over part or all of surface; leaves bluntly toothed to entire, 2–8 mm wide; flowers loosely spaced, adjacent calyces overlapping barely if at all; Florida panhandle ..... 2. *P. godfreyi*.
- C. Nutlets (2.1–)2.4–4.2 mm long, smooth; leaves usually sharply serrate, often wider than 8 mm; flowers usually tightly packed in inflorescence, adjacent calyces overlapping considerably; widespread ..... 12. *P. virginiana*.
- D. Larger leaves 2.5–4 times as long as wide, only 1 conspicuously clasping stem;

- 19–33 leafy nodes below inflorescence; flowers 17–24 mm long with calyx lobes 1–2.3 mm long; nutlets 3.1–3.5 mm long; Transylvania Co., N. Carolina ..... 12. *P. virginiana*.
- D. Two or more characters not as above; Louisiana to Manitoba and westward ..... E.
- E. Flowers 21–41 mm long with calyx lobes 2–4 mm long; all major leaves usually widest at to above middle of blade; Louisiana, Texas, northern Mexico ..... F.
- E. Flowers 9–23 mm long with calyx lobes 0.7–2 mm long; some major leaves usually widest below middle of blade, often near base of blade; north-central and northwestern U.S., central and western Canada ..... G.
- F. Rootstock bearing one to many elongate, horizontal secondary rhizomes, each terminating in a perennating bud; glandular dots present on calyx and conspicuous on upper leaf surface of dried specimens ..... 9. *P. correllii*.
- F. Perennating buds borne directly on rootstock or at ends of short, vertical secondary rhizomes, horizontal rhizomes lacking; glandular dots usually absent from calyx and absent or inconspicuous on upper leaf surface of dried specimens ..... 8. *P. digitalis*.
- G. Flowers on dried specimens 9–16 mm long (longer when fresh); nutlets 2.1–3.3 mm long; at least a few stalked glands usually present on corolla; leaves widest near or below middle of blade, never above middle, the upper pairs usually widest near base of blade; sometimes with majority of stem leaves bluntly toothed; widespread in northwestern U.S. and western Canada ..... 10. *P. parviflora*.
- G. Flowers on dried specimens 14–23 mm long (longer when fresh); nutlets 2.8–4.0 mm long; stalked glands usually absent from corolla; leaves widest above to below middle but usually not near base of blade; majority of stem leaves always sharply serrate; Alberta, Saskatchewan, Manitoba, N. Dakota ..... 11. *P. ledinghamii*.
- H. One or more leaves clasping stem ..... J.
- H. Leaves sessile or petiolate, but none clasping stem ..... U.
- J. Leaves of second pair below terminal raceme longer than the internode above; glandular dots present on calyx and conspicuous on upper leaf surface of dried specimens; larger leaves sharply serrate and no more than 3 times as long as wide; northern Mexico ..... 9. *P. correllii*.
- J. Two or more characters not as above; not occurring in Mexico ..... K.
- K. Rootstock bearing one to many elongate, horizontal secondary rhizomes, each terminated by a perennating bud ..... L.
- K. Perennating buds borne directly on rootstock or at ends of short, vertical secondary rhizomes, horizontal rhizomes lacking ..... Q.
- L. Flowers 22–36 mm long; all or most of larger stem leaves acute to attenuate at apex; axis of raceme densely pubescent, always with some (usually many) trichomes 0.2–0.25 mm long; west of Mississippi River ..... M.
- L. Flowers smaller, or half or more of larger leaves obtuse at apex, or axis of raceme minutely puberulent, few if any trichomes more than 0.15 mm long (mostly less than 0.1 mm); widespread in southeastern U.S. .... N.
- M. Flowers deep lavender to reddish violet; some leaves usually bluntly toothed or repand; petiolate lower leaves often present at anthesis; southwestern Louisiana and southeastern Texas ..... 5. *P. longisepala*.
- M. Flowers very pale lavender to white; all leaves sharply serrate; petiolate leaves usually deciduous before anthesis; southwestern Arkansas and northwestern Louisiana ..... 7. *P. angustifolia*.
- N. At least one pair of upper stem leaves usually widest at base of blade; flowering calyx tube (1–)2–4 mm long; flowers always less than 20 mm long; base of plant often conspicuously swollen, much thicker than central part of stem; Mississippi Valley and westward ..... 4. *P. intermedia*.
- N. Upper stem leaves widest above to below middle of blade but rarely at base; flowering calyx tube 3–7(–8) mm long; flowers often longer than

- 20 mm; base of plant rarely conspicuously swollen, usually little thicker than central part of stem; Atlantic and Gulf coastal plains from Virginia to Florida ..... P.
- P. Leaves of uppermost pair below terminal raceme often no larger than the floral bracts, those of second pair 0.4–3.2 cm long and rarely more than three-tenths as long as internode above; principal stem leaves usually widest at to above middle of blade; roadside ditches, open pine-woods, and glades, rarely growing in shade ..... 1. *P. purpurea*.
- P. Leaves of uppermost pair below terminal raceme usually considerably larger than the floral bracts, those of second pair (1.5–) 2.0–12.8 cm long and three-tenths as long as to longer than the internode above; principal stem leaves usually widest at to below middle of blade; wooded river swamps and fresh and brackish marshes, frequently growing in deep shade ..... 3. *P. leptophylla*.
- Q. Most or all of the larger leaves sharply serrate; largest leaves on dried specimens not more than 2.5 cm wide (wider when fresh) and rarely less than 5 times as long as wide ..... R.
- Q. Most or all of the larger leaves bluntly toothed to entire, or largest leaves more than 3 cm wide or less than 5 times as long as wide ..... S.
- R. Corolla deep lavender to reddish violet; stem with 7–10 nodes below inflorescence; petiolate lower stem leaves frequently present at and after anthesis; eastern Texas ..... 6. *P. pulchella*.
- R. Corolla usually very pale lavender to white; stem with 9–20 nodes below inflorescence (if in Texas, 11–20 nodes); petiolate lower stem leaves usually deciduous before anthesis; southwestern Georgia to Texas, north to Missouri, Kansas ..... 7. *P. angustifolia*.
- S. Largest leaves mostly concentrated in lower third of stem; most leaves of upper two-thirds of stem sharply serrate; Texas .... 6. *P. pulchella*.
- S. Largest leaves more evenly spaced throughout stem, or, if concentrated in lower third of stem, then most leaves of upper two thirds of stem bluntly toothed to entire; southeastern U.S., including Texas ..... T.
- T. Axis of raceme densely pubescent to tomentose, the trichomes mostly 0.2–0.3 mm long; calyx lobes at anthesis generally 2–4 mm long, many or all of them attenuate or cuspidate; Louisiana and eastern Texas ..... 8. *P. digitalis*.
- T. Axis of raceme puberulent to pubescent, the trichomes rarely as much as 0.2 mm long; calyx lobes at anthesis generally 1–2 mm long, mostly merely acute; Carolinas, Georgia, Florida ..... 1. *P. purpurea*.
- U. All or most of larger leaves sharply serrate and acute to attenuate at apex; leaves of second pair below terminal raceme a fifth as long as to about equalling the internode directly above ..... V.
- U. Half or more of larger leaves bluntly toothed to entire and/or obtuse at apex, or leaves of second pair below terminal raceme less than a fifth as long as or longer than the internode above ..... W.
- V. Axis of raceme densely pubescent, some (usually many) trichomes 0.13–0.25 mm long; sterile bracts absent from inflorescence; usually blooming April to mid-July ..... 7. *P. angustifolia*.
- V. Axis of raceme minutely puberulent, few if any trichomes more than 0.1 mm long; sterile bracts frequently present below the flowers; usually blooming July to October ..... 12. *P. virginiana*.
- W. All or most of larger leaves sharply serrate ..... 12. *P. virginiana*.
- W. Half or more of larger leaves bluntly toothed to entire ..... X.
- X. Leaves of second pair below terminal raceme rarely more than three-tenths as long as the internode above; open pinelands, glades, and roadsides from N. Carolina to Florida ..... 1. *P. purpurea*.
- X. Leaves of second pair below terminal raceme a third as long as to twice as long as the internode above; swamps, marshes, and river and lake margins from Quebec to Florida and west to Tennessee ..... Y.

- Y. Lowest leaves present at or after anthesis usually petiolate, petioles often more than 2 cm long, some petiolate leaves (if present) among largest leaves on plant; wooded swamps and fresh and brackish marshes of coastal plain from extreme southeastern Virginia to Florida . . . . . 3. *P. leptophylla*.  
 Y. All leaves at and after anthesis lacking petioles or, if present, petioles not exceeding 2 cm and the petiolate leaves rarely among largest leaves on plant; gravelly banks and islands of rivers and lakes from Quebec to Maryland, south through mountains to northern Tennessee . . . 12. *P. virginiana*.

## 1. *Physostegia purpurea* (Walter) Blake

*Prasium?* *purpureum* Walt. Fl. Carol. 166. 1788. LECTOTYPE: Specimen labeled *P. purpureum* Walt. by S. F. Blake on pg. 87 of the bound herbarium of Thomas Walter (BM, not seen; photo seen in GH).

*Physostegia purpurea* (Walt.) Blake, *Rhodora* 17: 134. 1915.

*Dracocephalum purpureum* (Walt.) McClintock ex Gleason, *Phytologia* 4: 24. 1952.

*Dracocephalum obovatum* Elliott, *Sketch Bot. S. Carol. & Georg.* 2: 86. 1821. HOLOTYPE: Georgia, St. Mary's, *Baldwin s.n.* (CHARL, not seen; photo seen in GH).

*Physostegia virginiana* var. *obovata* (Ell.) Gray, *Synopt. Fl. N. Am.* 2: 383. 1878.

*Dracocephalum denticulatum* var. *obovatum* (Ell.) Farwell, *Pap. Mich. Acad. Sci. Arts & Lett.* 1: 97. 1923.

*Physostegia obovata* (Ell.) Godfrey ex Weath. *Rhodora* 44: 254. 1942.

Erect perennial herbs to 14 dm high, with (5-)7-11(-22) nodes below the inflorescence, largest leaves sometimes concentrated in lower third of stem, the inflorescence thus appearing subscapose. Primary rhizome unbranched or with few branches, vertical or horizontal, up to 15 cm long. Lowest 1-6(-11) pairs of stem leaves petiolate or all leaves sessile; petiole, when present, up to 6.5 cm long; blades of lower and middle stem leaves 1-16 cm long, 0.2-4.4 cm wide, extremely variable in shape, from linear to spatulate to broadly obovate, oblong, elliptical, or pandurate, widest at to above the middle of the blade, base attenuate, cuneate, or slightly auriculate, at least a few leaves usually clasping the stem, apex obtuse to rounded or less frequently acute, margin repand or bluntly toothed, the upper leaves sometimes sharply serrate. Upper stem leaves greatly reduced, often little larger than the floral bracts (those of second pair below the terminal raceme 0.4-3.2 cm long and rarely more than three-tenths as long as the internode above), linear to narrowly lanceolate, sometimes narrowly oblanceolate or elliptical, apex acute, margin sharply serrate to entire. Flowers borne in 1-6(-10) racemes, raceme axis densely puberulent to pubescent throughout or sparsely so to glabrous near base (rarely sparsely puberulent to subglabrous throughout), trichomes frequently up to 0.17 mm long, rarely to 0.2 mm; floral bracts ovate to lanceolate, acute to attenuate, 2-4(-6) mm long, 1-2.5 mm wide; flowers 15-34 mm long, loosely to tightly spaced. Calyx conspicuously glandular-punctate or not, never bearing stalked glands, tube at anthesis 3-7(-8) mm long, lobes acute (rarely a few cuspidate), (0.8-)1-2.3(-3) mm long; calyx at fruit maturity (4-)5-9(-11) mm long. Corolla white to lavender, usually spotted and streaked inside with purple, tomentulose to glabrous. Nutlets 2-3.1(-3.6) mm long, trigonal with concave to slightly convex sides, surface smooth. CHROMOSOME NUMBER:  $2n = 38$ .

REPRESENTATIVE SPECIMENS: **Florida.** Lee Co.: Fort Myers, *Moldenke* 690 (PENN). Orange Co.: 5 mi E of Bithlo, *Kral* 6559 (IA, DUKE, VDB, GH, FSU). Osceola Co.: 1 mi E of Kissimmee River on Fla-60, *Lakela* 25212 (VDB, NCU, SMU, FSU). **Georgia.** Irwin Co.: 5 mi N of Irwinville, *Wilbur* 3364 (IA, GA, SMU, FSU). **Lowndes Co.:** 5 mi E of Valdosta, *Godfrey & Houk* 62758 (SMU, FSU). **McIntosh Co.:** E of ridge on Bill Smith Rd., *Bozeman* 1091 (NCU). **North Carolina.** Columbus Co.: 5 mi SE of Old Dock, *Radford* 5322 (NCU, GH). **Johnston Co.:** 3.5 mi SE of Wendell, *Radford* 25198 (DAO, VDB, NCU). **Onslow Co.:** 11.7 mi N of Hollyridge, *Ahles & Haesloop* 28215 (NCU). **South Carolina.** Charleston Co.: 2 mi SSE of St. Paul, *Radford* 24522 (NCU, FSU). **Georgetown Co.:** 4 mi

SW of Andrews, *Godfrey & Tryon 149* (TENN, GH). **Horry Co.:** 1 mi NW of Loris, *Bell 13746* (GH, NCU).

**DISTRIBUTION AND HABITAT** (map: Fig. 14): moist openings and roadside ditches in pine-lands from east-central North Carolina to southern Florida, west to southwestern Georgia and adjacent parts of the Florida panhandle. The species occasionally occurs in cypress savannas in southern Florida. A report of *Physostegia purpurea* from Tennessee (Wofford & Dennis, 1976) is based on a misidentification. The specimen concerned (Wofford & Dennis 51757, TENN) is a member of *P. virginiana* ssp. *virginiana*.

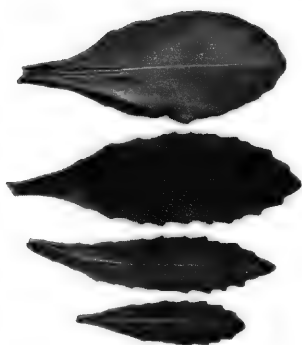
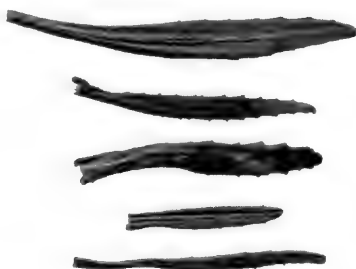
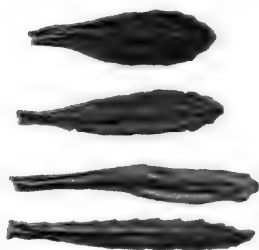
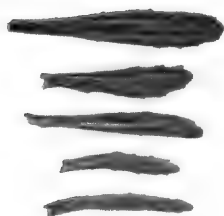
**FLOWERING:** early May through mid-August, except in the southern third of the Florida peninsula, where it may bloom at any time of the year.

**NOMENCLATURAL NOTES:** The application of the epithets *purpurea* and *denticulata* to this species is discussed elsewhere (Cantino, 1981b).

*Physostegia purpurea* exhibits clinal variation in several characters, the most conspicuous of which is leaf shape (Fig. 13). At the northern end of the range, in east-central North Carolina, the leaves are broadly obovate to elliptical or oblong, frequently as much as 3–4 cm wide. In southeastern North Carolina and eastern South Carolina, the largest leaves are mostly 1–2 cm wide. Although leaves as much as 2 cm wide can be found as far south as southern Florida, they are usually much narrower in that region, often as little as 0.2–0.5 cm wide. The transition is gradual, with considerable variation both within regions and within populations. For example, in a population in Pender Co., North Carolina (Cantino 975), the widest leaf per plant ranged from 1.4 to 3.1 cm in width. Near the other end of the cline, in a population in Sarasota Co., Florida (Cantino 1006), the width of the widest leaf ranged from 0.6 to 2.0 cm.

Another character that varies clinally in *Physostegia purpurea* is the degree of crowding of the flowers. In southern Florida, the flowers are always loosely spaced, adjacent calyces overlapping little if at all. More tightly packed flowers occur with increasing frequency as one moves northward through the range of the species, reaching a maximum in North Carolina, where over half of the specimens have tightly packed flowers with much overlap between adjacent calyces.

At least three other characters exhibit a north-south pattern of variation in *Physostegia purpurea*, but in contrast to the clinal variation in leaf width, there is for each of these characters a relatively abrupt transition line, on one side of which the character is monomorphic and on the other side polymorphic. In the Florida peninsula *P. purpurea* rarely if ever produces horizontal rhizomes, while north of about the 30th parallel, horizontal rhizomes may be present or absent, with much variation within populations. Throughout most of the range of the species, the axis of the raceme and the outside of the calyx are densely puberulent to pubescent. However, in southern Florida many specimens are only very sparsely puberulent, some approaching a glabrous condition. Plants with the usual dense puberulence are also

**PHYSOSTEGIA PURPUREA****N. CAROLINA****GEORGIA****N. CAROLINA****S. FLORIDA****GEORGIA**

CM

**S. FLORIDA**

common in southern Florida, and there is much variation within populations. The marked reduction of the upper stem leaves that is so characteristic of *P. purpurea* reaches an extreme state in the east-central and southern parts of the Florida peninsula (Volusia Co. to Collier Co.), where a growth form occurs in which all of the larger leaves are concentrated near the base of the plant, the raceme thus appearing almost scapose. This growth form is nearly unique within the genus, occurring elsewhere only in a very few specimens of *P. pulchella*. It is not, however, a consistent characteristic of any population.

Flower size varies geographically in *Physostegia purpurea*. In southwestern Georgia and the adjacent part of the Florida panhandle, the flowers of *P. purpurea* are among the smallest in the genus, ranging from 11 to 23 mm long on dried specimens (a few millimeters longer when fresh). Throughout the rest of its range the flowers are mostly 20–34 mm long, the only exceptions being a few specimens from eastern Georgia. The intrapopulational variation is great. In one population in Sarasota Co., Florida (Cantino 1006), the flowers ranged from 22 to 33 mm long. I found ranges nearly as great (21–30 mm; 20–29 mm; 25–34 mm) in populations in Camden Co., Georgia (Cantino 990) and Flagler and Lake Counties, Florida, respectively (Cantino 1001, 1004).

In spite of the extensive morphological variation in *Physostegia purpurea*, there are no clearly delimited infraspecific taxa. The variation in several characters is clinal, and of those characters in which there is a more abrupt transition between character states, no two of them have a geographically similar variation pattern. There is therefore not enough correlation among the character states to warrant the recognition of infraspecific taxa.

## 2. *Physostegia godfreyi* Cantino

*Physostegia godfreyi* Cantino, *Rhodora* 81: 415. 1979. HOLOTYPE: Florida, Gulf Co., wet pine flatwoods, and in shallow water of ditches, 7 miles S of Wewahitchka, 18-VI-1958, *Godfrey* 57086 (GH). ISOTYPES: FSU, IA, USF.

Erect, slender, perennial herbs to 1 m high, with 7–13 nodes below the inflores-

FIG. 13. Geographic variation in middle leaves of *Physostegia purpurea*: each leaf from a different plant, each cluster from a single population. Vouchers at GH. Upper left—Pender Co., NC (Cantino 975). Middle left—Columbus Co., NC (Cantino 978–980). Lower left—Glynn Co., GA (Cantino 989). Upper right—Camden Co., GA (Cantino 995). Middle right—Sarasota Co., FL (Cantino 1006). Lower right—Collier Co., FL (Cantino 1011–1014).



cence. Rhizome usually unbranched, vertical or horizontal, up to 10 cm long. Lowest 1-3(-5) pairs of stem leaves petiolate or, less frequently, all leaves sessile; petiole, when present, up to 3 cm long; blades of lower and middle stem leaves lacking any visible secondary venation, 1.5-7.5 cm long, 2-6(-8) mm wide, linear to narrowly oblong, spatulate, or oblanceolate (rarely lanceolate), often somewhat falcate, base attenuate, apex obtuse to acute, margin entire, repand, or remotely dentate, teeth blunt. Upper stem leaves greatly reduced in size, but otherwise similar to central leaves, those of second pair below the terminal raceme 0.8-1.5(-3.0) cm long and a fifth to a third (rarely half) as long as the internode directly above. Flowers borne in 1-3 (-5) racemes, raceme axis sparsely to densely puberulent near the apex and subglabrous at the base, trichomes rarely over 0.1 mm long, stalked glands scattered throughout; floral bracts ovate, 2-3.5 mm long, 1-2 mm wide; flowers 11-23 mm long, loosely spaced, adjacent calyces usually not overlapping at anthesis. Calyx not conspicuously glandular-punctate but bearing stalked glands, tube at anthesis 3-5.5 mm long, lobes acute, 0.6-1.8 mm long; calyx at fruit maturity 4-6.5 mm long. Corolla pale lavender, spotted and streaked inside with purple, puberulent or tomentulose to glabrous. Nutlets 1.7-2 mm long, trigonal, sides strongly convex when fully developed, usually verrucose over all or part of surface. CHROMOSOME NUMBER:  $2n = 38$ .

REPRESENTATIVE SPECIMENS (for a more complete list, see Cantino, 1979): **Florida. Bay Co.:** Calloway, 21-VI-1977, *Athey s.n.* (FSU). **Calhoun Co.:** 4 mi W of Blountstown, *Godfrey et al.* 53473 (FSU, GH). **Franklin Co.:** 6 mi S of Sumatra, *Kral & Godfrey* 15058 (VDB). **Gulf Co.:** 12 mi W of Wewahitchka, *Godfrey* 71370 (FSU, NCU). **Liberty Co.:** 3 mi N of Orange, *McDaniel* 4472 (FSU).

DISTRIBUTION AND HABITAT (map: Fig. 14): moist pine savannas in the lower Apalachicola region of the Florida panhandle.

FLOWERING: mid-May through late August.

In my discussion of the morphological and geographical relationships between *Physostegia godfreyi* and *P. purpurea* (Cantino, 1979), I stated that the Ochlockonee River forms the boundary between the ranges of the two species in the Florida panhandle, *P. purpurea* occurring strictly to the east of the river and *P. godfreyi* entirely or nearly entirely to the west. It has since come to my attention that *P. purpurea* has been collected west of the Ochlockonee River (*Godfrey* 65848, FSU), in Liberty Co., within about 5 miles of a site where *P. godfreyi* occurs. The specimen resembles many collections of *P. purpurea* from Wakulla Co., just east of the Ochlockonee River, and shows no sign of introgression with *P. godfreyi*.

### 3. *Physostegia leptophylla* Small

*Physostegia leptophylla* Small, Bull. N. Y. Bot. Gard. 1: 286. 1899. LECTOTYPE: Florida, Manatee River, VI-1878, South Florida Flora no. 10, *Garber s.n.* (NY), here designated. ISOLECTOTYPES: CM, GH, US, NY.

*Dracocephalum leptophyllum* (Small) Small, Flora of Miami, 163. 1913.

*Physostegia veroniciformis* Small, Fl. Southeastern U.S. 1028, 1337. 1903. HOLOTYPE: Georgia, near Sunbury, *LeConte s.n.* (NY?, missing).

*Dracocephalum veroniciformis* (Small) Small, Man. Southeastern Fl. 1156. 1933.

*Physostegia aboriginorum* Fern. *Rhodora* 45: 459. 1943. LECTOTYPE: Virginia, Norfolk Co., margin of Indian Creek, northeast of Northwest, 30-VI-1942, *Fernald & Long* 14397 (GH), here designated. ISOLECTOTYPES: GH, (PH, not seen).

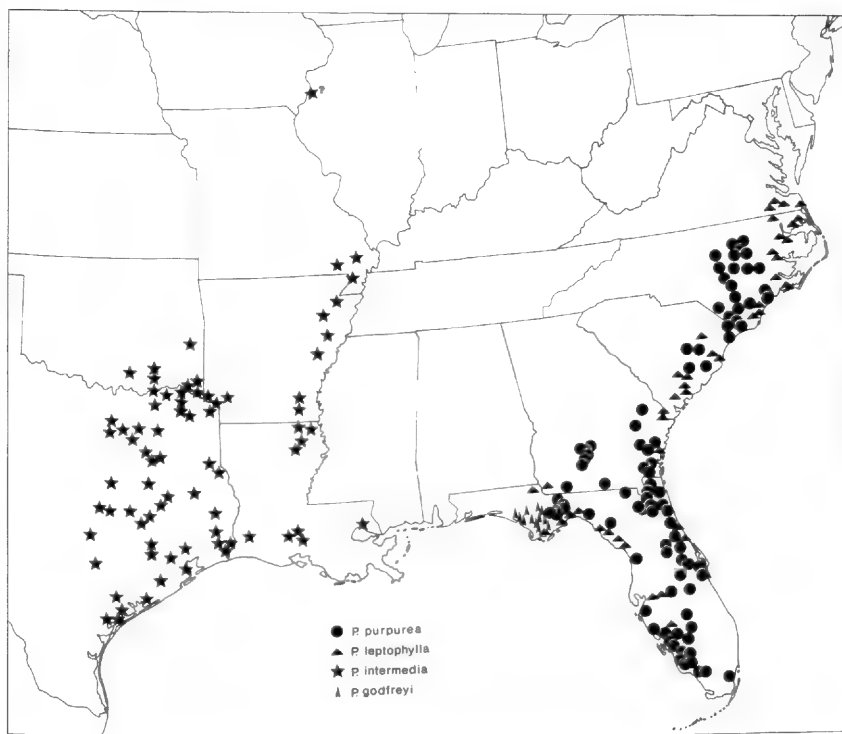


FIG. 14. Distribution map of *Physostegia purpurea*, *P. leptophylla*, *P. godfreyi*, and *P. intermedia*.

Erect perennial herbs to 14 dm high, with 7–15 nodes below the inflorescence. Primary rhizome branching to produce 1-many elongate, horizontal secondary rhizomes up to 40 cm long. Lowest (3–)4–9(–11) pairs of stem leaves petiolate, frequently still present at anthesis; petiole up to 6 cm long; blade 3–11 cm long, 1–3 cm wide, elliptical to lanceolate (rarely oblanceolate), base cuneate to attenuate (rarely rounded), apex obtuse to acute, margin entire, repand, or crenate. Sessile leaves of central part of stem 3–17 cm long, 0.5–3.3 cm wide, narrowly elliptical to lanceolate, occasionally oblanceolate, base cuneate, occasionally rounded or auriculate, at least a few leaves usually clasping the stem, apex acute to attenuate, margin bluntly toothed to repand, occasionally entire or sharply serrate. Upper stem leaves little to moderately reduced in size over central leaves (those of second pair below the terminal raceme [1.5–]2–13 cm long and three-tenths as long as to slightly longer than the internode directly above), often more attenuated apically than central leaves, but otherwise little different in shape. Flowers borne in 1–3(–6) racemes, raceme axis densely puberulent throughout or sparsely puberulent to glabrous at base, usually with few if any trichomes over 0.1 mm long; floral bracts lanceolate to ovate, attenuate, 2–6(–8) mm long, 1–2 mm wide; flowers 14–30 mm long, loosely spaced, adjacent calyces usually not overlapping at anthesis. Calyx conspicuously glandular-punctate or not, never bearing stalked glands, tube at anthesis 3.5–6 mm long, lobes acute to attenuate (occasionally a few cuspidate), 1–2.5(–3) mm long; calyx at fruit maturity 5–9.5 mm long. Corolla deep lavender to reddish violet, spotted and streaked inside with purple, sparsely (–densely)

puberulent or tomentulose to subglabrous. Nutlets 2.2–3.2 mm long, trigonal with concave to slightly convex sides, surface smooth. CHROMOSOME NUMBER:  $2n = 76$ .

REPRESENTATIVE SPECIMENS: **Florida.** **Franklin Co.:** Apalachicola, *Godfrey* 75840 (FSU). **Jefferson Co.:** Aucilla River bottom, *Kral & Godfrey* 2370 (FSU). **Levy Co.:** 7 mi S [W?] of Gulf Hammock, *Kral* 6495 (GH, IA, DUKE, VDB, FSU). **Wakulla Co.:** Newport, *Godfrey* 62831 (VDB, SMU, FSU). **Georgia.** **Chatham Co.:** Onslow Island, *Duncan* 21021 (MISS). **North Carolina.** **Jones Co.:** 5 mi NE of Pollocksville, *Sears* C322 (NCU). **Onslow Co.:** 4.2 mi SE of Gum Branch on Half Moon Creek, *Ahles & Haesloop* 28312 (NCU). **Pender Co.:** along NC-210, 2.6 mi E of US-117, *Ahles & Haesloop* 28054 (NCU). **South Carolina.** **Colleton Co.:** Edisto River at US-17, *Leonard & Radford* 1693 (MISS, WVA, GH, TENN, NCU, GA, CM, SMU, FSU, NO). **Virginia.** **Southampton Co.:** Nottoway River, Monroe Bridge, *Fernald & Long* 13122 (GH, GA, SMU, WVA, TENN).

DISTRIBUTION AND HABITAT (map: Fig. 14): wooded river swamps, fresh and brackish marshes from extreme southeastern Virginia to south-central Florida, west to southwestern Georgia and adjacent parts of the Florida panhandle.

FLOWERING: late April through early August.

Small stated in the protologue of *Physostegia leptophylla* that the "original specimens" were collected by Garber (So. Fla. Fl. No. 10). There are four sheets of this widely distributed collection at the New York Botanical Garden, where Small was working at the time the name was published. Of the four, one of them is too incomplete to have served as the primary basis for Small's comprehensive description, and one was transferred to NY from the Princeton University herbarium in 1945, long after the name was published. The choice of one of the remaining two sheets as the lectotype is problematical. Both were transferred to NY from other institutions, one from Columbia College (previously transferred to Columbia from Franklin and Marshall College, Lancaster, Pennsylvania) and one from the New York College of Pharmacy. Small could easily have seen either, but the Columbia College specimen has been selected because it is in better agreement with the description in one detail (petiole length) and because Small attended Franklin and Marshall College and received his doctorate from Columbia College before joining the New York Botanical Garden (Barnhart, 1938). He almost certainly would have seen this specimen, and he may well have been responsible for its transfer from Franklin and Marshall College to Columbia.

*Physostegia veroniciformis* Small appears from the description to be a taxonomic synonym of *P. leptophylla*, but the small flower size of the former is uncharacteristic of the latter. Unfortunately the type specimen, listed by Small as having been deposited in the herbarium of Columbia College (now part of the herbarium of the New York Botanical Garden), is missing.

Two practically identical sheets of the type collection of *Physostegia aboriginorum* Fernald are in the Gray Herbarium. Because both correspond equally well to the description and both have been annotated

TABLE 18. DISTINGUISHING CHARACTERISTICS OF *PHYSOSTEGIA LEPTOPHYLLA* AND *P. INTERMEDIA*.

<i>P. leptophylla</i>	<i>P. intermedia</i>
Uppermost leaves infrequently widest at base of blade	Uppermost leaves usually widest at base of blade
Flowering calyx tube 3.5–6 mm long	Flowering calyx tube (1–)2–4 mm long
Base of plant rarely conspicuously swollen	Base of plant frequently conspicuously swollen
Length ÷ width of fruiting calyx tube 0.8 to 1.5, rarely 2	Length ÷ width of fruiting calyx tube 0.5 to 1

“Type no.” by Fernald, the selection of one as the lectotype was necessarily arbitrary. Both sheets include leaves, rhizomes, roots, and mature flowers, but only one includes mature nutlets; this specimen was therefore chosen as the lectotype.

I have discussed elsewhere (Cantino, 1981b) the nomenclatural confusion surrounding the epithet *denticulata*, which has been applied incorrectly to *Physostegia leptophylla* by Fernald (1950) and others.

The morphological overlap between *Physostegia leptophylla* and the sympatric but reproductively isolated species, *P. purpurea*, has been discussed elsewhere (Cantino, 1981b). There is a roughly comparable amount of morphological overlap between *P. leptophylla* and two other species with which it is allopatric—*P. longisepala* and *P. intermedia*. The differences between *P. leptophylla* and *P. longisepala* are discussed under the latter species. *Physostegia intermedia* occupies swamp and marsh habitats in the Mississippi Valley and westward, similar to those frequented by *P. leptophylla* on the Atlantic coastal plain. There is no single morphological character that will, in itself, reliably distinguish the two species, but there are four morphological characters that will, in combination, distinguish them (Table 18). In addition, *P. leptophylla* and *P. intermedia* differ in chromosome number (38 pairs vs. 19 pairs, respectively).

#### 4. *Physostegia intermedia* (Nuttall) Engelmann & Gray

*Dracocephalum intermedium* Nutt. Trans. Am. Phil. Soc. 5: 187. 1837. LECTOTYPE: Red River, Nuttall s.n. (BM), here designated.

*Physostegia intermedia* (Nutt.) Engelm. & Gray, Boston Journ. Nat. Hist. 5: 257. 1845.

*Physostegia micrantha* Lundell, Wrightia 2: 8. 1959. HOLOTYPE: Texas, Titus Co., off Hwy 49, about 1 mile SE of Mount Pleasant, in open wet bottom land of Hart Creek, 29-V-1958, Lundell 15075 (LL, not seen). ISOTYPES: GH, NY.

Erect perennial herbs to 12 dm high, with 9–16(–20) nodes below the inflorescence. Primary rhizome branching to produce 1-many elongate, horizontal secondary and tertiary rhizomes up to 40 cm long. Stem often conspicuously swollen at base. Lowest 3–8 pairs of stem leaves petiolate, usually deciduous before anthesis; petiole up to 6 cm long; blades of lower and middle stem leaves 3–14 cm long, 0.3–1.5 cm wide, all lanceolate or some leaves oblanceolate to narrowly elliptical, base attenuate to cuneate on lower leaves, rounded to auriculate upwards, at least a few leaves clasping the

stem, apex acute to attenuate, margin repand, entire, or bluntly toothed, teeth few and widely spaced. Upper stem leaves little to moderately reduced in size over central stem leaves (those of second pair below the terminal raceme 1.7–9[–12] cm long and a third as long as to nearly as long as the internode directly above), lanceolate, attenuate, usually widest at or very near the auriculate-clasping base. Flowers borne in 1–5(–10) racemes, raceme axis densely puberulent to pubescent throughout or sparsely so to glabrous towards the base, trichomes frequently up to 0.15 mm long, rarely to 0.2 mm; floral bracts lanceolate or less frequently ovate, attenuate, (1.5–)2–5(–6) mm long, 1–1.5(–2.5) mm wide; flowers normally 9–19 mm long (shorter if anthers aborted), loosely spaced, adjacent calyces usually not overlapping at anthesis. Calyx not conspicuously glandular-punctate, never bearing stalked glands, tube at anthesis (1.2–)2–4 mm long, lobes acute (rarely a few cuspidate), (0.7–)1–2(–2.8) mm long; calyx at fruit maturity (3–)4–7 mm long. Corolla lavender, spotted and streaked inside with purple, puberulent to tomentulose. Nutlets 2–2.5(–2.9) mm long, trigonal with concave to slightly convex sides, surface smooth. CHROMOSOME NUMBER:  $2n = 38$ .

REPRESENTATIVE SPECIMENS: **Arkansas.** Ashley Co.: Mist, *Demaree* 15091 (OKL, SMU). **Craighead Co.:** Lake City, *Demaree* 5089 (TENN, GH, TEX). **Drew Co.:** Tillar, *Demaree* 21129 (WTU, SMU). **Louisiana.** Morehouse Parish: 2 mi S of Galion, *Thomas & Marx* 34669 (NCU). **St. Martin Parish:** 3.2 mi SE [of Lafayette?] on La-353, *Zammit* 20 (LAF). **Missouri.** Stoddard Co.: 1 mi W of junction of Hwy 153 & 60, E of Essex, *Steyermark* 85099 (MISS). **Oklahoma.** Johnston Co.: 4 mi SE of Tishomingo, *Taylor & Taylor* 4154 (SMU, OKL). **Texas.** Madison Co.: ca. 2 mi E of junction of Hwy 21 and Trinity River, *Nixon* 4036 (NCU). **Rains Co.:** 9.8 mi S of Point, *Van Vleet* 1374 (SMU). **Refugio Co.:** ca. 2 mi E of Refugio, *Jones* 1803 (SMU, FSU). **Waller Co.:** entrance to Austin State Park, near Sealy, *Correll & Edwin* 16438 (GH, NCU, LL).

DISTRIBUTION AND HABITAT (map: Fig. 14): swamps, marshes, river bottoms, wet meadows, and drainage ditches, from southeastern Missouri (one record each in Kentucky and Illinois) south to the Gulf Coast of Louisiana, and west to central Texas and southeastern Oklahoma. The collection locality of the Kentucky record is unknown ("barrens of Kentucky," C. W. Short, GH). The record of *Physostegia intermedia* from west-central Illinois (Henderson Co.) is very likely erroneous. A specimen of *P. intermedia* at the Field Museum is mounted on the same sheet with one of *P. virginiana*, and the sheet is stamped as being part of the Harry N. Patterson herbarium, purchased in 1900. The single label shared by the two specimens cites the collection locality as "prairies near Oquawka" and the collector as Patterson, but there is no collection number or date. *Physostegia intermedia*, a species of swamps rather than prairies, is not otherwise known from Illinois. *Physostegia virginiana*, on the other hand, is common in Illinois prairies. Patterson listed *P. virginiana*, but not *P. intermedia*, in his catalogues of the plants of the vicinity of Oquawka (1874) and of Illinois (1876). All of this suggests that the anomalous specimen of *P. intermedia* may have been mistakenly associated with the Oquawka collection locality, possibly by Patterson himself, but more likely by someone sorting or mounting his collection after its purchase.

FLOWERING: late March through late July.

In the protologue of *Dracocephalum intermedium*, Nuttall cited no specimens but stated that the species occurs "on the prairies in moist places, from Arkansas to Red river." I have seen two specimens (BM, PH) that might be considered as candidates for the lectotype, both of which correspond well to the description. As is characteristic of Nuttall's specimens, they are accompanied by only the briefest collection data, the specimen from the British Museum bearing the words "Red River," and the specimen from the Philadelphia Academy labeled simply "Ark." Both labels are in Nuttall's handwriting, and on both there

is an asterisk preceding the specific epithet. An asterisk, as Pennell (1950) has pointed out, was Nuttall's notation to indicate a new species or genus.

Pennell (1936) related that until 1818, Nuttall kept few specimens for himself, presenting "a complete series of his plants" to the Academy of Natural Sciences in Philadelphia, but that starting with the Arkansas collections he reserved an increasing proportion of his better specimens for his own personal collection, which he took with him when he returned to England in 1842. Thus, Pennell went on to say, "We may consider that his later types are in London, with isotypes in Philadelphia." Accordingly, I have selected as the lectotype the specimen in the British Museum.

Although the label data on the lectotype is brief, it is possible to obtain more precise information from Nuttall's published account of the journey (Nuttall, 1821; Pennell, 1936). Nuttall's explorations of the Red River were confined to the 15-mile stretch immediately upriver from the mouth of the Kiamichi River in what is now Choctaw Co., Oklahoma. He collected in that area from May 23 through June 13 of 1819.

*Physostegia micrantha* Lundell is based on a single population in Titus Co., Texas. It differs from *P. intermedia* in having very small flowers (5–7 mm long) with aborted anthers, but it resembles *P. intermedia* in all other characteristics. Plants with aborted anthers and an accompanying reduction in flower size are quite common in some populations of *P. virginiana* ssp. *virginiana* (see p. 32) and occur sporadically elsewhere in the genus. The specimens upon which *P. micrantha* is based are without doubt simply another example of this phenomenon. William F. Mahler has collected a series of specimens from the type locality of *P. micrantha* (Mahler 6458 a–h, SMU), some of which exhibit the floral characteristics of *P. micrantha* while others have the larger flowers and fertile anthers of *P. intermedia*.

##### 5. *Physostegia longisepala* Cantino sp. nov.

Herba perennis erecta ad 1 m alta, nodis 9–15 infra inflorescentiam. Caudex rhizomata secundaria horizontalia ad saltem 15 cm longa ferens. Paria foliorum caulinarum 4–8 infra petiolata, saepe sub anthesi persistentia; petiolus ad 3.5 cm longus; lamina folii petiolati 5–8 cm longa, 1–1.5 cm lata, elliptica, oblonga vel oblanceolata, base cuneata vel attenuata, apice obtuso vel acuto, marginibus repandis vel sparse dentatis, dentibus obtusis. Folia caulina media sessila, 5–12 cm longa, 0.5–1.7 cm lata, oblanceolata, elliptica vel lanceolata, base attenuata, cuneata, rotundata vel auriculata, pro parte maxima amplexantia, apice plerumque acuto vel attenuato, marginibus repandis, obtusi-dentatis, vel serratis (raro integris). Folia caulina superna magnopere vel modice deminuta, lanceolata vel elliptica, saepe prope basem laminae amplexantem latissima. Racemi 1–7, axe dense pubescenti, trichomatibus longioribus 0.15–0.25 mm longis; bracteae florales lanceolatae, attenuatae, (3–)4–6(–7) mm longae, 1–2 mm latae; flores

23–32 mm longi, rare vel dense positi. Calyx sub anthesi tubulari-campanulatus, tubo 4–8 mm longo, dentibus attenuatis vel cuspidatis, 2–3.5 mm longis. Corolla intense lavandulacea vel rubro-violacea, parte interior maculis atro-purpureis. Nucula 3–3.3 mm longa, trigona, lateribus laevibus. HOLOTYPE: Louisiana, Calcasieu Parish, 2 miles north of Edgerly, 18-V-1968, J. W. Thieret 28876 (SMU). ISOTYPE: LAF.

Erect perennial herbs to 1 m high, with 9–15 nodes below the inflorescence. Primary rhizome branching to produce 1-many elongate, horizontal secondary rhizomes up to at least 15 cm long. Lowest 4–8 pairs of stem leaves petiolate and frequently still present at anthesis; petiole up to 3.5 cm long; blade of petiolate leaves 5–8 cm long, 1–1.5 cm wide, elliptical, oblong, or oblanceolate, base cuneate to attenuate, apex obtuse to acute, margin repand or with a few widely spaced blunt teeth. Sessile leaves of central part of stem 5–12 cm long, 0.5–1.7 cm wide, elliptical to oblanceolate downwards on stem and elliptical to lanceolate upwards, base attenuate to cuneate downwards on stem and rounded to auriculate upwards, most leaves clasping the stem, apex usually acute to attenuate, margin repand, bluntly toothed, or serrate. Upper stem leaves moderately to greatly reduced in size over central leaves (those of second pair below the terminal raceme 2.7–6 cm long and three-tenths as long as to about half as long as the internode directly above), lanceolate to elliptical, often widest near the clasping base of the blade. Flowers borne in 1–7 racemes, raceme axis densely pubescent, some (usually many) of the trichomes 0.15–0.25 mm long; floral bracts lanceolate, attenuate, (3)–4–6(–7) mm long, 1–2 mm wide; flowers 23–32 mm long, loosely to tightly spaced. Calyx not conspicuously glandular-punctate, lacking stalked glands, tube at anthesis 4–8 mm long, lobes attenuate to cuspidate, 2–3.5 mm long;

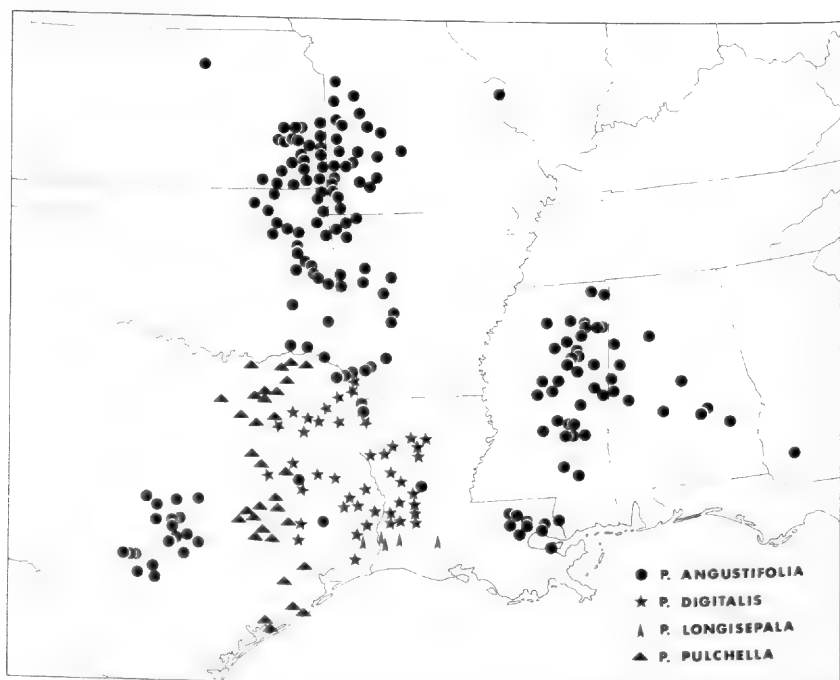


FIG. 15. Distribution map of *Physostegia angustifolia*, *P. digitalis*, *P. longisepala*, and *P. pulchella*.

calyx at fruit maturity 7.5–10 mm long. Corolla deep lavender to reddish violet, spotted or streaked inside with purple, puberulent or tomentulose to subglabrous. Nutlets (few available) 3–3.3 mm long, surface smooth. Chromosome number unknown.

**SPECIMENS EXAMINED:** **Louisiana. Acadia Parish:** near Crowley, *Debaillon* 3 (MO); near Crowley, *Dormon s.n.* (BH); near Crowley, *Dormon* 3 (SMU). **Bienville Parish:** grown in a garden (originally collected near Crowley, Acadia Parish), *Ewan* 19233 (GH, NO). [Note: the above four collections were apparently all from the same clump in Caroline Dormon's garden, originally transplanted from Crowley by Mary S. Debaillon.] **Calcasieu Parish:** 1.5 mi SW of Starks, *Thieret* 23545 (SMU); 4 mi S of Gillis, *Shinners* 23637 (SMU, ILL, NCU). **Texas. Jasper Co.:** near Evadale, *Correll* 32936 (LL).

**DISTRIBUTION AND HABITAT** (map: Fig. 15): moist prairies, thickets, and ditches, in southwestern Louisiana and southeastern Texas; apparently rare.

**FLOWERING:** mid-May through mid-June.

The 12 specimens upon which *Physostegia longisepala* is based bear some resemblance to *P. leptophylla*, *P. angustifolia*, and *P. pulchella*, but the extent to which they differ from each of these species is too great to permit their inclusion in any of them (Table 19). The most distinctive characteristic of *P. longisepala* is indicated by the name I have chosen; the calyx lobes at anthesis are relatively long for *Physostegia*. Every specimen has at least some calyx lobes 2.5 mm long

TABLE 19. DIAGNOSTIC CHARACTERS OF *PHYSOSTEGIA LONGISEPALA* IN RELATION TO THE 3 MOST SIMILAR SPECIES

<i>P. longisepala</i>	<i>P. leptophylla</i>
Longest calyx lobes 2.5–3.5 mm long; frequently cuspidate	Calyx lobes rarely over 2.5 mm long; infrequently cuspidate
Longest trichomes on raceme axis 0.2–0.25 mm long	Longest trichomes on raceme axis 0.1–0.13 mm long
Lower stem leaves usually oblanceolate	Lower stem leaves elliptical to lanceolate (rarely oblanceolate)
Stem leaves commonly sharply serrate	Leaves bluntly toothed, repand, or entire (rarely sharply serrate)
<i>P. longisepala</i>	<i>P. pulchella</i>
Longest calyx lobes 2.5–3.5 mm long; frequently cuspidate	Calyx lobes rarely over 2.2(–2.5) mm long; infrequently cuspidate
Horizontal secondary rhizomes produced	Horizontal secondary rhizomes never produced; rhizomes short and vertical
Lowest 4–8 stem nodes bear petiolate leaves	Lowest 1–4 stem nodes bear petiolate leaves
Stem with (9–)11–15 leafy nodes below inflorescence	Stem with 7–10(–12) leafy nodes below inflorescence
<i>P. longisepala</i>	<i>P. angustifolia</i>
Corolla deep lavender to reddish violet	Corolla usually very pale lavender to white
Horizontal secondary rhizomes produced	Horizontal secondary rhizomes rarely produced
Lowest 4–8 stem nodes bear petiolate leaves; some usually persistent through anthesis	Lowest 1–4 stem nodes bear petiolate leaves; these usually deciduous by anthesis



or longer, and on most specimens many or all of them are cuspidate. In *P. pulchella* and *P. leptophylla* they rarely exceed 2.5 mm in length at anthesis and are infrequently cuspidate. However, this character does not distinguish *P. longisepala* from *P. angustifolia*; calyx lobes of the length found in *P. longisepala* are at the upper end of the range of variation seen in *P. angustifolia*, and the cuspidate shape is frequent in the latter species. *Physostegia longisepala* differs from *P. angustifolia* in flower color, the form of the rhizome, and the number of pairs of petiolate leaves (Table 19).

In a discussion of *Physostegia pulchella*, Lundell (1969) noted that a collection from Jasper Co., Texas (Correll, Johnston & Edwin 22299), which he included within *P. pulchella*, is notable for having "strong lateral rhizomes." He suggested that it might represent a distinct taxon. I have not seen the specimen, but it was collected within a few miles of the site where Correll 32936 was collected and, like the latter specimen, probably represents *P. longisepala*.

## 6. *Physostegia pulchella* Lundell

*Physostegia pulchella* Lundell, *Wrightia* 2: 4. 1959. HOLOTYPE: Texas, Kaufman Co., north side of US-175, ca. 1 mile E of Crandall, in wet bottom land along stream bed, 12-V-1959, Lundell 16026 (LL, not seen). ISOTYPES: F, GH, NY.

Erect perennial herbs to 14 dm high, with 7–10(–12) nodes below the inflorescence. Rhizome unbranched or with few branches, strictly vertical, up to 6 cm long. Lowest 1–4 pairs of stem leaves petiolate, some usually present at anthesis; petiole up to 6.5 cm long; blade 2.5–11 cm long, 0.6–1.7 cm wide, narrowly elliptical to lanceolate or oblanceolate, base cuneate to attenuate, apex obtuse, margin entire, repand, or remotely crenate or dentate. Sessile leaves of lower and central part of stem often having 1–3 pairs of weak primary veins (other than the midrib) arising from base of blade, 3–15 cm long, 0.5–2 cm wide, lanceolate to oblanceolate or spatulate, base usually auriculate-clasping, apex acute or obtuse, margin usually sharply serrate to base of blade. Upper stem leaves scarcely or greatly reduced in size over central leaves (those of second pair below the terminal raceme 1.8–6.5[–10] cm long and one-third as long as to fully as long as the internode directly above), usually with 1–3 pairs of weak primary veins arising from base of blade, lanceolate, less frequently elliptical or oblanceolate, the sessile base auriculate and clasping the stem, apex attenuate, margin sharply serrate to base of blade, the uppermost pair sometimes serrate only at base or entire. Flowers borne in 1–3(–7) racemes, raceme axis densely pubescent towards apex and sparsely pubescent to glabrous at base, some (usually many) of the trichomes 0.13–0.2 mm long, often to 0.25 mm long; floral bracts lanceolate to ovate, attenuate, 2–5(–6) mm long, 1–2(–3) mm wide; flowers 16–30 mm long, loosely to tightly spaced. Calyx not conspicuously glandular-punctate, lacking stalked glands, tube at anthesis (3)–4–6 mm long, lobes acute to attenuate (occasionally a few cuspidate), 1–2.2(–2.5) mm long; calyx at fruit maturity 6–9 mm long. Corolla deep lavender to reddish violet, spotted or streaked inside with purple, puberulent, occasionally tomentulose or glabrous. Nutlets 2.2–3 mm long, trigonal with concave to slightly convex sides, surface smooth. CHROMOSOME NUMBER:  $2n = 38$ .

REPRESENTATIVE SPECIMENS: **Texas.** Burleson Co.: 9.6 mi NE of Lyons, *Cory* 51642 (SMU, MICH). Collin Co.: 1.6 mi NE of Royse City, *Cory* 55813 (SMU, NO). **Delta Co.:** 1.6 mi NE of Cooper, *Shinners* 28452 (SMU, NO, FSU, NCU). **Grayson Co.:** N of Denison,

*Gentry 1236* (SMU). **Grimes Co.:** 5 mi from Navasota on FM-159, *Massey 108* (SMU). **Hunt Co.:** 2.1 mi S of Commerce, *Shinners 28448* (GH, SMU, NO, FSU, BH). **Kaufman Co.:** 2 mi E of Terrell, *Shinners 10087* (SMU). **Lamar Co.:** 4.6 mi WSW of Paris, *Shinners 14843* (SMU). **Matagorda Co.:** College Port, *Demaree 61548* (OKL, SMU). **Navarro Co.:** 6 mi S of Richland, *Cory 51540* (SMU). **Robertson Co.:** Hearne, *Lundell & Lundell 10378* (NCU, SMU).

DISTRIBUTION AND HABITAT (map: Fig. 15): moist meadows, river bottoms, and ditches in eastern Texas. Thieret (1971) has reported *P. pulchella* from Louisiana on the basis of two collections that I have included within *P. longisepala* (one of them the type of the latter). I have seen no specimens from Louisiana that fit within my circumscription of *P. pulchella*.

FLOWERING: early April through early June (rarely to late June).

*Physostegia pulchella* shares many morphological characteristics with *P. angustifolia*, and the two species frequent similar habitats; they are probably closely related. The most conspicuous difference between them is the color of the corolla, which is deep lavender to reddish violet in *P. pulchella* and very pale lavender to pure white in *P. angustifolia*. I am aware of a single specimen of *P. pulchella* with white flowers (*Fleetwood 9780*, TEX), and Lundell (1969) mentions having seen a specimen of *P. angustifolia* with reddish purple corollas, but exceptions of this sort are rare.

In *Physostegia pulchella* there are usually 7–10 stem nodes below the inflorescence (very rarely 12), and the blooming period lasts from the beginning of April to the beginning of June. *Physostegia angustifolia* has 9–20 nodes and blooms from April through July; however, in Texas where the two species are parapatric (Fig. 15), *P. angustifolia* has 11–20 nodes and starts flowering in mid-May, when *P. pulchella* is approaching the end of its blooming period. In *P. pulchella* the petiolate lower stem leaves tend to persist longer than in *P. angustifolia*, often up to or beyond the time of anthesis; they are therefore frequently present on herbarium specimens of the former but usually lacking on specimens of the latter.

## 7. *Physostegia angustifolia* Fernald

*Physostegia angustifolia* Fern. *Rhodora* 45: 462. 1943. HOLOTYPE: Mississippi, Chickasaw Co., roadside bank near Egypt, 18-V-1933, *Weatherby & Weatherby 6318* (GH).

ISOTYPES: NY, TENN, GH.

*Dracocephalum virginianum* var. *album* Nutt. Trans. Am. Phil. Soc. 5: 187. 1837.

Type: "Arkansa," Nuttall s.n. (BM).

*Physostegia edwardsiana* Shinners, Field & Lab. 19: 167. 1951. HOLOTYPE: Texas, Blanco Co., between Johnson City and Dripping Springs, off Hwy 290, in marshy area, 8-VI-1945, *Lundell & Lundell 13851* (SMU). ISOTYPES: LL, MICH.

Erect perennial herbs to 17 dm high, with 9–18(–20) nodes below the inflorescence. Rhizome unbranched and strictly vertical, 2–4(–10) cm long, or (infrequently) branching to produce 1-many elongate, horizontal rhizomes up to 20 cm long. Lower and middle stem leaves all sessile or lowest 1–4(–7) pairs petiolate, the petiolate leaves usually early deciduous; sessile leaves 3–21 cm long, 0.3–2(–2.7) cm wide, lanceolate

to oblanceolate, occasionally almost linear, base cuneate to narrowly truncate, often somewhat auriculate, usually clasping the stem at least slightly, apex acute to attenuate, the lowest leaves occasionally obtuse, margin sharply serrate, rarely bluntly toothed or entire. Upper stem leaves usually much reduced in size over central stem leaves (those of second pair below the terminal raceme (0.7–)1–5(–6) cm long and an eighth as long as to two-thirds as long as [or rarely longer than] the internode directly above), similar in shape to central stem leaves, but often entire or only remotely serrate. Flowers borne in 1–5(–8) racemes, raceme axis densely pubescent throughout, some (usually many) of the trichomes 0.13–0.2 mm long, often to 0.25 mm long; floral bracts lanceolate, attenuate, mostly 3–6 mm long and 1–2.5 mm wide (the lowest pair sometimes as much as 12 mm long); flowers (18–)22–33(–36) mm long, tightly packed, adjacent calyces at anthesis mostly overlapping a quarter to half or more of their lengths. Calyx conspicuously glandular-punctate or not, lacking stalked glands, tube at anthesis (3.5–)4–7 mm long, lobes acute to cuspidate, (1–)1.5–2.5(–3) mm long; calyx at fruit maturity (6.5–)7–10(–10.5) mm long. Corolla pale lavender to white (rarely brighter lavender), spotted and sometimes streaked inside with purple, puberulent to tomentulose. Nutlets 2–3(–3.5) mm long, trigonal with concave to slightly convex sides, surface smooth. CHROMOSOME NUMBER:  $2n = 38$ .

REPRESENTATIVE SPECIMENS: **Alabama.** **Montgomery Co.:** 2 mi S of Montgomery, *Kral & Demaree* 30947 (VDB, SMU, FSU). **Sumter Co.:** 3.3 mi S of Dancy, *Kral* 42992 (VDB). **Arkansas.** **Hempstead Co.:** Fulton, *Palmer* 8028 (MO, PH). **Yell Co.:** Plainview, *Demaree* 63819 (KANU, VDB, NCU, SMU, MIN). **Georgia.** **Baker Co.:** 1 mi NE of Newton, *Thorne* 4372 (GA, F, MO, CU). **Kansas.** **Cherokee Co.:** 1 mi N of Columbus, *McGregor* 15659 (NY, KANU, NCU, GH, SMU). **Montgomery Co.:** 3 mi E of Sycamore, *McGregor* 14380 (KANU, NCU, SMU). **Louisiana.** **Caddo Parish:** 3.2 mi E of Trees City, *Shinners* 26178 (GH, SMU). **St. Tammany Parish:** Covington, near entrance to Pontchartrain Causeway, *Demaree* 49985 (YPI, PH, SMU). **Mississippi.** **Kemper Co.:** E of Scooba, *Jones* 12542 (MISS, NY, GH, GA). **Lee Co.:** near Verona, *Cooley & Ray* 5247 (GH, VDB, NCU, FSU). **Missouri.** **McDonald Co.:** roadside and in Blackjack-Post Oak savanna, *Buck* 255 (OKL). **Oklahoma.** **Ottawa Co.:** 0.5 mi NE of Quapaw, *Wallis* 7260 (KANU, NCU, GA, TEX, SMU, OKL). **Sequoyah Co.:** 0.5 mi S of Gore, *Wallis* 7495 (KANU, NCU, TEX, SMU, OKL). **Texas.** **Bowie Co.:** 0.5 mi W of Hooks, *Lundell & Lundell* 16039 (NY, GH, LL). **Burnet Co.:** 4 mi W of Bertram, *Rogers, Albers & Barksdale* 6870 (PH, MICH, F, TEX).

DISTRIBUTION AND HABITAT (map: Fig. 15): moist prairies, meadows, ditches, river bottoms, and marshy areas, from extreme southwestern Georgia (1 record) and eastern Alabama to central Texas, north to Missouri and Kansas.

FLOWERING. early April through the third week in July (rarely the end of July).

*Physostegia angustifolia* is the archetype of the polythetic species. It is easily recognized by a suite of correlated traits, not one of which is reliably diagnostic in itself. The leaves of *P. angustifolia* are usually sharply serrate, but in one population in Oklahoma (*Cantino* 1079, GH) some plants have entire leaves. The leaves usually clasp the stem to some degree, but when they are particularly narrow the clasping base is inconspicuous or lacking. The rhizome is usually short and strictly vertical, but elongate horizontal rhizomes are produced by many plants in a limited area of northwestern Louisiana and southwestern Arkansas (*Lundell* 16032, LL, GH, NY, TEX; *Moore* 6057, GH; *Cantino* 1074, GH). The corolla is characteristically very pale lavender to white, but reddish violet floral variants are known.

A character that is highly useful in distinguishing *Physostegia angustifolia* from the sometimes similar *P. virginiana* ssp. *praemorsa* is

the length of the trichomes that compose the raceme vesture (Fig. 6a,b). The distinction is quite evident at a magnification of 10x, but a higher magnification (60x) is necessary to quantify it. *Physostegia angustifolia* consistently has some (and usually many) trichomes 0.13 to 0.25 mm in length, while *P. virginiana* ssp. *praemorsa* rarely has even a few over 0.1 mm long. Exceptions are extremely rare in both taxa, accounting for at most 1–2% of the specimens. The exceptions in *P. virginiana* ssp. *praemorsa* are widely scattered through its range, whereas in *P. angustifolia* the exceptions are concentrated in north-western Arkansas.

The distribution of *Physostegia angustifolia* (Fig. 15) is strikingly discontinuous; it is composed of three discrete sections in which the species has been abundantly collected, separated by an extensive area where it appears to be rare. Surprisingly, there are no consistent morphological differences between the plants of the three areas; the interpopulational variation within the easternmost range segment is at least as great as the variation between the three segments. Shinnars (1951) has recognized the plants from the Edwards Plateau region as *P. edwardsiana*, asserting that they differ from *P. angustifolia* in being slightly taller, having a later blooming period, and in having leaves that are serrated only in the apical two-thirds of the blade (versus all the way to the base in *P. angustifolia*). I have not found any of these distinctions to survive a wider survey of *P. angustifolia*, and I agree with Lundell (1969) who synonymized *P. edwardsiana* under *P. angustifolia*.

A widely distributed collection made by Roland Harper north of Tuscaloosa, Alabama is problematical (Harper 3531). The population from which the specimens were collected in 1936 is now extinct due to the damming of the North River to form Lake Tuscaloosa, but enough specimens are in existence (13 plants on 8 sheets) to provide a sample of the morphological variation in the population.

Although the collection is more similar to *Physostegia angustifolia* than to anything else, there are five characters in which three or more specimens have a character state atypical of the species, and one of them, the presence of stalked glands in the inflorescence, is unknown in *P. angustifolia*. The glands are present on three specimens (F, NY, PH), where they are produced in abundance on the calyx and sparingly on the axis of the raceme. In 4 of the 13 specimens the raceme vesture consists of trichomes that are shorter than is usual in *P. angustifolia*, few of them exceeding 0.1 mm in length. In 4 of the 13 specimens, the flowers are arranged rather loosely in the raceme, a condition that is infrequent in *P. angustifolia*. At least the lower leaves on nearly all of the specimens are bluntly toothed to entire, and in 5 specimens the leaves do not clasp the stem. Both of these condi-

tions occur infrequently in *P. angustifolia*, entire leaves much more rarely than non-clasping leaf bases.

The only other taxon to which the Tuscaloosa plants bear any resemblance is *Physostegia virginiana* ssp. *virginiana*. Although the presence of stalked glands in the inflorescence of some specimens might suggest affinities with *P. virginiana*, in which such glands occur frequently, the majority of the Tuscaloosa plants differ from *P. virginiana* in having leaves that clasp the stem slightly and in having longer trichomes (frequently over 0.1 mm) on the raceme axis, both conditions characteristic of *P. angustifolia* and extremely rare in *P. virginiana* south of the Ohio River.

Perhaps the most likely explanation for the high variability of the population is that it represents a hybrid swarm, possibly a remnant of a rather old hybridization event. Morphology points to *Physostegia angustifolia* and *P. virginiana* ssp. *virginiana* as likely parents, but the absence of the latter from Alabama (see Fig. 17) argues against a recent hybridization. These two taxa might, however, have been sympatric in central Alabama during the Wisconsin glaciation, when the range of *P. virginiana* probably shifted southward to some extent. Another unusual specimen, collected along the Chattahoochee River in Early Co., Georgia (Thorne 5395, CU), also appears to be intermediate between *P. virginiana* and *P. angustifolia*, in that it possesses the stalked glands and non-clasping leaves of the former and the longer trichomes of the latter; Wisconsin-age sympatry and hybridization could account for the characteristics of this collection as well as the Tuscaloosa population.

In view of the extensive variation within the Tuscaloosa population in characters that are usually diagnostic of *Physostegia angustifolia*, I cannot state with certainty that the population represents that species. For the same reason, it is not possible to describe a new taxon at the specific or infraspecific level based on that population. There are some specimens (e.g., the left-hand specimen on the sheet at WIS) that do not differ in any way from normal *P. angustifolia*, while others (F. NY) differ in three to four characters. This interesting population is best left without formal recognition.

## 8. *Physostegia digitalis* Small

*Physostegia digitalis* Small, Bull. Torrey Bot. Club **25**: 613. 1898. LECTOTYPE: Louisiana, *Hale s.n.* (NY), here designated.

Erect, robust, perennial herbs to 2 m high, with 9–13(–16) nodes below the inflorescence. Rhizome strictly vertical and usually unbranched, up to 10 cm long. Lower and middle stem leaves all sessile or the lowest 1–4 pairs petiolate, the petiolate leaves early deciduous; sessile leaves often having 1–3 pairs of weak primary veins (other

than the midrib) arising from base of blade, 5–17 cm long, 1.5–7 cm wide, broadly oblanceolate or obovate to elliptical, less frequently ovate, base rounded to cuneate, usually somewhat auriculate and strongly clasping the stem, apex acute (to acuminate) upwards on stem and obtuse (to acute) downwards, margin repand to subentire or bluntly toothed (rarely a few leaves sharply serrate). Upper stem leaves much reduced in size over central leaves (those of second pair below the terminal raceme 1–3[–6] cm long and less than a fourth as long as to longer than the internode directly above), oblanceolate to lanceolate, the sessile base cuneate and sometimes slightly clasping, apex attenuate, margin sharply serrate, sometimes bluntly toothed or entire. Flowers borne in 1–11 racemes, raceme axis densely pubescent to tomentose throughout, trichomes mostly 0.2–0.3 mm long, a few stalked glands occasionally present; floral bracts lanceolate to ovate, attenuate, 3–9 mm long, 1.5–4 mm wide; flowers 25–41 mm long, tightly packed, adjacent calyces at anthesis overlapping half or more of their lengths. Calyx never conspicuously glandular-punctate but occasionally bearing stalked glands, tube at anthesis 4–8.5 mm long, lobes mostly attenuate to cuspidate, 1.5–4 mm long; calyx at fruit maturity 7–13 mm long. Corolla pale lavender to whitish, usually spotted inside with purple, glabrous to subglabrous, occasionally sparsely puberulent. Nutlets 2–3(–3.3) mm long, trigonal, sides usually slightly concave, surface smooth. CHROMOSOME NUMBER:  $2n = 38$ .

REPRESENTATIVE SPECIMENS. **Louisiana.** **Beauregard Parish:** 8 mi W of Longville, *Thomas* 30929 (NLU). **De Soto Parish:** S of Evelyn on La-177, *Thomas* 45729 (NLU). **Vernon Parish:** 8.3 mi S of Leesville, *Shinners* 20597 (GH, SMU). **Texas.** **Bowie Co.:** New Boston, *Lundell* 13995 (LL, SMU). **Hardin Co.:** Clear Lake Estates, between Kountze and Silsbee, 4 July 1970, *Amerson & Watson s.n.* (SMU). **Harrison Co.:** 0.8 mi E of Hallsville, *Shinners* 28600 (NCU, FSU). **Jefferson Co.:** between Cheek and Fannett, *Lundell & Lundell* 14733 (US, LL, SMU). **Upshur Co.:** 8.5 mi N of Ore City, *Shinners* 18965 (SMU). **Van Zandt Co.:** 6.3 mi S of Canton, *Van Vleet* 1629 (SMU).

DISTRIBUTION AND HABITAT (map: Fig. 15): moist, open pinewoods in western Louisiana and eastern Texas.

FLOWERING: mid-June through late July.

The two specimens that were cited in the protologue as being "the original specimens" can be found, mounted together on a single sheet, at the New York Botanical Garden. Both were collected in Louisiana, one by W. M. Carpenter and one by Josiah Hale. Of the two, the Hale specimen is the more consistent with Small's description, the leaves and floral bracts of the Carpenter specimen being smaller than those described in the protologue. For this reason, I have selected the Hale specimen as the lectotype.

*Physostegia digitalis* is among the most distinctive species in the genus and exhibits little geographical variation. It is easily recognized by its overall robustness, its large, broadly obovate to elliptic, entire to bluntly toothed leaves, its densely crowded flowers with long, attenuate to cuspidate calyx lobes, and its densely pubescent to tomentose raceme axis, the trichomes composing the vesture being the longest in the genus (mostly 0.2–0.3 mm long). A few specimens of *P. purpurea* from eastern North Carolina (e.g., *Ahles & Haesloop* 30027, NCU), which are at the broad end of the leaf shape gradient exhibited by that species, bear a superficial resemblance to *P. digitalis*. How-

ever, they are easily distinguished on the basis of the length of the trichomes on the raceme axis, those of *P. purpurea* rarely reaching and never exceeding 0.2 mm in length. In addition, the calyx lobes of *P. purpurea* are rarely cuspidate and are generally shorter than those of *P. digitalis*.

### 9. *Physostegia correllii* (Lundell) Shinnery

*Dracocephalum correllii* Lundell, *Wrightia* 1: 165. 1947. HOLOTYPE: Texas, Val Verde Co., along stream near the International Bridge at Del Rio, 26-VI-1946, *Correll & Correll* 12890 (LL; missing, not seen). ISOTYPE: SMU.  
*Physostegia correllii* (Lundell) Shinnery, *Rhodora* 51: 120. 1949.

Erect, robust, perennial herbs to 13 dm high, with 10–24 nodes below the inflorescence. Primary rhizome branching to produce an extensive system of elongate, horizontal secondary and tertiary rhizomes up to 50 cm long. Lowest 3–6 pairs of stem leaves petiolate and usually early deciduous. Central stem leaves sessile, conspicuously glandular-punctate when dried, the venation conspicuous, with 1–3 pairs of primary veins (other than the midrib) arising from the base of the blade, 3–9(–17) cm long, 1–5(–8) cm wide, broadly elliptical to obovate or occasionally ovate, base cuneate to rounded and clasping the stem at least slightly, apex acute to acuminate (occasionally a few lower leaves, or leaves on side branches resulting from damage to main shoot, may be obtuse), margin sharply serrate to base of blade, occasionally bluntly toothed or entire. Upper stem leaves gradually reduced, similar in shape and only slightly smaller than central leaves, those of second pair below the terminal raceme 2–5(–10) cm long and nearly as long as to more than twice as long as the internode directly above. Flowers borne in 1–5(–9) racemes, raceme axis densely pubescent to puberulent, at least a few nonglandular trichomes over 0.1 mm long, stalked glands usually scattered throughout; floral bracts ovate to lanceolate, attenuate, (3–)4–6(–7) mm long, 1.5–3 mm wide; flowers 21–33 mm long, tightly packed, adjacent calyces at anthesis usually overlapping half or more of their lengths. Calyx conspicuously glandular-punctate, usually bearing stalked glands as well, tube at anthesis 3–6(–7) mm long, lobes acute to cuspidate, 2–4 mm long; calyx at fruit maturity 5.5–9(–10.5) mm long. Corolla lavender, boldly spotted and streaked inside with purple, tomentulose to subglabrous and sometimes bearing a few stalked glands. Nutlets 2–3.1 mm long, trigonal with flat to strongly convex sides, surface smooth. CHROMOSOME NUMBER:  $2n = 38$ .

SPECIMENS EXAMINED: **United States.** **Louisiana.** Cameron Parish: 9 mi E of Grand Lake, *Cantino* 1064 (GH). St. Charles Parish: ditch along Mississippi River levee and river road, Montz, near parish line, *Montz* 3416 (LAF, NO). **Texas.** Bexar Co.: San Antonio, *Wilkinson* 44 (MO); San Antonio, *Wilkinson* 83 (MO); near San Antonio, 1900–1902, *Wilkinson* s.n. (MO). Galveston Co.: east side of High Island, *Waller* 3659 (GH). Harris Co.: 6 mi N of Humble, *Boon* 108 (TEX). Travis Co.: Colorado River bank at Montopolis bridge, *Tharp* 53–202 (TEX). Val Verde Co.: Del Rio, *Cory* 4674 (GH); 1 mi N of International Bridge to Villa Acuna, *Correll & Johnston* 18204 (LL); 2 mi S of Del Rio, *Correll & Johnston* 19427 (LL). **Zapata Co.:** Old Zapata, *Villarreal* 30 (SMU). **Mexico.** Coahuila: Saltillo, *Palmer* 2043 (GH); Monclova, *White* 1781 (GH, MICH); Muzquiz, 1936, *Marsh* s.n. (TEX); Melchor, Muzquiz, *Latorre* 47 (TEX). **Nuevo Leon:** near Monterrey, 14-VII-1888, *Pringle* s.n. (LL, VT); Monterrey, Santa Catarina, *Arsene* 6224 (GH, US, MO) [=Abbon 82]; Cercado, *Salinas et al.* 16M14 (TEX). **Sonora:** Near Santa Cruz, *Wright* 653 [1536] (GH, PH).

DISTRIBUTION AND HABITAT (map: Fig. 16): river bottoms and ditches, from southern

Louisiana to northeastern Mexico (1 record from Sonora); widespread but rare.

FLOWERING: the third week of June through the end of September.

*Physostegia correllii* is characterized by having rather broad leaves, rarely more than four times as long as wide, at least the upper ones with one to three pairs of weak primary veins (in addition to the midrib) arising from the clasping base of the blade (Fig. 4d), by the presence of conspicuous glandular dots on the calyx and upper leaf surface (conspicuous in dried material only), and by the production of elongate, horizontal rhizomes.

There are two rather odd specimens of a single collection (White 1781, GH, MICH) from near Monclova in Coahuila, Mexico, whose affinities are clearly with *Physostegia correllii* but which differ in having entire to subentire leaves that are somewhat narrower than is usual in the species. Since the leaves of *P. correllii* are usually serrate, a case could be made for recognizing a new variety on the basis of these specimens. However, two collections (Latorre 47, Marsh s.n.) from Muzquiz, a town about 100 miles from Monclova, appear to be intermediate between the Monclova collection and the more usual forms of *P. correllii*; although the leaves on these two specimens are as narrow as those from Monclova, their margins are remotely but sharply serrate. With collections of *P. correllii* as scarce as they are, it would seem unwise to recognize a variety when there is evidence that it may represent the endpoint of a cline of variation, the apparent morphological gap between it and the rest of the species being possibly only a collecting gap.

The distribution of *Physostegia correllii* exhibits a sizable disjunction (Fig. 16) owing to the existence of a single collection from northern Sonora, Mexico (Wright 1536, GH, PH). The Wright specimens have slightly smaller leaves and less crowded flowers than is usual in *P. correllii*, but they are not otherwise distinctive. Although the gap between the site of the Wright collection and the nearest collection site of *P. correllii* to the east stands out as a particularly large disjunction, the species as a whole appears to be rather sparsely distributed over a large area, perhaps due to disruption of a formerly more continuous range.

*Physostegia correllii* is classed as "endangered" in the 1974 Smithsonian report to the Congress of the United States and in the more recent revision of that list (Ayensu & DeFilipps, 1978). It has recently been recommended that its status be changed to "threatened" (R. S. Irving, personal communication). As rare as it is, and tending as it does to grow in habitats subject to human and natural disturbance (e.g., roadside ditches, river bottoms), there can be no doubt that it



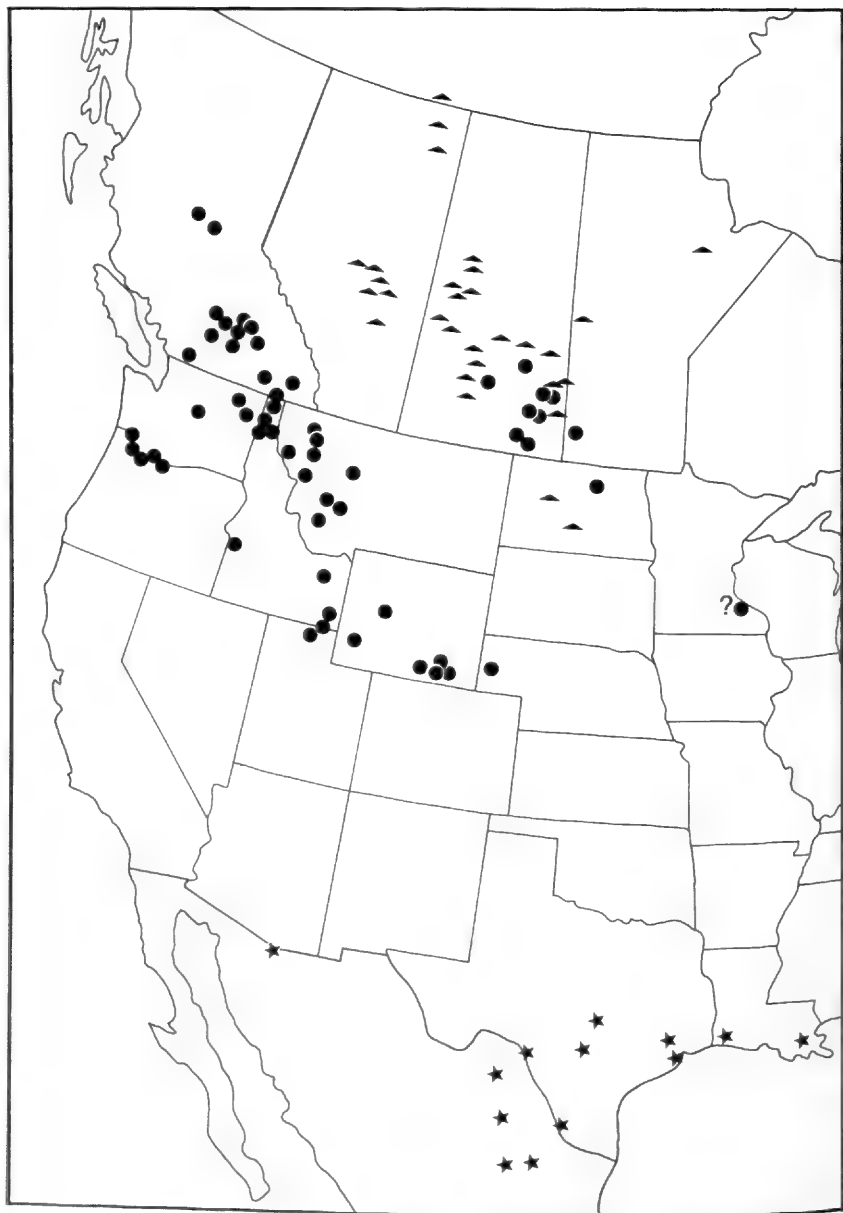


FIG. 16. Distribution map of *Physostegia correllii* (stars), *P. parviflora* (circles), and *P. ledinghamii* (triangles).

is in an extremely vulnerable position. Every effort should be made to protect the few remaining populations.

# 10. *Physostegia parviflora* Nuttall ex Gray

*Physostegia parviflora* Nutt. ex Benth. in D.C. Prodr. 12: 434. 1848. As synonym.

*Physostegia parviflora* Nutt. ex Gray, Proc. Am. Acad. 8: 371. 1873. Not valid (no description; cites *P. parviflora* Nutt. ex Benth., itself not a valid name).

*Physostegia parviflora* Nutt. ex Gray, Synopt. Fl. 2: 383. 1878. Not *Dracocephalum parviflorum* Nutt. Gen. N. Am. Pl. 2: 35. 1818. Lectotype: Columbia R., Nuttall s.n. (BM), here designated.

*Physostegia virginiana* var. *parviflora* (Nutt. ex Gray) Boivin, Nat. Canad. 93: 575. 1966.

*Dracocephalum nuttallii* Britton in Britt. & Brown, Ill. Fl., 2nd ed., 3: 117. 1913.

Based on *P. parviflorum* Nutt. ex Benth.; not superfluous because the combination *Dracocephalum parviflorum* would be a later homonym of *D. parviflorum* Nutt.

*Physostegia nuttallii* (Britt.) Fassett, Rhodora 41: 525. 1939.

Erect perennial herbs to 7 dm high, with 9–15 nodes below the inflorescence. Rhizome branched or unbranched, vertical or more frequently horizontal, up to at least 12 cm long. Lower and middle stem leaves all sessile or the lowest pairs petiolate, the petiolate leaves early deciduous; sessile leaves usually having 1–3 pairs of weak primary veins (other than the midrib) arising from base of blade, 2–10.5(–13.5) cm long, 0.3–2.3(–3.3) cm wide, lanceolate or narrowly ovate to elliptical, never widest above middle of blade, base cuneate in lowest leaves, truncate to rounded upwards, most or all leaves clasping the stem strongly, apex obtuse to attenuate, margin sharply to bluntly toothed, the lower leaves sometimes subentire. Upper stem leaves little reduced, slightly smaller to slightly larger than central leaves (those of second pair below the terminal raceme 2–11 cm long and two-thirds as long as to twice as long as the internode directly above), usually with 1–3 pairs of weak primary veins arising from base of blade, ovate to lanceolate, at least 1 pair usually widest near base, the base rounded to broadly truncate and strongly clasping the stem, apex acute to attenuate, margin sharply to bluntly toothed. Flowers borne in 1–8(–12) racemes, raceme axis densely puberulent, nonglandular trichomes never more than 0.15 mm long, stalked glands scattered throughout; floral bracts ovate to lanceolate, acute to attenuate, mostly 2–4 mm long and 1.5–2.5 mm wide (the lowest pair sometimes up to 11 mm long); flowers 9–16 mm long, tightly packed, adjacent calyces at anthesis overlapping half or more of their lengths. Calyx not conspicuously glandular-punctate but always bearing stalked glands, tube at anthesis (2.5–)3–5 mm long, lobes acute, 0.7–2 mm long; calyx at fruit maturity 4.5–7.5 mm long. Corolla lavender to reddish violet, spotted and streaked inside with purple, densely puberulent to subglabrous, occasionally tomentulose, usually bearing a few stalked glands. Nutlets 2.1–3.3 mm long, trigonal with flat to slightly convex sides, surface smooth. CHROMOSOME NUMBER:  $2n = 38$ .

REPRESENTATIVE SPECIMENS: **Canada. British Columbia.** 1 mi N of S end of Mara Lake, *Calder & Savile 11834* (DAO, ALTA); Vanderhoof, *Calder et al. 13539* (DAO); upper Arrow Lake, 16 mi N of Nakusp, *Calder 37145* (DAO). **Manitoba.** Virden, *Scoggan 11196* (GH). **Saskatchewan.** Weyburn, 17 July 1938, *Bolton s.n.* (SCS); Qu'Appelle Valley Region, S of Ellisborough, *deVries 214* (DAO). **United States. Idaho.** Bonner Co.: Camp Bay, Lake Pend Oreille, *Pennell 21281* (GH, PH). **Canyon Co.:** Falk's Store, *Macbride 314* (NY, IA, GH, WTU, MO, ILL, RM, US). **Montana.** Flathead Co.: Flathead Lake, *Somers, Muensch & Muensch 11386* (CU, WTU). **North Dakota.** Benson Co.: Leeds, 31 July 1907, *Lunell s.n.* (NY, IND). **Oregon.** Multnomah Co.: Rooster Rock Park, just E of Portland, *Taylor & Staudt 4264* (DAO). **Utah.** Cache Co.: 2 mi W of Mendon,

Smith 1889 (RM). Washington. Clarke Co.: mouth of Lewis River, 6 Sept 1892, *Henderson s.n.* (WTU). Pend Oreille Co.: 3 mi SW of Usk, Kreager 320 (WTU). Wyoming. Albany Co.: 12 mi S of Laramie, Porter 6021 (DAO, NY, GH, WTU, SMU, RM).

DISTRIBUTION AND HABITAT (map: Fig. 16): wet meadows, ditches, gravelly and marshy areas along lake shores and river banks, from central British Columbia south to Oregon, northern Utah, and Wyoming, and from southeastern Saskatchewan to northern North Dakota. A single specimen, collected in 1883 at Lake City, Minnesota (*Manning s.n.*, NY), would appear to represent a considerable eastward extension of the range of *Physostegia parviflora*. However, the validity of the record is questionable. A second specimen (GH) collected by Manning on the same date is a representative of *P. virginiana* ssp. *virginiana*. Neither specimen is in any way uncharacteristic of the taxon to which it belongs. There are no additional collection data accompanying either specimen to indicate whether or not they were collected at the same site. In the absence of any other record of *P. parviflora* east of north-central North Dakota, I suspect that the Manning specimen may have been collected elsewhere and mislabeled.

FLOWERING: late June to mid-September.

*Index Kewensis* cites two references to the name *Physostegia parviflora*, but in neither instance was the name validly published. The first publication was by Bentham, who attributed it to Nuttall but merely listed the name in synonymy with *P. imbricata* Hook., without referring to any earlier published description. The second reference in *Index Kewensis* is to a use of the name by Gray which has no nomenclatural status. It consists only of a reference to the earlier invalid publication of the name by Bentham and lacks a description. The earliest valid publication appears to be that of Gray (1878). He again attributed the name to Nuttall, citing Bentham's initial publication of it as well as his own use of the name in 1873, but for the first time a description was provided.

I have seen two specimens (BM, PH) that would undoubtedly be considered to be type material if Nuttall, himself, had published a description of the species. Both are labeled in Nuttall's hand as being *Physostegia parviflora*, and the collection data on both consist solely of the name "Columbia R." Because the first description to accompany a publication of this name was supplied not by Nuttall, but by Gray, the situation is more complicated. However, it seems best to choose one of the two Nuttall collections as the lectotype inasmuch as Gray and Nuttall are known to have been in frequent contact during Nuttall's later years in North America (Graustein, 1967). It is highly probable that Gray saw either Nuttall's specimens of *Physostegia parviflora* or a manuscript based on them, and that his own description was based directly on these materials. Bentham's original citation of "*P. parviflora* Nutt.! mss." in synonymy with *P. imbricata* Hook. indicates that a manuscript description of some kind existed at that time; Nuttall supplied many such descriptions to Torrey and Gray (Graustein, 1967).

It is not surprising that of the two specimens of *Physostegia par-*

*viflora*, the one in the British Museum is by far the better (see p. 69), the collection in the herbarium of the Philadelphia Academy being but a fragment. The specimen in the British Museum fits Gray's description perfectly. It is not unlikely that Gray saw it, either before Nuttall left for England or after Nuttall's death, when his personal collection was deposited in the British Museum. Gray spent a year in England beginning in September of 1868 (Dupree, 1968), and he would presumably have had the opportunity to examine Nuttall's specimens at that time. In consideration of these facts, I have chosen as the lectotype of *Physostegia parviflora* the specimen in the British Museum. According to Graustein (1967), Nuttall collected *P. parviflora* during the midsummer of 1835 at The Dalles, a narrows of the Columbia River in the region where it forms the border between Wasco County, Oregon and Klickitat County, Washington.

*Physostegia parviflora* is characterized by its small and densely crowded flowers, the presence of stalked glands on the calyx and corolla, and the broadly clasping upper stem leaves, some of them usually widest near the base of the blade. The only species with which it could be confused is *P. ledinghamii*. The distinctions between the two species and the probable hybrid origin of the latter are discussed elsewhere (Cantino, 1981a).

A cladistic analysis based on morphological characters (see p. 46) suggests that *Physostegia correllii* is the closest extant non-hybrid relative of *P. parviflora*. Although not strikingly similar in overall appearance, the two species share several characters that are infrequent in the genus as a whole. The most unusual characteristic of *P. parviflora* is the presence of stalked glands on the corolla. I have been able to find at least a few on better than 95% of the specimens of *P. parviflora*. These glands are also present on a quarter of the specimens of *P. correllii* and a third of those of *P. ledinghamii*. This trait is very rare elsewhere in the genus, although stalked glands are present on the calyx and the axis of the inflorescence in several other species. A second uniting characteristic is the unusual leaf venation that is universally present in *P. correllii* and occurs in about 90% of the specimens of *P. parviflora*. In addition to the midrib, there are one to three pairs of weak primary veins that arise from the clasping leaf base and ascend part way up the blade. This venation also occurs commonly in *P. pulchella* and *P. digitalis* and infrequently in several other species, but it is more prominent in *P. correllii* and *P. parviflora* than in the others.

The distribution of *Physostegia parviflora* exhibits a notable disjunction (Fig. 16), the two segments of the range separated by a gap that is 350 miles wide at its narrowest point. It is probable that the species had a more continuous distribution shortly after the most re-

cent glaciation and has since been eliminated from the intervening zone by the advent of drier climatic conditions. This hypothesis is supported by palynological evidence that the intervening prairie region was occupied by a spruce-dominated forest during the Wisconsin glaciation. This spruce forest was replaced by prairie vegetation about 12,000 years ago in Kansas and Nebraska and about 10,000 years ago in south-central Canada (Wright, 1970; Ritchie, 1976).

# 11. *Physostegia ledinghamii* (Boivin) Cantino

*Physostegia ledinghamii* Boivin ex Fraser & Russell, Annot. List Pl. Sask.: 36. 1953.  
As synonym.

*Dracocephalum ledinghamii* (Boivin) Russell, Ledingham & Coupland in Fraser & Russell, Annot. List Pl. Sask.: 36. 1953. No description; cites only an unpublished basionym.

*Physostegia virginiana* var. *ledinghamii* Boivin, Nat. Canad. 93: 574. 1966. First valid publication of the basionym. HOLOTYPE: Saskatchewan, Swift Current District, Caribou, "15 milles au nord, platière sablonneuse de la Saskatchewan du Sud," 28-VII-1952, Boivin & Alex 9978 (DAO).

*Physostegia ledinghamii* (Boivin) Cantino, Rhodora 83: 111. 1981.

Erect perennial herbs to 1 m high, with 9–16 nodes below the inflorescence. Primary rhizome branching to produce 1-many elongate, horizontal secondary and tertiary rhizomes. Lower and middle stem leaves all sessile or the lowest 1–5 pairs petiolate, the petiolate leaves usually early deciduous; sessile leaves sometimes having 1–3 pairs of weak primary veins (other than the midrib) arising from base of blade, 4–15 cm long, 0.5–3 cm wide, narrowly elliptical to lanceolate or oblanceolate, base cuneate to narrowly truncate, at least the upper leaves clasping the stem slightly, apex acute to attenuate or the lower ones sometimes obtuse, margin sharply serrate or the lowest ones bluntly toothed to subentire. Upper stem leaves gradually reduced, often only slightly smaller than central leaves (those of second pair below the terminal raceme 3–13 cm long and about as long as to nearly three times as long as the internode directly above), occasionally with a few weak primary veins arising from base of blade, lanceolate to narrowly elliptical, widest at to below middle of blade but usually not near the base, the base cuneate to rounded and clasping the stem, apex attenuate, margin sharply serrate. Flowers borne in 1–7(–9) racemes, raceme axis densely pubescent; floral bracts ovate to lanceolate, attenuate, mostly 2.5–4.5 mm long and 1–2.5 mm wide (lowest pair sometimes up to 11 mm long); flowers 14–23 mm long, tightly packed, adjacent calyces at anthesis usually overlapping half or more of their lengths. Calyx not conspicuously glandular-punctate but bearing stalked glands, tube at anthesis (3–)3.5–5.5 mm long, lobes acute, 1–2 mm long; calyx at fruit maturity (5–)6–8 mm long. Corolla lavender to reddish violet, spotted and streaked inside with purple, densely puberulent to subglabrous, occasionally tomentulose, sometimes bearing a few stalked glands. Nutlets 2.8–4 mm long, trigonal with flat to slightly convex sides, surface smooth. CHROMOSOME NUMBER:  $2n = 76$ .

REPRESENTATIVE SPECIMENS: **Canada. Alberta.** Fort Saskatchewan, *Turner 4979* (ALTA); near Manola, 26 July 1968, *Rusconi s.n.* (ALTA); near Clyde, ca. 45 mi N of Edmonton, *McCalla E2692* (ALTA). **Manitoba.** Le Pas, 21 July 1936, *Howe s.n.* (DAO, TRT, SCS). **Northwest Territories.** Salt River, *Loan 137* (DAO, ALTA, MO). **Saskatchewan.** Tisdale, *Breitung 1790* (DAO, ALTA, SMU); island S of North Battleford in North Saskatchewan River, *Frankton 945* (DAO); Green Lake Village, *Harms 16792* (DAO, GH). **United States.** **North Dakota.** McLean Co.: Ft. Berthold Indian Reservation, *Heidenreich 210* (OKL).

DISTRIBUTION AND HABITAT (map: Fig. 16): low, wet woods and swampy areas along

lake shores and stream banks, from northeastern Alberta to northeastern Manitoba, south to North Dakota.

FLOWERING: early July through late August.

See Cantino (1981a) for a discussion of the probable hybrid origin of *Physostegia ledinghamii* and a table of the diagnostic characters by which it can be distinguished from its putative parents, *P. virginiana* and *P. parviflora*.

## 12. *Physostegia virginiana* (L.) Bentham

Erect perennial herbs to 18 dm high, with 10–34 nodes below the inflorescence. Primary rhizome branched or unbranched, vertical or horizontal, up to 65 cm long. Lower and middle stem leaves all sessile or the lowest 1–7 pairs petiolate, the petiolate leaves usually early deciduous; sessile leaves 2–18 cm long, 0.2–4.4(–5.5) cm wide, most often elliptical to oblanceolate, varying to lanceolate, ovate, obovate, spatulate or linear, base attenuate to cuneate, less frequently rounded, rarely clasping the stem, apex acute to attenuate (occasionally the lower leaves obtuse and rarely all leaves obtuse), margin most often sharply serrate, less frequently bluntly toothed and rarely entire. Upper stem leaves scarcely to greatly reduced in size over central stem leaves and similar in shape, those of the second pair below the terminal raceme 0.8–11 cm long and a third as long as to four times as long as the internode directly above. Flowers borne in 1–16(–20) racemes, raceme axis densely puberulent to pubescent throughout or sparsely so to glabrous towards base, nonglandular trichomes rarely more than 0.15 mm long with stalked glands sometimes intermixed; floral bracts lanceolate to ovate, attenuate, mostly 2–8 mm long and 1–2.5 mm wide (the lowest bracts occasionally larger and intergrading with foliage leaves); sterile floral bracts often present below the flowers; flowers (13–)14–37 mm long, tightly to loosely spaced, adjacent calyces overlapping or not. Calyx conspicuously glandular-punctate or not, sometimes bearing stalked glands, tube at anthesis 2.5–8 mm long, lobes acute to attenuate (occasionally cuspidate), (0.6–)0.8–3 mm long; calyx at fruit maturity 4–10(–11) mm long. Corolla reddish violet to lavender to white, usually spotted and streaked inside with purple, densely puberulent or tomentulose to glabrous. Nutlets 2.1–4.2 mm long, trigonal with concave to convex sides, surface smooth. CHROMOSOME NUMBER:  $2n = 38$ .

### ARTIFICIAL KEY TO THE SUBSPECIES (NATIVE PLANTS ONLY)

This key is not intended to be used for cultivated forms of *Physostegia virginiana*; these are variable in morphology and may in some cases represent artificial intersub-specific hybrids. Garden escapes frequently key to ssp. *praemorsa* at couplet D. In-

asmuch as the vast majority of the specimens that actually represent ssp. *praemorsa* will key out at couplet A, those keying to this subspecies at couplet D should be viewed with suspicion, particularly if they were not collected in the region specified in the first lead of the latter couplet.

Rhizome distinctions are illustrated in Fig. 1, leaf bases in Fig. 4(a,c), and sterile bracts in Fig. 9a.

- A. Perennating buds borne directly on rootstock or at ends of short, vertical secondary rhizomes, the clones forming tight clumps. .... 12b. *P. virginiana* ssp. *praemorsa*.
- A. Perennating buds borne at ends of elongate, horizontal secondary rhizomes originating on rootstock, the clones forming widely spreading stands. .... B.
- B. Leaves 2.5–4 times as long as wide, the largest 4–8 cm long, some clasping stem slightly; Transylvania Co., N. Carolina. .... 12b. *P. virginiana* ssp. *praemorsa*.
- B. Leaves either longer or narrower than the above, all of them merely sessile; widespread. .... C.
- C. Flowers on dried specimens 13–24 mm long (longer when fresh). .... 12a. *P. virginiana* ssp. *virginiana*.
- C. Flowers on dried specimens 25–35 mm long (longer when fresh). .... D.
- D. Inflorescence usually bearing 3 to many pairs of sterile bracts below flowers; prairies, cedar glades, limestone barrens, and occasionally along streams; scattered through Tennessee, northern parts of Georgia and Alabama, eastern Arkansas, perhaps in Kentucky and southern Illinois. .... 12b. *P. virginiana* ssp. *praemorsa*.
- D. Inflorescence rarely bearing more than 2 pairs of sterile bracts below flowers; margins of rivers, streams, lakes, and bays; Lake Erie to southern Quebec, south commonly to Maryland and West Virginia, sparingly to central Virginia and northeastern Tennessee. .... 12a. *P. virginiana* ssp. *virginiana*.

## 12a. *Physostegia virginiana* (L.) Benth, ssp. *virginiana*

NAMES BASED ON CULTIVATED FORMS OF *PHYSOSTEGIA VIRGINIANA*, INCLUDING NATURALIZED ESCAPES.

*Dracocephalum virginianum* L. Sp. Pl. 2: 594. 1753. LECTOTYPE: Linn. Herb. Cat. no. 746.1 (LINN, not seen; photo seen at GH), designated by Epling, Journ. Bot. 67: 10. 1929.

*Physostegia virginiana* (L.) Benth. Bot. Reg. sub tab. 1289. 1829. Not validly published because the combination is not explicitly proposed (Art. 33.1, 1978 Int. Code Bot. Nom.).

*Physostegia virginiana* (L.) Benth. Lab. Gen. et Sp. 504. 1834. First valid publication of the combination.

*Dracocephalum denticulatum* Ait. Hort. Kew. 2: 317. 1789. HOLOTYPE: BM (not seen); photographs seen at GH. Taxonomic affinities of the type are not absolutely certain (Cantino, 1981b).

*Physostegia denticulata* (Ait.) Benth. Bot. Reg. sub tab. 1289. 1829. Not validly published because the combination is not explicitly proposed.

*Physostegia virginiana* var. *denticulata* (Ait.) Gray, Synopt. Fl. N. Am. 2: 383. 1878, not Chapman 1860.

*Physostegia denticulata* (Ait.) Britton, Mem. Torr. Bot. Club 5: 284. 1894.

*Physostegia virginiana* forma *denticulata* (Ait.) Benth. ex Sieb. & Voss, Vilm. Blum. 1: 856. 1895.

*Dracocephalum lancifolium* Moench, Meth. Pl. 410. 1794. Superfluous name (*D. virginianum* L. cited in synonymy).

*Dracocephalum speciosum* Sweet, Br. Fl. Gard. 1: tab. 93. 1825. Not *D. speciosum* Benth. in Wallich, Pl. Asiat. Rar. 1: 65. 1830. Type unknown.

*Physostegia speciosa* (Sweet) Sweet, Hort. Brit., ed. 2, 406. 1830.

- Physostegia virginiana* var. *speciosa* (Sweet) Gray, Synopt. Fl. 2: 383. 1878.  
*Physostegia virginiana* forma *speciosa* (Sweet) Benth. ex Sieb. & Voss, Vilm. Blum. 1: 856. 1895.  
*Dracocephalum virginianum* var. *speciosum* (Sweet) Farwell, Pap. Mich. Acad. Sci. Arts & Lett. 1: 97. 1923.  
*Physostegia imbricata* Hook. in Curt. Bot. Mag., new ser., 9: tab. 3386. 1835. TYPE: in the Hooker Herbarium (K).  
*Dracocephalum louisianum* Hort. in Lem. Hort. Univ. 4: 298. 1845. Type unknown.  
*Dracocephalum louisianum* Hort. in Karsch, Phan. Fl. Prov. Westf. 797. 1853. Type unknown.  
*Dracocephalum regelii* Hort. ex Sieb. & Voss, Vilm. Blum. 1: 856. 1895. As synonym.  
*Physostegia latidens* House, Bull. N.Y. St. Mus. 176: 38. 1915. HOLOTYPE: New York, along roadside and in a field west of State Road, just south of Utica, 10-VIII-1912, *Haberer 3084* (NYS).  
*Physostegia nivea* Lundell, Wrightia 5: 70. 1974. HOLOTYPE: Texas, Dallas Co., cultivated in garden; plants from Strybing Arboretum, San Francisco, California. 10-VI-1974, *Lundell 18837* (LL). ISOTYPE: GH.

NAMES BASED ON WILD REPRESENTATIVES OF *P. VIRGINIANA* SSP. *VIRGINIANA*.

- Physostegia formosior* Lunell, Bull. Leeds Herb. 2: 7. 1908. LECTOTYPE: North Dakota, Ward Co., in the timber along Souris River at Minot, 22-VIII-1908, *Lunell 883* (MIN), selected by Elizabeth McClintock but never published. ISOLECTOTYPES: MIN(2).  
*Dracocephalum formosius* (Lunell) Rydberg, Brittonia 1: 95. 1931. Not *Dracocephalum formosum* Gontsch. Not. Syst. Herb. Inst. Bot. Acad. Sci. URSS 7: 101. 1938.  
*Physostegia virginiana* var. *formosior* (Lunell) Boivin, Nat. Canad. 93: 574. 1966.  
*Physostegia speciosa* var. *glabriflora* Fassett, Rhodora 41: 377. 1939. HOLOTYPE: Wisconsin, Racine, *Hale s.n.* (WIS).  
*Physostegia granulosa* Fassett, Rhodora 41: 377. 1939. HOLOTYPE: Canada, Prov. Quebec, Cap-Rouge, greves estuariennes, 21-VIII-1928, *Marie-Victorin 28178* (WIS). ISOTYPE: GH.  
*Physostegia virginiana* var. *granulosa* (Fassett) Fernald, Rhodora 45: 464. 1943.  
*Dracocephalum virginianum* var. *granulosum* (Fassett) Core, Castanea 37: 301. 1972.  
*Physostegia formosior* forma *alba* J. W. Moore, Rhodora 52: 58. 1950. HOLOTYPE: Minnesota, Roseau Co., growing in wet ground 1/4 mile northwest of Warroad, 2-VIII-1939, *Moore & Moore 11399* (MIN).  
*Physostegia virginiana* forma *alba* (Moore) Boivin, Nat. Canad. 93: 574. 1966.  
*Physostegia virginiana* var. *elongata* Boivin, Nat. Canad. 93: 573. 1966. HOLOTYPE: Canada, Prov. Quebec, Ile Perrot, marecages au bord des eaux, 1-IX-1927, *Marie-Victorin & Rolland-Germain 29005* (DAO). ISOTYPES: DAO, GH.

Primary rhizome usually branching to produce an extensive system of elongate, horizontal secondary and tertiary rhizomes up to 65 cm long. Central stem leaves 0.3–4.3(–5.5) cm wide, elliptical to lanceolate, oblanceolate, or spatulate, margins sharply serrate, less frequently bluntly toothed, rarely entire. Flowers borne in 1–16(–20) racemes, raceme axis pubescent or puberulent, nonglandular trichomes frequently up to 0.15 mm long, rarely to 0.20 mm; sterile floral bracts usually not present below flowers; flowers (13–)14–28 mm long, tightly to loosely spaced, adjacent calyces overlapping or not. Calyx tube at anthesis 2.5–6(–7) mm long, lobes (0.6–)0.8–2.2(–3) mm long; calyx at fruit maturity 4–9.5(–11) mm long. Nutlets 2.1–4.2 mm long. CHROMOSOME NUMBER:  $2n = 38$ .

REPRESENTATIVE SPECIMENS (native range of ssp. *virginiana*): **Canada.** Manitoba. Brandon, *Stevenson 552* (DAO); Morden, *Scoggan 11486* (GH, MIN, ALTA). Ontario. Welland Co.: Point Abino, *Glowne 2926* (BH, PENN). York Co.: Center Island, Toronto, *Watson 190* (TRT). Quebec. Montmorency Co.: Ile d'Orleans, 2 mi E of Ste-Pétronille, *Perras 71–758* (OS, SCS). Quebec Co.: Cap Rouge, *Marie-Victorin 21570* (DAO, GH, PH). United States. Illinois. Peoria Co.: N of Averyville, Peoria, *Chase 3690* (ILL). Indiana. Allen Co.: S of Fort Wayne, *Deam 2552* (IND). Hamilton Co.: just N of Noblesville, *Deam*



12141 (IND). **Iowa.** Cedar Co.: 0.5 mi SE of Rochester, *Fay* 1283 (IA). **Johnson Co.:** Lake McBride State Park, 12 Aug 1956, *Pfeifer s.n.* (IA). **Kansas.** Douglas Co.: 2 mi S of Lone Star, *McGregor* 615 (KANU). **Kentucky.** Jefferson Co.: Islands at Falls of Ohio, 1840, *Short s.n.* (CM, PH). **Maryland.** Montgomery Co.: Stubblefield Falls, *Killip* 32175 (MICH). **Michigan.** Houghton Co.: Otter Lake, *Hyypio* 350 (MSC, MICH). **Minnesota.** Blue Earth Co.: 2 mi SW of Mankato, *Moore* 25309 (MIN). Roseau Co.: 1/4 mi NW of Warroad, *Moore & Moore* 11400 (TEX, WIS, KANU, MIN, OKL, SMU). **Missouri.** Andrew Co.: 2.5 mi SW of Amazonia, *Steyermark* 70052 (F). **New York.** Essex Co.: Lake Champlain, Mullen Bay, *Muenschner, Manning & Maguire* 503 (NCU, CU). **North Dakota.** McHenry Co.: Towner, 12 Aug 1908, *Lunell s.n.* (US, MIN, NY, PH, MO). Pembina Co.: St. Thomas, *Larson* 3522 (KANU). **Ohio.** Ottawa Co.: Bay Twp., Winous Point, *Lowden* 766 (OS). Van Wert Co.: 3.5 mi N of Delphos, *Stuckey* 6327 (OS). **Pennsylvania.** Erie Co.: Presque Isle, 12 Aug 1879, *Guttenberg s.n.* (CM). **Lycoming Co.:** W branch of Susquehanna River opposite Jersey Shore, *Westerfeld & Wahl* 3009 (OKL, SMU, FSU, DAO, WVA, DUKE, NCU). **South Dakota.** Vermillion (near Big Stone Lake), *Johnson* 90 (IA, NY, GH, MICH, WTU). **Vermont.** Chittenden Co.: Burlington, Lake Champlain, *Charette* 695 (DAO, VT, FSU, SMU). **West Virginia.** Barbour Co.: Arden, 22 June 1973, *Bush s.n.* (WVA). **Preston Co.:** Erwin, 23 July 1959, *Bartholomew & Vail s.n.* (US, LL, MO, SMU, FSU, DAO, MSC, NY, GH, DUKE, TENN, NCU, GA). **Wisconsin.** Buffalo Co.: Mississippi River bottoms opposite Wabasha, Minnesota, *Fassett & Hotchkiss* 3456 (MIN, GH).

DISTRIBUTION AND HABITAT (map: Fig. 17): river and stream banks, lake and bay shores, drainage ditches, marshes, estuaries, and other moist sites, from Quebec to Manitoba, south to northeastern Kansas, southern Illinois, northern Tennessee, and eastern Virginia.

FLOWERING: mid-June through mid-October.

The type specimen of *Dracocephalum virginianum* L. appears to be a cultivated plant. Epling (1929), who selected one of the two specimens in the Linnean Herbarium, believed it to be of garden origin. After examining a photograph of the specimen, I have no reason to disagree with his interpretation. Although the species is based on a cultivated plant, the application of the specific epithet to one of the two native subspecies does not present a problem.

*Physostegia virginiana* was cultivated in Europe at least as early as 1674 (Boccone, 1674), and the cultivars grown there at the time of Linnaeus probably were the offspring of more than one introduction. It seems reasonable to assume that most if not all of the introductions before 1753, when Linnaeus described the species, originated from the eastern seaboard of North America near the few major settlements within the range of *P. virginiana*. The more southerly subspecies occurs from western Virginia and central North Carolina to northeastern Mexico, north to central Missouri, northern Illinois, and western Ohio (Figs. 17 and 18). The northern subspecies occurs naturally within 60 miles of Philadelphia, within 40 miles of Baltimore, and along the St. Lawrence River in the vicinity of both Montreal and Quebec City. Because the latter subspecies probably gave rise to the plants cultivated in 18th century Europe, of which the lectotype of *Dracocephalum virginianum* is a representative, it is the most reasonable candidate to bear the specific epithet.

*Physostegia virginiana* is the most widespread and variable species

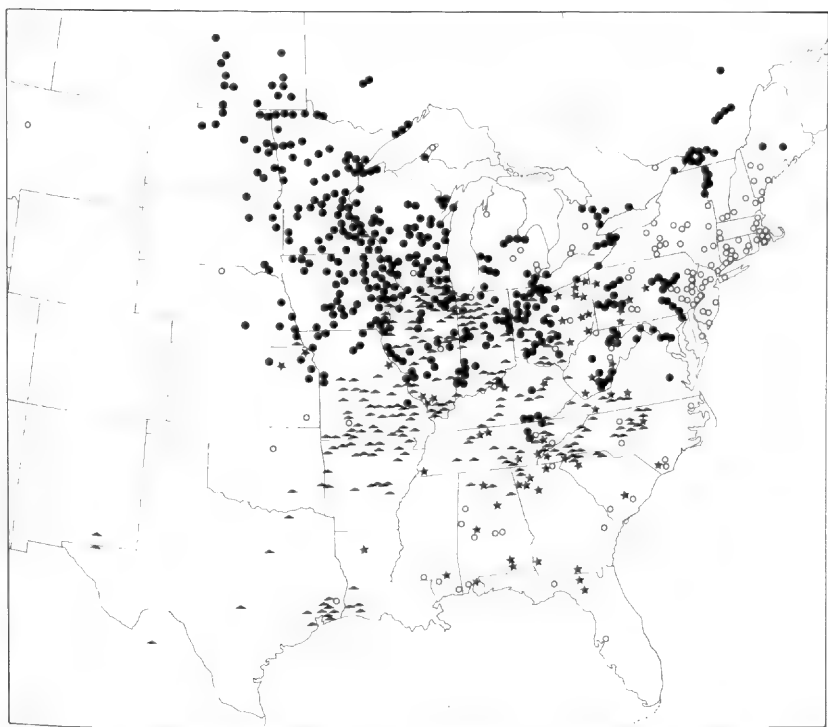


FIG. 17. Distribution map of *Physostegia virginiana*. Ssp. *virginiana* (closed circles); ssp. *praemorsa* (triangles); garden escapes (open circles); uncertain subspecific affinities, probably mostly garden escapes (stars).

in the genus. Intraspecific taxa have been described in piecemeal fashion, but Boivin (1966) has made the only attempt to apportion the variation within the entire species into a limited number of precisely defined varieties. While his approach is laudable, his attempt to define his eight varieties so that they are mutually exclusive has produced a collection of rather artificial taxa. Most of the varieties Boivin recognizes correspond to real morphogeographical entities, but the sharply defined limits he provides are not a true reflection of the natural situation, where there is considerable morphological overlap.

Illustrative of the problem is the degree of intergradation that exists between two varieties of *Physostegia virginiana* that are among the most distinctive and widely accepted—var. *granulosa* and var. *formosior*. The former ranges from the St. Lawrence River and Lake Champlain to West Virginia and northern Tennessee, and the latter

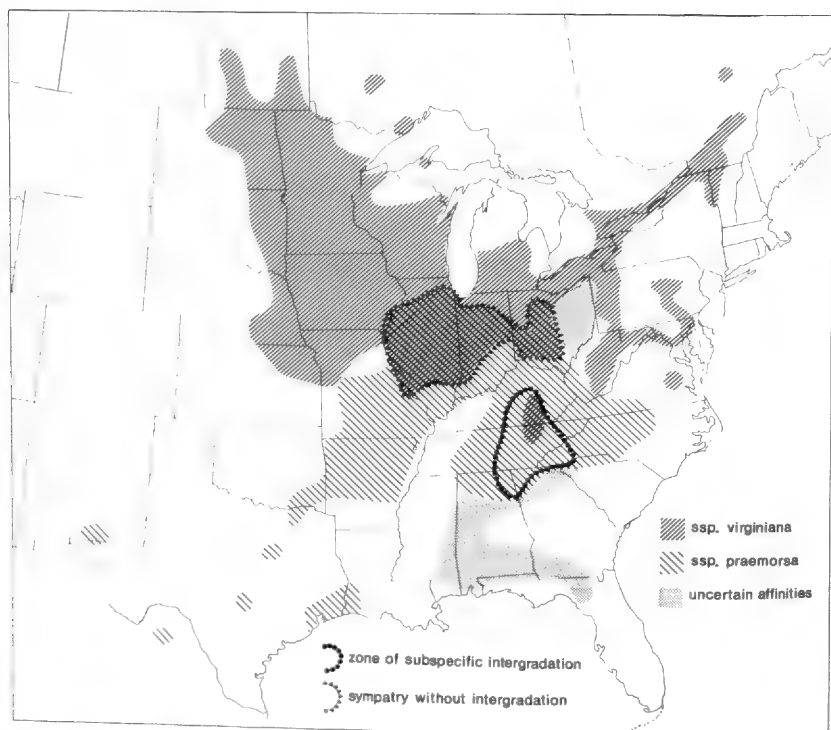


FIG. 18. Subspecific sympatry and intergradation in *Physostegia virginiana*. Plants of "uncertain affinities" are probably garden escapes (see text). Definite garden escapes have been omitted.

from Manitoba to Michigan, south to northeastern Kansas and south-central Ohio. Not only is there overlap in all the characters that distinguish the two varieties when they are delimited in such a way that they are strictly allopatric, but they intergrade through a series of populations connecting their geographic ranges. The plants that frequent the shores of Lake Erie and Lake Ontario resemble var. *formosior* in some characters, var. *granulosa* in others, and are intermediate in others yet (Table 20). Specimens from the western end of Lake Erie, nearest to the range of var. *formosior*, resemble that variety more closely than do those from Lake Ontario or the eastern end of Lake Erie. My observations of populations at both ends of Lake Erie suggest that intrapopulational variation is not great and that they are probably not hybrid swarms. The intergradation between the two varieties is more plausibly a case of simple clinal variation rather than the result of hybridization.

TABLE 20. INTERGRADATION OF *PHYSOSTEGIA VIRGINIANA* VAR. "GRANULOSA" AND VAR. "FORMOSIOR".

<i>P. virginiana</i> var. " <i>granulosa</i> "	<i>P. virginiana</i> of Lake Erie, Ontario	<i>P. virginiana</i> var. " <i>formosior</i> "
Plants 2-10 dm high	Plants 4-14 dm high	Plants 3-16 dm high
Widest leaf 0.5-1.8(-2.2) cm wide	Widest leaf 0.5-2.0 cm wide	Widest leaf (0.5-)1.2-4.2 (-5.5) cm wide
Leaf serrations frequently confined to apical half of blade	Leaf serrations confined to apical half of blade, or not	Leaf serrations rarely confined to apical half of blade
Apices of leaf teeth blunt or sharp	Apices of leaf teeth sharp	Apices of leaf teeth sharp
Some stem leaves usually widest above middle of blade	Stem leaves widest above middle of blade, or not	Stem leaves rarely widest above middle of blade
Flowers loosely or tightly spaced	Flowers tightly spaced	Flowers tightly spaced
Leaf length of second pair below terminal raceme ÷ length of internode above = 0.3-1.8(-2.1)	Leaf length of second pair below terminal raceme ÷ length of internode above = (0.7-)0.9-2.3 (-3.1)	Leaf length of second pair below terminal raceme ÷ length of internode above = 1.2-3.8
Fruiting calyx (5-)6-9.5 (-11) mm long	Fruiting calyx 5-8(-10) mm long	Fruiting calyx (4-)4.5-7 mm long
Length ÷ width of fruiting calyx = 1-2	Length ÷ width of fruiting calyx = 0.8-1.7	Length ÷ width of fruiting calyx = 0.7-1.2

There is little point in formally recognizing varieties that intergrade as completely as do var. *granulosa* and var. *formosior*. However, there is too much geographic variation in the species to ignore completely. Instead, I have recognized two wide-ranging subspecies. They are easily distinguished throughout most of their range but intergrade in one of their two regions of sympatry (Fig. 18). Because the two subspecies do not intergrade in the other (larger) zone of sympatry, and because the number of cases of intergradation is much less than when a system of numerous varieties is used, the proposed classification involving two subspecies is preferable on both theoretical and pragmatic grounds.

The best distinction between the subspecies is the form of the rhizome. *Physostegia virginiana* ssp. *virginiana* nearly always produces elongate, horizontal rhizomes (Fig. 1a), each terminated by an overwintering bud. Subspecies *praemorsa* usually lacks horizontal rhizomes; its perennating buds are borne either directly on the rootstock (Fig. 1b) or at the ends of short, vertical rhizomes that branch off

from the lower portion of the rootstock and ascend directly to the surface.

Exceptions occur in both subspecies. Depauperate individuals of *ssp. virginiana* may not produce any horizontal rhizomes. I have seen few examples of this in the field, but it occurs commonly enough in the greenhouse. In addition, there is a population of plants in Hardy Co., West Virginia (Cantino 908, GH) that resemble the local race of *ssp. virginiana* but lack horizontal rhizomes. Throughout much of the range of *ssp. praemorsa*, horizontal rhizomes are never produced. It is primarily in the eastern half of Tennessee and adjacent parts of Georgia, Alabama, and North Carolina that members of some populations that otherwise appear to be *ssp. praemorsa* possess horizontal rhizomes. The two subspecies intergrade in this region, a situation that is discussed below.

Garden transplant experiments indicate that intraspecific variation in the form of the rhizome is not merely a plastic response to edaphic conditions. Thirty plants from 10 populations of *ssp. virginiana* and 70 plants from 18 populations of *ssp. praemorsa* were grown together in the garden. With the exception of a few depauperate individuals of *ssp. virginiana*, they all produced the same rhizome morphology as that produced in their natural habitat.

A second character correlated with the short, vertical rhizome of *ssp. praemorsa* is the production of empty floral bracts below the flowers in response to a long photoperiod (see p. 25). There are two requirements that must be satisfied if the empty bracts are to be produced: first, the plant must have the genetic potential to respond to the proper photoperiod; and second, the proper photoperiod must be provided. Because the latter requirement is not always satisfied under natural conditions, an observed absence of empty bracts is of no taxonomic significance, but the presence of the bracts is a reasonably good diagnostic character for *ssp. praemorsa*.

The determination of the degree of correlation between the two defining characters of *ssp. praemorsa* requires experimental manipulation. Nineteen plants (from 9 populations) that lacked horizontal rhizomes and 28 plants (from 8 populations) that possessed them were grown under a 16-hour photoperiod (see p. 25 for further details of the study). Seventeen of the 19 plants (89%) that lacked horizontal rhizomes produced empty bracts, whereas 27 of the 28 plants with horizontal rhizomes (96%) failed to produce empty bracts. Although the sample size was small, the plants tested were taken from widely scattered populations, so the results should be reasonably representative of the degree of correlation that exists in nature. Only specimens from natural populations were included in this study; empty bract production is quite common in the cultivated forms of *Physo-*

*stegia virginiana*, all of which have horizontal rhizomes.

The subspecies are sympatric in parts of Illinois, Indiana and Ohio (Fig. 18), where they occupy somewhat different habitats, ssp. *praemorsa* most often growing in prairie vegetation or on open wooded slopes, while ssp. *virginiana* is most frequently found in swampy areas along rivers, lakes, and man-made ditches. In this region the two subspecies differ in several additional characters that are diagnostic locally but do not hold true throughout the range of the species (i.e., degree of reduction of the upper stem leaves, leaf texture, and flower length). They have been treated as distinct species in at least two floristic works of the region (Deam, 1940; Jones, 1963), and hybridization between them is probably infrequent because of their differing habitats. There are a number of collections from the Chicago area that may be hybrids, but outside of that area there is very little evidence of intersubspecific hybridization. If ecological isolation is indeed preventing hybridization, it would not be surprising to see a breakdown of isolation in areas where human disturbance is extensive.

There is a smaller zone of subspecific sympatry in southeastern Kentucky and northeastern Tennessee (Fig. 18), where the two taxa intergrade both ecologically and morphologically. Subspecies *virginiana* is confined to streamsides in this area; ssp. *praemorsa* occurs along streams occasionally but is found more frequently in open woods, limestone barrens, and prairie-like sites. The foliar and floral characteristics that distinguish the two subspecies farther north do not hold true in Kentucky and Tennessee, and even the primary characters, rhizome morphology and the potential to produce empty floral bracts, are less well correlated in this region than elsewhere.

The most interesting aspect of the intraspecific variation pattern of *Physostegia virginiana* is the existence of two separate regions of subspecific sympatry, in one of which the subspecies intergrade, while in the other they remain ecologically and morphologically distinct. This situation is most adequately explained by a hypothesis of circular overlap (Mayr, 1963). Subspecies *praemorsa* and "var. *formosior*" of ssp. *virginiana*, the two infraspecific taxa of *Physostegia virginiana* that co-occur without intergradation in the Lower Great Lakes States, are connected by a chain of intermediates. "Variety *formosior*" intergrades with the eastern race of ssp. *virginiana* ("var. *granulosa*") via a group of morphologically intermediate populations along Lake Erie (Table 20 and related text). "Variety *granulosa*," in turn, intergrades with ssp. *praemorsa* in eastern Tennessee and parts of adjacent states (the "zone of subspecific intergradation" in Fig. 18). This pattern of morphological variation can be explained by hypothesizing a divergence of ssp. *virginiana* from ssp. *praemorsa* (or the divergence of both subspecies from a common ancestor) in or near the "zone of

subspecific intergradation," followed by their northward migration along separate pathways, concomitant with continued morphological and ecological divergence. By the time they came into secondary contact in the Lower Great Lakes States, they had attained both ecological isolation and a high degree of morphological distinctness. The hypothesized route of the migration and its timing in relation to the Wisconsin glaciation are discussed elsewhere (Cantino, 1980: 256–268).

The frequent naturalization of cultivated *Physostegia virginiana* presents a problem when one is identifying seemingly wild specimens to subspecies. The cultivated forms apparently always produce the horizontal rhizomes characteristic of native ssp. *virginiana*, but some cultivars bear a closer resemblance to ssp. *praemorsa* in other aspects of their morphology. Although the cultivated specimen upon which Linnaeus based the species was almost certainly a member of the subspecies that, for this reason, must be referred to as ssp. *virginiana*, there is no reason to assume that all modern cultivars are purebred descendants of the forms cultivated in 18th century Europe. Some of the showier forms of ssp. *praemorsa* may have been collected by horticulturalists and included in breeding programs. This would explain the much more frequent production of empty bracts in cultivated forms of *P. virginiana* than in wild forms of ssp. *virginiana*, as well as the resemblance of some cultivars to ssp. *praemorsa* in above-ground vegetative morphology. Because the genetic background of modern cultivars is unknown, they cannot reasonably be placed in either subspecies and should not be identified below the species level.

*Physostegia virginiana* commonly escapes from cultivation, and it is probable that even some populations in undisturbed sites owe their origin to the escape of garden plants. The recognition of garden escapes has presented the most serious problem in parts of the southeastern United States, where there are no indisputably native populations with which to compare. Subspecies *praemorsa* occurs commonly across the northern part of Alabama, Georgia, and South Carolina, but I have seen only a scattering of specimens of *Physostegia virginiana* from south of the Appalachian section of these states and from neighboring Mississippi and Florida ("uncertain affinities" in Fig. 18). Many have horizontal rhizomes and the remainder lack underground parts. Because of the relative rarity of collections from that region and the association of many of them with disturbed habitats, I suspect that most such collections represent garden escapes. However, some of the collections come from seemingly natural habitats, and one of these (Thorne 5395, CU) is unlike any cultivated form I have seen.

There is agreement among authors of floristic works that most records of *Physostegia virginiana* from New England, eastern New York, New Jersey, and eastern Pennsylvania represent escapes from culti-

vation (e.g., Britton, 1889; Graves, et al., 1910; Taylor, 1915; Hoffman, 1922; Wagner, 1943; Schaeffer, 1949; Fernald, 1950; Seymour, 1969; Domville & Dunbar, 1970; Harris, 1975). This is supported by herbarium label data indicating that the majority of the specimens from this region were collected along roads, railroads, and in other disturbed areas. *Physostegia virginiana* is absent from many of the older floras dealing with the region, substantiating this view.

The recent spread of *Physostegia virginiana* in the Philadelphia area is particularly well documented. There is no mention of it in Barton's (1818) listing of the indigenous and naturalized plants within a 10-mile radius of Philadelphia. A more recent flora of Philadelphia and vicinity (Keller & Brown, 1905), which covers much of southeastern Pennsylvania, records the species only from the shores of the Susquehanna River, where it is apparently native. In Bucks County, north of Philadelphia, *P. virginiana* was unknown in 1876 (Thomas & Moyer, 1876) and known from but a single locality in 1932 (Benner, 1932). It has been collected from at least four additional sites in Bucks County since then, as well as from numerous localities in nearby Berks, Lehigh, Montgomery, and Philadelphia Counties.

A second example is provided by the Boston area, where *Physostegia virginiana* is somewhat less common than in southeastern Pennsylvania. The species is not mentioned in early 19th century floristic works dealing with Boston (Bigelow, 1824) or Massachusetts (Hitchcock, 1835; Dewey, 1840). In Middlesex County, just northwest of Boston, Dame and Collins (1888) recorded it from only one locality, where it was "probably an escape from cultivation." I have seen more recent specimens from three other sites in Middlesex County, and it now occurs sporadically in most of the counties in eastern Massachusetts.

On the basis of a similar historical approach, it can be stated with near certainty that *Physostegia virginiana* is native nowhere in New Jersey, southeastern New York, Pennsylvania east of the Susquehanna River, or New England, except along the shores of Lake Champlain and possibly the Kennebec and Penobscot Rivers in Maine. Less certain is the status of collections from central New York, central and western Pennsylvania, and eastern Ohio, but it is likely that most records from these areas also represent garden escapes. In Ohio, Newberry (1860) recorded the species from the central and western parts of the state only. Transeau and Williams (1929) mapped it as occurring in eastern Ohio, but only in the counties adjoining Lake Erie. The scattering of more recent collections from nonlacustrine eastern Ohio are probably all escapes from cultivation. In New York, House (1924) states that *P. virginiana* is native from Lake Champlain and Oneida County southward and westward, but 19th century floras dealing with



central and western New York, except the Buffalo-Niagara area where it is apparently native, either do not mention the species (Paine, 1865; Beckwith & Macauley, 1896; Clute, 1898) or indicate that it is known only as an escape from cultivation (Burgess, 1877; Dudley, 1886). In Pennsylvania west of the Susquehanna River, it appears to be native only along the Allegheny-Monongahela-Ohio river system, including several tributaries.

The ostensibly greater abundance of garden escapes in the northeastern states than in the rest of the range of the species is very likely due to the preference of collectors for uncommon or unfamiliar plants. Where *Physostegia virginiana* is native and abundant, the occasional naturalized garden plant will go unnoticed, whereas in the northeast and parts of the southeast, where native *P. virginiana* is rare or absent, garden escapes are much more likely to be collected as a novelty.

The preparation of the distribution map (Fig. 17) has been difficult because the structure of the greatest diagnostic value in distinguishing the two native subspecies—the rhizome—is missing from many herbarium specimens, and because naturalized garden forms of the species are frequently intermediate between the native subspecies. The usual problem is not one of determining to which of the two native subspecies a particular specimen belongs, but whether it represents a native population or a garden escape.

There is no character that is universally useful in distinguishing native plants from garden escapes. However, there are character states frequent enough among the cultivated forms to be of use in certain limited regions, where these traits are absent from native populations. The elongate, horizontal rhizome of the cultivated forms facilitates the recognition of garden escapes in regions where only ssp. *praemorsa* is native. The frequent presence of sterile bracts below the flowers in garden plants helps to distinguish them from native ssp. *virginiana*. The leaves of cultivated plants are usually sharply and deeply serrate, in contrast to the shallowly and bluntly toothed leaves of the Appalachian race of ssp. *virginiana*. Cultivated forms often have five or more racemes, whereas ssp. *praemorsa* and the Appalachian race of ssp. *virginiana* usually do not have more than three. The upper leaves of garden plants are usually not much smaller than the middle leaves, while those of ssp. *praemorsa* and the Appalachian race of ssp. *virginiana* are often much reduced in size. Native ssp. *virginiana* from Wisconsin and Iowa northwestward appears similar to some of the frequently encountered cultivars, but the native plants tend to have shorter calyx tubes and longer trichomes on the axis of the raceme than do most garden forms. If the calyx tube is 4 mm or less long and the axis of the raceme includes some nonglandular tri-

chomes more than 0.1 mm long, then the specimen is almost certainly native. However, the lack of trichomes over 0.1 mm long or the possession of a longer calyx tube does not necessarily indicate that the plant is an escape. Because of their unreliability, these characters must be used with caution.

The proposed infraspecific classification of *Physostegia virginiana* is not without problems. Although the majority of the collections from most parts of its range can be assigned to a subspecies, there are a number of specimens from the southeastern United States that cannot. Indeed, if the southern Appalachian "zone of subspecific intergradation" is, in fact, occupied by the ancestral complex from which the two subspecies diverged, it may not even be reasonable to try to assign specimens from that area to one or the other of the subspecies. The subspecific classification may be similarly inapplicable in Alabama, Mississippi, and Georgia if the specimens from there are relics of the Wisconsin-age range of the ancestral complex.

There is no perfect solution when one is attempting to subdivide a species in which there is circular overlap. If no infraspecific taxa are recognized, the classification will be rejected by those familiar with the region of overlap, where there will be two morphologically and ecologically distinct taxa going by the same name. If the two overlapping "arms" of the species are given formal recognition, as I have chosen to do, the classification will be satisfactory in the region of overlap but problematical in the source area where the two lines diverged. I can only offer the pragmatic suggestion that, in the case of *Physostegia virginiana*, the two subspecies be recognized where they are distinct but that no effort be made to distinguish them in the southern Appalachian region where they intergrade.

**12b. *Physostegia virginiana* (L.) Benth.  
ssp. *praemorsa* (Shinners) Cantino comb. nov.**

- Physostegia praemorsa* Shinners, Field & Lab. 19: 166. 1951. HOLOTYPE: Texas, Fannin Co., 0.6 mi WSW of Honey Grove, chalk outcrop, larger plants from ditch bank, smaller from dry chalk, 16-X-1949, *Shinners 11980* (SMU). ISOTYPE: SMU.
- Dracocephalum variegatum* Ventenat, Descr. Pl. Nouv. Jard. Cels, tab. 44. 1801. Superfluous name (*Prasium incarnatum* Walt. cited in synonymy).
- Physostegia variegata* (Vent.) Benth. Bot. Reg. sub tab. 1289. 1829. Not validly published because the combination is not explicitly proposed.
- Physostegia virginiana* forma *candida* Benke, Am. Midl. Nat. 16: 423. 1935. HOLOTYPE: Illinois, Cook Co., Arlington Heights, 25-VIII-1934, *Benke 5681* (F). ISOTYPES: GH, US.
- Physostegia serotina* Shinners, Field & Lab. 24: 17. 1956. HOLOTYPE: Louisiana, Calcasieu Parish, clay ditch bank on east side of Lake Charles, 9-X-1955. *Shinners 22108* (SMU). ISOTYPES: GH, NY, DUKE, MICH, GA, TEX, WIS, BH, FSU, SMU.
- Physostegia virginiana* var. *reducta* Boivin, Nat. Canad. 93: 572. 1966. HOLOTYPE: Indiana, Cass Co., prairie patch, low sandy area along R.R., 1/2 mile east of Lake Cicott, 26-IX-1936, *Friesner 10132* (DAO). ISOTYPES: NY, GA, OKL, SMU, CU, ILL.

Rhizome short, unbranched, and strictly vertical, or (infrequently) branching to produce elongate, horizontal secondary rhizomes up to 20 cm long. Central stem leaves 0.2–3(–4.4) cm wide, elliptic to oblanceolate, varying to obovate, ovate, spatulate, lanceolate, or linear, the margin sharply serrate. Flowers borne in 1–8 racemes, raceme axis puberulent, nonglandular trichomes usually not more than 0.1 mm long (rarely to 0.13 mm); sterile floral bracts (up to 40 pairs) frequently present below the flowers; flowers (16–)18–37 mm long, usually tightly packed, adjacent calyces at anthesis usually overlapping a quarter to half or more of their lengths. Calyx tube at anthesis (3.5–)4–8 mm long, lobes (0.8–)1–3 mm long; calyx at fruit maturity 6–10 (–11) mm long. Nutlets (2.5–)2.9–3.8(–4) mm long. CHROMOSOME NUMBER:  $2n = 38$ .

REPRESENTATIVE SPECIMENS: **Mexico. Coahuila.** Mpio. de Muzquiz, Rincon de Maria, *Wendt et al.* 1265 (GH). **United States. Alabama.** Colbert Co.: S side of Littleville, *Kral* 44026 (VDB). **Morgan Co.:** Lacey's Springs, *Kral* 48532 (VDB). **Arkansas. Lonoke Co.:** Grand Prairie, *Demaree* 22473 (SMU, MIN, NY, MO). **Prairie Co.:** Hazen, *Demaree* 54730 (SMU, NCU). **Illinois. Vermilion Co.:** Fithian, *Gates* 2170 (MICH). **Indiana. Porter Co.:** 1 mi E of Crisman, *Deam* 21260 (IND). **White Co.:** 3.2 mi S of Reynolds Center, *Webster & Webster* 7129 (NCU, DUKE, MSC). **Iowa.** Muscatine Island, 6 Sep 1895, *Refert s.n.* (IA). **Kentucky. Madison Co.:** Big Hill, *McFarland* 30 (BH, F, GH, NY, PH, IND, US, OKL, WVA, PENN, DUKE, TENN, MICH, MIN, SMU, MO, WIS). **Louisiana. Calcasieu Parish:** Lake Charles, 3.1 mi S of McNeese campus, *Thieret* 27966 (GH, FSU). **Missouri. Benton Co.:** 8 mi NE of Warsaw, *Stephens* 36317 (KANU). **Wright Co.:** 3 mi N of Manes, *Steyermark* 25084 (F). **Nebraska. Richardson Co.:** NE corner of sec. 33, R15E, T3N, *Shildneck C-7140* (KANU). **New Mexico. Eddy Co.:** S. Fork of Big Canyon, E scarp of Guadalupe Mts., *Wendt & Lott* 2126 (GH). **North Carolina. Ashe Co.:** Bluff Mt., *Radford et al.* (*Bozeman et al.*) 45258 (NCU, GA, VDB, TENN, SIU, GH, NY, WVA, MISS, VPI, FSU, MIN, SMU, CM, TEX, LL, WIS, WTU, IND). **Jackson Co.:** 10 mi E of Cherokee, *Correll & Correll* 22533 (LL). **Ohio. Adams Co.:** 2 mi E of Lynx, *Terrell* 1034 (OS). **Marion Co.:** E of Marion, 28 Aug 1939, *Fullerton s.n.* (OS). **South Carolina. York Co.:** just E of York, *Bell* 10097 (NCU). **Tennessee. Blount Co.:** near Rich Gap, *Greene* 4054 (TENN). **Rhea Co.:** between Dayton and Pikeville, *Rogers* 44236 (VPI, TENN). **Texas. Jefferson Co.:** 9 mi W of Beaumont, *Cory* 50021 (NY, GH, MICH, US, SMU, RM). **Liberty Co.:** 3.5 mi E of Moss Hill, *Correll* 34000 (LL). **Virginia. Tazewell Co.:** S side of US-19, 1 mi SW of Little River Branch, *Smyth* 1102 (VPI).

DISTRIBUTION AND HABITAT (map: Fig. 17): western Virginia and central North Carolina to southeastern New Mexico and northeastern Mexico, north to central Missouri, northern Illinois, and northwestern Ohio (one record in extreme southeastern Nebraska, one in southeastern Minnesota). This subspecies occurs in an extraordinary variety of habitats, including prairies, limestone glades and barrens, calcareous outcrops, open woodlands, stream margins, and roadside ditches.

FLOWERING: June through October, rarely to mid-December.

*Physostegia virginiana* ssp. *praemorsa* exhibits considerable variation in the length/width ratio and overall size of the leaves, the degree of reduction of the upper leaves, the presence or absence of stalked glands in the inflorescence, and the size and color of the flowers. However, in contrast to the situation in ssp. *virginiana*, the major part of the variation occurs among populations in the same general area, rather than between regional races. A few races are discernible, but they are less distinct from one another than is the case in ssp. *virginiana*.

The most distinctive race comprises a cluster of populations in southwestern Louisiana and southeastern Texas, separated by 200 miles from their nearest consubspecific neighbor and by 300 miles

from the main body of the subspecies. Shinnors (1956) based his *Physostegia serotina* on representatives of this race, recognizing their affinities to *P. praemorsa* Shinnors, but stating that "*P. serotina* is a larger plant with larger, much deeper-colored corollas which have a more pronounced basal tube, the limb flaring well above the calyx when fully expanded." In addition, the race is characterized by having rather narrow, crowded leaves and a great many empty bracts below the flowers. All of these character states occur commonly elsewhere in the subspecies, and in rare instances they are found in combination in geographically distant populations that are very unlikely to form a monophyletic group with "*P. serotina* Shinnors." For example, a few collections from calcareous cedar glades in northern Alabama are very similar to the type collection of *P. serotina* (e.g., Kral 44026, VDB; Kral 48532, VDB), as are some from the same habitat in Missouri. In northern Alabama, I have seen plants that resemble the type of *P. serotina* intermixed in populations with others that are of the usual Appalachian form of *P. virginiana* ssp. *praemorsa*. Parallel evolution within the subspecies is the most plausible explanation for this situation.

A second distinctive, but very local race occurs at two sites near the Horsepasture River in Transylvania Co., North Carolina (Bannister & Anderson 298, DUKE; Hardin 2297, FSU, GA; Rodgers 62330b, DUKE; Cantino 946, GH). The rather short, broad leaves of these plants are unusual in *Physostegia virginiana* but can be found in a few populations of ssp. *praemorsa* in Polk Co., Arkansas (McWilliam 589, GH, WIS; Backholz 273, WIS). More unusual is the slightly clasping leaf base of this variant (Fig. 4c), a trait that I have observed in only two other

TABLE 21. DISTINGUISHING CHARACTERISTICS OF *PHYSOSTEGIA* *ANGUSTIFOLIA* AND *P. VIRGINIANA* SSP. *PRAEMORSA*.

<i>P. angustifolia</i>	<i>P. virginiana</i> ssp. <i>praemorsa</i>
Flowering April-late July	Flowering (June-) July-December (August-December in zone of sympatry)
Sterile bracts never present below flowers	Sterile bracts frequently present below flowers
Longest nonglandular trichomes on raceme axis 0.13-0.2(-0.25) mm long	Longest nonglandular trichomes on raceme axis not more than 0.1(-0.13) mm long
Stalked glands never present on raceme axis	Stalked glands frequently present on raceme axis
Nutlets 2.0-3.0(-3.5) mm long	Nutlets (2.5-)2.9-3.8(-4) mm long
Leaf base frequently clasping stem	Leaf base rarely clasping stem (never in zone of sympatry)

specimens of *P. virginiana* (Wilkinson s.n., US, CU, from Mansfield, Ohio).

A barely discernible race of *Physostegia virginiana* ssp. *praemorsa* occurs in prairie habitats in Illinois, Indiana, and Ohio, and in a few sites in the extreme eastern parts of Iowa and Missouri. The leaves of these plants tend to be a bit narrower and the upper ones more reduced than is usual in the subspecies. A similar form occurs in isolated prairie patches in Arkansas and Tennessee. The strong resemblance of this prairie ecotype of *P. virginiana* ssp. *praemorsa* to *P. angustifolia* has caused confusion in floristic works. The two taxa can be reliably distinguished on the basis of the length of the trichomes on the axis of the inflorescence (see discussion of this character under *P. angustifolia*). A number of other distinguishing characters, mostly less reliable but more readily observable, are listed in Table 21.

#### EXCLUDED OR DUBIOUS NAMES

- Physostegia truncata* Benth. Lab. Gen. et Sp. 505. 1834. = *Brazoria truncata* (Benth.) Engelm. & Gray.
- Physostegia virginiana* var. *denticulata* Chapm. Fl. South. U.S. 325. 1860. Not *P. virginiana* var. *denticulata* (Ait.) Gray, 1878. Apparently not based on *Dracocephalum denticulatum* Ait.; type unknown; description insufficient to determine affinities.
- Prasium*? *incarnatum* Walter, Fl. Carol. 165. 1788. Probably based on a member of *Physostegia*, but description insufficient to determine specific affinities. Blake's lectotypification of the name with a specimen of *Physostegia virginiana* in the "Walter Herbarium" should be rejected because the specimen disagrees with the description (Cantino, 1981b).

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# SPECIES OF *DRABA*, *LESQUERELLA* AND *SIBARA* (CRUCIFERAE)

REED C. ROLLINS

Vigorous field activity in western North America, particularly in connection with rare and endangered species programs, has brought to light new and interesting taxa in the family Cruciferae. Often several trips to the populations of these new finds were necessary to obtain appropriate material for an adequate study. I am indebted to Barbara Williams of the Shasta-Trinity National Forest staff, Redding, California, for making two trips back to the site where she first collected specimens of *Draba carnosula*. She provided significant notes on the plants as they occur in the field. My thanks to Dr. Thomas Van Devender of the Arizona Natural Heritage Program, Tucson, Arizona, who first sent material of *Sibara grisea*. Also, I am grateful to Dr. Richard Spellenberg of New Mexico State University, Las Cruces, New Mexico, and his wife Marie. They made special collections of *Sibara grisea*, including flowers fixed for morphological studies and buds for chromosome counts. Unfortunately, we did not get positive results from the fixed buds. Research reported in this paper was supported by National Science Foundation Grant DEB78-08766.

## DRABA

The seeds of the large genus *Draba* are almost universally without wings. Among North American species, only two have, in the past, been known that possess winged seeds. These are *D. pterosperma* Payson and *D. asterophora* Payson, both with relatively limited geographical ranges. *Draba pterosperma* appears to be present only in the Marble Mountains of Siskiyou County, California and *D. asterophora* occurs in the mountains of extreme western Nevada and limitedly in the Sierra Nevada Mountains of California. A third species with winged seeds (Fig. 1), not previously known in fruit or with mature seeds, has recently been found near Mt. Eddy in Trinity County, California. This has prompted me to examine the winged nature of the seeds in these three species in relation to the seeds of other species of *Draba*. Murley (1951) states that a distal wing tip is occasionally present on the seeds of *D. glabella* Pursh var. *megasperma* Fern. & Knowlt. However, I have examined over one hundred seeds of this taxon without being able to confirm this observation.

In most species of *Draba*, the seeds are plump and oblong to oval. Often they are tapered toward the funicular attachment and thus take the general shape of a tear-drop. All seeds of these shapes are without the slightest suggestion of a wing. Usually they are slightly com-



FIG. 1. *Draba carnosula* O. E. Schulz. Photograph of Williams 386 (GH). Photo by A. Coleman.

pressed perpendicular to the backs of the cotyledons, which are in an accumbent position with respect to the radicle. The very different winged seeds of the three species mentioned above are similar in that they are strongly flattened, with winged margins that vary from 0.5 to 1.5 mm. wide toward the distal end of the seed. The wings, varying in width, border the seeds all the way around except for the funicular area. The wing is an extension of the outer epidermal layer which forms a sac-like structure enveloping the seed as well as extending beyond it in three directions. In *D. asterophora* and *D. pterosperma*, the epidermal layer forming the wing is loose and often wrinkled over the seed surface but in *D. carnosula* the epidermal layer is very tight-fitting over the seed. Also, the cells of the wing are smaller and the wings themselves are more rigid than those of the other species.

In view of the substantial differences between the winged seeds of the three species under review and those of the bulk of *Draba*, it is pertinent to ask whether the winged seed character has any implications for the generic limits of *Draba*. Winged seeds of the type seen in these species are common in *Arabis*. Were it not for the yellow flowers and scapose habit, *D. carnosula* could possibly be accommodated in *Arabis*. This is not true of *Draba asterophora* and *D. pterosperma*. They are definitely *Draba*-like in habit and in every other character except for the winged seeds. We have not found it difficult to accept both winged and wingless seeds in the genus *Arabis* (Rollins, 1941) and it is my conclusion that the same position must be adopted with respect to *Draba*. Payson (1917) noted that *D. asterophora* and *D. pterosperma* are not closely related but rather appear to be independently related to other species of *Draba*. In the case of *D. carnosula*, there is no apparent close relative among the North American species of *Draba*. Certainly it is not to be associated with *D. howellii*.

*Draba carnosula* O. E. Schulz (1927, p. 82) was described with only a few lines. Subsequently it was treated by Hitchcock (1941) as *D. howellii* var. *carnosula*, again with only a brief characterization. Because of this a full description is given.

Perennial; scapose; caudex simple or occasionally branched, branches slender and straw-colored; leaves rosulate in a small dense cluster, entire, obovate, obtuse, non-petiolate, 4–8 mm. long, 3–4 mm. wide, thickish, glabrous on flat surfaces but margined with simple or branched trichomes, these forked or with 3 or 4 branches; stems one or two, without leaves or bracts, simple, slender, glabrous, 6–12 cm. tall; inflorescence 3- to 6-flowered; flowers remote; sepals ca. 3 mm. long; petals yellow, 5–6 mm. long; filaments slender, ca. 4 mm. long; anthers ovate, ca. 1 mm. long; fruiting pedicels slender, divaricately ascending, straight, glabrous, 4–6 mm. long; siliques divaricately ascending to erect, glabrous, broadly lanceolate to elliptic-lanceolate, flat usually tapering above and below, 13–22 mm. long, 4–6 mm. wide; terminal silique usually erect on an axis up to 12 mm. long, an aborted flower pedicel scar is on the

axis; valves with a strong nerve from base to narrowed apex that subtends the style; styles slender, 2–3 mm. long; stigmas nearly entire, only slightly larger in diameter than styles; septum entire, translucent, central nerve absent or indistinct; ovules 4–6 in each loculus; seeds flat, orbicular, 3–4 mm. in diameter including wings, wings 1–1.5 mm. wide, cotyledons accumbent.

SPECIMENS STUDIED: **California. Trinity Co.:** on a dry, rocky, open hillside in ultrabasic soil at 7,900 ft. elevation, T40, R5W, Sec. 18, Weed Quadrangle, Shasta-Trinity National Forest, near Mt. Eddy, 27 Aug. 1980, *Barbara Williams* 386 (GH); along trail out of basin above upper Deadfall Lake toward pass, vicinity of Mt. Eddy, 8 Aug. 1979, *Barbara Williams* 270 (UC).

*Draba carnosula* is an unusual species in several ways in addition to having widely winged seeds. The fruits are so large in comparison to the size of the basal rosettes and the stems so slender that the plants look top heavy (Fig. 1). The leaf rosettes are scarcely more than 1 cm. across. The siliques are few in number on a given scape. They are remote from each other giving a distinctive appearance to the infructescence.

#### LESQUERELLA

In our treatment of *Lesquerella* (Rollins and Shaw, 1973) we called attention to the disjunct populations of *L. wardii* which differed somewhat from each other but not in a way that seemed to require nomenclatural recognition. For several years, I have been particularly interested in plants of the populations on the Kaibab Plateau of northern Arizona which have shorter styles and on the average a higher number of ovules than Utah material of the species. On the same day in August, 1957, I collected late season plants at two different sites between Jacob Lake and the entrance to the north rim of Grand Canyon National Park. A few days earlier, I had collected typical *L. wardii* on the Aquarius Plateau in Garfield County, Utah. In making comparisons in the field, I was impressed with the differences between these disjunct populations. Another chance to look for the Arizona population with the hope of field study came in June, 1979. To my surprise, the plants we found were white-flowered, not yellow as had been expected. Correlated with the unusual white-flowered feature is a very different trichome type than is present in *L. wardii*. This material represents an undescribed species. Apparently we were too early in the season to find the Arizona populations of *L. wardii* that we had sampled in 1957.

#### *Lesquerella kaibabensis* Rollins, sp. nov.

Perennial with a thickened simple or rarely branched caudex, densely pubescent, trichomes similar throughout; stems prostrate, arising below a terminal cluster of

leaves that form a flat rosette, less than 1 dm. long; radical leaves entire (1)-2-4(-5) cm. long, (5)-8-41(-18) mm. wide, petiole slender, 1-3 times as long as the blade, blades broadly ovate to nearly orbicular, abruptly narrowed to petiole; foliar and cauline trichomes with 3-5 primary radial unfused branches, minutely granular on surface, branches usually forked; cauline leaves cuneate at base, lower sometimes nearly petiolate, narrow to broadly oblanceolate, 5-10 mm. long, obtuse to somewhat acute, usually less than 6 per stem; inflorescences congested, short, few-flowered; pedicels divaricately ascending; straight to slightly sigmoid with young fruit, 5-8 mm. long; sepals narrowly oblong, boat-shaped, 5-6 mm. long, ca. 1.5 mm. wide, outer pair slightly saccate at base; petals spatulate, white, erect, 8-10 mm. long, 2.5-3.5 mm. wide; paired stamens 4-5 mm. long, anthers ca. 1 mm. long; siliques elliptical to broadly oblong, 6-8 mm. long, slightly compressed contrary to plane of septum, densely pubescent, tips of trichomes somewhat flaring, valve interior glabrous; septum entire; styles usually pubescent, 1-2 mm. long; ovules 5-7 in each loculus; funiculi attached to septum by ca. 1/3 their lengths, mature seeds unknown.

Herba perennis pubescentibus; trichomatibus radiis 3-5 non coalescentibus autem probe basin furcatis; caulibus prostratis 5-10 cm. longis; foliis radicalibus rosulatis petiolatis integris (1)-2-4(-5) cm. longis, (5)-8-14(-18) mm. latis, laminis late ovatis vel orbicularibus; foliis caulinis cuneatis anguste vel late oblanceolatis 5-10 mm. longis; inflorescentiis congestis; petalis erectis albis spathulatis 8-10 mm. longis 2.5-3.5 mm. latis; pedicellis adcententibus vel divaricatis 5-8 mm. longis; siliquis ellipticis vel late oblongis parum obcompressis 6-8 mm. longis; stylis pubescentibus 1-2 mm. longis; loculis 5-7 ovulatis; seminibus maturis ignotis.

Holotype in the Gray Herbarium, collected on a limestone-clay knoll, 18.6 miles south of Jacob Lake on road to the north entrance of Grand Canyon National Park, Coconino County, Arizona, June 8, 1979, *Reed C. and Kathryn W. Rollins 79191*. (Isotypes to be distributed.)

The short inflorescences, prostrate stems, and long petioled radical leaves, together with the nonbranching caudex and elongated, somewhat compressed siliques, are features shared by *Lesquerella kaibabensis* and *L. wardii*. Undoubtedly these two species are closely related. But the trichomes with only three to five primary branches, which are forked and with ascending tips, that characterize *L. kaibabensis* are strikingly different from those of *L. wardii* where the 5-7 rayed trichomes are more massive toward the center and the tips lie flat on the leaf surfaces. The siliques are larger and the styles shorter in *L. kaibabensis* than in *L. wardii* except that in the Arizona populations of both species the styles are nearer to the same length. In *L. kaibabensis*, the silique-valves are peculiarly uneven, with depressions and slightly raised portions. This was noticed in the field so it is not a result of drying, but the exact meaning of this feature cannot be assessed without further collections to establish its constancy in the species as a whole. An important difference between the species is in the flower color, white in *L. kaibabensis* and yellow in *L. wardii*.

#### SIBARA

The species group to which *Sibara grisea*, newly described below, belongs occurs in Mexico and west Texas, primarily in the lower Rio



Grande Valley and adjacent areas. Up to now, we have not seen *Sibara* from farther north in the Texas-New Mexico region except for the more widespread and different *S. virginica* which occurs in central and southern Texas eastward in the southeastern states, and with a skip to southern California.

### *Sibara grisea* Rollins, sp. nov.

Annual, greyish green, branched beginning at base, glabrous throughout, slightly fleshy, some branches erect, others ascending, 1-2(-3) dm. tall; leaves monomorphic, pinnately lobed, petiolate, not auriculate, 3-7(-20) cm. long, 1.5-3(-4) cm. wide, lateral lobes broadly oblong to ovate, entire to shallowly sinuate-dentate, terminal lobe triangular, shallowly dentate, larger than lateral lobes; flowers minute; sepals broadly oblong, spreading at anthesis, nonsaccate, green then turning purplish, 2 mm. or less long, slightly more than 1 mm. wide; petals white, spatulate, narrowed to a slender claw, not unguiculate, spreading, 3.5 mm. or less long; stamens spreading, filaments white, anthers oblong, curved, ca. 0.5 mm. long, attached below middle; infructescences 5-15 cm. long, usually extending nearly length of stem; pedicels divaricately ascending, rarely more widely spreading, straight, 5-10 mm. long, reduced upward, scarcely expanded at summit; siliques straight, divaricately ascending, compressed parallel to septum, 2-3 cm. long, 1.5-2.0(-2.5) mm. wide, one-nerved from base to apex with a very short but noticeable gynophore; styles less than 0.5 mm. to 1.5 mm. long; stigmas entire to very faintly lobed, smaller to equal in diameter to style tip on fruits; seeds in a single row, yellowish, compressed, slightly longer than broad, narrowly winged, ca. 1.5 mm. long, ca. 1.2 mm wide, mucilagenous when wetted; cotyledons accumbent.

Herba annua ramosa griseo-viridis glabra plus minusve crassa 1-2 dm. alta; foliis pinnatifidis lobatis petiolatis nonauriculatis 3-7 cm. longis 1.5-3.0 cm. latis; floribus minutis; sepalis nonsaccatis viridis vel purpureis ca. 2 mm. longis, petalis albis anguste-spathulatis ca. 3.5 mm. longis nonunguiculatis; pedicellis rectis divaricatis 5-10 mm. longis, siliquis linearibus rectis 2-3 cm. longis, 1.5-2.0 mm. latis; stylis ca. 0.5 mm. vel 1.5 mm. longis, seminibus oblongis ca. 1.2 mm. latis; cotyledonibus accumbentibus.

Holotype in the Gray Herbarium, abundant in limestone cliff areas, Marble Canyon, Sacramento Mountains, Otero County, New Mexico, elevation ca. 4,400 ft., June 4, 1979, T. R. Van Devender, J. L. Betacourt and M. L. Wimberly s.n. Isotype (ARIZ).

OTHER SPECIMENS STUDIED. **New Mexico.** **Otero Co.:** about 3.5 mi. due E of U.S. Hwy. 70 through Alamogordo, in Marble Canyon of W slope of Sacramento Mts., ca. 5,000 ft., 11 May 1980, *Richard and Marie Spellenberg 5500* (GH); same area, 4 miles E of U.S. Hwy. 70, ca. 6,000 ft., 11 May 1980, *Richard and Marie Spellenberg 5507* (GH). **Texas.** **Hudspeth Co.:** limestone soil, oak-juniper community, Pine Canyon, Guadalupe Mountains National Park, 3 June 1974, *Larry C. Higgins 8535* (WTS).

It is with some hesitancy that the Higgins sheet, consisting of only one plant, is referred to *Sibara grisea* because it differs from the type collection in having longer tapering styles and angular instead of rounded leaf lobes. This collection may represent a different infraspecific taxon at least, or there is a possibility that a distinct species is represented. More complete specimens from the Guadalupe Mountains are needed for a clarification of the situation.

The nearest relative of *Sibara grisea* is *S. runcinata* (Wats.) Roll. which occurs in southwestern Texas and Mexico. In my treatment of

*Sibara* (Rollins, 1947), *S. viereckii* (Schulz) Roll. was recognized but this is now referred to *S. runcinata* as a synonym. *Sibara grisea* is completely glabrous whereas *S. runcinata* is hirsute with simple spreading trichomes toward the base of the stems, more sparsely so on the leaves. The styles on the mature fruits of *S. runcinata* are much longer than in *S. grisea* and the cauline leaves are sessile with auricles usually clasping the stems instead of being petiolate as in the latter species. In the more northerly populations of *S. runcinata*, the auriculate cauline leaves are more definite than in the more southerly material. The problem is that often there is but a single cauline leaf present on a plant. If this occurs near the base of the stem, the leaf usually resembles the basal leaves which are uniformly petiolate and have no auricles. If a cauline leaf occurs near the middle or on the upper part of the stem, then it is auriculate. The unreliability of this feature to mark off a taxon has led us to abandon the recognition of *S. viereckii*.

*Sibara grisea* grows both on cliffs and at the base of cliffs or otherwise nearly barren clayey soil. In the open, the plants are erect and if in a sunny location, they are grey-green. Plants growing on the cliff-face are often appressed to the cliff and in shady places they are less gray and more green than those growing in the open. The plants tend to be fleshy and very brittle. There is a considerable range in the size of the individual plants as is characteristic of many annual species.

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AUGUSTUS FENDLER'S COLLECTION LIST:  
NEW MEXICO, 1846-1847

*Reed C. Rollins*

THELYPODIOPSIS AND SCHOENOCRAMBE  
(CRUCIFERAE)

*Reed C. Rollins*

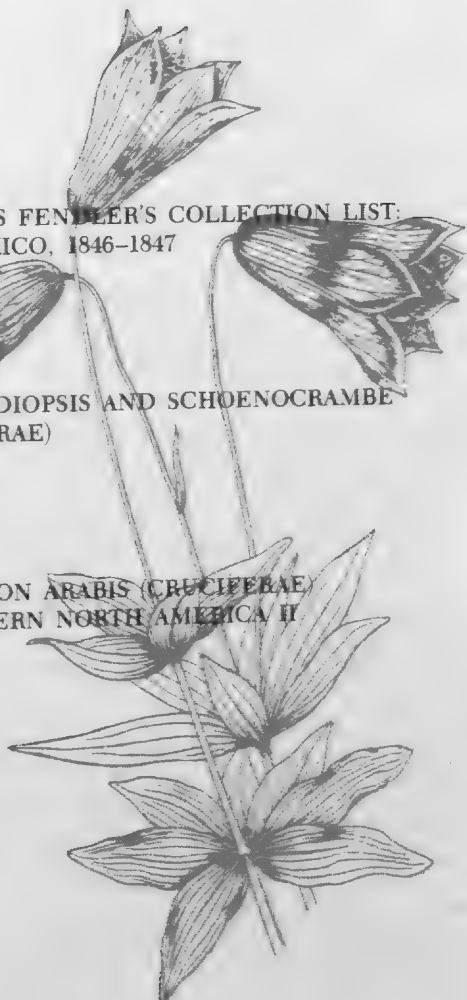
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1846-1847

ELIZABETH A. SHAW

INTRODUCTION

"My needle is slow to settle—varies a few degrees and does not always point due southwest, it is true, and it has good authority for this variation, but it always settles between west and south-southwest. The future lies that way to me, and the earth seems more unexhausted and richer on that side." The words were written by Henry Thoreau (1862); the feelings had long been shared by many Americans, Asa Gray among them. There had developed awareness of the west and conviction that the United States soon must extend to the Pacific—the "manifest destiny" of the nation.

Gray's interest in the west developed early. Even before his first trip to Europe, in 1838-1839, Gray had had a taste of this barely known flora through seeing the plants collected by Lewis and Clark, by Edwin James, by Bradbury, and by Nuttall which he had studied in Philadelphia and in Torrey's herbarium. But when he saw in Glasgow the herbarium of William Hooker, and in England the herbaria of Lambert and others, there was spread before him an array of new and fascinating things from other collectors working in the northern Rockies and in Oregon.

Gray now was hooked. He was totally committed to North American botany and he was acutely aware of the botanical terra incognita of the southern part of the Rocky Mountains. Soon after his return to the United States, Gray met George Engelmann, a German physician and botanist practicing medicine in St. Louis. Engelmann was well situated, at the entry to the west, where he could watch the flood of people headed out over the prairies, and sign up for his own causes, those who seemed interested in plants. Gray, back in Cambridge, had the resources of books and of herbarium which allowed him to work on those new plants which would be coming in, and the Gray-Engelmann partnership soon was established.

Their first efforts were not successful. Engelmann was in touch with John Charles Frémont, but the plants collected by Frémont in 1842 in the Wind River Mountains of Wyoming and in the South Pass of Colorado went to John Torrey. Torrey forwarded the *Compositae* to Gray who found them interesting enough to write to Torrey (5 Dec., 1842). ". . . Lieut. F. must be *indoctrinated* & taught to collect both dried spec. & seeds. Tell him he shall be *immortalized* by having the 999th *Senecio* called *S. Fremonti* . . ." The next summer Frémont led an expedition up the Arkansas and north to the Columbia River, but he seemed always reluctant to take along any scientific assistant,



and was noticeably unwilling to share either the work or the glory which might result. So Frémont again did the collecting of plants himself, but this time much of the material was lost, some by the fall of a pack mule into a chasm, some soaked in a flood on the Kansas River. Back in St. Louis, Frémont, to Engelmann's annoyance and disappointment, refused to allow these water-logged parcels be opened and the plants dried, so many specimens were irreparably damaged. Those remaining again went to Torrey.

Frémont was not the only string to the Gray-Engelmann bow. In Silliman's Journal for April-June, 1843, Gray advertised that, ". . . three enterprising botanists are now engaged in exploring the most interesting portions of the *far West*, and that their collections of dried plants will be offered to subscribers, in sets, as they come to hand." Two of the three were Karl Geyer and Friederich Lüders, young Germans whom Engelmann knew at St. Louis, who were in the field with a party led by a wealthy Scot, Sir William Stewart. Lüders lost his plants when his canoe capsized on the Columbia. Geyer had better luck and came eventually to Fort Vancouver on the Columbia. However, from here Geyer sailed to England and offered his plants to Hooker, an act of perfidy which much annoyed Engelmann and Gray, especially Gray who had finally to buy a set of the plants for himself.

The third collector was Ferdinand Lindheimer, also a friend of Engelmann. Lindheimer started in 1843 to collect in eastern Texas with the thought, at least on the part of Gray, that he would work westward and go eventually to Santa Fe. Plants did indeed come in from Lindheimer, but rather than pushing to the west, Lindheimer married and settled in the German community at New Braunfels. Gray's frustration now was acute. He wrote on 8 April, 1846, to Engelmann, "What is Lindheimer about? Why is not his last year's collection yet with you? We had just got things going, and we can sell fifty sets right off of his further collections, and he can go on and realize a handsome sum of money if he will only work now! And he will connect his name forever with the Texan flora!"

But it was 1846 and changes were coming to the southwest. On 13 May, President Polk proclaimed that a state of war existed between the United States and Mexico. On the same day, the state of Missouri was asked to provide one thousand volunteer cavalry; by the end of the month these troops had been placed under the command of Colonel Stephen Kearny and Kearny's "Army of the West" had been ordered to Santa Fe and thence westward to occupy California. Gray seized the opportunity. He wrote on 30 May to Engelmann, "We must have a collector for plants living and dry to go to Santa Fe, with the Government Expedition. If I were not so tied up, I would go myself. Have you not some good fellow you can send? We could prob-

ably get him attached somehow so as to have the protection of the army, and if need be I could raise two hundred dollars as an outfit . . . Someone must go into this unexplored field." Luck was at last with the partnership. Four weeks later, Engelmann could tell Gray, "I believe I have found a young man . . . His name is, if I am right, A. Fendler."; and on 3 July, "He has now concluded to go, accompanied by his brother; his name is Augustus Fendler."

Compared to his contemporaries in the southwest—to Lindheimer or to Charles Wright—Augustus Fendler is little known. The bare facts of his life are given in "An Autobiography and Some Reminiscences of the Late Augustus Fendler," edited by William Canby, and published in the *Botanical Gazette* in 1885.

Fendler was born in 1813 at Gumbinnen in East Prussia, now Gusev in the Russian S.S.R. He came to the United States in 1836 and after working in Philadelphia and New York, Fendler wandered west in 1838, to Texas and then to St. Louis. In 1844 Fendler returned to Germany and at Königsberg met Ernst Meyer. Meyer suggested to Fendler, who had by then worked at various trades, that sets of dried plants from the American west could easily be sold in Europe. Fendler found this idea attractive, and back in St. Louis, turned to Engelmann for advice, assistance, and books. Around St. Louis, Fendler "practiced" collecting and preparing specimens, but Engelmann dissuaded him from trying to sell in Europe sets of plants already familiar there and suggested that Fendler gain more experience and then turn toward Santa Fe.

Fendler thus was on the scene, but even by the summer of 1846, he had little experience in handling plants, and Engelmann was modest in telling Gray about him. On 25 June, Engelmann wrote to Gray, ". . . he cannot yet be called a botanist, nor even a collector.", but Engelmann believed him to be sound and thought that plans for Fendler's trip should at once be made. Gray was to write to Secretary of War Marcy to get permission for Fendler to travel with a military party and to arrange for his transportation. Engelmann would provide him with paper, lend him one hundred dollars ("relying on your wealthy friends in Boston etc. to refund the money"), and do what he could to smooth Fendler's way with the authorities at Fort Leavenworth. Engelmann saw clearly, and coldly, the problems which could arise, "The money advanced would be refunded after the sale of the plants, or by sending plants and seeds, etc. But in case of his death or of the loss of his collections, or (which I do not fear) of his proving false [a memory of Geyer], that advanced money would be lost."

Preparations were made with remarkable speed. By the end of July a letter from Secretary Marcy had reached Fort Leavenworth and

Fendler was ready. He and his brother left St. Louis on 1 August for the fort, armed with fifty dollars from W. S. Sullivan, one hundred and twenty dollars from John Amory Lowell, a supply of paper from Engelmann (as well as "full written instructions"), and the promise that they would travel free of charge with the army. Engelmann was pleased that Fendler was on his way after only six weeks of preparation and began, ". . . to hope a little more from this country for science."

#### FENDLER'S ROUTE: THE ROAD TO SANTA FE

The "Army of the West" followed the Santa Fe trail which by 1846 was a well-defined road, for the wagons of traders had been traveling for twenty-five years over its length of more than eight hundred miles. A very brief account of Fendler's route was provided by Engelmann for the preface to Gray's *"Plantae Fendlerianae Novi-Mexicanae"* (1849), but there are many other sources of information on the trail and thus about Fendler's collecting localities. An early one, popular at the time, is Josiah Gregg's *"Commerce of the Prairies or the Journal of a Santa Fe Trader,"* published in 1844 and still fine reading. Also valuable is Wislizenus' *"Memoir of a Tour to Northern Mexico"* (1848) which has a good map showing most of the localities cited by Fendler. Useful, too, is Emory's *"Notes of a Military Reconnaissance"* (1848) which has a general botanical appendix by John Torrey, a treatment of cacti by Engelmann, and a report on natural history by James Abert with another list of plants prepared by Torrey. This, too, has a map. These two reports on the trail are of particular interest for both Wislizenus and Emory traveled over it only eight weeks before Fendler did. Among recent books, I have found most useful Riddle's *"Records and Maps of the Old Santa Fe Trail"* (1963) and Stocking's *"The Road to Santa Fe"* (1971). And there is the chapter on Fendler in McKelvey's (1955) incomparable *"Botanical Exploration of the Trans-Mississippi West 1790-1850."*

The Fendlers left Fort Leavenworth, Kansas, on 10 August, 1846, with Colonel Sterling Price's Second Missouri Mounted Volunteers. Twelve of the fourteen companies in this command went to Santa Fe by the Cimarron cutoff, across the Oklahoma panhandle, and into northeastern New Mexico. Two companies, and the Fendlers, were detailed to travel up the Arkansas River to Bent's Fort, near La Junta, Colorado, there to meet a commissary train which was to be escorted to Santa Fe (Berry, 1964).

In August there was no real road between Fort Leavenworth and the trail, about twenty-five miles to the south. Fendler's party seems simply to have headed south from the fort and to have picked up the trail near Olathe, Kansas. The first locality on the trail which is cited

by Fendler, on 12 August, is Lone Elm, south of Olathe in Johnson County. For ease of reference I shall use both modern place names, whether or not they were in use in Fendler's time, and the names used by Fendler, many of which are no longer in use.

The trail ran west-southwestward across Kansas through Council Grove, past McPherson, to Great Bend where travellers reached the Arkansas River and turned upstream. Above Great Bend there were several crossings of the river; a "lower crossing" near Ford (Ford County), two "middle crossings" between Cimarron and Charleston (Gray County), and the "upper crossing," near Lakin in Kearny County. From each of these a trail ran across the Cimarron Desert, the "Waterscape" of travellers, to the waterholes on the Cimarron River in southwestern Kansas, joining finally in Grant County and continuing as the Cimarron cut-off into New Mexico. This was the shortest and driest route to Santa Fe, taken by most of the companies under Price's command.

There was also the mountain route, an arm of the trail which continued up the Arkansas into Colorado. The Fendlers went this way to Bent's Fort. The arrival of the troops was noted by Francis Parkman, "On the 6th [September] two companies of volunteers of Price's rgt. came up to our camp—a set of undisciplined ragamuffins." (Parkman, ed. Wade, 1947).

From Bent's Fort the trail ran southwestward, nearly over route 350, to Trinidad, Colorado, thence over the Raton Pass into New Mexico. About fifteen miles south of Raton, New Mexico, the mountain route forked, the eastern road soon forking again, so that there were three routes through Colfax County, New Mexico. The westernmost road ran through Cimarron, thence south through Rayado. The middle road ran from a point north of Maxwell southwestward to Rayado and there joined the western road. The eastern branch ran farther to the south, then turned to the west and joined the others about twelve miles west of Colmor. Fendler's party probably used the middle road. The mountain route then ran south to Watrous where the Cimarron cutoff came in from the northeast. It was a single trail from this point and, nearly following route 85, continued into Santa Fe.

Fendler was in Santa Fe from 11 October, 1846, until 9 August, 1847. He arrived too late in the season to do much collecting, but in the spring of 1847 he started work along the Santa Fe Creek and on the nearby plains. Fendler never got far from the town, probably from his lack of money and from his fear of Indians. He did make two trips, on 8 May and on 24 and 25 May, 1847, to "Rio del Norte," the Rio Grande, about twenty miles west of the town. Unfortunately he got no more than ten or twelve miles into the mountains east of

Santa Fe. Standley (1910) pointed out that, ". . . if he had gone further he would have found hundreds of plants not in his collections. Fifteen or 20 miles away he would have found a subalpine flora that would have been rich in plants then undescribed."

Fendler would, no doubt, have stayed longer in Santa Fe, but he had run out of money. Presence of the troops had driven prices up quickly. As early as 8 November 1846, Fendler wrote to Engelmann that prices were two to three times higher than in St. Louis. In this same letter Fendler suggested to Engelmann that he and his brother could manufacture matches, very expensive in Santa Fe and in short supply, and asked Engelmann to send raw materials and instructions, but this scheme seems to have come to nothing. During the spring of 1847 Gray tried to raise money among his usual donors in Boston, but these efforts came also to nothing, and by summer Fendler must have been very short indeed of money.

The Second Missouri and the Fendlers left Santa Fe for Fort Leavenworth on 9 August, 1847, by the shortest route. Fendler thus retraced his route of the year before to Watrous, New Mexico, where the Cimarron route turned to the northeast. From Watrous the trail ran across the southeastern corner of Colfax County, then through Union County a few miles north of Sofia, Mt. Dora, and Seneca. It crossed into Oklahoma just to the south of Mexhoma. In Oklahoma the trail continued north to Cold Spring, east of Kenton (Cimarron County), on the Cimarron River; and then followed the Cimarron into Kansas. Still following the Cimarron, the trail continued into southern Grant County; from here one could turn northward for the crossings of the Arkansas. Fendler's party took the trail to the middle crossings and then followed the river down to Great Bend. From here the trail to Fort Leavenworth was nearly that of a year before. Fendler reached the fort on 24 September, 1847, and left the next day for St. Louis. His last cited locality is "bank of the Missouri River, about Washington [Missouri]" on 27 September, 1847.

#### FENDLER'S COLLECTIONS AND THE COLLECTION LIST

On his return to St. Louis, Fendler worked with Engelmann to order his plants into families, beginning with Ranunculaceae, and following the Candolleian sequence through "Polypetalae," "Monopetalae," "Apetalae," gymnosperms, monocotyledons, and vascular cryptogams. Fendler also prepared from his notes kept day-to-day a list of the collections, arranged by family, and numbered from "1," "*Clematis ligusticifolia*," through "1026," referred by Fendler to Characeae. A copy of this list, packed with information on places and dates of collection, on plant habits and habitats, went with the plants to Gray.

The plants came to Gray over several months. On 20 December, 1847, he wrote to Engelmann that the families up to Rosaceae had arrived, "The specimens are perfectly charming! So well made, so full and perfect. Better never were made." The rest were in Gray's hands by the next summer and he then worked over the whole collection. By November, Gray had prepared for communication to the American Academy of Arts and Sciences, "*Plantae Fendlerianae Novi-Mexicanae*," including families from Ranunculaceae through Compositae, published in February, 1849, with the promise, "to be continued." But that was the end of it. As happened so often, Gray prepared for publication those families through the Compositae, a favorite of his, but there were then other demands on his time and no more family treatments of Fendler's plants appeared, although Gray did, of course, eventually describe those things he considered to be new to science.

The plants and the publication have always presented problems—some of Fendler's making, others attributable to Gray. The Compositae, the last family treated in the publication, fall about half way through the dicotyledons in the Candollean sequence. As a result, only half of Fendler's collections are dealt with in "*Plantae Fendlerianae*." For these Gray extracted from the collection list locality data, months of collection, and some, but certainly not all, information on habit and habitat. However, for the rest, apart from those Gray described as "new," or may have mentioned incidentally, this information has not been available. The printed labels for the sets state only "*Plantae Novo-Mexicanae/A. Fendler coll./1847*" and no one concerned with distribution seems to have added other information.

Then in compiling the collection list, Fendler often included two or more collections—which he thought to be the same—under one number. In some cases, these had been made at the same place. Thus, number 37 of the list has these data: "Santa Fe; upper part of the creek valley, foot of mountains. 7 July–10 August, 1847." But other numbers in Fendler's list comprise collections made at different places. Number 92 of the collection list has this entry: "15–26 August, 1847. Between Vegas and Moro River [New Mexico] and a few miles east of Cold Spring (Cimarron) [Oklahoma]."

The sets offered for sale were made up by Engelmann and Fendler, not by Gray. In a few cases they lumped two or three of Fendler's numbers, each already perhaps including two or more individual collections, into a single distribution number. Thus material distributed as "Fendler 93", *Linum perenne*, included number 91 of the list, collected at Santa Fe, and number 92, just mentioned above, made up of plants collected in New Mexico and Oklahoma. Gray's copy of Fendler's list is neatly written in a now faded ink with Fendler's own numbers lightly pencilled in. In the families up to Compositae, the final distribution numbers, under which these plants are cited, were

added in red ink by Engelmänn before sending the list to Gray, and the lumpings thus are easily noted. The numbers in red ink are those used in "*Plantae Fendlerianae*" and run through "295," the first of the *Compositae*, distributed as "*Vernonia noveboracensis*."

Engelmänn felt that he had neither the expertise nor the time to arrange the *Compositae* and following families, so these he left to Gray (Engelmänn to Gray, 15 Feb., 1848). He wrote again to Gray on 27 February, 1848, "Fendler is so situated [for money] that he cannot wait with the distribution of his plants; he will therefore distribute them now with my red numbers (in your Catalogue [copy of the collection list]) as far as they go and then with his own numbers in pencil, so that the subscribers can alter them afterwards so as to correspond with the printed Catalogue numbers. As far down as *Vernonia* you could then adopt in the printed Catalogue the red numbers, but farther on you arrange the plants as you think best, and add to the end of each notice in brackets: (Fendler's Catalogue Nro 714 or whatever it may be) or (F.C. 714) something like Hookers Catalogue of Geyers' plants."

Gray explained this in a footnote on page 61 of "*Plantae Fendlerianae*," "From this onward, the numbers inclosed in parentheses, and usually placed after the habitat, are those under which the specimens have been distributed." Thus in the published treatment of the *Compositae* the numbers which enumerate the taxa run sequentially from "295," "*Vernonia noveboracensis*, var." through "462," "*Sonchus asper*," but these numbers have only rarely been used in citing the specimens. Of the specimens of Fendler's *Compositae* which I have seen, only a few have on the label both the original distribution number, that is, the number which is used in the collection list and cited in parentheses in "*Plantae Fendlerianae*"; and the taxon number used in "*Plantae Fendlerianae*." Many subscribers seem not to have added this latter number.

Fendler's presentation of dates and of localities can also be troublesome. In her chapter on Fendler, McKelvey (1955) concluded that the collection list does not provide an itinerary, "since the plants are arranged according to families and the dates and localities supplied are covering ones. For example his no. 1 bears the notation: 'Santa Fe, 1st-19th July, 1847. Moro River 15th August. Creek bottom land, near the water climbing to the tops of trees and shrubs. Also the Rio de los Animas between Bent's Fort and Santa Fe. Fruit: 15th August-16th January.'" That the dates are "covering ones" may be so; I suspect that in most cases they are not. Thus it is likely that "1st-19th July, 1847" refers only to collections made on those two days, not to some unknown number of collections made between those dates. In fact it makes no difference to the user in most cases.

It is no easier and no more helpful to refer any individual plant to a collection made on one of two days than to try to refer it to some one of nineteen days. I do not agree that Fendler's itinerary cannot be worked out. That is easily done; the dates and localities are there; they are easily tied together and the localities are shown on contemporary maps.

The plants eventually were offered for sale as "*Plantae Novo-Mexicanae*." Gray had been much impressed by them and hoped that Fendler would return to the west, but this was not to be. On his return to St. Louis, Fendler was sadly short of money—the financial problems from Santa Fe remained, the sets did not sell as quickly as Gray had hoped, and some of the purchasers were slow in paying. The buyers paid ten cents per number; thus, John Amory Lowell paid for his set of 513 numbers, fifty-one dollars and thirty cents. The money went to Fendler, but he had large debts owed to Engelmann, and he had to support himself and his brother. Fendler complained to Engelmann and Gray about the lack of profit in plant collecting, but he was, nevertheless, willing to go again into the field.

Early in the summer of 1849 he set out with a military party from Fort Leavenworth towards the Platte River, but the group was led by an inexperienced officer. As a result of this man's mismanagement, Fendler's wagon with paper and other supplies was overturned in a flooded creek. Fendler, his equipment lost or badly damaged, was forced to turn back to St. Louis where he found that all of his remaining possessions had been lost in a fire which destroyed much of the waterfront of the city. Fendler was now very much discouraged. A few months later he left St. Louis for Panama and although he later spent many years in the United States, he had nothing more to do with the west.

The collection list is presented so that Fendler's plants, which include the first collections of importance from Santa Fe, and which in many cases are the types of names published by Gray and by others, can be more easily used. This published list is not an exact transcription of Gray's copy, for I have in many entries modified Fendler's erratic and inconsistent use of marks of punctuation, and I have deleted "st" and "th" from dates, but there are no other changes in Fendler's own wording.

#### SUMMARY OF DATES AND LOCALITIES, EN ROUTE TO AND FROM SANTA FE

1846. **Kansas.** Aug. 11: 8, 10, 15, 18 miles south Fort Leavenworth; 2, 4, miles south of Kansas River. Aug. 12: few miles south of lower ferry of Kansas River; 20 miles from the ferry; Lone Elm. Aug. 13:



Lone Elm; 60, 80 miles west of Independence [distances cited for Aug. 13–17 as “west of Independence” are exaggerated by 20–40 miles]. *Aug. 14*: Black Jack Point; Hickory Point; 90 miles west of Independence. *Aug. 15*: 100, 117 miles west of Independence. *Aug. 16*: 117, 120 miles west of Independence; 30 miles east of Council Grove. *Aug. 17*: 118, 120 miles west of Independence; 110 Mile Creek; few miles east of Bluff Creek; 30, 25, 20, 15, few miles east of Council Grove. *Aug. 18*: 15, 12, 10, 5 miles east of Council Grove. *Aug. 19–26*: Council Grove. *Aug. 27*: 30 miles west of Council Grove. *Aug. 28–30*: no collections listed. *Aug. 31*: between Cow Creek and Little Arkansas River; Cow Creek. *Sept. 1*: between Cow Creek and Walnut Creek. *Sept. 2–3*: Walnut Creek. *Sept. 3*: Walnut Creek. *Sept. 4*: no collections listed. *Sept. 5*: Arkansas River. *Sept. 6*: 15 miles east of ford of Arkansas River. *Sept. 7–9*: no collections listed. *Sept. 10*: 5 miles south of ford of Arkansas River. *Sept. 11–15*: no collections listed. **Colorado.** *Sept. 16*: 20 miles east of Big Sand Creek. *Sept. 17*: 10 miles east of Big Sand Creek; few miles east of Big Sand Creek. *Sept. 18*: no collections listed. *Sept. 19*: 42, 32 miles east of Bent’s Fort. *Sept. 20*: 6 miles east of Bent’s Fort. *Sept. 21–22*: no collections listed. *Sept. 23*: 3 miles above Bent’s Fort; Bent’s Fort. *Sept. 24–26*: no collections listed. *Sept. 27*: 20, 25, 27 miles south of Bent’s Fort; 15 miles northeast Rio de los Animas. *Sept. 28*: Rio de los Animas. **New Mexico.** *Sept. 29*: Raton Mountains. *Sept. 30*: Raton Creek; between Raton and Bermejo Creek. *Oct. 1*: between Bermejo and Rio Colorado; 3 miles north of Rio Colorado; 8 miles south of Rio Colorado. *Oct. 2–3*: Poñi Creek. *Oct. 4*: Poñi Creek; Rayado Creek; few miles south of Rayado Creek. *Oct. 5–8*: no collections listed. *Oct. 9*: between San Miguel and Santa Fe; between San Miguel and Pecos. *Oct. 10*: few miles east of Pecos.

1847. **New Mexico.** *Aug. 10*: 8 miles east of Santa Fe; between Santa Fe and Pecos; Pecos; from Santa Fe to San Miguel; between Santa Fe and Ojo de Bernal. *Aug. 11*: between Pecos and San Miguel. *Aug. 12*: between Pecos and San Miguel; San Miguel. *Aug. 13*: 18 miles west [east?] of Pecos; Ojo de Bernal. *Aug. 14–17*: San Miguel to east of Rock Creek. *Aug. 14*: between San Miguel and Vegas; 15, 12, 10, 8, 7, 6, 5, miles west of Vegas; Vegas; 2 miles east of Mora River [prob. wrong date—at Mora on Aug. 15]. *Aug. 15*: between Vegas and Mora River; Mora River. *Aug. 16*: Mora River. *Aug. 17*: Mora River; 2 miles east of Mora River; east of Rock Creek [wrong date—at Rock Creek on Aug. 22]. *Aug. 18*: 2, 5, 6, 8 miles east of Mora River. *Aug. 19*: no collections listed. *Aug. 20*: Ocate Creek; Rio Colorado; Rabbit Ear Creek [wrong date—at Rabbit Ear Creek on Aug. 25]; Middle Spring of the Cimarron [impossible for this date]. *Aug. 21*: between Ocate Creek and Rio Colorado; Rio Colorado; be-

tween Rio Colorado and Rock Creek. *Aug. 22:* Rock Creek. *Aug. 23:* 7 miles west [east?] of Rock Creek; Rock Creek; 7 miles east of Rock Creek. *Aug. 24:* between Rock and Rabbit Ear Creeks. *Aug. 25:* Rabbit Ear Creek; few miles west of McNees' Creek; between Rabbit Ear and McNees' Creek; McNees' Creek; east of McNees' Creek. **Oklahoma.** *Aug. 26:* between McNees' Creek and Cold Spring; Cold Spring; few miles east of Cold Spring. *Aug. 27:* Upper Spring of Cimarron. *Aug. 28:* few miles west of Cimarron; crossing of the Cimarron; between Cimarron crossing and Willow Bar; Willow Bar. **Oklahoma-Kansas.** *Aug. 29:* Willow Bar, between Willow Bar and Middle Spring; Middle Spring; 10, 16 miles east of Middle Spring. **Kansas.** *Aug. 30:* 16 miles east of Middle Spring; 18 miles west of Lower Spring. *Aug. 31:* few miles west of Lower Spring; Lower Spring. *Sept. 1:* Sand Creek. *Sept. 2:* 40 miles southwest of crossing of Arkansas River; Pawnee Fork [wrong date—at Pawnee Fork on Sept. 8]. *Sept. 3:* 4 miles south of the Arkansas River crossing; Walnut Creek [wrong date—must have passed Walnut Creek on Sept. 8]. *Sept. 4:* no collections listed. *Sept. 5:* 3 miles west of Fort Mann. *Sept. 6:* no collections listed. *Sept. 7:* between Coon Creek and Pawnee Fork. *Sept. 8:* Pawnee Fork; between Pawnee Fork and Cow Creek. *Sept. 9:* Cow Creek. *Sept. 10-14:* no collections listed. *Sept. 15:* Turkey Creek; Cottonwood Creek. *Sept. 16:* Cottonwood Creek; few miles east of Cottonwood Creek. *Sept. 17:* 16 miles west of Council Grove; Council Grove. *Sept. 18:* Council Grove; Bluff Creek. *Sept. 19:* between Bluff Creek and 110 Mile Creek. *Sept. 20:* few miles west, few miles east of 110 Mile Creek. *Sept. 21:* 18 miles east of 110 Mile Creek; upper ferry of Kansas River. *Sept. 22:* upper ferry of Kansas River; 6 miles north of upper ferry. *Sept. 23:* between Kansas River and Fort Leavenworth. *Sept. 24:* few miles south of Fort Leavenworth. **Missouri.** *Sept. 25:* bed of Missouri River a few miles above Liberty. *Sept. 26:* banks of Missouri River below Liberty. *Sept. 27:* banks of Missouri River above Washington.

#### LOCALITIES CITED BY FENDLER

*Arkansas River crossing or ford:* There were at least four important places of crossing. The "lower crossing" was at Mulberry Creek near the town of Ford, Ford Co., Kansas. There were two "middle crossings" west of Cimarron, Gray County; the easternmost between Cimarron and Ingalls, the western one between Ingalls and Charleston. This western crossing is suggested by Stocking (1971) to be either the last, or the most used, for it is the clearest on aerial photographs. This may have been Fendler's locality. The "upper crossing" was near Lakin, Kearny County.

*Bent's Fort* (mountain route): This was Bent's old fort or Fort William, used from 1828 to 1853. It stood on the north bank of the Arkansas River about four miles east of La Junta, Colorado.

*Big Sand Creek* (mountain route): Now Big Sandy Creek, this creek enters the Arkansas a few miles east of Lamar, Prowers Co., Colorado.

*Bermejo Creek* (mountain route): Now spelled "Vermejo," this creek enters the Canadian River a few miles south of Maxwell, Colfax Co., New Mexico. Fendler's party probably crossed the Vermejo six or seven miles west of Maxwell.

*Black Jack Point*: In Fendler's time a grove of oaks, the locality is in Douglas Co., Kansas, about eight miles southwest of Gardner.

*Bluff Creek*: The trail crossed this creek about three miles north of Bushong, Lyon Co., Kansas.

*Cimarron route*: Ran from the Arkansas crossings southwestward to the Cimarron River in southwestern Kansas and the Oklahoma panhandle, then across the northeastern corner of New Mexico to Wabasha and Santa Fe. This direct route was taken by Fendler on his return to St. Louis (August, September, 1847).

*Cimarron River* (Cimarron route): The crossing or ford of the Cimarron was near Willow Bar, about ten miles north northwest of Keyes, Cimarron Co., Oklahoma. For the Cimarron springs, see the individual entries.

*Coon Creek*: drains into the Arkansas near Kinsley, Edwards Co., Kansas.

*Cold Spring* (Cimarron route): about twelve miles northwest of Boise City, Cimarron Co., Oklahoma.

*Cottonwood Creek*: crossed by the trail about one mile from Durham, Marion Co., Kansas.

*Council Grove*: on the Neosho River, Morris Co., Kansas.

*Cow Creek*: crossed the trail just west of Lyons, Rice Co., Kansas.

*Fort Leavenworth*: on the Missouri River, just north of Leavenworth, Kansas.

*Fort Mann*: a short-lived military post west of Dodge City, Ford Co., Kansas.

*Independence*: just east of Kansas City, Missouri, this was for many the starting point of the road to Santa Fe.

*Kansas River*: The "lower ferry" was perhaps Grinter's ferry, just west of Kansas City; the "upper ferry" may have been Pappan's ferry at the site of Topeka, Kansas.

*Liberty*: Clay Co., Missouri.

*Little Arkansas River*: crossed by the trail a few miles southwest of Windom, McPherson Co., Kansas.

*Lone Elm*: about four miles east of Gardner, Johnson Co., Kansas.

*Lower Spring*: about two miles west of US 270 near the Grant—Stevens county line, Kansas.

*McNees' Creek* (Cimarron route): crossed by the trail a few miles west of Mexhoma, Oklahoma; just into Union Co., New Mexico.

*Middle Spring* (Cimarron route): about two miles west of the bridge carrying Kansas route 27 over the Cimarron, Morton Co., Oklahoma.

*Mora River*: crossed by the trail near the town of Watrous, Mora Co., New Mexico.

*Ocate Creek* (Cimarron route): crossed by the trail about ten miles east of Colmar, Union Co., New Mexico.

*Ojo de Bernal*: about five miles southwest of Tecolote, San Miguel Co., New Mexico.

*One Hundred and Ten Mile Creek*: crossed by the trail just east of Scranton, Osage Co., Kansas. The name refers to the distance from Fort Osage, Missouri.

*Mountain route*: Ran upstream from the Arkansas crossings to Bent's Fort, thence over the Raton Pass into New Mexico where it met the Cimarron route at Watrous, Mora County. Fendler's party took this route to Santa Fe (September, October, 1846).

*Pawnee Fork*: crossed by the trail near Larned, Pawnee Co., Kansas.

*Pecos*: western part of San Miguel Co., New Mexico.

*Poñi Creek* (mountain route): now Ponil Creek; crossed by the trail a few miles east of Cimarron, Colfax Co., New Mexico.

*Rabbit Ear Creek* (Cimarron route): crossed by the trail between Grenville and Mt. Dora, Union Co., New Mexico.

*Raton Creek* (mountain route): crossed by the trail near Raton, Colfax Co., New Mexico.

*Raton Mountains* (mountain route): Colorado—New Mexico. The trail crossed by the Raton Pass, between Starkville, Las Animas Co., Colorado and Raton, Colfax Co., New Mexico.

*Rayado Creek* (mountain route): crossed by the trail at Rayado, Colfax Co., New Mexico.

*Rock Creek* (Kansas): crossed by the trail about five miles east of Council Grove, Morris Co., Kansas.

*Rock Creek* (New Mexico—Cimarron route): crossed by the trail a few miles northeast of Sofia, Union Co., New Mexico.

*Rio Colorado*: Canadian River. Fendler cited the Rio Colorado as a collecting locality on 1 Oct., 1846. The party probably was between Springer and Colfax, New Mexico on the mountain route and Fendler's locality must be a tributary of the Canadian. He was again on the Rio Colorado on 21 Aug., 1847, this time on the Cimarron route which forded the Canadian a few miles south of Taylor Springs, Colfax Co., New Mexico.

*Rio de los Animos* (mountain route): the Purgatoire River; i.e., Rio de las Animas Perdidas en Purgatorio. The trail crossed the river about twelve miles northeast of Trinidad, Las Animas Co., Colorado.

*Rio del Norte*: the Rio Grande, about twenty miles west of Santa Fe.

*Sand Creek* (Cimarron route): crossed by the trail seven to nine miles southwest of Ulysses, Grant Co., Kansas.

*San Miguel*: a few miles south of US 85 in the southwestern part of San Miguel Co., New Mexico.

*Turkey Creek*: crossed by the trail near McPherson, McPherson Co., Kansas.

*Upper Spring* (Cimarron route): about two miles west of the point at which US 287 crosses the Cimarron River, Cimarron Co., Oklahoma.

*Waggon Mound*: Wagon Mound, Mora Co., New Mexico.

*Walnut Creek*: crossed by the trail a few miles west of Ellenwood, Barton Co., Kansas.

*Washington*: Franklin Co., Missouri, about forty miles west of St. Louis.

*Willow Bar* (Cimarron route): about 2½ miles south of Colorado—Oklahoma state line; about ten miles north of Keyes, Cimarron Co., Oklahoma.

*Vegas*: Las Vegas, San Miguel Co., New Mexico.

#### NOTES ON THE COLLECTION LIST

1. Each entry represents plants which Engelmann and Fendler referred to a single taxon, but an entry can include one or more separate collections.

2. Material enclosed in quotation marks consists of annotations written into the manuscript by Engelmann or by Gray.

3. The first number cited is always that originally used in the enumeration.

4. For numbers 1–327 of the list, the number immediately following and enclosed in parentheses is a distribution number assigned, and written into the manuscript, by Engelmann. In a few cases, e.g., (50) and (71), the distribution number includes two (rarely three) of Fendler's numbers; i.e., (50) includes "55" and "57;" (71) includes "77" and "78." These distribution numbers, which run from (1) through (295), are those used by Gray in "*Plantae Fendlerianae*" to enumerate species in families Ranunculaceae through Valerianaceae, plus "*Vernonia noveboracensis* var.," the first taxon in the Compositae. For these groups it is these numbers which have always been used in citing the collections.

5. From this point on, Engelmann turned over to Gray the task of assigning distribution numbers. For the remaining Compositae (the last family published in "Plantae Fendlerianae") Gray assigned numbers which actually are the running numbers in Fendler's manuscript. In the Compositae the numbers which enumerate taxa run sequentially from 295 ("Vernonia noveboracensis var.") through 462 ("Sonchus asper"), but Gray cited in the text the numbers "under which the specimens have been distributed," that is, Fendler's numbers, and these are used in citing collections. N.B.: "295" is a distribution number assigned by Engelmann; "296" and following numbers to the end of the Compositae are merely sequential numbers. Starting with the Lobeliaceae, Gray continued to use the manuscript numbers for distribution numbers.

Thus in the following pages: (a) in the Compositae the first number for each entry is the running number in the manuscript and is also the number under which the collection was distributed; the second number given is that used in the sequential listing of taxa in "Plantae Fendlerianae;" the name cited is that used in "Plantae Fendlerianae"; in a few cases the collection was named—by Gray's annotation in the collection list—but was not cited in "Plantae Fendlerianae"—these are so indicated; (b) from the beginning of the Lobeliaceae to the end of the list, the number given is both that used in the manuscript and the distribution number.

#### COLLECTION LIST: 1846–1847

- 1 (1) Santa Fe, 1–19 July, 1847. Moro River, 13 August. Creek bottom land, near the water, climbing to the tops of trees and shrubs. Also Rio de los Animas between Bent's Fort and Santa Fe.
- 2 = No. 1. Fruit. 15 August–16 January.
- 3 (3) Santa Fe, 12 May–3 June. Foot and sides of steep rocks in shady places near the creek. Climbing over shrubs.
- 4 (2) Council Grove, 21 August, 1846. Creek bottom land. = 5.
- 5 A few miles east of Council Grove, 17 August, 1846. High bank of a dried-up creek.
- 6 (4) A few miles east of Santa Fe, creek valley in the mountains. Shady places, foot of rocks near irrigating ditch. 16–24 June, 1847.
- 6b "Anemone cylindrica—in fruit" A few miles south of Kansas River. 22 September, 1847.
- 7 (5) Santa Fe, eastern mountain range. 17–26 April. Lesser hills at the foot of mountains, on gently sloping northern declivities; tolerably good soil.

8 (6) Sunny margin of the creek, 6 miles above Santa Fe (in the mountains). Fertile soil. 3 June, 1847.

9 (7) Santa Fe, 2 May–19 October. Creek bottom, wet places. Form large patches by sending off runners in all directions.

10 (8) Santa Fe, 26 April–16 June. Creek bottom, moist places. Stem upwards of 18 inches high.

11 (9) Santa Fe, creek valley in the mountains; fertile soil between rocks; also, sunny side of mountains. 26 April–3 June.

12 (10) Poñi Creek, between Bent's Fort and Santa Fe. Bottom land, near the creek, amongst willows. 3 October, 1846.

13 (11) Banks of Moro River. Low fertile soil. 15 August, 1847.

14 (12) Santa Fe, creek bottom, between the mountains; damp shady places, fertile soil. 20 May–3 June in flower. 8 July—in fruit. Sepals 4, white; petals none; stamens 23 or 24.

15 (13) Santa Fe, creek valley, shady places, margins of irrigating ditches at the foot of perpendicular rocks. 13 June–1 July in flower. 19 July in fruit. Flowers dioecious.

16 "I find no specimen with this number, but suppose that a form of the last number, *Thalictrum*, is meant by it." Bottom land of Moro River, 15 August, 1847.

#### BERBERIDACEAE

17 (14) 26 April–15 May, 1847. Upper part of Santa Fe creek valley. Sides of mountains, near the top as well as the foot of them; also on the creek bottom. Evergreen leaves, most of them partly eaten by animals. Fruit ripens by the 28th of July.

18 (15) Santa Fe Creek, foot of steep and rocky banks, not far from the water. Shrubs of from 3–4 feet high. 28–31 May, 1847. Some specimens have the lower leaves sharp serrate.

#### PAPAVERACEAE

19 "One of the varieties of *Argemone mexicana*; I find no specimen with this number." 3 September, 1846. Walnut Creek, rather low prairie. Valves of the capsula, 4, with prickles, the points of which are directed towards the apex.

20 "*Argemone mexicana*, a less hispid form" 27 August, 1847. Upper Spring (Cimarron River); prairie. Valves of the capsula 3 and 4 with prickles, the points of which are directed away from the apex.

21 (16) 7 June–28 July, 1847. Santa Fe. Low, level, sandy places, in the neighbourhood of fields. From upwards of 2 feet high. Socially in great numbers.

#### FUMARIACEAE

22 (17) 15 April–20 July, 1847. Santa Fe, creek valley, between rocks, generally near the creek; also, moist gravelly parts of

the creek bed, exposed to occasional inundations of the creek.

## CRUCIFERAE

23 (38) On the lesser hills west of Santa Fe, sterile pebbly, and dry soil, gently sloping declivities (both sunny and northern) amongst stones. Fruit: 29 April–7 June.

23 (39) Santa Fe, dry gravelly hills, 24 May, 1847.

24 (40) Santa Fe, lesser hills, 2 May, 1847. A fruiting specimen, very different from those of no. 23; also some differences in the leaves.

25 (41) 15 April–11 May, 1847. Santa Fe; creek bed, in parts exposed to inundations; gravelly moist soil; petals 4, white.

26 (42) 8–24 May, 1847. Rio de Norte, sunny side of ravines. Silicles more crowded and somewhat dotted; stem nearly smooth.

27 (46) Mountain valleys, from Santa Fe east to Rabbit Ear Creek. 10–20 August, 1847. There seem to be 2 different forms of this plant.

28 (44) 19 March–5 June, 1847. Santa Fe; creek bottom in the mountains; also foot of mountains. Petals 4, white.

29 (18) 8 May–17 August, 1847. Rio del Norte, flat, sandy bank, washed by the water; east to Mora River.

30 (19) 25 May–23 June, 1847. Santa Fe; creek bottom, low wet places.

31 (21) 29 June–25 July, 1847. Santa Fe Creek, low wet places and margin of the creek.

32 (45) 16 June–17 July, 1847. Santa Fe; eastern mountain range, near the irrigating ditch of a field.

33 (20) Santa Fe; wet meadows and moist places of the creek bottom. 27 May–29 June, 1847.

34 = 33 "Nasturtium = 33" Santa Fe, 12 July, 1847. Moist soil near irrigating ditches.

35 (27) 30 March–15 May, 1847. Santa Fe, creek valley. Moist, sandy soil in parts of the creek bed, exposed to occasional inundations. Rarely on hills between rocks.

36 (24) 13–18 July, 1847. Santa Fe; sunny side of a hill, amongst rocks.

37 (22) 7 July–10 August, 1847. Santa Fe, upper part of the creek valley, foot of mountains.

38 = 27 (23) 7–28 July, 1847.

39 (23) 26 July, 1847. Santa Fe Creek, margin of the water. Flowers minute.

40 (24) 11 August–15 August, 1847. Mountainous region from Santa Fe to Vegas.

41 (25) 6 June–28 July, 1847. Santa Fe, creekbottom in the mountains; margin of the creek; also in shady moist places.



- 41 $\beta$  (26) 24 June, 1847.  
 42 (32) 24 April–19 May, 1847. Santa Fe, dry gravelly hills; petals 4, yellow; plant rather socially.  
 43 (33) 14–17 August, 1847. San Miguel to east of Rock Creek. Spots of fertile and loose soil on high prairies.  
 44 (34) 15 May–12 July, 1847. Santa Fe Creek valley, level somewhat damp ground, foot of mountains.  
 44 $\beta$  (35) Rio del Norte, 24 May, 1847. On a ledge of rock high up on the steep mountain—bank of the river.  
 45 (28) 15 May–16 June, 1847. Margin of Santa Fe Creek in the mountains.  
 46 (43) 8 May–28 July, 1847. Santa Fe Creek, shady steep declivities and foot of mountains. More rarely in the creek bottom and low banks of the creek.  
 47 (37) 21 June–26 July, 1847. Santa Fe, near irrigating ditches not far from fields.  
 48 (29) 15 August, 1847. Bank of Moro River.  
 49 (31) 16 June–28 July, 1847. Santa Fe, margin of the Creek, 5 miles east of Santa Fe, in the mountains.  
 50 (30) 16–24 June, 1847. Santa Fe Creek, foot of mountains.

## CAPPARIDACEAE

- 51 (36) 27 September, 1847. 15 miles north east of Rio de los Animas, between Bent's Fort and Santa Fe.  
 52 (48) 21–28 August, 1847. From Rio Colorado to the crossing of the Cimmaron River. Rather low places.  
 53 (47) 28 August, 1847. Between crossing of the Cimmaron River and Willow Bar. Deep sandy soil.  
 54 (49) 7 June–19 October, 1846–47. Santa Fe, low level places (somewhat sandy) near the town, also near the Creek. East as far as Cow Creek. Annual herb.  
 54 $\beta$  Flower white, the same.

## VIOLACEAE

- 55 (50) 8 September, 1847. Pawnee Fork, steep bank of the river, loose soil.  
 56 (51) 15 May–28 June, 1847. Santa Fe, creek bottom in the mountains; shady damp places, fertile soil; sometimes margin of the Creek.  
 57 (50) 26 April–28 June, 1847. Santa Fe, creek valley. Margin of the creek and low level places.

## CISTACEAE

- 58 (52) 13 August, 1846. 60 miles west of Independence.

## HYPERICACEAE

- 59 (53) 16 June–28 July, 1847. Santa Fe, creek bottom in the mountains, margin of the creek and moist places.

## CARYOPHYLLACEAE

60 (63) 12 May–25 June, 1847. Santa Fe, eastern mountains, creek bottom, near the creek, between stone piles. Sepals 5; petals 5 (by abortion 4), cleft, ([small sketch here] inside of a petal showing the 2 little elevations near the base of the blade), alternate; stamens 10 (5 higher than the rest).

61 (59) 15 May, 1847. Santa Fe Creek valley, foot of mountains gently sloping declivities between stones (only in one region). Petals white.

62 (55) Santa Fe, Creek valley in the mountains, open level tract, where cattle and horses were always grazing. Also between Santa Fe and Pecos. 28 July–10 August, 1847.

63 (61) 20 May–16 June, 1847. Santa Fe, creek bottom in the mountains, near the creek. Petals 5, ([small sketch here] cleft) [part of floral diagram here]. Plant viscid, especially the upper part of it.

64 (62) 16 June, 12 July, 1847. Santa Fe, Creek valley in the mountains between rocks near the creek.

65 (54) 2 May–3 June, 1847. Santa Fe, Creek valley, moist level soil. Flowers minute; petals white.

66 (65) 3–19 July, 1847. Santa Fe, Creek valley in the mountains, margin of the creek.

67 (64) 15–28 July, 1847. Santa Fe, Creek bottom in the mountains.

68 (57) 14 August, 1847. Prairies, 5 miles west of Vegas. Flowers white.

69 (56) 14 August, 1847. 8 miles west of Vegas, woodland on the mountain region, shady places. Differs from no. 62 in size and shape of its bracts.

70 (66) 14 August, 1847. Woodland 6 miles west of Vegas.

71 (58) 14 August, 1847. 2 miles east of Moro River, at the foot of high rocks.

72 (67) 24 September, 1847. A few miles south of Fort Leavenworth.

73 (60) 10 August, 1847. A few miles east of Santa Fe.

## ILLECEBRACEAE

74 (68) 21 September, 1847. Creek bottom about 20 miles east of 110 Creek.

75 (69) 17 September, 1846. A few miles east of Big Sand Creek (between crossing of the Arkansas River and Bent's Fort). High prairies, gravelly soil. Also: 14 August–17 September, 1847. From San Miguel to Council Grove; loose soil.

76 (70) 25 August, 1847. A few miles west of McNees's Creek.

## PORTULACACEAE

- 77 (71) 28 July, 1847. Santa Fe, Creek bottom, in the mountains, on a level tract of grazing ground.
- 78 (71) 25 August, 1847. Between Rabbit Ear and McNees's Creeks. Flower lilac.
- 79 (72) 3 September, 1847. Sand hills 4 miles south of the crossing of Arkansas River. Flower fine red, the size of a dime.
- 80 (73) 3 September, 1847. Crossing of the Arkansas River, sand hills south of that river. Flower red, near the size of half a dime.
- 81 (74) 3 August, 1847. Santa Fe, common in waste places about town. Flower, deep yellow.

## MALVACEAE

- 82 (75) 13 June–8 August, 1847. Santa Fe, yards and waste garden places.
- 83 (76) 31 August, 1847. A few miles west of Lower Spring (Cimarron).
- 84 = 85 (76) "the same as last" 8 September, 1847. Banks of Pawnee Fork.
- 85 (77) 24 & 25 August, 1847. Low moist places at Rabbit Ear and McNees's Creeks.
- 86 (79) 30 June–31 July, 1847. Santa Fe, moist meadows.
- 87 (80) 24 June–28 July, 1847. Santa Fe, Creek bottom, near the creek.
- 88 (81) 8 June–30 July, 1847. Santa Fe, neighbourhood of fields and waterducts.
- 89 (78) 7 June–4 August, 1847. Santa Fe, wet meadows and near the walls of gardens and fields.
- 90 (82) 24 May–3 September, 1847. Santa Fe, plains and foot of the lower hills, near ditches. East to Rock Creek. Also Poñi Creek, between Bent's Fort and Santa Fe.

LINEACEAE (*sic*)

- 91 (83) 23 May, 1847. Santa Fe, level rather fertile tracts; petals 5, blue.
- 92 (83) 15–26 August, 1847. Between Vegas and Moro River and a few miles east of Cold Spring (Cimarron).
- 93 (85) 4 May–18 July, 1847. Hills about Santa Fe, gravelly dry soil. Flowers fugacious in the highest degree.
- 94 (85) 3–11 June, 1847. Santa Fe, in an old dry irrigating ditch. This plant seems to differ from the preceeding one in having the claw of the petals of the same colour of the blade, while the preceeding one has the upper part of the claw brown. "This 85 may be a mere variety of 84 or a peculiar species which could be named *L. puberulum*; probably the first."

- 95 (85) 29 August, 1847. Between Willow Bar and Middle Spring (Cimarron).  
 96 (85) 16-26 August, 1847. Moro River to Cold Spring (Cimarron River).  
 97 (84) 29 August, 1847. 16 miles east of Middle Spring (Cimarron River).  
 98 (86) 15-20 September, 1847. Prairie, between Turkey Creek and 110 Creek.

## GERANIACEAE

- 99 (87) 15 April-20 October, 1846-1847. [i.e., April, 1847] Santa Fe, Creek bottom and foot of hills not far from the creek. Found a plant of this kind in flower even as late as 21 December when the greater part of the creek valley was covered with deep snow.  
 100 (88) 3 June-28 July, 1847. Santa Fe, Creek valley, shady places, moist soil near the creek. I never found this plant growing in very dry localities.  
 101 (89) 31 May-28 July, 1847. Santa Fe Creek, near irrigating ditches at the foot of mountains.  
 102 (90) 18 August, 1847. 5 miles east of Moro River, bottom land.  
 103 (89) 18 August, 1847. Seems to differ from no. 101 only in its color. 6 miles east of Moro River.

## OXALIDACEAE

- 104 (91) 7 July-8 August, 1847. Santa Fe, margin of irrigating ditches and in low wet places.  
 105 "Marsilea without fructification!" 24 May, 1847. Rio del Norte. Leaves floating on the surface of the water in shallow places.  
 106 (92) 7 September, 1847. Between Coon Creek and Pawnee Fork. Road side.

## BALSAMINACEAE

- 107 (93) 14-24 August, 1847. 90 miles west of Independence to Council Grove, creek bottom, rich soil.

ZANTHOXYLACEAE (*sic*)

- 108 (94) 25 May, 1847. Rio del Norte. Steep and rocky banks (trap formation). Shrubs from 7 to 10 feet high, leaves of an agreeable odor.  
 108a (95) 8 May, 1847. Rio del Norte. Deep ravines in the mountains.  
 109 (96) 21 September, 1847. Kansas River, bottom land, a few miles south west of the upper ferry.  
 110 (97) 8 July, 1847. Santa Fe, Creek valley. steep rocky mountain sides. 26 April, 1847. Fruit specimen, from the preceeding year, in the same locality.

111 (98) 11-24 June, 1847. Santa Fe, Creek valley in the mountains, shady bank. Upwards of 4 feet high. Socially.

112a (99) 25 May, 1847. Fruit specimens. Rio del Norte. Precipices of the mountains and steep rocky banks of the river. Shrub from 3-8 feet high, possesses a peculiarly disagreeable odor. The berries of this shrub leave greasy spots on the paper in being dried. Also: 16 August, 1847. Moro River; rocky hillside; ripe fruit.

112b (99) 8 May, 1847. Rio del Norte. Flower specimens from the same regions as no. 112a.

#### ZYGOPHYLLACEAE

113 (100) 24 May-6 August, 1847. Rio del Norte and Santa Fe. Open level places, loose soil about town, near fields and waste places; adnate to the ground. The leaves of this plant when wet impart to the paper a yellow dye.

#### ACERACEAE

114a (102) male specimen. 22 April, 1847. Santa Fe, eastern mountain range, creek valley, near the margin of the creek and in low situations at a small distance from the same. Large trees, lower part of the trunk generally very knotty, which seems to arise from the many wounds the tree receives early in spring, in order to draw the sap from it. This sap is gathered in holes cut in the trunk of the tree at a little distance from the wounded places.

114b female specimens.

114c leave [*sic*] and fruit specimens. 3 April-12 May, 1847.

115 (102) 8 September, 1847. Pawnee Fork, creek bottom.

116 (101) 12-18 May, 1847. A shrub 15 feet high, of slender growth, in shady places near the creek, eastern mountains, Santa Fe. 31 May-6 June, fruit.

#### CELASTRACEAE

117 (103) 17 August, 1846. 25 miles east of Council Grove.

118 (104) 20 September, 1847. Shady bottom land of 110 Creek. Somewhat twining.

119a (106) flower specimen: 24 & 25 June, 1847. Santa Fe, eastern mountains, sunny side. fruit specimen: 28 July, 1847, in fruit. A shrub about 1½ feet high and 2 feet in diameter.

119b (105) 15 May-3 June, 1847. Santa Fe, Creek valley in the mountains. Foot of mountains, shady steep declivities, in soil consisting of decomposed rocks intermixed with vegetable mould. An evergreen shrubby plant about 1 foot high. Their roots consisting for the greater part in the older branches which by coming in contact with the ground send down rootlets and are therefore but slightly covered with soil.

#### VITACEAE

120 (108) 17 August, 1847. 2 miles east of Moro River, at the foot of high rocks.

121 (108) 28 July, 1847. Santa Fe, creek valley, between rocks.

122 (107) 25 May, 1847. Rio del Norte. Steep, desolate places of its high rocky bank, near the water, with their tendrils fastened to other shrubs.

## POLYGALACEAE

123 (109) 13 August, 1847. Low prairie, a few miles west of Vegas.

124 (110) 25-28 August, 1847. From Rabbit Ear Creek to Willow Bar. Road side.

## LEGUMINOSAE

125 (111) 1 October, 1846. Between Colorado and Bermejo Creeks, level prairie, good soil.

126 (111) 3 June-10 July, 1847. Santa Fe, creek valley, foot of mountains.

127 (113) 8 May, 1847. Rio del Norte. Shady places, in deep ravines between rocks.

128 (111) 7 July, 1847. Santa Fe, creek valley.

129 (111) 17 August, 1847. 2 miles east of Moro River.

130 (112) 25 June, 1847. Santa Fe, neighbourhood of a field.

131 (115) 8 May-25 July, 1847. Santa Fe, creek valley; most abundant near irrigating ditches in the lower part of the valley. Flowers of different colors, but most generally of a deep crimson which turns into deep blue in drying. This plant I have never observed to be eaten by any domestic animal. In fruit, 30 June.

132 (116) 31 May-3 June, 1847. Santa Fe, lower part of mountainsides. Flower of a rusty color.

133 (117) 5 September, 1847. 3 miles west of Fort Mann (near the Arkansas River). Banks of a creek.

134 (119) 28 August, 1847. Willow Bar, low wet bank of the creek.

135 (121) 18 August, 1846. Low places in the prairies, 12 miles east of Council Grove. Also: Santa Fe, 23 June-4 July, 1847. Creek valley and in waste places about town and near fields. Plant viscose and leaves a print of its shape in green color on the paper.

136 (122) 14 August-9 September, 1847. From San Miguel to Cow Creek, high priaries.

137 (123) 29 August, 1847. Between Willow Bar and Middle Spring (Cimarron River).

138 (124) 14 October, 1846. Santa Fe prairie.

139 (125) 14 August, 1847. 7 miles west of Vegas, in woodland. Plant 2-3 feet high.

140 (126) 17 August, 1846-8 September, 1847. 120 miles west of Independence to Pawnee Fork. Shrub from 3 to 5 feet high.

141 (127) 10 July-15 September, 1846-1847. n.b.: 15 Sep-

tember, 1846 Santa Fe, margin of irrigating ditches, near fields. Also: low prairies near the Arkansas River.

142 (132) 19 May–19 June, 1847. Santa Fe. Dry gravelly hills, sunny sides. A shrub of dwarfish growth,  $\frac{1}{2}$  to 1 foot high; stem and branches very crooked and confusedly entangled in each other. Fruit specimen: 21 June, 1847.

143 (133) 21 May–25 August, 1847. Santa Fe, sunny sides and foot of stony gravelly hills. East of McNees's Creek.

144 (131) 27 August–3 September, 1847. Upper Spring (Cimarron River) to Walnut Creek. Prairie.

145 (129) 15–27 August, 1847. From Vegas to Upper Spring (Cimarron). Prairie.

146 (130) 29 August, 1847. Willow Bar (Cimarron), sandy soil.

147 (128) 28 August, 1847. Between the Crossing of the Cimarron River and Willow Bar; low sandy places on the prairie.

148 (127) 20 September, 1847. A few miles west of 110 Creek. Prairies.

149 (134) 28–29 August, 1847. Between the Crossing of the Cimarron and Middle Spring. Sandy soil.

150 (135) 11–26 July, 1847. Santa Fe, near fields. 14 August, 1846. About 90 miles west of Independence; steep side of a rocky bluff. 20 August, 1847. Middle Spring (Cimarron).

151 (136) 21 September, 1847. Prairies a few miles southwest of the upper ferry of the Kansas River.

152 (137) 14 August, 1847. 5 miles west of Vegas.

153 (138) 13–29 August, 1847. Between Willow Bar and Middle Spring (Cimarron). Sandy soil. Also: Ojo de Bernal.

154 (139) 30 August, 1847. 18 miles west of Lower Spring (Cimarron). Prairie.

155 (140) 3 October, 1846. Poñi Creek (between Bent's Fort and Santa Fe). Also: 15 June, 1847. Santa Fe, creek bottom, near the water.

156 (141) 7 June and 19 October, 1846–1847. [i.e., October, 1846 & June, 1847] Santa Fe, low somewhat wet places about town.

157 (142) 23 June, 1847. Santa Fe; enclosed field, amongst weeds and cornstalks.

158 (143) 2–6 September, 1847. Between Fort Mann (Arkansas River) and Walnut Creek; high prairie.

159 (146) 24 April–9 May, 1847. Plains about Santa Fe, red sandy soil; socially, of rather low depressed growth, but in patches from 1–2 feet diameter. I never observed that this plant had been eaten by any animal whatever.

160 (147) 10–15 May, 1847. Together with the preceeding one, flower white.

- 161 (171) 15-26 August, 1847. From Moro River to Cold Spring (Cimarron). Prairie.
- 162 (148) 22 April-28 May, 1847. Santa Fe, gravelly hills and lesser mountains amongst rocks.
- 163 (149) 8-25 May, 1847. Rio del Norte and Santa Fe. Stony hills.
- 164 (151) Santa Fe, 28 May, 1847. Dry gravelly hills.
- 165 (156) 25 May, 1847. Rio del Norte. Near its bank.
- 166 (152) 26 August, 1847. Between McNees's Creek and Cold Spring (Cimarron).
- 167 (153) 13 August, 1847. Neighbourhood of Ojo de Bernal.
- 168 (154) 5 August, 1847. Moro River, prairie.
- 169 (155) 25 August, 1847. Between Rabbit Ear and McNees's Creeks.
- 170 (150) 15 August, 1847. Moro River, prairie.
- 171 (144) 21 August, 1847. Between Colorado and Rock Creek. Low Prairie.
- 172 (157) 10 August, 1847. Between Santa Fe and Pecos. Woodland in the mountains.
- 173 (161) 8-25 May, 1847. Rio del Norte; loose sandy soil, not far from the river, especially around and between low shrubs. Flower sometime white.
- 174 (159) 19 April-28 June, 1847. Santa Fe; sunny and steep declivities of stony hills.
- 175 (159) 28 May-28 June, 1847. Santa Fe.
- 176 (156) 24 May, 1847. Santa Fe.
- 177 (158) 11 July, 1847. Santa Fe, hills.
- 178 (160) 3-13 June, 1847. Santa Fe; sunny hillside, between rocks, under protection of shrubs.
- 179 (164) 16 September, 1847. Cottonwood Creek to Kansas River; dry prairies.
- 180 (165) 24 September, 1847. 8 miles south of Fort Leavenworth; gullies along the road side.
- 181 (166) 8 May-30 June, 1847. Santa Fe. Level places on the neighbourhood of fields and irrigating ditches; rather socially.
- 181b Fruit: 30 June-2 August, 1847.
- 182 (167) 21 June, 1847. Santa Fe. Flower light rose color.
- 183 (168) 24 June-8 July, 1847. Santa Fe, creek valley in the mountains, foot of mountains.
- 184 (169) 3 October, 1846. Poñi Creek, between Bent's Fort and Santa Fe; low prairies.
- 185 (170) 2 May-3 June, 1847. Santa Fe, creek valley 5 miles above Santa Fe. Foot of mountains, and in level moist places.
- 186 (172) 18 September, 1847. Council Grove; creek bottom.



- 187 (173) 28 August, 1847. A few miles west of the ford of Cimarron River and at Willow Bar, road side.
- 188 (174) 31 August, 1847. A few miles west of the Lower Spring (Cimarron).
- 189 (180) 14 August, 1847. Between San Miguel and Vegas.
- 190 (179) 4 October, 1846. A few miles south of Rayado Creek (between Bent's Fort and Santa Fe), hillside, gravelly soil. 10–25 August, 1847. A few miles east of Santa Fe to McNees's Creek.
- 191 (178) 14 August, 1846. Black Jack Point; low prairies. 29 August, 1847. Between Willow Bar and Middle Spring (Cimarron).
- 192 (177) 21 August, 1846. Council Grove, grassy hillside.
- 193 (181) 27 August, 1847. Upper Spring (Cimarron), hillside.
- 194 (114) 8 August, 1847. Santa Fe, cultivated.
- 195 (145) 11 August, 1846. 2 miles south of Kansas River; woods, roadside. 15 August, 1846. About 100 miles west of Independence; on the more elevated places of the creek bottom.
- 196 (175) 21 August, 1846. Council Grove, low places. Plant from 4–6 feet high.
- 197 (118) 24 August, 1846. Council Grove, sloping bank of the creek and in the bottom land.
- 198 (120) 24 August, 1846. Council Grove, creek bank.
- 199 (162) 16 August, 1846. 117 miles west of Independence; bank of a creek and in bottom land.
- 200 (163) 16 August, 1846. 117 miles west of Independence; bank of a creek and in bottom land.
- 200<sup>2</sup> (176) 7 June, 1847. Santa Fe, gravelly hillside, socially.

## ROSACEAE

- 201 (182) 22 August, 1847. Rock Creek; creek bottom.
- 202 (186) 17 August, 1847. 2 miles east of Moro River; foot of high rocks.
- 203 (183) Santa Fe, creek valley; at no great distance from houses. Trees of about 30 or 40 feet high, branches spreading very much. 20 April, 1847. in flower. 20 May, 1847. in leaf.
- 204 (185) 28 May–3 June, 1847. Santa Fe Creek; steep rocky banks, at the margin of the creek. 15 July in fruit.
- 205 (187) 2–16 June, 1847. Santa Fe Creek, foot of hills. A shrub about 1 foot high.
- 205<sup>b</sup> 28 July, 1847, in fruit.
- 206 (190) 28 May–12 July, 1847. Santa Fe Creek, bottom land, margin of the water; fertile soil.
- 207 (192) 16 June, 1847. Santa Fe, margin of the creek, in the mountains.
- 208 (193) 24 May–4 October, 1846–7. Rio del Norte and Rayado Creek (between Bent's Fort and Santa Fe). Sides of ravines and

- steep rocky banks of the river. Shrub from 2 to 5 feet high. [N.B.: Rayado Creek = 4 October, 1846; Rio del Norte = 24 May, 1847.]
- 209 (195) 3-28 July, 1847. Santa Fe, creek bottom, near the water.
- 210 (196) 11 August, 1846. 18 miles south of Fort Leavenworth.
- 211 (191) 17 August, 1846. 15 miles east of Council Grove; creek bottom.
- 212 (197) 24 June-15 July, 1847. Santa Fe, creek valley; sunny side of mountains between rocks, 11 miles above Santa Fe. Plant viscose.
- 213 (201) 16 August, 1847. Moro River, hillside.
- 214 (202) 25 June-8 July, 1847. Santa Fe, creek valley in the mountains, 9 miles above Santa Fe; foot of mountains, sunny side.
- 215 (199) 1-15 July, 1847. Santa Fe, creek bottom; also foot of hills not far from the creek, sunny side.
- 216 (203) 22 June-26 July, 1847. Santa Fe, creek bottom, margins of the creek.
- 217 (198) 16-25 June, 1847. Santa Fe, creek bottom, moist soil.
- 218 (200) 15 May-24 June, 1847. Santa Fe, creek bottom and moist meadows.
- 218<sup>b</sup> (197) 19 October, 1846. Santa Fe, damp places.
- 219 (204) 3 June, 1847. Santa Fe, creek bottom, at some distance from the water.
- 220 (205) 16 June-15 July, 1847. Santa Fe, creek valley in the mountains 9 miles above Santa Fe, foot of mountains.
- 221 (206) 26 April-3 June, 1847. Santa Fe Creek. Sunny declivities of the mountains; more frequently at the foot of mountains, and in the valley not far from the creek. Socially and intermixed with the following one.
- 222 (207) 22 April-15 May, 1847. Santa Fe, creek valley. In similar situations with the preceding one, though generally not so high up on the mountains.
- 223 (208) 11-26 June, 1847. Santa Fe, bank of the creek, shady places. 28 July, in fruit.
- 224 (209) 31 May-24 June, 1847. Santa Fe, creek valley in the mountains, shady place near an irrigating ditch. Petals 5, alternate, perpendicular and at right angles to the sepals.
- 225 (210) 16-24 June, 1847. Santa Fe Creek, near its margins.
- 226 (211) 22 August, 1847. Rock Creek, creek bank amongst other shrubs.
- 227 (212) 22 August, 1847. Rock Creek, bottom land.

- 228 (212) 15 August, 1847. Banks of Moro River.  
 229 (213) 7-8 July, 1847. Santa Fe, creek valley in the mountains, 9 miles above Santa Fe, sunny side of mountains.  
 230 (184) 30 April, 1847. Santa Fe, neighbourhood of houses.  
 230<sup>2</sup> (188) 15 July, 1847. Santa Fe, upper part of the creek; steep sunny sides of mountains. Shrub about 4 feet high.  
 230<sup>3</sup> (189) 21 August, 1847. Rio Colorado, thin layers of soil upon and between ledges of rocks, near the river bank.  
 230<sup>4</sup> (194) 3-15 July, 1847. In fruit. Santa Fe Creek valley in the mountains; sunny side of steep rocky mountains. A shrub 8 to 10 feet high.

## LYTHRACEAE

- 231 (214) 25 August, 1846. Council Grove, creek bed.  
 232 (214) 18 September, 1847. Bluff Creek bottom, about 16 miles east of Council Grove. 20 September, 1847. Bottom of 110 Creek.  
 233 (215) 21 August, 1846. Council Grove.  
 234 (215) 11 August-21 September, 1846-7. 18 miles south of Fort Leavenworth, and prairies a few miles southwest of the upper ferry of Kansas River. [N.B. 11 August, 1846 = 18 miles south of Fort Leavenworth.]

## ONAGRACEAE

- 235 (216) 24 June-28 July, 1847. Santa Fe, Creek valley in the mountains, in ravines; flowers purple.  
 236 (217) 16 June-30 September, 1846-7. Santa Fe, creek bed, gravelly wet places near irrigating ditches, grassy margin of the creek. Also: Raton Creek (between Bent's Fort and Santa Fe) creek bottom in the mountains. [N.B. 30 September, 1846 = Raton Creek; 16 June, 1847 = Santa Fe.]  
 237 (230) 24 May-18 July, 1847. Santa Fe, sunny hillside; also: Rio del Norte, bank of the river; flower of a sulphur color, which turns to be red in a few days after opening and in drying.  
 238 (222) 28 May-12 July, 1847. Santa Fe, creek valley. In different localities on soil that was dug up in the spring to elevate the sides of an irrigating ditch. Also: on the sunny side of a small hill in places where the soil was full of ants. Petals white, but turning into red when drying.  
 239 (223) 8-10 May, 1847. Rio del Norte, gravelly soil near the river. Petals white, showy. Also: Santa Fe.  
 240 (218) 24 June, 1847. Santa Fe, creek valley in the mountains; foot and sunny sides of mountains. Plant 2-3 feet high.  
 241 (219) 19 September, 1847. Prairie between Bluff Creek and 110 Creek.

- 242 (220) 12 August, 1846. Dry prairies, 20 miles south of the lower ferry of the Kansas River. Plant 4 feet high.
- 243 (223) 19 June–28 July, 1847. Santa Fe. In and near fields on rather elevated places, Flowers white.
- 243b the same with white flowers. 12 July, 1847. Santa Fe.
- 244 (221) 3–28 July, 1847. Santa Fe, hillside near a field.
- 245 (230) 28 August, 1847. A few miles west of the ford of the Cimarron River.
- 246 (230) = 237, foliis angustioribus. 23–31 August, 1847. 7 miles west of Rock Creek to a few miles west of the Lower Spring (Cimarron River).
- 247 (228) 16 June–19 July, 1847. Santa Fe, creek bottom.
- 248 (229) 25 August, 1847. McNees's Creek. Sandy hillside.
- 249 (229) 21–28 August, 1847. Low prairies from Rio Colorado to the ford of the Cimarron River.
- 250 (229) 13–15 August, 1847. Ojo de Bernal to Vegas.
- 251 (224) the same as 243, fol. integr. 23 June–18 July, 1847. Santa Fe, near irrigating ditches. Also: 28 August, 1847. Between the ford of the Cimarron River and Willow Bar. Sand.
- 252 (224) the same as last, more canescent. 29 August, 1847. About 10 miles east of Middle Spring (Cimarron).
- 253 (225) 21 September, 1847. Creek bottom, about 20 miles east of 110 Creek.
- 254 (225) 17 August, 1846. 20 miles east of Council Grove, dry prairies.
- 255 (226) 24 August, 1846. Council Grove, low places.
- 256 (227) 1 September, 1847. Sand Creek, margin of a low swampy place.
- 257 (231) 17 May–2 August, 1847. Santa Fe, near fields. Sepals 4, reflexed; petals 4, alternate, light rose color changing to deep red. 18 June, 1847. Santa Fe. Petals white changed to yellow. 3 September, 1846. Walnut Creek, rather low prairie.
- 258 (232) 28–29 August, 1847. Between Willow Bar and Middle Spring (Cimarron).
- 259 (233) 12 August, 1846. A few miles south of the lower ferry of the Kansas River. Bottom land.
- 260 (234) 27 August, 1846. 30 miles west of Council Grove; creek bank. 15 August, 1847. Bottom land of Moro River. Plant upwards of 15 feet high at Willow Bar.
- 260<sup>b</sup> (234) 1 September, 1846. Between Cow Creek and Walnut Creek, low prairie. Flower white.
- 261 (235) 21 September, 1847. 10 miles southwest of the upper ferry of Kansas River, prairie. Plant 4–5 feet high.

262 (236) 18 September, 1847. Bluff Creek, bottom land, near the water.

263 (237) 12 August, 1846. A few miles south of the lower ferry of the Kansas River.

264 (238) 15 May–7 June, 1847. Santa Fe, in the water of a pond near its margin.

#### LOASACEAE

265 (239) 1 August, 1846. Council Grove, on hills between rocks. [N.B.: date must be incorrect; Fendler left Fort Leavenworth only on 10/11 August.]

266 (242) 21 June–19 July, 1847. Santa Fe, near fields. Flower very seldom open in the daytime.

267 (240) 21 August, 1847. Between Rio Colorado and Rock Creek, low prairie. Stem 3–4 feet high, much branching.

268 (242) 17 September, 1846. Gravelly and pebbly hillsides, from the ford of the Arkansas River to Bent's Fort.

269 (243) 17 August, 1847. 2 miles east of Moro River, low prairies.

270 (240) 25 August, 1847. McNees's Creek. 2 September, 1847. Pawnee Fork; prairies. Stem 4 feet high, flower vespertile.

#### CACTACEAE

271 (244) 8 July, 1847. Santa Fe. To cactus n. 1. Eastern mountain range at a moderate height and near the foot of mountains, between pieces of rock. Also: frequently on the road from Bent's Fort to Santa Fe, on hills and high prairies. Plant not more than 2 inches above the ground. Subglobose or obovate with the upper part hemispherical. Either solitary or in pairs. There are some in which the root sends up several subterranean branches which ramify again and again in elongating, until they reach the surface, where each ramification bears a globose plant at its apex. Spines straight, radiating at right angles to the axes of their respective mammaeform or conical tubercles, white, thin, more like fine bristles with the exception of from 2–4 stronger ones, which are mostly of a red color and make larger angles with the axes of their respective tubercles.

272 (247) 15 May, 1847. To cactus no. 3. Santa Fe. Higher regions of the mountains, steep and rocky sunny declivities. Also: on elevated plains somewhat sandy. Plant generally growing in large clusters; the young plants growing from the sides of the old one, in the dividing line of the subterranean part of the stem from that part above the ground, that is, close to the soil. Sometimes in clusters of 14 individual plants. Alternate ribs and furrows, the ribs beset with radiating spines, (generally 9 in number), nearly in a tangential plane to the apex, and a tenth one in the center, erect, much longer than the rest and of a darker color. Ribs 10, rarely 11.

273 (249) 9-21 June, 1847. To cactus no. 4. Santa Fe, high level somewhat sandy prairie. Young plants growing from the old ones in the same manner as in the preceding no. Plant: 10 ridges, (generally) 7, radiating, tangential rather stout spines, with a larger somewhat curved and oblique standing one in the center and pointing more or less towards the apex of the plant. The younger spines are more or less dark colored, of a lighter shade near the apex. Many of the spines are more or less dark colored, of a lighter shade near the apex. Many of the spines are flattened.

274 (248) 31 May-13 June, 1847. To cactus no. 5. Santa Fe. Higher regions of the mountains, steep and rocky sides. Also: on elevated, broken, somewhat sandy plains. 7 ridges, mostly 3 to 5, somewhat curved, stout, flattened spines with a sharp edge or ridge running on the inside from the base to the apex; length of spines about 1 inch; no central one.

275 (251) 21 June, 1847. To cactus no. 6. Santa Fe. 3 to 8 miles southwest of the town. Elevated plains, somewhat sandy soil; in spreading clusters of from 2-4 feet diameter. I never found them in the mountains or on high hills.

276 (250) 25 May-9 June, 1847. To cactus no. 7 and 8. Santa Fe. Both grow in sandy, pebbly and generally on sterile soil. spreading over 2 to 3 feet diameter. Plant no. 7 flat, round, somewhat obovate joints, with 7 rows of spiny nodes on each side, each row containing 7 nodes which are beset with fine rigid bristles. The plant of no. 8 has much larger and smoother joints, which are also oblong obovate.

277 (252) 19 June-29 June, 1847. To cactus no. 9. Santa Fe. Foot of the mountains, on moderate hills and high prairies. Upwards of 6 feet high and the lower part of the stem in some instances 5 inches diameter. Spines sheathing. Fruit lateral as well as terminal, either dry and hard, or soft and yellow. 22 December, 1846. The yellow fruit adheres to the branches as strong as ever, and has not changed in its appearance in the least since the 1 November. This kind of cactus seems to stand the cold much better than the flat jointed kinds, no. 7 and 8. They are sometimes used on the tops of mud walls, for the same purpose as broken glass bottles are used in other countries.

278 (246) 4 May-9 June, 1847. To cactus no. 11. Santa Fe. Eastern mountain range, sunny declivities of the smaller mountains, between rocks.

279 (245) 15-21 May, 1847. To cactus no. 12. Santa Fe, valley of the lesser hills; loose sandy clay, seemingly good soil.

## GROSSULARIACEAE

280 (256) 16 August, 1847. Moro River, rocky hillside.

- 281 (256) 30 May, 1847. 5 miles southwest of Santa Fe. In a dry valley between the lesser hills. Leaves viscoose and of a peculiar odor.
- 282 (257) 15-22 August, 1847. From Moro River to Rock Creek, bottom land and near the banks. 3 to 5 feet high.
- 283 (254) 25 May, 1847. Rio del Norte. Steep and rocky banks of that river. Shrub about 4 feet high.
- 284 (254) = 283. 8-25 May, 1847. Rio del Norte, ravines.
- 285 (254) 29 May, 1847. Santa Fe. Shrub 3 feet high.
- 286 (255) 12 May, 1847. Santa Fe, mountains.
- 287 (253) 11-28 May, 1847. Santa Fe, margin of the Creek.
- 288 (255) 2-12 May, 1847. Santa Fe Creek, shady bank, a few steps from the creek. Shrub 4 feet high.

## CUCURBITACEAE

- 289 (258) 14 August, 1846. Hickory Point, about 80 miles west of Independence.
- 290 (259) 22 August, 1847. Rock Creek, bottom.
- 291 (260) 21-30 June, 1847. Santa Fe, margin of a pond and near fields in hollows.
- 292 (261) 19-31 July, 1847. Santa Fe, fields.

## CRASSULACEAE

- 293 (262) 3 August, 1847. Santa Fe, sides of rocks in the mountains near the Creek. Damp rich soil. Sepals 5, white; petals none; stamens 10? Flowers minute; leaves thick, fleshy.
- 294 (263) 18 September, 1847. Bluff Creek, bottom.

## SAXIFRAGACEAE

- 295 (264) 16 June-28 July, 1847. Santa Fe; northern declivities of mountains, on rocks. Leaves green throughout the winter.
- 296 (265) 12 May-24 June, 1847. Santa Fe Creek. Steep shady rocky banks.
- 297 (266) 24 June-8 July, 1847. Santa Fe Creek, sunny steep sides of the mountains between rocks. 11 miles above Santa Fe.
- 297<sup>2</sup> (267) 6-22 June, 1847. Santa Fe Creek bank near the water, where the creek is walled in on both sides by high rocks.

## UMBELLIFERAE

- 298 (268) 18 September, 1847. Bluff Creek, bottom.
- 299 (269) 18 September, 1847. Bluff Creek, bottom.
- 300 (270) 15 August, 1847. Moro River bank.
- 301 (271) 8 August, 1847. Santa Fe Creek bottom.
- 302 (272) 2-25 June, 1847. Santa Fe Creek, fertile soil, margin of water.
- 303 (273) 16 June-8 July, 1847. Santa Fe Creek, margin of the water.
- 304 (274) 24 April-30 May, 1847. Santa Fe. Gently sloping

declivities amongst the gravelly hills. Rather good soil.

305 (275) 24 April, 1847. Santa Fe. Socially and together with the preceding one, found only in one locality.

306 (278) naturalized around Santa Fe [N.B.: entire entry in hand of A. Gray.]

307 (276) 26 April–3 July, 1847. Santa Fe Creek, sunny declivities, foot of mountains.

308 (277) 17 August, 1847. 2 miles east of Moro River. Elevated rocky region.

#### CORNACEAE

309 (279) 20 September, 1847. Bottomland of 110 Creek.

310 (280) 28 May–13 June, 1847. Sandy, steep and rocky bank of Santa Fe Creek, close to the water. Shrub about 12 feet high.

#### LORANTHACEAE

311 (281) 4 November, 1846; 17 March, 1847. Neighbouring hills about Santa Fe and elevated plains. I found this plant growing only upon the branches of the two kinds of shrub cedar that grow about Santa Fe, and on one other tree. It occurs sometimes in clusters of over 1 foot diameter and 3/4 foot high. Wherever they are found, they are found on many neighbouring trees (socially). Leafless. The berry is globose of a light champaign colour, with a tinge of red when dried, glossy. Berries on short branchlets, 1, 2, rarely 3 together. The lines of dilation of the tops of any pair of adjacent joints are at right angles to each other. Branches more wrinkled after than before drying.

312 (282) 2 March, 1847. Santa Fe, mountain range; declivities of the lower mountains. Only on Coniferae no. 830, in much smaller and thinner clusters than the preceding one. Branches somewhat quadrangular. Berries smaller, on styles. The branches of the tree, on which this plant grows, seem to be much injured by it.

313 (283) 7 March–20 April, 1847. Santa Fe, mountain range. Lower part of the mountains in ravines. Only found on Coniferae no. 831. The branches of the tree, on which this plant grows, are likewise injured by it.

#### CAPRIFOLIACEAE

314 (284) 8 September, 1847. Pawnee Fork. Creek bottom.

315 (285) 2 October, 1846. Poñi Creek (between Bent's Fort and Santa Fe).

316 (284b) 7 July, 1847. Santa Fe Creek bottom.

317 (286) 2–16 June, 1847. Santa Fe Creek, margin of the water. A shrubby plant about 4 feet high.

#### RUBIACEAE

318 (287) 16 June–7 July, 1847. Santa Fe Creek, shady bank near an irrigating ditch.

319 (288) 15–28 July, 1847. Santa Fe Creek valley. Sunny



side of high mountains. Petals 4, pale yellow.

320 (289) 16–29 June, 1847. Santa Fe; wet places near irrigating ditches.

321 (290) 12–23 August, 1846. From Lone Elm west to Council Grove. Low prairie. also: near a pool of standing water.

322 (291) 17–30 May, 1847. 7 miles southwest of Santa Fe. Foot of dry gravelly hills, tolerably good soil. Flower bluish red.

323 (292) 26 August, 1847. Between McNees's Creek and Cold Spring (Cimarron). Prairie.

324 (292) 19 August, 1846. Council Grove, on hills, in crevices of rocks.

#### VALERIANACEAE

325 (293) 15–18 August, 1847. Vegas to Moro River. Elevated rocky region.

326 (294) 22 April–20 May, 1847. Santa Fe Creek; foot of mountains, shady steep declivities; rich soil in corners of the rocks. Flower branchlets each pair at right angles to the next pair below or above. Inflorescence centrifugal. Each flower branchlet is subtended by a bract. Petals 5, light rose colour, nearly white. 3–6 June, 1847, in fruit.

#### COMPOSITAE

327 295. *Vernonia noveboracensis* var. 3 September, 1847. Ford of the Arkansas River. Bottom land.

328 299. *Liatris punctata*. 14–28 August, 1847. San Miguel to Willow Bar (Cimarron). Prairies.

328b 299. *Liatris punctata*. 14 August, 1846. Hickory Point; prairies. Leaves larger and more narrow; bract of the flowers more pointed.

328c 299. *Liatris punctata*. 30 August–15 September, 1846–7. Walnut Creek to Cottonwood Creek; dry prairies. Flower spikes more crowded; bracts of the flowers more acuminate. In one specimen flower white.

329 300. *Liatris spicata*. 30 August, 1847. Middle Spring (Cimarron). Low prairie. Plant 4–6 feet high.

330 301. *Liatris pycnostachya*. 11 August, 1846. 18 miles south of Fort Leavenworth; dry prairies.

331 298. *Liatris squarrosa*  $\delta$  *intermedia*. 15 September, 1847. Prairies between Turkey Creek and Cottonwood Creek.

332 297. *Liatris squarrosa*. 8 miles south of Fort Leavenworth.

333 302. *Liatris scariosa*. 10 August–16 September, 1847–46. Region about Council Grove and to Fort Leavenworth; high prairies.

333b 302. *Liatris scariosa*. Council Grove; high prairies. Inflorescence different from the preceding one.

- 334 445. *Tetradymia inermis*. 26 July, 1847. Santa Fe; sunny side of a hill. Shrub 3 feet high, the only one shrub of this kind seen by me.
- 335 306. *Brickellia grandiflora*. 22, 23 August, 1847. Near Rock Creek; steep rocky side of a ravine.
- 336 identified in the collection list as *Eupatorium ageratoides*, but not cited in "Plantae Fendlerianae." 18 September, 1847. Council Grove; creek bottom.
- 337 311. *Eupatorium perfoliatum*. 24 September, 1847. 8 miles south of Fort Leavenworth; low prairie.
- 338 identified in the collection list as *Eupatorium purpureum*, but not cited in "Plantae Fendlerianae" 23 September, 1847. Creek bottom, north of Kansas River.
- 339 309. *Clavigera brachyphylla*. 17 August, 1847. 2 miles east of Moro River; foot of high rocks.
- 340 304. *Kuhnia eupatorioides*. 17 August, 1846. 18 miles east of Council Grove.
- 341 352. *Linosyris graveolens*. 23 September, 1846. Bent's Fort, gravelly dry hills. A shrub 2 to 4 feet high.
- 342 305. *Kuhnia eupatorioides*  $\gamma$  *gracilis*. 15 August, 1847. Bottom of Moro River. 2 to 3 feet high.
- 343 identified in the collection list as *Kuhnia eupatorioides*, but not cited in "Plantae Fendlerianae" 7, 8 September, 1847. Between Cow Creek and Pawnee Fork. Prairies.
- 344 309. *Eupatorium purpureum*. 15 August, 1846. About 100 miles west of Independence; creek bottom.
- 345 310. *Eupatorium ageratoides*. 15 August, 1846. 100 miles west of Independence; creek bottom.
- 346 308. *Brickellia californica*. 16 August, 1847. Moro River; hillside between rocks. Also: 18 August, 1847. 8 miles east of Moro River, bottom land.
- 347 307. *Brickellia fendleri*. 8-28 July, 1847. Santa Fe Creek, 11 miles above Santa Fe, foot of mountains, sunny side.
- 348 335. *Diplopappus ericoides*. 10 May-19 June, 1847. Santa Fe, side of ravines in very dry places.
- 349 336. *Townsendia sericea*  $\beta$  *papposa*. 19 April-10 May, 1847. Santa Fe, gently sloping declivities of hills, less frequently on grassy places.
- 350 337. *Townsendia fendleri*. 11 May-2 August, 1847. Santa Fe, hillsides, gravelly soil.
- 351 338. *Townsendia strigosa*. 4-15 May, 1847. Santa Fe, gravelly hills.
- 352 312. *Dieteria coronopifolia*. 10 August-10 September, 1846-7. Walnut Creek to the ford of Arkansas River [Sept., 1846];

loose somewhat sandy soil. Also: a few miles east of Santa Fe [Aug., 1847].

353 340. *Townsendia eximia*. 28 June–15 August, 1847. Santa Fe Creek, sides of high mountains, to Moro River; prairies.

354 identified in the collection list as *Aster novae-angliae*, but not cited in "Plantae Fendlerianae" 22, 23 September, 1847. Shady creek bank and low prairies, a few miles north and south of the upper ferry of the Kansas River.

355 316. *Aster sericeus*. 16–19 September, 1847. Prairies 20 miles west of Council Grove to Fort Leavenworth.

356 315. *Aster sagittifolius*. 17 September, 1847. Council Grove; creek bottom.

357 315. *Aster sagittifolius*. 17 August–23 September, 1847. 15 miles east of Council Grove, and a few miles north of the upper ferry of the Kansas River; creek bottom.

358 not identified and not cited in "Plantae Fendlerianae" 23 September, 1847. Prairies and creek banks, between Kansas River and Fort Leavenworth.

359 "I do not find this." 28 Sept., 1846. Rio de los Animas (between Bent's Fort and Santa Fe), bottom land.

360 320. *Aster simplex*. 3 July–3 August, 1847. Corners of a walled in pasture.

361 "the same as last," but not cited in "Plantae Fendlerianae" 15 August–3 October, 1846–7. Banks of the Moro River and bottom of Põni Creek (between Santa Fe and Bent's Fort).

362 313. *Aster laevis*. 28 July, 1847. Santa Fe Creek valley in the mountains, 9 miles above Santa Fe, foot of mountains.

363 326. *Aster divaricatus*. 3 September, 1847. Ford of Arkansas River, south side, bottom land.

364 323. *Aster* n. sp.? 17 August, 1847. 2 miles east of Moro River.

365 322. *Aster miser*  $\gamma$  *diffusus*. 22 Sept., 1847. Creek banks and bottoms a few miles north of the upper ferry of Kansas River; 5–6 feet high.

366 314. *Aster azureus*. 21 Sept., 1847. Prairies, 12 miles southwest of the upper ferry of Kansas River.

367 319. *Aster multiflorus*  $\gamma$  *commutatus*. 22 Aug., 1847. Rock Creek, bottom land.

368 318. *Aster multiflorus*. 16–21 Sept., 1847. Cottonwood Creek to the upper ferry of Kansas River.

369 324. *Aster oblongifolius*. 17 Sept., 1847. Prairies and creek bottoms about Council Grove.

370 321. *Aster carneus*. 3 Sept., 1846. Banks of Walnut Creek.

- 371            325. *Aster oblongifolius*. 23 Aug., 1847. 7 miles east of Rock Creek.
- 372            317. *Aster fendleri*. 20 Aug., 1847. Ocate Creek and Rio Colorado.
- 373            314. *Egletes humilis*. 25 May, 1847. Santa Fe Creek valley, foot of a hill.
- 374            333. *Erigeron cinereum*. 11 April–11 May, 1847. Santa Fe; sunny declivities, foot of hills near irrigating ditches, socially.
- 375            332. *Erigeron canum*. 17 May–3 June, 1847. Santa Fe; gravelly hills; also: foot of mountains, dry places.
- 376 = 384      331. *Erigeron macranthum*. 28 July, 1847. Santa Fe Creek, valley, sides of high mountains 10 miles above Santa Fe.
- 377            327. *Erigeron candense*. 12 July–20 Oct., 1846–7. Santa Fe Creek bottom, margin of the creek.
- 378            363. *Conyza subdecurrens*. 28 July, 1847. Santa Fe, foot of mountains; high up the creek.
- 379            identified in the collection list as *Boltonia glastifolia*, but this species is not mentioned in "Plantae Fendlerianae" 16 September, 1847. Prairie, a few miles east of Cottonwood Creek.
- 380            333. *Erigeron cinereum*. 24 May–11 June, 1847. Rio del Norte, low sandy bank. Also: Santa Fe, creek bottom in the mountains.
- 381            334. *Erigeron flagellare*. 20 May–22 June, 1847. Santa Fe Creek bottom, low moist places.
- 382            328. *Erigeron divaricatum*. 7 Sept., 1847. Between Coon Creek and Pawnee Fork, roadside.
- 383            329. *Erigeron bellidiastrum*. 28 Aug., 1847. A few miles west of the ford of Cimarron River and Willow Bar; deep sand.
- 384 = 376      330. *Erigeron macranthum*. 3–15 July, 1847. Santa Fe Creek, high mountains, 11 miles above Santa Fe.
- 385            333. *Erigeron cinereum*. 31 May–19 July, 1847. Santa Fe Creek valley, near irrigating ditches.
- 386            357. *Prionopsis ciliata*. 28 Aug.–1 Sept., 1847. Between Willow Bar and Cow Creek, low prairies.
- 387            346. *Solidago speciosa*  $\beta$  *angustata*. Santa Fe Creek valley, sides of high mountains.
- 387b           350. *Solidago incana*. 27 July, 1847. Santa Fe.
- 388            342. *Gutierrezia euthamiae*. 23 Sept., 1846. Bent's Fort. Also: 8 July–10 Aug., 1847. Santa Fe, gravelly hills.
- 389            347. *Solidago rigida*. 22 Aug., 1846. Council Grove, prairies.
- 390            358. *Grindelia squarrosa*. 24 June–3 Aug., 1847. Santa Fe Creek bottom; also: moist meadows and near irrigating ditches.
- 391            360. *Chrysopsis villosa*. 11 June–6 Aug., 1847. Santa Fe

Creek valley, sunny hillsides between rocks. Also: 10 Oct., 1846. A few miles east of Pecos.

391 361. *Chrysopsis canescens*. 12 July–1 Sept., 1847. From Santa Fe to Sand Creek, dry prairies.

391 362. *Chrysopsis canescens* var. *nana*. 17 Aug., 1847. 2 miles east of Moro River. Elevated rocky region.

392 359. *Heterotheca scabra*  $\beta$  *nuda*. 29–31 Aug., 1847. Middle Spring to Lower Spring (Cimarron); low prairies.

393 356. *Haplopappus gracilis*. 19 Oct., 1846. Creek bottom, Santa Fe.

394 354. *Haplopappus spinulosus* var. *glaber*. 16 miles east of Middle Spring, prairies.

395 355. *Haplopappus spinulosus* var. *canescens*. 24 May, 1847. Between Santa Fe and the Rio del Norte.

396 364. *Eclipta erecta*. 26 Sept., 1847. Banks of the Missouri River, below Liberty.

397 369. *Melampodium cinereum*. 17 Sept., 1846. 10 miles east of Big Sand Creek, high prairies, gravelly soil. Also: 8 May, 1847. Rio del Norte.

398 365. *Silphium integrifolium*. 21 Sept., 1847. High prairies, a few miles southwest of the upper ferry of Kansas River.

399 366. *Silphium perfoliatum*. 23 Sept., 1847. Creek bank 5 miles north of Kansas River.

400 381. *Zinnia grandiflora*. 7 June–4 Oct., 1846–47. Santa Fe. Dry gravelly hillsides. Also: Rayado Creek 4 Oct., 1846 (between Bent's Fort and Santa Fe), foot of a hill; gravelly soil.

401 367. *Engelmannia pinnatifida*. 29 Sept., 1846. Raton Mountains.

402 = 410 372. *Ambrosia coronopifolia*. Santa Fe, near garden walls, moist soil. 2 August, 1847.

403 identified in the collection list as *Ambrosia coronopifolia*, but not cited in "Plantae Fendlerianae" 16, 17 Sept., 1847. Region about Council Grove.

404 identified in the collection list as *Ambrosia coronopifolia*, but not cited in "Plantae Fendlerianae" 26 July, 1847. Santa Fe Creek, valley near the creek.

405 373. *Ambrosia longistylis*. 26 July–10 Aug., 1847. Santa Fe Creek bottom and other low level places. Branches mostly decumbent, upwards of 3 feet long.

406 378. *Franseria tenuifolia*. 13 July, 1847. 3 Oct., 1846. Poñi Creek (between Bent's Fort and Santa Fe), low prairies. Also: Santa Fe, foot of hills near an irrigating ditch.

407 374. *Ambrosia longistylis*, var. 6 Aug. 1847. Santa Fe Creek bottom.

- 408 376. *Franseria hookeriana* var. 20 Sept., 1846. Dry Creek, 6 miles east of Bent's Fort, sandy bed of the creek. 28 August, 1847. Willow Bar, deep sand.
- 409 375 bis. *Franseria hookeriana*. 19 Oct., 1846. Santa Fe, near the creek.
- 410 = 402 identified in the collection list as *Ambrosia coronopifolia*, but not cited in "Plantae Fendlerianae" 13 Aug., 1846. dry prairie at Lone Elm camp. 8 Sept., 1847. Pawnee Fork.
- 411 377. *Franseria discolor*. 21 Aug., 1847. Between Rio Colorado and Rock Creek.
- 412 379. *Franseria tomentosa*. 2 Sept., 1846. Walnut Creek, high part of the bank.
- 413 370. *Iva ciliata*. 1-3 Sept., 1847. Sand Creek. Low wet places in the prairie, east of Fort Leavenworth.
- 414 375. *Ambrosia aptera*. 22 Aug. 1847. Rock Creek, bottom land. 22 Aug., 1846-2 Sept., 1846. Council Grove to Walnut Creek, 8 to 10 feet high.
- 415 371. *Cyclachaena xanthiifolia*. 8 Aug.-17 Aug., 1847. Santa Fe—2 miles east of Moro River, bottom land. 8 to 10 feet high.
- 416 371. *Cyclachaena xanthiifolia*. 10-22 Aug., 1847. Santa Fe to Rock Creek. Bottom land, 6 to 10 feet high.
- 417 384. *Rudbeckia laciniata*. 3 June-19 July, 1847. Santa Fe Creek bottom, close to the water.
- 418 identified in the collection list as *Rudbeckia laciniata*, but not cited in "Plantae Fendlerianae" 17 Aug., 1846. About 20 miles east of Council Grove, creek bottom.
- 419 385. *Rudbeckia subtomentosa*. 11 Aug., 1846. 15 miles south of Fort Leavenworth.
- 420 368. *Berlandiera lyrata*. 11-12 Aug., 1847. Between Pecos and San Miguel, woodland on the mountains.
- 421 403. *Ximenesia encelioides*  $\delta$  *cana*. 30 May-29 Sept., 1847. Santa Fe, waste gardens and about wheatfields, foot of hills. Also: Rio de los Animas, Raton mountains, valley.
- 422 387. *Lepachys columnaris*  $\beta$  *pulcherrima*. 13 Aug., 1847. 18 miles west of Pecos, valley.
- 423 386. *Lepachys columnaris*. 10 Aug., 1847. Between Santa Fe and Pecos.
- 424 388. *Lepachys columnaris*  $\beta$  *pulcherrima*. 7 July-3 Oct., 1846-47. Santa Fe [7 July, 1847], waste fields and level tracts, near waterducts. Ojo de Bernal and Põni Creek [3 Oct., 1846], prairies.
- 425 393. *Helianthus mollis*. 13 Aug. & 21 Sept., 1847-46. Dry prairies between 110 Creek and Fort Leavenworth.
- 426 392. *Helianthus rigidus*. 3 July, 1847. Santa Fe, waste garden place.

- 427            394. *Helianthus maximiliana*  $\beta$  *asperrimus*. 3 Sept., 1847. South side of ford of Arkansas River, bottom land.
- 428            389. *Helianthus lenticularis*. 23 June–28 July, 1847. Waste fields and Santa Fe Creek valley, 3 miles above Santa Fe.
- 429            390. *Helianthus petiolaris*. 29 Aug., 1847. Middle Spring (Cimarron), low places on the prairie, 8 to 12 feet high.
- 430            382. *Heliopsis laevis*. 15 Aug., 1847. Bottom land of Moro River.
- 431            395. *Heliopsis trachelifolius*. 16 Aug., 1846. Creek bottom, about 30 miles east of Council Grove.
- 432            396. *Heliomeris multiflora*. 23 Aug., 1847. 7 miles east of Rock Creek, bottom land.
- 433            383. *Heliopsis laevis*  $\beta$  *gracilis*. 26 Aug., 1846. Council Grove, creek bed near the water.
- 434            391. *Helianthus orgyalis*. 14 Aug., 1846. Hickory Point, low prairie.
- 435            402 *bis*. *Bidens connata*. 25 Sept., 1847. Dry part of the bed of Missouri River, a few miles above Liberty.
- 436            408. *Lowellia aurea*. 26–27 Aug., 1847. Between Cold and Upper Spring (Cimarron).
- 437            identified in the collection list as *Bidens*, but not cited in "Plantae Fendlerianae" 26 Sept., 1846. Dry part of the Missouri River bed, a few miles below Liberty.
- 438            identified in the collection list as *Bidens frondosa*, but not cited in "Plantae Fendlerianae" 25 Sept., 1847. Banks of Missouri River near Liberty.
- 439            402 *bis*. *Bidens connata*. 17 Sept., 1847. A few miles west of Council Grove, low places.
- 440            not identified in the collection list; not cited in "Plantae Fendlerianae" 10 Aug., 1847. Between Santa Fe and Pecos.
- 441            397. *Coreopsis tinctoria*. 17 Aug., 1847. a few miles east of Moro River, low places.
- 442            397. *Coreopsis tinctoria*. 5–9 Sept., 1846–47. Between Coon Creek and Pawnee Fork, shallow hollows in the prairie (said to be made by the buffaloes in wallowing).
- 443            402. *Bidens frondosa*. 3 Sept., 1847. South side of the ford of Arkansas River, bottom land.
- 444            398. *Coreopsis involucrata*. 20 Sept., 1847. A few miles east and west of 110 Creek, hollows in the prairie.
- 445            *Cosmidium gracile*. 24 May–1 Sept., 1846–47. Santa Fe, foot of hills near irrigating ditches. Also: Rio del Norte–Cow Creek.
- 446            identified in the collection list as *Cosmidium gracile*, but not cited in "Plantae Fendlerianae" 1 Oct., 1846. 3 miles north of Rio Colorado; valley in the prairies.

- 447 399. *Cosmos bipinnatus*. 14 Aug., 1847. 10 miles west of Vegas, woodland.
- 448 399. *Cosmos bipinnatus*. 20 Oct., 1846. Santa Fe Creek, bottom.
- 449 401. *Bidens tenuisecta*. 3 Oct., 1846. Poñi Creek (between Santa Fe and Bent's Fort), margin of the creek bank.
- 450 412. *Gaillardia pinnatifida*. 13 June–26 July, 1847. Santa Fe, foot of dry stony hills.
- 451 413. *Gaillardia pinnatifida* var. 23 Aug., 1847. 7 miles east of Rock Creek. Bracts, subtending the heads of flowers, much longer than on the preceding one.
- 452 414. *Gaillardia pinnatifida* var. 24 May, 1847. Rio del Norte, foot of hills.
- 453 410. *Gaillardia lanceolata*. 1 Sept., 1846. Between Cow and Walnut Creeks.
- 454 411. *Gaillardia pulchella*. 28 Aug–8 Sept., 1847. Ford of the Cimarron River and Pawnee Fork.
- 455 415. *Palafoxia hookeriana*  $\beta$  *subradiata*. 25 Aug.–20 Sept., 1847–46. Between Rabbit Ear Creek and Willow Bar, deep sand. Also: sandy bed of Dry Creek (between ford of Arkansas River and Bent's Fort).
- 456 419. *Hymenopappus luteus*. 5 May–11 July, 1847. Santa Fe, sloping sides of dry hills.
- 457 421. *Actinella argentea*. 19 April–7 June, 1847. Santa Fe, stony gravelly hills, sunny as well as northern declivities; rather socially.
- 458 416. *Schkuhria neo-mexicana*. 7 July–6 Aug., 1847. Santa Fe, margin of fields, near walls.
- 459 identified in the collection list as *Dysodia chrysanthemoides*, but not cited in "Plantae Fendlerianae" 10 July, 1847. Santa Fe Creek, bottom and margin of the creek.
- 460 423. *Actinella richardsonii* var. *floribunda*. 8 June–13 July, 1847. Santa Fe, rocky hills as well as plains and creek bottom.
- 461 10 July, 1847. A monstrosity of this plant, showing the structure of a compositae flower plainly.
- 461 409. *Riddellia tagetina*. 22 June–31 July, 1847. Santa Fe Creek, valley, foot of hills near irrigating ditches. Also: 9 Oct., 1846. Between San Miguel and Santa Fe, woodland, near the road.
- 462 identified in the collection list as *Melampodium*, but not cited in "Plantae Fendlerianae" 10 Aug., 1847. From Santa Fe to San Miguel.
- 463 417. *Hymenopappus flavescens*. 28 Aug., 1847. A few miles west of Willow Bar (Cimarron River), deep sand.
- 464 417. *Hymenopappus flavescens*. 14 Aug., 1847. Between San Miguel and Vegas.



- 465            418. *Hymenopappus tenuifolius*. 13-23 Aug., 1847. Ojo de Bernal to Rock Creek, prairies.
- 466            422. *Actinella scaposa* var. *mutica*. 11, 12 Aug., 1847. Pecos to San Miguel, woodland.
- 467            424. *Helenium autumnale*. 17 Aug., 1847. A few miles east of Moro River; bottom land.
- 468            424. *Helenium autumnale*. 20 Sept., 1847. From 110 Creek to Fort Leavenworth; low places in the prairies.
- 469            420. *Bahia oppositifolia*. 10-26 Aug., 1847. 8 miles east of Santa Fe to Cold Spring (Cimarron River), low places and sides of ravines.
- 470            441. *Senecio longilobus*. 17 May-4 Nov., 1846-47. Santa Fe, mountain sides and foot of hills. 2 to 3 feet high.
- 471 = 460 identified in the collection list as *Actinella richardsonii* var. *floribunda*, but not cited in "Plantae Fendlerianae" 8 June, 1847. Santa Fe, hills, amongst rocks. On leaves and stems there are scattered bright, shining dots.
- 472            442. *Senecio longilobus*. 18-26 July, 1847. Foot of a hill, Santa Fe.
- 473            442. *Senecio longilobus*. 22 June-25 July, 1847. Santa Fe Creek, valley. Also: 19 Oct., 1846.
- 474            440. *Senecio filifolius*  $\beta$  *fremontii*. This number is so identified in the collection list, although "(474)" is not cited in "Plantae Fendlerianae" 8 Sept., 1847. Pawnee Fork. 27 Sept., 1846. 27 miles south of Bent's Fort.
- 475            443. *Senecio eremophilus*. "(475)" is pencilled into the GH copy of "Plantae Fendlerianae" in the hand of Sereno Watson. 20 Oct., 1846 & 22 June, 1847. Santa Fe Creek, bottom, not far from the creek.
- 476            438. *Senecio aureus*. This number is so identified in the collection list, although "(476)" is not cited in "Plantae Fendlerianae" 22 June, 1847. Santa Fe Creek bottom.
- 477            437. *Senecio exaltatus*. "(477)" is pencilled into the GH copy of "Plantae Fendlerianae" in the hand of Sereno Watson. 26 April-3 June, 1847. Santa Fe Creek valley, foot of mountains 10 miles above Santa Fe.
- 478            444. *Senecio fendleri*. Santa Fe Creek valley; foot of mountains 11 miles above Santa Fe.
- 479            439. *Senecio aureus*  $\gamma$  *borealis*. "(479)" is pencilled into the GH copy of "Plantae Fendlerianae" in the hand of Sereno Watson. 15 May-3 June, 1847. Santa Fe Creek, foot of hills.
- 480            444. *Senecio fendleri*. 3 June, 1847. Santa Fe, foot of mountains, 12 miles above Santa Fe.

- 481 436. *Erechtites hieracifolia*. Creek banks, 5 miles south of Fort Leavenworth.
- 482 380. *Xanthium echinatum*. 4 Aug., 1847. Santa Fe, waste places.
- 483 identified in the collection list as *Xanthium echinatum*, but not cited in "Plantae Fendlerianae" 3 Sept., 1846. Bank of Walnut Creek.
- 484 probably 448. *Cirsium altissimum*; "(584)" in "Plantae Fendlerianae," but that number in the collection list falls in Scrophulariaceae. 17 Aug., 1846. High bank of a creek.
- 485 446. *Cirsium canescens*. 31 May–17 June, 1847. Santa Fe, sunny side of mountains, lower part.
- 486 447. *Cirsium ochrocentrum*. Santa Fe, mountainsides.
- 487 455. *Macrorhynchus purpureus*. 16 June–28 July, 1847. Santa Fe Creek bottom, grassy places.
- 488 454. *Crepis ambigua*. 2 June–10 Aug., 1847. Santa Fe Creek bottom, level grassy places. From the root, when broken, there is exuding a white, milky juice.
- 489 450. *Hieracium longipilum*. 21 Sept., 1847. High prairies about 12 miles southwest of the upper ferry of the Kansas River.
- 490 453. *Malacothrix sonchoides*. 24 May, 1847. Rio del Norte, river bottom, low sandy bank.
- 491 457. *Lactuca elongata*  $\gamma$  *sanguinea*. 17 Aug., 1847. A few miles east of Moro River.
- 492 459. *Mulgedium pulchellum*. 21 Aug., 1847. Between Rio Colorado and Rock Creek. Also: 3 Sept., 1847. Walnut Creek.
- 493 451. *Nabalus asper*. 17 Sept., 1847. 16 miles west of Council Grove, high prairies. Plant 2–3 feet high.
- 494 460. *Mulgedium floridanum*. 22 Aug., 1846. Council Grove, creek bottom.
- 495 456. *Taraxacum palustre* var. *latifolium*. 15 May, 1847. Santa Fe Creek bottom, near the bank.
- 496 452. *Lygodesmia juncea*. 3 Oct., 1846. Poñi Creek (between Bent's Fort and Santa Fe), low prairies.
- 497 452. *Lygodesmia juncea*. 30 June–12 July, 1847. Santa Fe, in and about fields. The flowers consisting generally of 5 ligules, which at the lower part form tubes (each ligule containing a separate flower: stamens and pistil), all the intermediate space filled up with chaff. From this plant when broken exudes a yellow-greenish juice, which in coming on the atmosphere soon shows some of the properties of Indian rubber. Enveloping scales of the flower head higher than the pappus. Lower leaves entire, linear. Stem and branches striated. Flower red and light bluish.

- 498            449. *Stephanomeria runcinata*. 9 June–1 July, 1847. Santa Fe, foot of dry hills, although not far from irrigating ditches or fields.
- 499            353. *Haplopappus spinulosus*. 30 May–10 Oct., 1846–47. Santa Fe, sandy and gravelly very little inclined places, generally not very far from irrigating ditches. Also: about Pecos and Walnut Creek.
- 500            456. *Taraxacum palustre* var. *latifolium*. 15 May–25 June, 1847. Santa Fe Creek bottom, near the bank.
- 501            456. *Taraxacum palustre* var. *latifolium*. 15–20 May, 1847. Santa Fe Creek bottom, moist fertile soil.
- 502            462. *Sonchus asper*. 7–13 June, 1847. Santa Fe, waste places about town and along garden walls.
- 503            450. *Hieracium longipilum*. 13 Aug., 1846. 80 miles west of Independence, stony hill.
- 504            458. *Lactuca graminifolia*. 3 July, 1847. Santa Fe Creek valley, 12 miles above Santa Fe, high up on the mountains. No expanded flowers by which I could tell its color.
- 505            458. *Lactuca graminifolia*. 8 July, 1847, Santa Fe Creek valley; flower yellow.
- 506            459. *Mulgedium pulchellum*. 8–25 July, 1847. Santa Fe Creek, hillside facing the creek, loose gravelly soil. Flowers blue.
- 507            461. *Sonchus oleraceus*. 23 June–10 July, 1847. Santa Fe, along the inside of field walls, near irrigating ditches.
- 508            461. *Sonchus oleraceus*. 11–23 June, 1847. Santa Fe Creek valley.
- 509            426. *Achillea millefolium*. 16 June–20 Oct., 1847–46. Santa Fe Creek bottom, moist meadows, also foot of mountains.
- 509b           426. *Achillea millefolium*. identified in the collection list but not cited by number in "Plantae Fendlerianae" 13 July, 1847. Santa Fe. Flowers rose color.
- 510            428. *Artemisia canadensis*. 17 Aug., 1847. 2 miles east of Moro River, rocky elevated place. Also: 1 Oct., 1846. 8 miles south of Rio Colorado (between Bent's Fort and Santa Fe).
- 511            427. *Artemisia dracunculoides*. 15 Aug., 1847. Bottom of Moro River.
- 512            433. *Artemisia frigida*. 3 Oct., 1846. Poñi Creek, prairie. 23 Aug. 1847. 7 miles east of Rock Creek.
- 513            431. *Artemisia ludoviciana*. 26 July, 1847. Santa Fe Creek valley.
- 514            431. *Artemisia ludoviciana*. 26 Aug.–3 Oct., 1846. Council Grove to Poñi Creek, low prairie.
- 515            431. *Artemisia ludoviciana*. 17 Sept., 1847. Prairies, a few miles west of Council Grove.
- 516            429. *Artemisia filifolia*. 24 Aug., 1847. Between Rock and Rabbit Ear Creeks.

- 517 430. *Artemisia discolor*. 31 July, 1847. Santa Fe, foot of a hill.
- 518 432. *Artemisia vulgaris*. 15 July, 1847. Santa Fe Creek bottom close to the creek.
- 519 434. *Gnaphalium sprengelii*. "(519)" is pencilled into the GH copy of "Plantae Fendlerianae" in the hand of Sereno Watson. 10-14 Aug., 1847. Between Santa Fe and Vegas. Mountain woodland, low places.
- 520 identified in the collection list as "Gnaphalium too poor to say" 23 Aug., 1846. Council Grove, hill.
- 521 435. *Antennaria dioica*. 21 May-3 June, 1847. Santa Fe, hills at the foot of the higher mountains (northern declivities).
- 522 435. *Antennaria dioica*. 6 May-3 June, 1847. Together with the preceding one.
- 523 435. *Antennaria dioica*. 15 May-3 June, 1847. Santa Fe, hills at the foot of the higher mountains (northern declivities); together with no. 521.
- 524 435. *Antennaria dioica*. 26 April-3 June, 1847. Santa Fe Creek; hills at the foot of mountains.
- 525 349. *Solidago incana*. 23 Aug., 1847. 7 miles east of Rock Creek.
- 526 407. *Dysodia chrysanthemoides*. 14-16 June, 1847. Santa Fe Creek bottom, margin of an irrigating ditch.
- 527 343. *Gutierrezia sphaerocephala*. 27-29 Aug., 1847. Upper Spring (Cimarron) to Middle Spring, low prairie.
- 528 344. *Amphiachyris dracunculoides*. 21 Sept., 1847. High prairies a few miles southwest of the upper ferry of Kansas River.
- 529 351. *Solidago lanceolata*. 3 Sept., 1847. Ford of Arkansas River (south side) wet bottom land. 17-21 Sept., 1847. Council Grove to the upper ferry of Kansas River.
- 530 348. *Solidago ulmifolia*. 21 Sept., 1847. Prairie, about 10 miles southwest of the upper ferry of Kansas River.
- 531 345. *Solidago speciosa*. 21 Sept., 1847. High prairies, a few miles southwest of the upper ferry of Kansas River.
- 532 Identified in the collection list as *Solidago rigida*, but not cited by number in "Plantae Fendlerianae" 21 Sept., 1847. The same locality as the preceding one.
- 533 339. *Townsendia grandiflora*. 21 Aug., 1847. Between Ocate Creek and Rio Colorado, low prairie.
- 534 405. *Heterospermum tagetinum*. 14 Aug., 1847. 12 miles west of Vegas; woodland.
- 535 296. *Pectis angustifolia*. 10 Aug., 1847. Between Santa Fe and Pecos.

- 536            406. *Flaveria angustifolia*. 30 Aug., 1847. 18 miles west of Lower Spring (Cimarron).  
 537            425. *Amauria dissecta*. 14-17 Aug., 1847. A few miles east of Moro River.  
 538            404. *Sanvitalia aberti*. Between Santa Fe and Pecos; woodland.

## LOBELIACEAE

- 539            20 September, 1847. Creek bank, a few miles west of 110 Creek. Flower blue, sometimes purple.  
 540            17 August, 1846. About 118 miles west of Independence, creek bottom. 3-15 September, 1847. Ford of Arkansas River to Cottonwood Creek, banks and creek bottoms.

## CAMPANULACEAE

- 541            22 September, 1847. Woodland about 6 miles north of the upper ferry of Kansas River. Flower blue.  
 542            22 September, 1847. Bottom land of Kansas River.  
 543            16 June-28 July, 1847. Santa Fe Creek, 9 miles above Santa Fe, sunny side of mountains between rocks.

## ERICACEAE

- 544            16-17 June, 1847. Santa Fe Creek, overshadowed margin of the creek.  
 545            28 July, 1847. Santa Fe, ravines high up on the mountains.  
 546            26 April-2 May, 1847. About 6 miles east of Santa Fe, creek bottom. Shady declivities of the mountains. Evergreen. Wild turkies eat the berries as soon as the snow that covered them is melted away.

## AQUIFOLIACEAE

- 547            25 May, 1847. Rio del Norte, steep and rocky bank of the river. A shrub about 10 feet high.

## PRIMULACEAE

- 548            1 April-15 May, 1847. Santa Fe Creek; gravelly places of its bed exposed to inundations, moist soil. Petals light rose color nearly white. Some few specimens I found to have been preserved under the snow throughout the winter.  
 549            3-16 June, 1847. Santa Fe Creek, sunny margin, deep fertile soil. Flower of a very fine purple color before drying.  
 550            15-18 August, 1847. Bottom land about Moro River.

## PLANTAGINACEAE

- 551            10 May-26 August, 1847. Santa Fe. Dry valley between the lesser hills, tolerably good soil. Also creek valley, sides of hills not far from the creek. Also Rio del Norte and a few miles east of Cold Spring (Cimarron).

- 552 6 June–25 July, 1847. Santa Fe Creek bottom, near the creek.  
 553 17 August, 1846. About 120 miles west of Independence.

## PEDALIACEAE

- 554 31 August, 1847. Lower Spring (Cimarron), prairie.

## ACANTHACEAE

- 555 25 August, 1846. Council Grove, gravel of the creek bed.  
 556 11 August, 1846. 10 miles south of Fort Leavenworth. Flower blue.  
 557 22 September, 1847. Woodland about 6 miles north of the upper ferry of the Kansas River.

## SCROPHULARIACEAE

- 558 3 June–7 July, 1847. Santa Fe Creek bottom, margins of the creek, wet soil.  
 559 27 May–9 June, 1847. Santa Fe. Near and in springs and rivulets.  
 560 11 May–19 October, 1847. Santa Fe Creek bottom, low sandy margin of the creek, wet soil.  
 561 2 September, 1847. Pool of water on the prairies, 40 miles southwest of the ford of Arkansas River.  
 562 20 August, 1846. Council Grove, creek bottom.  
 563 26 April–16 June, 1847. Santa Fe Creek bottom, margin of the water, flat sandy wet banks. Petals blue with violet stripes, the lower one smaller than the rest and of a lighter blue. Flower fugacious.  
 564 31 May–8 July, 1847. Santa Fe Creek, margins of the water, partly immersed. Flower blue, fugacious in a high degree.  
 565 17 August, 1846. About 25 miles east of Council Grove.  
 566 24 August, 1846. Council Grove, creek bottom, fertile soil. Plant 18 feet high.  
 567 18 September, 1847. Bluff Creek, bottom.  
 568 14 August, 1846 and 18 September, 1847. Bluff Creek and Hickory Point, bottom land.  
 569 25–26 August, 1847. Between Rabbit Ear Creek and Cold Spring (Cimarron). Sandy hillside.  
 570 20 September, 1847. From 110 Creek to Fort Leavenworth; low prairies.  
 571 3 September, 1847. Arkansas bottom, wet places, south of its ford.  
 572 23 August, 1846. Council Grove, low places between hills. Flower lilac, fugacious.

- 573 18 August, 1846. 5 miles east of Council Grove; also 21 September, 1847. Dry prairies a few miles southwest of the upper ferry of Kansas River.
- 574 18 August, 1846. 10 miles east of Council Grove. Prairie.
- 575 21 May–26 July, 1847. Santa Fe, dry gravelly hills.
- 576 4–28 May, 1847. Santa Fe, gravelly hills, dry soil.
- 577 14 August, 1846. Hickory Point, prairie.
- 578 10 August, 1847. Between Santa Fe and Pecos, woodland.
- 579 12 August, 1847. Neighbourhood of San Miguel.
- 580 1–12 July, 1847. Santa Fe Creek, hillside; flower white.
- 581 22 June–3 July, 1847. Santa Fe Creek bottom. Also: 11 miles above Santa Fe, on sides and ravines of high mountains (where the moisture is greater than in the plains of Santa Fe).
- 582 15 May–3 July, 1847. Santa Fe Creek; shady, gently sloping declivities, foot of mountains. Petals white, stamens 2, nearly twice the length of the petals.
- 583 28 July, 1847. Santa Fe Creek, shady sides of mountains, 11 miles above Santa Fe.
- 584 29 April–15 July, 1847. Santa Fe, gravelly hills and sides of mountains; Rio del Norte; Poñi Creek, and Rayado Creek (between Bent's Fort and Santa Fe). 4 October, 1846.
- OROBANCHACEAE
- 585 4 October, 1846. Rayado Creek (between Bent's Fort and Santa Fe); gravelly valley.
- VERBENACEAE
- 586 30 April–20 October, 1846–1847. Waste fields and low valleys in the mountains, Santa Fe. Also: between Rayado and Ocate Creeks [20 Oct., 1846].
- 587 24 May–31 July, 1847. Santa Fe, Creek bottom.
- 588 22 June–31 July, 1847. Santa Fe, Creek bank.
- 589 8 May, 1847. Rio del Norte; flat sandy bottom not far from the river.
- 590 19 October, 1846. Santa Fe, Creek valley, gravelly moist soil.
- 591 23 October, 1846. Santa Fe, Creek bottom. 27 August, 1847. Upper spring (Cimarron), bottom.
- 592 28 August, 1847. 1 September, 1847. Willow Bar, low sandy places, also: Sand Creek, low places in the prairies.
- 593 21 September, 1847. 18 miles east of 110 Creek.
- 594 12 August, 1847. Neighbourhood of San Miguel, prairies.
- 595 15 August, 1847. Moro River bottom.

- 596 22 September, 1847. Bottom land of Kansas River.  
 597 11 June–31 July, 1847. Santa Fe, Creek bottom. In some specimens the flower white.  
 598 4 September, 1847. Ford of Arkansas River to Pawnee Fork, bottom land.  
 599 17 August, 1846. About 30 miles east of Council Grove, bottom land.  
 600 16 August, 1846. About 120 miles west of Independence; creek bed, wet places.  
 601 21 August–6 September, 1847. Rio Colorado to Pawnee Fork; low places on the prairie.

## LABIATAE

- 602 10 August–10 October, 1847. A few miles east of Santa Fe to Moro River; mountain valleys and prairies.  
 603 25 June–15 July, 1847. Santa Fe Creek; foot of mountains (sunny side).  
 604a 16 June–18 September, 1847. Santa Fe to Bluff Creek, bottom land.  
 604b same specimen with white flowers.  
 605 22 August–27 September, 1846. Council Grove; also: about 25 miles south of Bent's Fort.  
 606 9 June–20 October, 1847. 1846. [i.e., 20 Oct., 1846; 9 June, 1847.] Santa Fe Creek bottom, also sides of hills, between rocks not far from irrigating ditches.  
 607 29 September, 1847. [date certainly wrong] Between Kansas River and Fort Leavenworth, prairies. Flower white.  
 608 10–16 August, 1847. Pecos to Moro River; woodland in the mountains, low valleys.  
 609 1–31 July, 1847. Santa Fe Creek bottom; in moist shady places.  
 610 14–18 August, 1847. A few miles west of Vegas to Moro River.  
 611 18 August, 1847. 6 miles east of Moro River, bottom land.  
 612 11 August, 1846. 8 miles south of Fort Leavenworth.  
 613 17 August, 1846. About 25 miles east of Council Grove.  
 614 23 June–20 October, 1846–47. Santa Fe Creek bottom, near irrigating ditches 23 June, 1847; Ford of the Arkansas River and east of Council Grove.  
 615 15 August, 1846. 117 miles west of Independence, creek bottom.  
 616 20 August, 1846. Council Grove, creek bottom.  
 617 14–17 August, 1847. A few miles west of Vegas to Moro River; woodland and prairies.



618 10 August–4 October, 1846–47. Pecos. Ojo de Bernal to Rock Creek [10 Aug., 1847]. Also: Poñi and Rayado Creek (between Bent's Fort and Santa Fe), in valleys.

619 13 August, 1846–23 September, 1847. Kansas River bottom.

620 24 May–31 July, 1847. Santa Fe, sunny hillsides facing the creek, between rocks; also: between rocks near irrigating ditches—Rio del Norte.

621 3 July–10 August, 1847. Santa Fe Creek valley in the mountains, sunny mountain sides between rocks; also stone piles near a field.

#### BORAGINACEAE

622 21 August, 1847. Between Rio Colorado and Rock Creek. Low prairies.

623 28 August, 1847. Willow Bar, deep sandy soil.

624 11 August, 1846. 4 miles south of Kansas ferry, low prairie. 23 August, 1847. 7 miles east of Rock Creek.

625 26 April–3 June, 1847. Santa Fe Creek Bottom, foot of hills at some distance from the water.

626 24 May–28 July, 1847. Santa Fe Creek bottom, moist fertile soil at the margin of the water.

627 24 June–15 July, 1847. Santa Fe, high up the creek, sunny side of mountains. In bunches of  $1\frac{1}{2}$  foot diameter and 2–2½ foot high. Flower short and small.

628 20 May–3 June, 1847. Santa Fe Creek valley, bottom land and foot of hills. Flower long but narrow.

629 19 April & 15 May, 1847. Santa Fe, stony side of hills (sunny side). Flowers long and large.

629b 3 October, 1846. Poñi Creek (between Bent's Fort and Santa Fe). Bottom prairie, good soil. The root of this plant is said by the Mexicans to be good (when boiled) to cure sores. Also: 25 August, 1847. Between Rabbit Ear and McNees's Creeks.

630 18 September, 1847. Bluff Creek, bottom land.

631 25 August, 1847. McNees's Creek, sandy hillside.

632 29 April–24 May, 1847. Declivities of dry gravelly hills southwest of Santa Fe. Flower white.

633 25 June–15 July, 1847. Santa Fe Creek up the mountains; sunny side of mountains between rocks.

634 4 May–9 July, 1847. Santa Fe, valleys between dry and gravelly hills; also: creek valley close to fields.

635 7–15 July, 1847. Santa Fe, Creek valley near a field.

636 19 May–31 July, 1847. Santa Fe, valleys between the gravelly hills where they run out onto the plains.

637 18 September, 1847. Bluff Creek, bottom land.

- 638 7 July, 1847. Santa Fe Creek valley.  
 639 17-23 August, 1847. Rio Moro to Rock Creek; elevated prairies.  
 640 24 April-30 May, 1847. Santa Fe, valleys between the gravelly hills south west of Santa Fe.

## HYDROPHYLLACEAE

- 641 3-16 June, 1847. Santa Fe Creek, 8 miles above Santa Fe; shady damp places on ledges of rocks.  
 642 3 June-28 July, 1847. Santa Fe Creek bottom, low rather moist places.

## HYDROLEACEAE

- 643 30 May-21 June, 1847. 5 miles southwest of Santa Fe, loose tolerably good soil in a valley between the hills. Petals deep violet.  
 644 10-14 August, 1847. Santa Fe to Vegas; woodland valleys in the mountains.

## POLEMONIACEAE

- 645 18 August, 1847. Low bottom land of Moro River.  
 646 11 May-25 July, 1847. Santa Fe. Creek valley; on hills, also foot of hills near irrigating ditches. Flower red.  
 647 14 August, 1847. 12 miles west of Vegas.  
 648 4 May-31 May, 1847. Santa Fe; valleys between the gravelly hills southwest of Santa Fe, where they run out onto the plains. Petals white anthers of a bluish green color.  
 649 24 May, 1847. Rio del Norte, low bank between rocks. Flower blue.  
 650a 8 May, 1847. Rio del Norte, shady places in ravines, between rocks.  
 650b 28 August-1 September, 1847. Between ford of the Cimarron River and Willow Bar; sandy soil. Also: Sand Creek.  
 651 17 May, 1847. Santa Fe. Sunny side of a dry and gravelly hill. Only found in one place. 7 June, 1847, in fruit.  
 652 23 August, 1847. 7 miles east of Rock Creek, creek bottom.  
 653 24 June-28 July, 1847. Santa Fe, 19 miles up the Creek, high mountain side.  
 654 19 July, 1847. Santa Fe Creek bottom, fertile soil.  
 655 16 June-8 July, 1847. Santa Fe, high up the Creek. Sunny side of steep rocky mountains.

## CONVOLVULACEAE

- 656 11 August, 1846. 8 miles south of Fort Leavenworth; bottom land.  
 657 8 September, 1847. Pawnee Fork; steep bank.  
 658 18 September, 1847. Bluff Creek, bottom land.

- 659 9 July, 1847. Santa Fe; waste house gardens and margins of fields.
- 659b 6 September, 1846. About 15 miles east of the ford of Arkansas River; level prairies.
- 660 21 August, 1847. Between Rio Colorado and Rock Creek; also Sand Creek. 27 September, 1846. 20 miles south of Bent's Fort.
- 661 2 October, 1846. Between Poñi and Rayado Creek, gravely hillside.
- 12-22 August, 1847. Pecos to Rock Creek.
- 662 8-10 August, 1847. Santa Fe, cornfields; also: woodland between Santa Fe and Vegas.
- 663 10 August, 1847. Between Santa Fe and Pecos. Mountainous woodland.
- 664 14 June, 1847. Santa Fe; margin of an irrigating ditch in a waste lying garden.
- 665 10 August, 1847. Between Santa Fe and Pecos, woodland.
- 666 15 August, 1847. Moro River, bottom land.
- 667 23 September, 1847. Creek bottom, north of Kansas River. Flower white, showy.
- 668 25 May-11 July, 1847. Santa Fe, at the foot of dry hills (sunny side). Socially. Flower seldom seen expanded.
- 668b 10 August, 1847. Between Santa Fe and Pecos.

## SOLANACEAE

- 669 21 June-11 August, 1847. Santa Fe, Creek valley, about fields and irrigating ditches. Also from Santa Fe to Vegas; woodland, shady places around trees and shrubs.
- 670 28 May-11 June, 1847. Santa Fe Creek valley, close to an irrigating ditch at the foot of a hill.
- 671 7 June-1 October, 1847-6. Santa Fe; in back streets of the town and near fields, flat on the ground [7 June, 1847]. Also between Raton and Bermejo Creeks, level prairies [1 Oct., 1846].
- 672 6-11 August, 1847. Santa Fe, steep rocky sides of dry hills. Also from Santa Fe to Vegas, woodland in the mountains.
- 673 1 July-6 August, 1847. Santa Fe Creek valley, foot of mountains, sunny side.
- 674 18 August-29 August, 1847. Rock Creek to a few miles east of Council Grove; prairies.
- 675 17 July-13 August, 1847. Santa Fe Creek valley. Sunny declivities near the creek, loose soil. Also neighbourhood of Ojo de Bernal.
- 676 28, 29 August, 1847. A few miles west of Willow Bar to Middle Spring (Cimarron).

- 677 20-27 August, 1847. Ocate Creek to Upper Spring (Cimarron), low prairies.
- 678 6 June-9 July, 1847. Santa Fe, waste gardenplaces.
- 679 25 August, 1847. McNees's Creek, low prairie.
- 680 14 June-13 July, 1847. Margin of irrigating ditch in a waste garden. Stamens deep blue. Santa Fe.
- 681 21 June-30 August, 1847. Santa Fe—Middle Spring (Cimarron). Ravines and low places in the prairies; also: creek bottom. Between Poñi and Rayado Creeks.
- 682 31 May-31 July, 1847. Santa Fe, in and near fields. Also foot of mountains not far from the Creek.
- 683 11 June-18 July, 1847. Santa Fe Creek valley, between rocks at the foot of hills.
- 684 21 June-18 August, 1847. Santa Fe, gently sloping sides of ravines, loose soil; also in level places (creek bottom). Spreading on the ground. Flowers compound, consisting of two separate flowers. Also: 6 miles east of Moro River.
- 685 7 June-10 August, 1847. Santa Fe, waste gardens and yards; also between Santa Fe and Pecos.

## GENTIANACEAE

- 686 7 June-25 June, 1847. Santa Fe Creek valley, foot of mountains. Flies seem to be very fond of this plant. 4-5 feet high.
- 687 28 August-5 September, 1846-7. Prairies a few miles west of the ford of Cimarron River; also Arkansas River.
- 688 21 September, 1847. Prairies a few miles southwest of the upper ferry of Kansas River.
- 689 21-23 September, 1847. Creek bottom north of Kansas River, near its upper ferry.

## APOCYNACEAE

- 690 24 June-28 July, 1847. Santa Fe, steep rocky sides of mountains, facing towards the creek.
- 691 22 August, 1847. Rock Creek, bottom land.
- 692 19 August, 1846. Council Grove, bottom land of the creek.

## JASMINACEAE

- 693 31 May, 1847. Santa Fe, sunny hillsides between rocks, foot of hills and in valleys. Flower fugacious.

## ASCLEPIADACEAE

- 694 25 June-31 July, 1847. Santa Fe; foot of the mountains as well as of the lower hills.
- 695 11 June-1 July, 1847. Santa Fe, near fields.
- 696 11 June, 1847. Santa Fe, creek valley, sunny side of a stony hill.

- 697 17 August, 1847. 2 miles east of Moro River.  
 698 15–21 August, 1847. Moro River and Rock Creek.  
 699 21–25 August, 1847. Between Rio Colorado and Mc-  
 Nees's Creek.  
 700 18 September, 1847. Bluff Creek, bottom land.  
 701 22 August, 1847. Rock Creek, bottom land.  
 702 12 August, 1847. Neighbourhood of San Miguel.  
 703 21 September, 1847. 12 miles southwest of the upper  
 ferry of Kansas River.  
 704 12 August, 1846. A few miles south of Kansas River,  
 prairies.  
 705 14–25 August, 1847. Between San Miguel and McNees's  
 Creek.  
 706 25 August, 1847. Between Rabbit Ear and McNees's  
 Creek; high prairie.  
 707 24 May, 1847. Rio del Norte; flat sandy river bank, be-  
 tween stones.

## CHENOPODIACEAE

- 708 16 September, 1846. 20 miles east of Big Sand Creek;  
 sandy gravelly soil.  
 709 25 August, 1847–19 September, 1846. 32 miles east of  
 Bent's Fort, flat prairies near the bank of the Arkansas River. Also  
 McNees's Creek. A shrub 1½ to 3½ foot high and very much spread-  
 ing.  
 710 10 August, 1847. Between Santa Fe and Pecos; wood-  
 land.  
 711 22 August, 1847. Between Rio Colorado and Rock Creek.  
 Low parts of the prairie.  
 712 26 August, 1847. Between McNees's Creek and Cold  
 Spring; sandy soil.  
 713 10 August, 1847. Between Santa Fe and Pecos.  
 714 15–17 August, 1847. Moro River; prairie.  
 715 22 August, 1847. Rock Creek; bottom land.  
 716 10–11 August, 1847. Between Santa Fe and San Miguel;  
 woodland.  
 717 1 September, 1847. Sand Creek; low prairie.  
 718 17 & 21 August, 1847–46. Council Grove, dry prairie.  
 Also: a few miles east of Moro River.  
 719 23 June, 1847. Santa Fe, waste house gardens.  
 720 17 May–12 July, 1847. Santa Fe Creek valley; foot of  
 hills where the ground is occasionally irrigated.  
 721 23 August, 1847. 7 miles east of Rock Creek.  
 722 9 June–26 July, 1847. About houses, gardens, etc.  
 723 12 July, 1847. Santa Fe; margin of fields.

- 724 17 August, 1847. A few miles east of Moro River.  
 725 23 June–9 July, 1847. Santa Fe; about fields and yards.

## AMARANTHACEAE

- 726 17 September, 1846. About 10 miles east of Big Sand Creek; high prairie.  
 726 30 August, 1847. Middle Spring (Cimarron); prairie. The branches of this plant are not so spreading as in the preceding one.  
 727 12 August, 1847. Neighbourhood of San Miguel. Leaves smooth.  
 728 10 September, 1846. 5 miles south of the ford of Arkansas River.  
 729 14 August, 1847. 16 miles west of Vegas.  
 730 9 October, 1846. Between San Miguel and Pecos; roadside.  
 731 24 May–23 August, 1847. Santa Fe; yards and waste places. Also: Rock Creek, high prairies.  
 732 24 June, 1847. About houses and yards, near irrigating ditches. Santa Fe.  
 733 10 July, 1847. About houses and yards, near irrigating ditches. Santa Fe. Lower side of the leaves marked with red spots.  
 734 25 May–6 August, 1847. Santa Fe Creek valley. Also: Rio del Norte, sandy soil, between rocks, flat river bank.  
 735 14 June–11 July, 1847. Santa Fe Creek valley, foot of hills.  
 736 19 July, 1847. Santa Fe, near houses and fields.  
 737 14–21 August, 1846. Hickory Point to Council Grove, gullies.  
 738 3 September, 1846. Walnut Creek, creek bank.

## NYCTAGINAEAE

- 739 19 May–11 August, 1847. Santa Fe; flat somewhat moist places not very far from fields and irrigating ditches.  
 740 10 August–28 September, 1847. Between Santa Fe and Ojo de Bernal; mountains, woodland. Also: 28 September, 1846. Rio de los Animas, valley, tolerably good soil. Flowers seldom expanded (only in the morning).  
 741 22 August, 1847. Rock Creek, bottom land.  
 742 14 & 15 August, 1847. Vegas to Moro River. Leaves cordate, involucre of the flower somewhat tomentose.  
 743 19 September, 1846. 42 miles east of Bent's Fort; bank of the Arkansas River. 17 August, 1847. 2 miles east of Moro River; elevated rocky region.  
 744 11–17 August, 1846. Fort Leavenworth to Council Grove.  
 745 16 June–10 August, 1847. Santa Fe Creek valley, foot of hills, also near fields between rocks. Involucre of the flower con-

sisting of 5 segments and containing 3 flowers.

746 7 July–6 August, 1847. Santa Fe Creek valley near irrigating ditches, amongst the branches of undershrubs. Plants viscose. Flowers rarely to be seen opened except in the morning. Involucre resembling a calyx of 5 sepals.

POLYGONACEAE

747 17 August, 1847. 2 miles east of Moro River; foot of high rocky embankment.

748 8 September, 1847. Pawnee Fork, creek bottom.

749 29 August, 1847. Middle Spring (Cimarron); low places.

750 4 July–8 September, 1847. Santa Fe and Pawnee Fork, creek bottom.

751 17 September, 1847. Council Grove, creek bottom.

752 22 June–28 July, 1847. Santa Fe, margins of irrigating ditches.

753 9 July, 1847. Santa Fe Creek bottom.

754 14 June, 1847. Santa Fe, near irrigating ditches.

755 8 September, 1847. Pawnee Fork. Fruit winged.

756 14 August, 1846. Hickory Point, creek bottom. Seeds much smaller than in the preceding one.

757 22 August, 1847. Rock Creek, overshadowed deep ravine.

758 8 May, 1847. Between the Rio del Norte and Santa Fe; elevated grassy plains.

759 17 August, 1847. 2 miles east of Moro River, bottom land. 4–5 feet high.

760 21 June, 1847. Santa Fe; near the irrigating ditch of a field.

761 29 August, 1847. Middle Spring (Cimarron).

762 8 August, 1847. Santa Fe, pasture, wet moory places.

763 7 July–17 August, 1847. Santa Fe Creek valley, up in the mountains. Also: 2 miles east of Moro River, elevated rocky region.

764 10 August, 1847. Between Santa Fe and Pecos. Also: 15 July, 1847. Santa Fe Creek valley.

765 25 August, 1847. Between Rabbit Ear and McNees's Creeks.

766 16 August, 1847. Moro River; summit of a rocky hill, between ledges of rocks.

767 21 August, 1847. Between Rio Colorado and Rock Creek.

768 23 September, 1846. 3 miles above Bent's Fort, Arkansas River, on the rounded, very pebbly and sterile bluffs.

769 15–17 August, 1847. Moro River, rocky elevated region. Also: 2 October, 1846. Between Poñi and Rayado Creeks.

770 15 July, 1847. Santa Fe Creek valley, mountain side

between rocks. Leaves more or less persistent through the winter.

771 14 August, 1847. 15 miles west of Vegas.

772 1 September, 1846. Between Walnut and Cow Creeks.

773 28 August, 1847. Willow Bar in sand, socially. 5 to 6 feet high.

#### ELEAGNACEAE

774 28 July, 1847. Creek valley, 12 miles above Santa Fe, foot of mountains and in ravines.

#### ULMACEAE

775 25 May, 1847. Rio del Norte; somewhat elevated bank of the river, close to the water. A treelike shrub about 12 feet high, branches spreading.

#### EUPHORBIACEAE

776 25 May-13 July, 1847. Rio del Norte; lower part of ravines, sunny side. Also: Santa Fe, sunny steep side of stony hills. Also: 4 October, 1846. Between Poñi and Rayado Creeks.

777 17 August, 1846. A few miles east of Bluff Creek. 18 September, 1847. Bluff Creek, bottom land.

778 14 August, 1846. Hickory Point, creek bottom.

779 21 September, 1847. Creek bottom, 20 miles east of 110 Creek.

780 29, 31 August, 1846-47. Cow Creek [31 Aug., 1846] and Middle Spring [29 Aug., 1847] (Cimarron). Dry prairie.

781 30 June-19 October, 1846-47. Santa Fe, lower part of the town, creek valley, gravelly soil. Also: on steep sides of gullies, rather stony soil.

782 25 August, 1846. Council Grove, creek bottom.

783 19 June-8 September, 1847. Santa Fe, in and near fields. Pawnee Fork, steep banks of the river.

784 17 August, 1846. 120 miles west of Independence to Waggon Mound (New Mexico); in gullies and low places of the prairie.

785 16 & 17 September, 1847. 18 miles west of Council Grove to Fort Leavenworth.

786 2 May-28 July, 1847. Santa Fe Creek valley; foot and sunny sides of high mountains.

787 8 September, 1847. Pawnee Fork. Steep banks of the creek.

788 31 August, 1846. Between Cow Creek and little Arkansas River.

789 10-16 August, 1847. Between Santa Fe and Moro River. Around the stand of shrubs, mountainous country.

790 24 May, 1847. Rio del Norte, low sandy river bank, between stones. Leaves somewhat serrate, especially towards their apexes.



- 791 6-12 August, 1847. Santa Fe to San Miguel.  
 792 23 August, 1846. Council Grove; hills, ledges of rocks,  
 in crevices.  
 793 25 August, 1847. McNees's Creek, sandy hillside.  
 794 28 August & 1 September, 1847. Ford of the Cimarron  
 to Sand Creek; low prairies.  
 795 25 May-3 October, 1846-7. Rio del Norte [25 May,  
 1847], sandy soil, low river bank between rocks. Also: Santa Fe and  
 Poñi Creek [3 Oct., 1846].  
 796 30 June-10 July, 1847. Santa Fe; valleys between the  
 dry gravelly hills. Branches pilose.  
 797 6 June-18 August, 1847. Santa Fe, foot of hills.  
 798 8 September, 1847. Pawnee Fork; steep bank of the  
 creek, loose soil.  
 799 8 September, 1847. Pawnee Fork; prairie and steep bank  
 of the creek.  
 800 4 May-18 July, 1847. Santa Fe, sides of hills and moun-  
 tains.  
 801 21 June, 1847. Santa Fe, dry hillsides.  
 802 14 August, 1846. Hickory Point, dry bed of a creek.  
 802b 1 September, 1847. Sand Creek, prairie.  
 803 24-25 May, 1847. Rio del Norte.  
 804 7 June, 1847. Santa Fe. Differs from the preceding one  
 in its seeds.

## CUPULIFERAE

- 805 8 June, 1847. Santa Fe, eastern mountains. Shrub oak,  
 8 feet high.  
 806 8 June, 1847. Santa Fe, eastern mountains. A shrub  
 about 8 or 9 feet high.  
 807 6 June-1 November, 1846-47. Santa Fe, mountains. A  
 shrub about 9 feet high.  
 808 8 June, 1847. Santa Fe, mountains. A shrub 10 feet  
 high.  
 809 8 June-19 July, 1847. Santa Fe Creek valley; banks of  
 the creek and foot of mountains. A shrub 8-12 feet high.  
 810 6 June, 1847. Santa Fe, sides of mountains. Shrub 8-10  
 feet high.

## BETULACEAE

- 811 16-25 June, 1847. Santa Fe, upper part of the creek  
 valley, margin of the water. A shrub 15 to 20 feet high. 30 March-1  
 April in flower.

## SALICACEAE

- 812 28 April-15 May, 1847. Santa Fe Creek bottom, exposed  
 to the inundations of the creek. Shrub 10-14 feet high. In drying the

twigs leave a greasy mark on the paper. 30 March–1 April, 1847, in flower.

813 12–20 May, 1847. Santa Fe Creek bottom; margin of the creek and near irrigating ditches.

814 25 May, 1847. Rio del Norte; foot of steep mountain banks, amongst rocks near the water.

815 11–20 May, 1847. Santa Fe, margin of the creek. A tree-like shrub about 15 feet high. I could find no male flowers on this shrub.

816 30 April–2 May, 1847. Santa Fe Creek, bottom bank of the creek. Treelike shrub about 20 feet high.

817 12 May, 1847. Santa Fe, margin of the creek. The buds of this tree are coated with a very sticky substance, which resembles bees-wax, is transparent and in drying between paper is taken up by the latter and makes the same transparent and sticky also. April in flower.

818 Santa Fe. Close to the creek. Trees about 40 feet high; lower branchlets long, slender and pending; trees of a fine growth in the neighbourhood of a house. I could find no male flowers to this tree. 10 May in flower.

819 Santa Fe Creek bottom, 4 miles above Santa Fe. A tree with spreading branches; the bark is a shining white color, given to it by a coat of a very white powdery substance which easily comes off, adheres to clothes etc., with great tenacity. 12 April, 1847, in flower.

#### URTICACEAE

820 24 May, 1847. Rio del Norte, rocky bank of the river.

821 15 August, 1847. Moro River, bottom land.

822 18 August, 1846. 15 miles east of Council Grove, creek bottom, rich soil.

823 15 August, 1846. 100 miles west of Independence, creek bottom, fertile soil.

824 10 August, 1846. 8 miles south of Fort Leavenworth.

825 15 July, 1847. Santa Fe Creek, 6 miles above Santa Fe, foot of mountains.

826 15 August, 1847. Moro River, bottom land.

827 21 August, 1846. Council Grove, creek bottom. 15 miles south of Fort Leavenworth. 11 August, 1846. Ravine.

#### CONIFERAE

828 1 November, 31 January, 4 March, 1847. Santa Fe. In the higher part of the mountains about 5 or 6 miles east of Santa Fe. Especially on the northern declivity of a sharp mountain ridge where they are to be found in great numbers with but very few other trees between them, while the southern declivity of that same high ridge

is occupied by a long-leaved pine no. 831, to the exclusion of almost every other kind. The pistillate flower branches are to be found on the top part of the tree, the staminate ones on the lower branches. Bark of the younger trees smooth and of a white color, on old trees only the summit and the branches are smooth and whitish. The terminal buds of the branches furnished during the winter with a thick and transparent coat of a resinous substance. A kind of balsam or turpentine is elaborated in little cavities under the surface of the bark around the larger branches and the stem of the tree by which the surface is raised into scattered nodules. This turpentine is clear and of a very light color and has an agreeable odor. Trees 60–80 feet high, some of a very handsome pyramidical growth.

829           1 November, 23 February, 1847. Santa Fe. Eastern mountains, upper regions as well as along the higher part of the creek valley. I saw several trees of this kind from which the bark had been peeled, probably for the use of tanning leather. The trunks of some of the larger trees of this kind measure 7 feet in circumference, 5 feet above the ground.

830           30 March, 1847. Hills, eastern mountains, Santa Fe. A shrublike tree, which attains a greater height towards the summit of the mountains, but not above 20 feet. Mostly of a stunted depressed growth, branching near the ground. Also in great abundance on the elevated plains and hills west and southwest of Santa Fe. By far the greater part of the firewood that is brought into Santa Fe by the Mexicans is of this tree. 20 April in flower.

831           17 February, 2 March, 1847. Santa Fe, eastern mountain range; low hills as well as high mountains; seems to prefer the drier north sides of the mountains. Valuable timber trees. Their growth is above 90 or 100 feet high, straight and some of the trunks are of great dimensions.

832           8 February, 1847. Santa Fe. Eastern mountain range. Upper region of high mountains. Fruit suspended, truck 60 to 80 feet high; branchlets extremely flexible.

833           17 February, 1847. Santa Fe Creek bottom, about 7 miles above Santa Fe. A young, slender and straight tree about 20 feet high; branches arranged in whorls, around the trunk; branches easily broken with exuding rosin from the broken places. Leaves articulated, quadrangular; lower portion persistent to the branchlets. I found only two trees of this kind.

834           30 March, 1847, in flower. Santa Fe. A shrub (the highest from 10 to 15 feet) very common all around Santa Fe. Lower regions of the mountains, but more abundant on the dry gravelly hills southwest of Santa Fe, and on the plains adjoining them. They are found also on the summits of high mountains, but far less abundantly.

The branchlets of this shrub dry much quicker than those of the next following number.

835           30 April, 1847, in flower. Santa Fe, mountain valleys, in the neighbourhood of creeks. A shrub commonly of 12 to 15 feet high; some of its lowermost branches (near the ground) often  $\frac{1}{2}$  foot in diameter. A treelike shrub of this kind I saw near the Creek, whose main trunk measured 8 feet in circumference; the lowermost branches very much spreading and growing to a height of about 25 feet.

836           3 June, 1847, in flower. Santa Fe Creek valley, in shady places at no great distance from the Creek. Low shrubs from 1 to  $2\frac{1}{2}$  feet high, branches very tough.

## NAJADACEAE

837           21 June–17 July, 1847. Vicinity of Santa Fe, at the margin of ponds, immersed, leaves floating on the surface.

## ALISMACEAE

838           17 August, 1846. About 25 miles east of Council Grove, marshy ground, creek bed.

839           21–23 June, 1847. Santa Fe, shallow ponds. 17 July, in fruit.

840           2 September, 1847. Shallow pond-like collections of water in the prairies, 40 miles west of the ford of Arkansas River.

## ORCHIDACEAE

841           14 August–27 September, 1846. Low prairies 9 miles south of Fort Leavenworth; also about  $100^{\circ}$  west longitude, not far from the bed of the Arkansas River. Flowers white.

## IRIDACEAE

842           22 June–7 July, 1847. Santa Fe, low grassy places near irrigating ditches.

## SMILACEAE

843           18 June, 1847. Santa Fe, cultivated.

844           17 June, 1847. Santa Fe Creek valley; overshadowed bank of the creek.

845           3–10 June, 1847. Santa Fe, shady bank of the creek, fertile soil.

846           3–24 June, 1847. Santa Fe Creek valley, foot of mountains, shady places, northern declivities.

## LILIACEAE

847           8 July, 1847. Santa Fe, foot of mountains, creek valley.

848           28 June–1 October, 1846–7. Santa Fe to Rock Creek; also between Raton and Bermejo Creek (between Bent's Fort and Santa Fe). Near creeks and on level prairies, also foot of mountains.

849           3 June, 1847, in flower. Santa Fe, sunny steep declivities of mountains, between rocks; ever-green. The rhizomas of this plant which sometimes are to be found of 3 inches diameter, are used

by the Mexicans as a substitute for soap. For this purpose, they are mashed into pieces with a stone, hot water poured onto them, and the clothes rubbed with them. In drying the leaves I found that from their bases where they has been cut, some drops of a clear transparent substance, which was sticky like glue, but had no smell, was exuding. Some of the leaves over three feet long.

- 850           24 May–21 August in flower. Santa Fe to Rock Creek, at the foot of mountains, on shady declivities, around shrubs. Also on dry sterile hills about Bent's Fort, but more abundantly in the valleys between these hills. The rhizomas of this plant are likewise used as a substitute for soap. This plant does not seem to flower every year.
- 851           17 August, 1847. 2 miles east of Moro River. Elevated rocky region.

#### PONTEDERIAEAE

- 852           2 September, 1847. Pondlike collections of water in the prairies 40 miles southwest of the ford of Arkansas River. Flowers of a fine blue colour.

#### MELANTHACEAE

- 853           11 August, 1846. 8 miles south of Fort Leavenworth, high prairies.
- 854           28 July, 1847. Santa Fe Creek, 12 miles above Santa Fe, foot of mountains.

#### JUNCACEAE, CYPERACEAE & GRAMINEAE

- 855           6 June–26 July, 1847. Santa Fe, wet grassy places of the creek bottom.
- 856           20 May–17 August, 1847. Santa Fe and Rio Moro, elevated rocky regions not far from the water.
- 857           9 June–12 July, 1847. Santa Fe Creek, margin of the water.
- 858           16 June–28 July, 1847. Santa Fe Creek, margin of the water.
- 859           3 September, 1847. Ford of the Arkansas River, wet bottom land.
- 860           15 May–7 July, 1847. Santa Fe Creek, near the water.
- 861           3 June, 1847. Santa Fe Creek, bottom land exposed to inundations.
- 862           14 August, 1847. 12 miles west of Vegas, elevated rocky region.
- 863           22 August, 1846. Council Grove, shady place underneath projecting ledge of rocks, loose fertile soil.
- 864           28 July, 1847. Santa Fe Creek valley in the mountains.
- 864b          14 August, 1847. Between San Miguel and Vegas, open woodland. Flower white.

- 865 25 June–28 July, 1847. Santa Fe, foot of mountains near irrigating ditches.
- 866 14–25 August, 1847. San Miguel—McNees's Creek, sandy hillside.
- 867 27 August, 1846. 30 miles west of Council Grove, low place.
- 868 25 July–14 August, 1847. Santa Fe to Vegas, woodland.
- 869 13 August, 1846. 80 miles west of Independence. 3 September, 1847. Ford of the Arkansas River, wet bottomland.
- 870 18–26 September, 1847. Bluff Creek, bottom. [N.B. 26 September must be an error; Fendler on that day was near Liberty, Missouri.]
- 871 23 August, 1846. Council Grove, dry parts of the gravelly creekbed.
- 872 27 May–12 July, 1847. Santa Fe, margin of the creek.
- 873 26 April, 1847. Santa Fe Creek, low grassy bank.
- 874 27 May–18 July, 1847. Santa Fe, margin of a pond, wet soil.
- 875 21 May–7 June, 1847. Santa Fe, immersed in a pond.
- 876 3 September, 1847. Ford of the Arkansas River, wet bottom land.
- 877 3 September, 1847. Ford of the Arkansas River, low wet places near the river.
- 878 26 April–24 June, 1847. Santa Fe, margin of the creek and of irrigating ditches.
- 879 15 May, 1847. Santa Fe, Creek valley, moist places.
- 880 16 June, 1847. Santa Fe, margin of the creek in the mountains.
- 881 21 May–19 July, 1847. Santa Fe, margin of the creek.
- 882 31 May–16 June, 1847. Santa Fe Creek bank.
- 883 16 June–7 July, 1847. Santa Fe, margin of irrigating ditches.
- 884 15 May–24 June, 1847. Santa Fe Creek bank, near the water.
- 885 3 June, 1847. Santa Fe, shady bank of the creek, close to the water.
- 886 23 August, 1847. 7 Miles east of Rock Creek.
- 887 21 May–7 June, 1847. Santa Fe, wet meadows near a pond.
- 888 3 June, 1847. Santa Fe Creek valley, not far from the creek.
- 889 20 May–6 June, 1847. Santa Fe, margin of irrigating ditches.

- 890 17 April, 1847. Santa Fe Creek, moist places near the creek.
- 891 26 April, 1847. Santa Fe, foot of mountains, not far from irrigating ditches.
- 892 24-27 April, 1847. Santa Fe, wet meadow near a pond.
- 893 24 May, 1847. Rio del Norte, margin of the water on somewhat elevated banks, between rocks.
- 894 10 May-2 August, 1847. Santa Fe, dry loose and level ground; also sandy soil and gently sloping declivities.
- 895 27 August, 1847. Upper Spring (Cimarron River), bank of the river.
- 896 19 July-16 August, 1847. Santa Fe-Moro River, rocky bluffs.
- 897 27 August, 1847. Upper Spring (Cimarron River), margin of the water.
- 898 27 August, 1847. Upper Spring (Cimarron River), margin of the water.
- 899 19 June-10 August, 1847. Santa Fe, elevated places of the creek bottom; also near the irrigating ditches of fields.
- 900 19 August, 1846. Council Grove, bottom land.
- 901 3-19 July, 1847. Santa Fe, margin of irrigating ditches at the foot of mountains.
- 902 22 June-8 August, 1847. Santa Fe Creek bottom.
- 903 20 May-18 July, 1847. Santa Fe, dry valleys at the foot of hills, loose soil.
- 903b 31 July, 1847. Santa Fe Creek valley.
- 904 15 July, 1847. Santa Fe Creek valley, foot of hills.
- 905 19-31 July, 1847. Santa Fe Creek bottom.
- 906 21 September, 1847. Bottom land of Kansas River.
- 907 8-15 July, 1847. Santa Fe Creek valley near irrigating ditches.
- 908 8 June-15 July, 1847. Santa Fe Creek valley at the foot of hills, not far from the creek bank.
- 909 22 June-26 July, 1847. Santa Fe Creek valley, foot of hills.
- 910 16 June-12 July, 1847. Santa Fe.
- 911 17 August, 1846. 110 Creek, slopes of the creek bank.
- 912 21 May, 1847. Santa Fe, in a wet meadow.
- 913 25 August, 1847. McNees's Creek, sandy hillside.
- 914 15 August-18 September, 1847. 100 miles west of Independence to Bluff Creek, fertile bottom land.
- 915 12 August, 1847. Near San Miguel, open woodland.
- 916 7 July-16 August, 1847. Santa Fe-Moro River, foot of rocky hills.

- 917 28 July, 1847. Santa Fe Creek valley.  
 918 10-31 July, 1847. Santa Fe, foot of hills at the margin  
 of fields.  
 919 24 May-16 June, 1847. Rio del Norte-Santa Fe, side of  
 hills.  
 920 28 June-7 July, 1847. Santa Fe Creek valley, shady bank  
 of the creek.  
 921 24 June-28 July, 1847. Santa Fe, foot of mountains.  
 922 7-12 July, 1847. Santa Fe, side of mountains.  
 923 12-26 July, 1847. Santa Fe, side of mountains.  
 924 16 June-26 July, 1847. Santa Fe, protected by shrubs,  
 at the foot of hills near fields.  
 925 28 August, 1847. Between the ford of Cimarron River  
 and Willow Bar, deep sandy somewhat moist soil.  
 926 28 August, 1847. A few miles west of the ford of Cim-  
 arron River, high sandy prairie.  
 927 6 June-31 July, 1847. Santa Fe Creek valley, foot of  
 mountains.  
 928 16-22 June, 1847. Santa Fe Creek valley.  
 929 3-16 June, 1847. Santa Fe, margin of the creek in the  
 mountains.  
 929b 3 June-15 June, 1847. Santa Fe, margin of the creek in  
 the mountains.  
 930 27 May-12 July, 1847. Santa Fe, wet meadows.  
 931 27 May-15 July, 1847. Santa Fe, low wet meadows.  
 932 22 April-16 June, 1847. Santa Fe Creek valley, side of  
 mountains between rocks, also foot of mountains and steep rocky  
 banks.  
 932b 7 June, 1847. Santa Fe, margin of the creek.  
 933 18 September, 1847. Bluff Creek, bottom.  
 934 17-20 August, 1847. Ocate Creek to Moro River, ele-  
 vated rocky places.  
 935 23 August-26 September, 1847. Council Grove, gravelly  
 part of the creek. [N.B.: locality and dates do not agree.]  
 936 10-13 August, 1847. A few miles east of Santa Fe to the  
 neighbourhood of Ojo de Bernal; woodland.  
 937 25 May-26 July, 1847. Rio del Norte, steep bank be-  
 tween rocks; also Santa Fe, waste gardenland.  
 938 7 June-25 July, 1847. Santa Fe, along the mudwalls of  
 fields.  
 939 31 May-7 June, 1847. Santa Fe Creek, grassy somewhat  
 elevated parts of its bottom land.  
 940 26 July-23 August, 1847. Santa Fe, Rock Creek, dry  
 prairie.



- 941 16 June–7 July, 1847. Santa Fe Creek, foot of hills.  
 942 15 May, 1847. Santa Fe Creek.  
 943 30 April–24 June, 1847. Sunny bank of Santa Fe Creek.  
 944 9 June–29 July, 1847. Santa Fe Creek valley, wet soil near a spring.  
 945 1 June–28 August, 1847. Rio del Norte, low sandy bank; Santa Fe, flat sandy places to the ford of Cimarron River; also between Bent's Fort and Santa Fe.  
 946 17 May–19 July, 1847. Dry sandy plains between Santa Fe and the Rio del Norte; also Santa Fe, foot of hills near fields.  
 947 3–31 July, 1847. Santa Fe Creek, valley, foot of hills near fields.  
 948 13–23 August, 1847. Ojo de Bernal, Moro River and Rock Creek.  
 949 2 August–1 September, 1847. Rather high and dry prairies, Santa Fe to Little Arkansas River, from which region east it is only found occasionally, small isolated patches along the road as far as Council Grove.  
 950 13 August, 1847. Near Ojo de Bernal.  
 951 29 June–27 August, 1847. Santa Fe, Moro River to Council Grove.  
 952 14 August, 1846. A few miles west of Hickory Point, low wet bottom.  
 953 18 September, 1847. Bluff Creek, bottom.  
 954 24 September, 1847. 8 miles south of Fort Leavenworth, along the roadside.  
 955 24 May–28 August, 1847. Rio del Norte, slopes of somewhat elevated banks, also: a few miles west of the ford of Cimarron River, prairie.  
 956 28 August, 1847. A few miles west of the ford of Cimarron River, low prairies.  
 956b 3 July, 1847. Santa Fe Creek, valley up in the mountains.  
 957 3 July, 1847. Santa Fe Creek, valley not far from the creek.  
 958 3 June–19 October, 1846 & 47. Santa Fe Creek valley, gently sloping declivities, rather dry soil.  
 959 6 June–15 July, 1847. Santa Fe, margin of the creek.  
 960 9 June–10 August, 1847. Santa Fe, foot of dry hills, somewhat sandy soil.  
 961 8 September, 1847. Pawnee Fork, creek bottom, shady places.  
 962 26–28 July, 1847. Santa Fe Creek valley, near fields.  
 963 7 July, 1847. Santa Fe, margin of the creek.

- 964 24 September, 1847. Near Fort Leavenworth.
- 965 3 October, 1846. Bottom prairie and banks of Poñi Creek, fertile soil.
- 966 16 August, 1847. Moro River, hillside between rocks.
- 967 22 September, 1847. 6 miles north of the upper ferry of Kansas River.
- 968 13 August to 1 October, 1846-47. Ojo de Bernal & Rock Creek [13 Aug., 1847], elevated prairie, in spots where the soil is loose and fertile; also: between Bermejo and Colorado River [1 Oct., 1846], in similar localities.
- 969 1 June-1 October, 1846-47. Santa Fe-Vegas, and Colorado River; prairie valleys, good soil.
- 970 24 June-15 July, 1847. Santa Fe Creek valley near an irrigating ditch.
- 971 15 July, 1847. Santa Fe, not far from the creek, at the foot of mountains.
- 972 22 June-28 July, 1847. Santa Fe, margin of the creek.
- 973 30 May-6 August, 1847. Santa Fe, dry hillsides, gravelly soil.
- 974 8 September, 1847. Pawnee Fork, creek bottom.
- 975 24 May, 1847. Rio del Norte, sides of somewhat elevated banks fronting the water, between rocks.
- 976 1 Sept., 1847. Prairie at Sand Creek.
- 977 14 Aug., 1847. Between San Miguel and Vegas.
- 978 19 May-13 July, 1847. Rio del Norte and Santa Fe, sunny hillsides, between rocks.
- 979 17 May-6 Aug., 1847. Rio del Norte, sandy elevated places of the river bank, at some distance from the water; also Santa Fe, foot of hills, dry loose sandy soil, under protection of shrubs.
- 980 16 June-10 Aug., 1847. Santa Fe, foot of dry hills.
- 981 30 May-13 Aug., 1847. Santa Fe, dry gravelly valley; also neighbourhood of Ojo de Bernal.
- 982 17 Aug., 1847. 2 miles east of Moro River, foot of high rocks.
- 983 17-31 July, 1847. Santa Fe, waste fields; Rio del Norte, low sandy river bank.
- 984 29 Aug., 1847. Between Willow Bar and Middle Spring (Cimarron River).
- 985 15 May-3 June, 1847. Santa Fe Creek, bottom land at no great distance from the creek.
- 986 19 July, 1847. Santa Fe, grassy margin of an irrigating ditch.
- 987 12 Aug.-8 Sept., 1847. Pawnee Fork and Pecos, prairies.
- 988 16 July-3 Sept., 1847. Santa Fe Creek valley near fields;

Willow Bar, sandy wet bottomland; ford of Arkansas River, low bottom land.

989 27 Aug., 1847. Upper Spring (Cimarron River), margin of the water.

990 21 Sept., 1847. Prairie about 10 miles southwest of the upper ferry of Kansas River.

991 27 Sept., 1847. Bank of Missouri River above Washington.

992 12 Aug., 1847. 10 miles east of Pecos, low prairie.

993 21 July, 1847. Santa Fe Creek valley, not far from the creek.

994 16 Aug., 1847. Moro River, hillside between rocks.

995 17 Aug., 1846. Creek bottom near Council Grove.

996 26 July–8 Sept., 1847. Santa Fe Creek bottom; Ojo de Bernal, margin of a pond; ford of the Arkansas River, wet bottom land; Pawnee Fork, creek bottom.

997 12 Aug., 1847. 10 miles east of Pecos.

998 26 Aug., 1847. A few miles west of the ford of Cimarron River.

999 12 Aug., 1847. Ojo de Bernal, low grassy places in the mountains.

1000 3–24 June, 1847. Santa Fe Creek, margin of the creek.

1001 13–16 Aug., 1847. Ojo de Bernal—Moro River, summit of a rocky hill.

1002 15 May–12 July, 1847. Santa Fe, margin of the creek.

1003 24 Sept., 1847. 8 miles south of Fort Leavenworth, in ravines along the road side.

1004 17 Aug., 1847. A few miles east of Moro River, deep standing water.

1005 14 Aug., 1846. About 90 miles west of Independence, under water in a deep large pool.

1006 18 Sept., 1847. Bluff Creek bottom, submerged in the water of a shallow pool.

1007 & 1008 2 species. 17 Aug., 1847. A few miles east of Moro River, surface of deep standing water.

1009 29 April, 1847. Santa Fe, in a pond-like collection of water fed by a small spring.

#### EQUISETACEAE

1010 22 April–22 June, 1847. Santa Fe Creek bottom, near the creek and irrigating ditches; also Rio del Norte, low bank, margin of the water.

1011 8–22 May, 1847. Rio del Norte, low wet sandy bank of the river.

- 1012 22 June, 1847. Santa Fe, foot of hills, near the creek.  
 1013 4 March–2 May, 1847. Sunny bank of Santa Fe Creek.

## FILICES

- 1014 3 June, 1847. Santa Fe Creek valley, grassy places.  
 1015 12 April–11 November, 1846–7. Santa Fe, shady sides of mountains, near the foot as well as on the summit. In good soil under protection of rocks and roots, in crevices. Early in the spring, the leaves show a tendency to roll up as soon as the plant is taken from the ground. Mostly green throughout the winter.  
 1016 23 Feb., 1847. Eastern mountains, Santa Fe; sunny declivities in crevices of steep masses of rocks.  
 1017 8–25 May, 1847. Rio del Norte, deep ravines in the trap-formation, rachis flexuose, pinnae alternate.  
 1017b 22 August, 1846. Council Grove, underneath projecting ledges of rocks, high dry region. rachis straight, pinnae opposite.  
 1018 20 Aug., 1846. Council Grove, summit of a hill, deep crevices in the rock.  
 1019 28 July, 1847. Santa Fe Creek, 12 miles above Santa Fe, high mountains, shady places in ravines.  
 1020 5 June, 1847. Santa Fe Creek, bottom, near the creek.  
 1021 21 Aug., 1847. Council Grove, between rocks, in a ravine.  
 1022 15 May–24 June, 1847. Santa Fe Creek bottom, shady places at the foot of rocks, moist fertile soil.  
 1023 30 March–17 Aug., 1847. Santa Fe Creek, shady bank, between rocks, good soil. Also 2 miles east of Moro River, green throughout the winter.

## LYCOPODIACEAE

- 1024 13 Feb.–17 April, 1847. Santa Fe Creek, perpendicular side of rocks facing the creek, in the higher regions of the mountain range, as well as on the shady bank of the lower creek. Begins to be lively green in the month of March.  
 1025 16 Feb.–April, 1847. Santa Fe, between rocks in the upper region of the mountains.

## CHARACEAE

- 1026 29 April, 1847. Santa Fe, in a shallow pond fed by a spring.

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The collection list and the letters from George Engelmann to Asa Gray are in the archives of the Gray Herbarium and I am grateful to the Director of the Gray Herbarium for permission to use these materials.

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In many genera of the Cruciferae originally based on species from the Old World (*Arabis*, *Cardamine*, and *Draba*, for example) there has never been any doubt about their occurrence natively in the western hemisphere. *Sisymbrium* has been similarly treated as an inclusive genus with species in most parts of the world. But in the latter, treatments have fluctuated enormously. Such early floras dealing with North American plants as Hooker (1829–30) and Torrey and Gray (1838–40) interpreted *Sisymbrium* broadly and attributed many anomalous species to the genus. However, since these earlier works there has been a steady narrowing of the genus. Schulz (1924) was the primary architect of a reduced *Sisymbrium* as far as North American species are concerned. But Greene (1896) and Rydberg (1907) had already started the process. Schulz recognized that *Halimolobos*, although initially based on Mexican species, also included others from farther north [*H. diffusa* (Gray) Schulz and *H. virgata* (Nutt.) Schulz] formerly placed in *Sisymbrium*. Since then, other species north of Mexico, *H. mollis* (Hook.) Roll., *H. perplexa* (Hend.) Roll. and *H. whitedii* (Piper) Roll., were moved from either *Sisymbrium* or *Arabis* to *Halimolobos* (Rollins, 1943). In another direction, Schulz carved *Romanschulzia* and *Coelophragma* from *Sisymbrium*. The opposite trend was initiated by Payson (1922) when he assembled in *Sisymbrium* many species that had previously been recognized as belonging to *Thelypodium*. In doing so, he placed *Schoenocrambe* Greene, *Thelypodopsis* Rydb., and *Hesperidanthus* Rydb. into synonymy under *Sisymbrium*.

I have followed Payson in his realignment of *Sisymbrium* for many years, but it has been increasingly difficult to do so. The impact of new and increased knowledge of the North American species involved has been to emphasize their differences from *Sisymbrium* rather than their similarities. It is interesting and telling that Al-Shehbaz (1973) and Payson, (1923), both studying *Thelypodium*, came to different conclusions with regard to many of the species treated in the present paper. Payson regarded them as belonging to *Sisymbrium*, Al-Shehbaz as neither *Thelypodium* nor *Sisymbrium*. He transferred *Thelypodium* *ambiguum* Wats. [*Sisymbrium ambiguum* (Wats.) Pays.] and *Thelypodium linearifolium* (Gray) Wats. [*Sisymbrium linearifolium* (Gray) Pays.] to *Thelypodopsis* and at the same time accepted *Thelypodopsis* as Rydberg had originally constituted it. The weight of evidence favors the course taken by Al-Shehbaz with respect to those North American

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species referable to *Thelypodiopsis* but treated as *Sisymbrium* by Payson. I followed Al-Shehbaz in my study of *Thelypodiopsis* of Mexico (Rollins, 1976) in connection with the preparation of a treatment of the Cruciferae for Johnston's *Flora of the Chihuahuan Desert*. In doing so, I further narrowed *Sisymbrium* as far as its involvement with American species is concerned. In the present study, I have concluded that none of those North American species previously placed in *Sisymbrium* should remain there. *Sisymbrium* is now regarded as being an Old World genus which, and along with such genera as *Brassica*, *Diplotaxis*, *Eruca*, *Raphanus* et al., has only alien species in the North American flora.

Al-Shehbaz's action (1973) in bringing *Sisymbrium linearifolium* into *Thelypodiopsis* was important because it showed that species had connections with other species of the genus, but he apparently did not take fully into account its close relationship to *Schoenocrambe linifolia* (Nutt.) Greene [*Sisymbrium linifolium* Nutt.]. These two species can hardly be placed in separate genera. In this respect I cannot help but agree with Payson (1923) who, in writing of *Sisymbrium linifolium* says, "It seems very doubtful if there is any difference other than one of degree between the root system of this plant and of *Hesperidanthus* [*S. linearifolium*]. I should not hesitate to adopt a genus on very slight morphological grounds if it became evident that it was really distinct phylogenetically. In this case, however, there seems no reason to doubt the close relationship between *S. linifolium* and the related species [*S. linearifolium*] and neither is there significant grounds for maintaining them distinct generically."

Recent discoveries of new species (Welsh & Atwood 1977; Welsh, 1981) have filled in the gaps between *Thelypodiopsis* and *Schoenocrambe* to an extent that makes both of these genera pivotal between *Thelypodium* and *Sisymbrium*. The type species of *Schoenocrambe*, *S. linifolia*, has habitat phases that resemble *S. argillacea* Welsh & Atwood and *S. barnebyi* Welsh & Atwood on the one hand and *S. linearifolia* on the other. And there are no technical characters that are sufficiently fundamental to place these species in different genera from each other.

As in other genera of the Cruciferae, *Thelypodiopsis* and *Schoenocrambe* are not well-defined in the sense that all species in each genus are completely unlike those of any other genus. In fact, *Thelypodiopsis elegans* is fairly close to *Thelypodium sagittatum* and there are features of *Thelypodiopsis ambigua* that resemble those of *Thelypodium sagittatum*. Our generic concept is based on the premise that a genus is made up of a constellation of species that are putatively more closely related to each other than to the species of any other genus. Furthermore, the center of diversity represented by the

species of such a genus is different from the center of diversity of any other genus. At the fringe of this diversity there may be species that come close to the fringe of diversity of another genus, but taxonomically the submergence of one genus or the other is not required. The evolutionary connections in such a situation are clearer than in cases where an evident gap is present between the genera. The number of instances in the Cruciferae where two or more genera come together (Rollins, 1939, 1950, 1960) are so numerous that this is almost the rule rather than the exception. This argues for the relative "youth" of the family because the evolutionary connections between the genera are still present whereas in many "ancient" families great gaps between genera exist. Not only are *Thelypodopsis* and *Schoenocrambe* genera of the nature mentioned above as far as each other are concerned, they in turn are closely connected to other genera. This is particularly true of *Schoenocrambe* where *S. linifolia* is very close to *Sisymbrium polymorphum*, a species of central Asia and eastern Europe. In fact, *S. polymorphum* is somewhat out of place in *Sisymbrium* and may well be nearer its congeners in *Schoenocrambe*.

Geographically, the species of *Schoenocrambe* and *Thelypodopsis* occur most abundantly in western United States and northern Mexico. One species, *Schoenocrambe linifolia*, barely gets into Canada. The most northerly known stations are in British Columbia. The most southerly species is *Thelypodopsis alpina* which occurs in Guatemala. Several species, such as *Schoenocrambe linifolia*, *S. linearifolia*, and *Thelypodopsis elegans*, are relatively widespread and abundant. All three of these species are frequently collected and are well represented in herbarium collections. *Schoenocrambe linearifolia* occurs from Colorado and Utah to Coahuila, Mexico; *S. linifolia* occurs from British Columbia to Arizona and New Mexico. *Thelypodopsis elegans* is found in western Colorado, in the northern half of Utah, and in southwestern Wyoming. *Thelypodopsis purpusii* is infrequently collected but it has been collected at disjunct localities over a fairly wide range extending from northern Arizona to Coahuila. Otherwise, the species of *Thelypodopsis* and *Schoenocrambe* tend to be local in their occurrence and they are infrequently collected.

The flowers of several species, *Thelypodopsis ambigua*, *T. elegans*, and *T. juniperorum*, for example, are relatively large and showy. In these, both sepals and petals are purple-colored or whitish. In *T. ambigua* and *T. juniperorum* the petals are bright purple, those of *T. elegans* range from white to light purple. Only three species, *Schoenocrambe linifolia*, *Thelypodopsis aurea*, and *T. divaricata*, have yellow or yellowish flowers. In all others, the flowers are purplish, whitish, or white.



## THELYPODIOPSIS

**Thelypodopsis** Rydberg, Bull. Torr. Bot. Club 34: 432. 1907.

Erect annual or biennial (rarely perennial) herbs with one to several stems from the base, usually branched; glabrous or if pubescent, trichomes simple; leaves heteromorphic, basal leaves usually petiolate if present, often lacking on mature plants, cauline leaves remote to crowded, cuneate or petiolate in a few species, auriculate in most species, diminishing upward on the stem; flowers in lax to moderately dense racemes which terminate each branch; sepals glabrous or sparsely pubescent in a few species; petals narrowly lingulate to spatulate or obovate, white to purple (yellow in *T. aurea* and *T. divaricata*); pedicels slender, erect to widely spreading (reflexed in *T. retrofracta*); siliques terete or nearly so, infrequently somewhat torulose, narrowly linear, erect to widely spreading or rarely reflexed, sessile in most species, gynophorate in a few species; styles present or obsolete on the silique; stigmas bifid with lobes over the replum margins to nearly entire; seeds usually plump, oblong, wingless (except in *T. retrofracta* where they have a narrow distal wing); cotyledons incumbent, rarely obliquely incumbent to nearly accumbent. Type species *Thelyposiopsis elegans* (Jones) Rydberg.

## KEY TO THE SPECIES

- A. Cauline leaves ovate to broadly oblong, strongly auriculate, large auricles clasping the stem.
  - B. Basal leaves deeply pinnately lobed to pinnatifid, lower cauline leaves at least pinnatifid. Plants of Arizona to Texas and Mexico.
    - C. Siliques beaked, torulose; petals 8–10 mm. long; lower leaves and stems pubescent with spreading simple trichomes ..... 13. *T. incisa*.
    - C. Siliques rounded at apex, not beaked; petals 4–6 mm. long; lower leaves and stems glabrous ..... 12. *T. purpusii*.
  - B. Basal leaves and lower cauline entire or at most dentate (rarely somewhat incised in one phase of *T. elegans*).
    - D. Pedicels erect, mostly appressed to rachis; siliques less than 3 cm. long; plants biennial or perennial ..... 14. *T. versicolor*.
    - D. Pedicels divaricately ascending, widely spreading or slightly descending; siliques 4–10 cm. long; plants annual or biennial (except *T. wootonii* of Mexico which may be perennial).
    - E. Siliques stipitate, slender stipe 3–7 mm. long.
      - F. Sepals and petals purple; sepals erect during anthesis.
        - G. Plants glabrous throughout, coarse; styles 1 mm. or less long; pedicels at right angles to rachis, slightly curved upward, 1 cm. or less long (slightly longer in var. *erecta*) ..... 1. *T. ambigua*.
        - G. Plants pilose toward base of stem, stems slender; styles 2–3 mm long; pedicels divaricately ascending to widely spreading, 1–2 cm. long on lower mature siliques ..... 2. *T. juniperorum*.
      - F. Sepals and petals yellow; sepals spreading to somewhat reflexed during anthesis ..... 3. *T. aurea*.
    - E. Siliques sessile or with a short thick stipe less than 2 mm. long.
      - H. Lower cauline leaves oblong to ovate, acuminate to acute (rarely obtuse), widest below the middle.
        - I. Pedicels less than 1.5 cm. long, mostly ca. 1 cm. long; plants not rhizomatous.
          - J. Inflorescence lax, few-flowered; siliques few and remote; cauline leaves acuminate, scarcely reduced upward; plants of Guatemala ..... 8. *T. alpina*.
          - J. Inflorescence dense, many-flowered; siliques many and forming a dense infructescence; cauline leaves acute, reduced upwards.
            - K. Petals purplish, light lavender or white, gradually tapered from

blade to claw, spatulate, not constricted; sepals purplish, spreading, or if erect not forming an urn-shaped calyx.

L. Styles of developed siliques expanded at summit, club-shaped; plants sparsely pilose at least at base of stems; siliques straight to somewhat curved, usually not tortuous or torulose ..... 4. *T. elegans*.

L. Styles of developed siliques uniform in diameter, cylindrical; plants wholly glabrous or rarely pilose at base of stems; siliques tortuous and torulose ..... 5. *T. vermicularis*.

K. Petals yellow, sharply constricted between small oblong blade and broadened membranous claw; sepals yellowish, erect, connivent, forming an urn-shaped calyx ..... 6. *T. divaricata*.

I. Pedicels more than 1.5 cm. long, mostly ca. 2 cm. long; plants rhizomatous ..... 7. *T. wootonii*.

H. Lower cauline leaves pandurate or obovate, obtuse, rounded at apex; widest above the middle.

M. Pedicels widely spreading to arched downward; siliques loosely descending; somewhat arched to nearly straight ..... 11. *T. arcuata*.

M. Pedicels divaricately ascending; siliques divaricately ascending, straight ..... 9. *T. shinniersii*.

A. Cauline leaves narrowly oblong without auricles or petiolate (weakly auriculate in some plants of *T. vaseyi*, auricles not clasping stem).

N. Cauline leaves petiolate, sharply and deeply dentate to lobed, very thin, fruiting pedicels widely spreading ..... 10. *T. byiei*.

N. Cauline leaves cuneate at base, entire or rarely weakly dentate.

O. Siliques and pedicels ascending; siliques less than 2.5 cm. long, strongly torulose; petals white ..... 15. *T. vaseyi*.

O. Siliques and pedicels strongly reflexed; siliques 4 cm. or more long, not strongly torulose; petals purplish ..... 16. *T. retrofracta*.

**1. *Thelypodopsis ambigua* (S. Wats.) Al-Shehbaz, based on *Thelypodium ambiguum* S. Watson, Proc. Amer. Acad. 14: 290, 1879. *Sisymbrium ambiguum* (S. Wats.) Payson, Univ. Wyo. Publ. Sci. 1: 11, 1922. *Thelypodopsis ambigua* (S. Wats.) Al-Shehbaz, Contrib. Gray Herb. 204: 138, 1973.**

Annual or biennial, glabrous throughout, glaucous; stem single, coarse, branched above, up to a meter or more tall; basal leaves petiolate, ascending, oblanceolate, obtuse, coarsely and irregularly dentate to entire, up to 2 dm. long, 1–2 cm. wide; cauline leaves numerous, overlapping, auriculate, oblong to lanceolate, up to 1 dm. long, reduced upward, upper entire, lower often dentate; inflorescences dense with numerous flowers, greatly elongating in fruit; sepals purplish, erect, oblong, scarious-margined, non-saccate, 5–7 mm. long; petals deep purple, broadly spatulate, 10–12 mm. long, blade widely spreading to somewhat reflexed at anthesis, abruptly narrowed to claw; stamens slightly exserted; filaments slender; anthers curved, 3–4 mm. long; pedicels widely spreading, markedly expanded at summit, usually slightly curved upward, 6–9 mm. long; siliques widely spreading, somewhat curved downward to nearly straight, terete, slightly torulose, 5–9 cm. long, slightly more than 1 mm. in diameter, stipitate; stipe 3–5 mm. long; styles ca. 1 mm. long; stigma obscurely 2-lobed; seeds oblong, not winged, ca. 1.5 mm. long, less than 1 mm. wide. *n* = 11 (Rollins and Rüdénberg, 1971).

#### KEY TO THE VARIETIES

Petals deep purple; pedicels spreading at right angles to rachis; siliques widely spreading ..... 1a. var. *ambigua*.

Petals light purplish to nearly white; pedicels divaricately ascending; siliques ascending to erect ..... lb. var. *erecta*.

1a. *T. ambigua* (S. Wats.) Al-Shehbaz var. *ambigua*.

DISTRIBUTION: Arizona in Coconino, Mohave, and Yavapai counties. It was listed from Washington County, Utah, by Welsh and Reveal (1977) but the Palmer specimen (no. 27) cited came from Trumbull, Arizona.

FLOWERING: March–June.

HOLOTYPE: Long Valley, Mohave County, Arizona, 27 Mar 1858, *Newberry s.n.* (GH!).

OTHER SPECIMENS STUDIED: **Arizona. Coconino Co.:** between Ash Fork and Peach Springs, 12 May 1931, *McKelvey 2170* (GH); 1 mi. SE of Dinosaur, between Peach Springs and Seligman, 8 May 1967, *Rollins 67101* (GH). **Mohave Co.:** Peach Springs, June 1884, *Lemmon 3246* (GH, US); same locality 26 May 1884, *M. E. Jones 69* (GH); Arizona Strip District, T36N, R7W, S16, 7 Jun 1979, *Coombs & Bundy 2815* (BRY); 1 mi. E of Truxton, 7 May 1967, *Rollins 6796* (GH); Trumbull, 60 mi. S of St. George, Utah, 1887, *E. Palmer 27* (GH, NY 5 sheets, US); 1.6 mi. E of Mt. Trumbull, 25 May 1979, *N. H. Holmgren et al. 9169* (GH); ca. 3 mi. N of Mt. Trumbull, 20 May 1973, *Spellenberg et al. 3191* (GH). **Yavapai Co.:** 30 mi. NW of Wickenburg, 9 Jun 1968, *Barclay & Lockwood 3009* (GH).

1b. *T. ambigua* var. *erecta* Rollins, var. nov.

Herba biennis glabra, foliis integris, petalis purpureis vel albidis, pedicellis adcententibus vel divaricatis, siliquis erectis.

DISTRIBUTION: southern Utah and northern Arizona.

FLOWERING: April–May.

HOLOTYPE: Utah. Kane Co.: Kanab, 11 May 1941, *A. Eastwood & J. T. Howell 9300* (GH). Isotype (US).

OTHER SPECIMENS STUDIED: **Arizona. Mohave Co.:** clay hillside, piñon-juniper community, ca. 18 mi. W of Fredonia, 27 May 1968, *Higgins 1370* (GH); chinle formation, ca. 5 mi. N of Moccasin on Coral Pink Sand Dunes road, 19 May 1972, *Atwood & Higgins 3938* (BRY). **Utah. Kane Co.:** ca. 12 airline mi. NW of Fredonia, Arizona, 4 May 1970, *Welsh & Atwood 9706* (BRY).

The conspicuous flowers of *Thelypodopsis ambigua* are not exactly regular. Two petals are oriented on the upper side and two on the lower side of the nearly horizontal flower when it is at full anthesis. The anthers of the paired stamens protrude slightly from the center of the flower and are usually exposed to insects entering the flowers because the petal blades are either widely spreading or somewhat reflexed. The dense elongated racemes of deep purple flowers make *T. ambigua* a conspicuous member of the juniper woodland flora in places where it occurs in abundance.

Typical *Thelypodopsis ambigua* has a single, rather thick stem that is densely covered with overlapping thickish oblong leaves. Branching occurs well above the base. The lower leaves are erect, well-developed, and tend to persist at least through the early flowering period. In these respects, this species differs from its close relatives, *T. juni-*

*perorum* and *T. elegans*, both of which shed the lowermost leaves by the time flowering begins. These species usually branch beginning at the base (this is more consistent in *T. elegans* than in *T. juniperorum*). They have more ovate cauline leaves than is the case with *T. ambigua* and these tend to be more remote from each other on the stem.

2. *Thelypodiopsis juniperorum* (Payson) Rydberg, based on *Sisymbrium juniperorum* Payson, Univ. Wyo. Publ. Sci. 1: 12, 1923. *Thelypodiopsis juniperorum* (Payson) Rydberg, Fl. Rocky Mts. ed. 2: 1123, 1923. *Thelypodiopsis elegans* (Jones) Rydb. var. *juniperorum* (Pays.) Harrington, Man. Pl. Colorado 280, 1954.

Annual; stems erect, single and branched above or several branches arising just above base, pilose with simple flattened trichomes at base and at nodes, 3–10 dm. tall; basal leaves entire to irregularly dentate, oblanceolate, obtuse, narrowed to a winged petiole, 5–15 cm. long; cauline leaves auriculate, clasping the stem, lower oblong and obtuse, upper becoming elongated and lax in fruit; inflorescence terminating each branch; sepals erect, purple, oblong, non-saccate, 5–7 mm. long, 2–3 mm. wide; petals purple with an orbicular blade abruptly narrowed to a slender claw, 14–17 mm. long, 5–9 mm. wide, blade widely spreading at anthesis; stamens erect, slightly exserted, single and paired subequal; anthers erect, curved, 3–4 mm. long; pedicels widely spreading to divaricately ascending, glabrous to sparsely pilose, 1–2 cm. long; siliques ascending to nearly erect, stipitate, terete, torulose, glabrous, 5–9 cm. long, ca. 1 mm. in diameter; stipes slender, 3–6 mm. long; styles slightly expanded at apex, 2–3 mm. long; stigmas shallowly lobed, lobes over replum margin; seeds oblong, plump, not winged; cotyledons oblique to nearly accumbent.

DISTRIBUTION: west central Colorado.

FLOWERING: May–June.

HOLOTYPE: 6 mi. E of Montrose, Montrose County, Colorado, 15 Jun 1915, E. B. Payson 688 (RM!). Isotype (GH!).

OTHER SPECIMENS STUDIED: Colorado. Gunnison Co.: near Gunnison Canyon, 31 May 1913, Payson 97 (GH). Montrose Co.: 5.4 mi. N of turnoff to Black Canyon, off U.S. Hwy. 50, 28 May 1979, R. C. & K. W. Rollins 7994 (GH); 1.3 mi. N of turnoff to Black Canyon, 28 May 1979, R. C. & K. W. Rollins 7987 (GH); 2.2 mi. on Colo. Hwy. 347 from its junction with U.S. Hwy. 50, 24 Jul 1969, I. & M. Al-Shehbaz 6902 (GH); 4 mi. E of Cerro Summit, 27 May 1979, R. C. & K. W. Rollins 7975 (GH).

Although Payson believed *Thelypodiopsis juniperorum* to be somewhat intermediate between *T. ambigua* and *T. aurea*, I am convinced that it is much closer to *T. ambigua*. The plants are less robust, the inflorescence is much less dense than in *T. ambigua* and the presence of simple flat whitish trichomes toward the base of the stems in *T. juniperorum* will consistently separate it from that species.

Evidently *Thelypodiopsis juniperorum* is more local than most species of the genus. As I interpret it, the species includes only those populations with relatively large purple flowers and with long slender gynophores supporting the fruits. Thus delimited, some populations with a mixture of sessile fruits and short stoutish-stiped fruits referred by some to *T. juniperorum* fall within the rather polymorphic *T. elegans*. This type of material probably misled Harrington (1954) into believing that *T. juniperorum* is only a variety of *T. elegans*.

3. *Thelypodopsis aurea* (Eastwood) Rydberg, based on *Thelypodium aureum* Eastwood, *Zoe* 2: 227, 1891. *Thelypodopsis aurea* (Eastwood) Rydb., *Bull. Torr. Bot. Club* 34: 432, 1907. *Sisymbrium aureum* (Eastwood) Payson, *Univ. Wyo. Publ. Sci.* 1: 13, 1922.

Biennial or short-lived perennial, glabrous or sparsely pubescent toward base of stems with simple trichomes; stems erect, single or branching near base, branched above, 2–5 dm. tall; basal leaves oblanceolate, obtuse, irregularly dentate, glabrous, wing-petioled, 3–5 cm. long; cauline leaves oblong to lanceolate, auriculate, reduced and more acute upward; inflorescences terminating each branch, elongated in fruit; sepals oblong, non-saccate, yellow, spreading at anthesis, 5–7 mm. long, ca. 2 mm. wide; petals lingulate or spatulate, tapering gradually to a broad claw or with a slightly enlarged blade, yellow, 7–10 mm. long; stamens erect, not exserted; filaments of single and paired stamens subequal; anthers curved when dry; fruiting pedicels divaricately ascending, straight, 5–10 mm. long; siliques erect to slightly divaricate, slender, nearly straight, stipitate, 5–7 cm. long, somewhat torulose; stipe slender, 2–5 mm. long; styles ca. 2 mm. long; stigma two-lobed to nearly entire; immature seeds oblong, plump, wingless, ca. 2 mm. long, ca. 1 mm. wide.  $n = 11$  (Rollins and Rüdénberg, 1977).

**DISTRIBUTION:** southwestern Colorado, northwestern New Mexico and southeastern Utah.

**FLOWERING:** April–May.

**HOLOTYPE:** Durango, Colorado, *Eastwood* (CAS, not seen).

**OTHER SPECIMENS STUDIED:** **Colorado.** Montezuma Co.: Mancos, Jun 1892, *Eastwood s.n.* (GH, NY, US); SW Colorado, 1875, *Brandeggee* 1120 (GH); 1 mi. E of Utah state line, 23 Apr 1971, *Rollins & Stafleu* 7148 (GH); hills W of Mancos, 21 May 1943, *Ripley & Barneby* 5352 (NY); McElmo Creek valley, 20.6 mi. S of Cortez, 15 May 1981, *R. C. & K. W. Rollins* 8127 (GH). **New Mexico.** Sandoval Co.: foothills of Nacimiento Mts., east of Cuba, 26 May 1946, *Ripley & Barneby* 7571 (GH). **San Juan Co.:** steep slope below bluffs on the San Juan River, 1/2 mi. E of Four Corners Point, 22 Apr 1971, *Rollins & Stafleu* 7133 (GH); 7 mi. S of Shiprock, 19 Apr 1941, *Cutler* 4602 (GH). **Utah.** **San Juan Co.:** E of Aneth near Utah state route 262 just inside Utah, ca. 1/4 mi. from Colorado line, 23 Apr 1971, *Rollins & Stafleu* 7146 (GH); road cut, Utah state route 262, 5-1/2 mi. E of Aneth, 23 Apr 1971, *Rollins & Stafleu* 7147 (GH); 10 mi. SW of Blanding, 8 May 1933, *Harrison* 5937 (BRY); N end of Montezuma Creek, 6 mi. E of U.S. Hwy. 47, 8 May 1969, *Welsh et al.* 8914 (BRY); 15 mi. S of Blanding on road to Bluff, 13 May 1970, *Atwood* 2429 (BRY); 6 mi. above Bluff, 29 Apr 1961, *Shumway* 61 (BRY); 8 mi. W of Blanding, 19 May 1955, *Barneby* 12766 (NY).

Although it is one of the poorly collected species of *Thelypodopsis*, *T. aurea* is not uncommon in the area where it occurs as Dr. Frans Stafleu and I found in 1971 when we collected specimens from four separated populations in three different states. This was in the four corners area of Arizona, Colorado, New Mexico, and Utah. There we observed many populations additional to those we sampled, all in the valley of the San Juan River. In its habit of growth, *T. aurea* is somewhat similar to *T. ambigua*, often having a single stout stem that arises from a relatively heavy root. Some plants do branch at or near the base but in most, branching occurs above the middle of the stem. It does appear to be biennial. However, there is a good possibility that some plants persist beyond the second year.

Specimens of *Thelypodopsis aurea* are either completely glabrous or there may be simple spreading trichomes at the base of the stem.

On a given sheet, both glabrous and sparsely hirsute individuals may be found, showing that presence or absence of trichomes is not a characteristic that can be used for taxonomic purposes in this species. There is also some variation in the petal shape. This ranges from spatulate to broadly oblong.

**4. *Thelypodopsis elegans*** (Jones) Rydberg, based on *Thelypodium elegans* M. E. Jones, *Zoe* 4: 265, 1893. *Thelypodopsis elegans* (Jones) Rydb., *Bull. Torr. Bot. Club* 34: 432, 1907. *Streptanthus wyomingensis* A. Nelson, *Bull. Torr. Bot. Club* 26: 126, 1899. *Thelypodopsis wyomingensis* (A. Nels.) Rydb., loc. cit. *Thelypodium bakerii* Greene, *Pl. Baker.* 3: 8, 1901. *Thelypodopsis bakerii* (Greene) Rydb., loc. cit.

Annual or biennial; stems one to many from the base, branched above, sparsely to densely pilose toward base or sometimes pubescent throughout, 3–10 dm. tall; basal leaves entire or more rarely dentate, oblanceolate, acute to obtuse, with a short-winged petiole, glabrous or pilose on the under surface, 2–6 cm. long, 1–1.5 cm. wide; cauline leaves auriculate; lower oblong, acute to obtuse, entire or rarely dentate, glabrous or less frequently pilose on the lower surface; inflorescences dense, elongating usually glabrous, rarely pilose on the lower surface; flowers pale lavender or nearly white, non-saccate, greatly in fruit; sepals oblong, purplish to pale lavender or nearly white, non-saccate, divaricately ascending to erect, 5–7 mm. long; petals spatulate, pale purple to white, unguiculate, 10–14 mm. long; pedicels slender, divaricate, glabrous or less frequently sparsely pilose, 7–10 mm. long, expanded at summit; siliques sessile or with a thick gynophore 1 mm. or less long, terete, often torulose, straight or sometimes tortuose, divaricately ascending to more widely spreading, glabrous to sparsely pilose or rarely more densely so, 4–9 cm. long, ca. 1.5 mm. in diameter; styles 1–3 mm. long, often obclavate; stigmas 2-lobed, grooves shallow to prominent; seeds wingless, angular, oblong, ca. 1 mm. wide, less than 1.5 mm. long; radicle exceeding cotyledons; cotyledons incumbent to obliquely so.

**DISTRIBUTION:** western Colorado, Utah, southwestern Wyoming.

**FLOWERING:** May–June.

**HOLOTYPE:** Westwater, Grand County, Utah, 6 May 1891, M. E. Jones s.n. (POM!). Not 7 May 1891 as given in the protologue (cf. Rollins, 1971).

**REPRESENTATIVE SPECIMENS:** **Colorado.** Delta Co.: 2 mi. W of Delta, 25 May 1938, Rollins 2137 (GH, US). **Garfield Co.:** near Glenwood Springs, 13 Jun 1957, Rollins 57150 (GH). 2 mi. W of Rifle, 27 May 1938, Rollins 2202 (GH). **Gunnison Co.:** 3 mi. E of Sapinero, 23 May 1938, Rollins 2110 (GH). **Mesa Co.:** off U.S. Interstate 70, 5.7 mi. E of Utah border, 29 May 1979, R. C. & K. W. Rollins 79102 (GH); 10 mi. N of Mesa, 27 May 1938, Rollins 2195 (GH). **Moffat Co.:** Yampa Canyon near Chew Ranch, Dinosauro National Monument, 16 May 1948, Porter 4480 (GH); 10 mi. W of Maybell, 14 May 1948, Harrington 3888 (GH); 4 mi. E of Craig, 22 May 1979, Rollins 7937 (GH). **Montrose Co.:** Cimarron, 6 Jun 1901, Baker 32 (GH; US, isotypes of *Thelypodium bakerii*); 1.7 mi. E of Montrose, 28 May 1979, R. C. & K. W. Rollins 7982 (GH); Naturita, 4 May 1914, Payson 272 (GH). **Routt Co.:** 5 mi. W of Steamboat Springs, 18 May 1948, Harrington 3999 (GH). **Utah.** Duchesne Co.: 3.8 mi. E of Duchesne, 30 May 1979, R. C. & K. W. Rollins 79115 (GH). **Grand Co.:** 1.5 mi. N of Westwater, 29 May 1979, R. C. & K. W. Rollins 79105 (GH); off U.S. Interstate 70, 9 mi. E of Cisco exit, 29 May 1979, R. C. & K. W. Rollins 79106 (GH). **Uintah Co.:** bluff above Willow Creek, 11 mi. S of Ouray, 31 May 1979, R. C. & K. W. Rollins 79121 (GH); 1 mi. W of Rainbow, 4 Jun 1965, N. H. Holmgren et al. 1803 (GH); 2.5 mi. SW of Vernal, 30 May 1979, R. C. & K. W. Rollins 79118 (GH). **Wyoming.** Carbon Co.: 16

mi. N of Rawlins, 21 May 1979, *Reed C. and Richard C. Rollins* 7927 (GH); 8 mi. N of Baggs, 22 May 1979, *Reed C. & Richard C. Rollins* 7933 (GH). Sweetwater Co.: Green River, 30 May 1897, *Nelson* 3034 (GH, isotype of *Streptanthus wyomingensis*); same locality, 13 Jun 1936, 28 May 1938, *Rollins* 1177, 2217 (GH); 5 mi. N of Henry's Fork, 29 Jun 1951, *Rollins & Porter* 5140 (GH).

The variation in various features of *Thelypodopsis elegans* is frustrating because certain facies of the species are recognizable and show geographical integrity. However, to pin these down with consistent characters is elusive. Certain trends can be recognized. For example, there is increased pilosity on the leaves, stems, pedicels, sepals, and siliques as material from northern Colorado into southern Wyoming is examined. Some populations from southwestern Wyoming, the type locality for what has been called *Thelypodopsis wyomingensis*, tend to have torulose siliques and the styles are strongly expanded at the tip in many plants. But these features are not consistently correlated even in the same geographical area. Other characters, such as the length of the gynophore, if it is present, appear to be erratic. In a single population (*Rollins* 7933 from 4 miles east of Craig, Colorado), the siliques of a given plant may be virtually sessile or in different plants the gynophores may range up to at least 1 mm. long. The lengths of the siliques vary considerably.

*Thelypodopsis bakerii* was founded on plants with relatively shorter fruits than are present in typical *T. elegans* but several populations in the area where the type of *T. bakerii* was collected have plants with siliques that range well within the shortest limit of typical *T. elegans*. The siliques of plants in the "*T. bakerii*" area do average shorter than those in the type area of *T. elegans*. But this is not sufficiently definitive to provide the basis for the recognition of a separate taxon. Over most of the area where *T. elegans* occurs, the basal leaves and lower cauline leaves are entire or nearly so. There are occasional plants with sparsely dentate leaves but this is not the rule. However, from northern Colorado and southern Wyoming come specimens with lower leaves that are markedly dentate. This feature is correlated to some extent with increased pilosity. The possibility of recognizing nomenclaturally an infraspecific taxon based on these correlated features was recognized. However, specimens with transitional features were too numerous to permit clear distinctions to be made.

After studying 13 new collections especially obtained from populations where field observations were made at the time the material was taken, I have reluctantly come to agree with Payson (1922). In referring to this species, he stated that "to separate these forms is at present impossible since they seem to show no correlation to one another nor to geographical areas." I feel that Payson's statement is as appropriate now as it was when he made it. The 13 collections referred to were from different localities nearly throughout the range of *Thely-*

*podopsis elegans*, including the type areas of "*Thelypodium bakerii*," *Thelypodopsis elegans*, and "*Streptanthus wyomingensis*."

**5. *Thelypodopsis vermicularis* (Welsh & Reveal) Rollins, comb. nov.,** based on *Thelypodium sagittatum* (Nutt.) Endl. var. *vermicularis* Welsh & Reveal, Great Basin Nat. 37: 357, 1977.

Annual or biennial, glabrous throughout or rarely with a few trichomes near base; stems one to several from the base, branched above, 2–6 dm. tall; basal leaves few, quickly shed, broadly oblanceolate, obtuse, entire or with a few small remote teeth, 2–5 cm. long, 1–1.5 cm. wide, petiole shorter than blade; cauline leaves strongly auriculate and clasping, broadly ovate to oblong, obtuse to gradually narrowed toward apex, entire, reduced upward but not markedly so; inflorescence dense, elongating considerably in fruit; sepals loosely ascending to spreading during anthesis, oblong, white to purplish or greenish, non-saccate, 4.5–5.5 mm. long, 1.2–1.5 mm. wide; petals spatulate, white, tapering gradually from blade to broad claw, 9–11 mm. long, 3–4 mm. wide; stamens erect; anthers straight, 2–3 mm. long; pedicels widely spreading to divaricately ascending, slender, 5–8(–10) mm. long, abruptly expanded at apex; siliques erect or ascending, terete, torulose, tortuose, 2–4 cm. long, 1.2–1.5 mm. in diameter, sessile or with a short gynophore up to 1.5 mm. long; styles cylindrical, 1–2 mm. long; stigmas equalling but not exceeding styles in diameter; seeds narrowly oblong, wingless, plump, ca. 2 mm. long, ca. 1 mm. wide; cotyledons incumbent, radicle exceeding cotyledons.

**DISTRIBUTION:** Utah and eastern Nevada.

**FLOWERING:** April–June.

**HOLOTYPE:** Arapien shale formation, greasewood community, ca. 4 mi. SE of Sigurd, Sievier Co., Utah, 29 May 1972, *Welsh & Atwood 11718* (BRY!).

**OTHER SPECIMENS STUDIED:** **Nevada. White Pine Co.:** 3.9 km. N of U.S. Hwy. 50 on road to Long Valley, 20 Jun 1979, *N. H. & P. K. Holmgren 9373* (GH); along road to Duckwater, 20.3 mi. from U.S. Hwy. 50, 26 May 1979, *Williams 79-53-3* (BRY. GH). **Utah. Box Elder Co.:** Grouse Creek Valley on the Etna Road, south of Etna, 27 May 1973, *Albee 1355* (BRY); Grouse Creek Rd., 11.5 mi. N of Utah Hwy. 30, 27 May 1971, *N. H. & P. K. Holmgren 4862* (GH). **Iron Co.:** Escalante Desert near Lund, 8 May 1943, *Ripley & Barneby 4373* (GH). **Juab Co.:** Dugway Valley NW of Delta, 29 May 1981, *Tiehm 6516* (GH); E of Fish Springs Range on a *Sarcobatus* and *Atriplex* flat near Cane Springs, 9 May 1968, *Reveal & Thomas 984* (BRY. GH). **Millard Co.:** 6 mi. W of Hinckley, 9 May 1935, *Harrison 6301* (BRY); Wah Wah Valley, 27 May 1981, *Tiehm 6513* (GH); Black Rock Desert, 1 mi. N of Borden Siding, 14 May 1968, *R. C. Holmgren 536* (BRY); 2 mi. S of Black Rock Station, 4 May 1968, *R. C. Holmgren 534* (BRY); along hwy. to Topaz Mountain, 10 mi. W of Hwy. 6, 9 May 1979, *Atwood 7142* (BRY). **Salt Lake Co.:** Salt Lake, June 1869, *Watson 108* (GH); alkali area on way to Salt Lake, 12 Jun 1933, *Eastwood & Howell 376* (GH). **Sanpete Co.:** ca. 2 mi. E of Aurora, 5 Jun 1979, *R. C. & K. W. Rollins 79161* (GH); 1 mi. W of Gunnison, 23 Apr 1979, *Neese & Williams 7140* (BRY); South Valley allotment, T20S, R1W, S20, 25 May 1979, *Greenwood s.n.* (BRY); 15 mi. SSW of Levan, 24 Apr 1979, *Welsh et al. 18273* (BRY). **Sevier Co.:** S and E side of foothills, Jun 1938, *Carson s.n.* (BRY). **Tooele Co.:** Utah Hwy. 36, 6 mi. N of Vernon, 6 Jun 1970, *N. H. & P. K. Holmgren 4178* (GH). **Utah Co.:** E side of Coyote Pass, 1.2 mi. W of Utah Hwy. 68, 15 May 1968, *Weston 71* (BRY).

*Thelypodopsis vermicularis* is very closely related to *T. elegans* and a number of the specimens of it in herbaria have been so determined in the past. The complex variability of *T. elegans* obscured and made difficult the recognition of the consistent pattern of differences that



characterized *T. vermicularis*. Only after a number of specimens had been accumulated was it possible to be assured that such a pattern existed. Some of the oldest specimens were determined as *Thelypodium sagittatum* and as indicated above, var. *vermicularis* was described under that species. That *S. vermicularis* could have been considered to be varietal in a species of another genus emphasizes the closeness of the genera *Thelypodium* and *Thelypodopsis*.

The vermiform siliques and cylindrical styles are the most distinctive features of *Thelypodopsis vermicularis*, but the dense capitate inflorescences ultimately elongating into relatively long infructescences with numerous siliques tend to distinguish this species from *T. elegans* which has fewer flowers and fruits. In most of the specimens of *T. vermicularis* seen, the cauline leaves are broader, shorter, and more obtuse than those of *T. elegans*. However, there are enough exceptions to make leaf-shape unreliable as a distinguishing feature.

Geographically, *Thelypodopsis vermicularis* occurs west of the area occupied by *T. elegans*. It is found mostly in the western half of Utah. I have seen only two collections from eastern Nevada.

**6. *Thelypodopsis divaricata* (Roll.) Welsh & Reveal**, based on *Caulanthus divaricatus* Rollins, Contrib. Gray Herb. **201**: 8, 1971. *Thelypodopsis divaricata* (Roll.) Welsh & Reveal, Great Basin Nat. **37**: 355, 1977.

Annual or biennial, single stemmed and without a true basal rosette of leaves; stems erect, branched above or rarely simple, densely pubescent below with contorted and twisted flat simple trichomes to nearly glabrous, usually glabrous above, 2–10 dm. tall; lowest leaves densely overlapping, sessile but scarcely auriculate, entire to irregularly dentate, oblong, obtuse, sparsely pubescent to glabrous, 2–10 cm. long, 1–3 cm. wide; cauline leaves reduced upward changing shape from oblong to ovate and acute, auriculate and clasping the stem; inflorescences dense, elongating in fruit; sepals yellowish, erect, forming an urn-shaped calyx, sparsely pubescent, 3.5–5 mm. long; petals yellow with a whitish claw, 7–10 mm. long; claw broadened, ca. 2 mm. wide; blade oblong, folded and crisped, 3–5 mm. long, ca. 1 mm. wide; ovary sparsely pubescent; fruiting pedicels divaricately ascending to more widely spreading, straight, sparsely pubescent to glabrous, slender, 7–12 mm. long; siliques terete, straight, nearly erect to divaricately ascending or more widely spreading, sparsely pubescent to glabrous, 4–8 cm. long, 1–1.5 mm. in diameter, sessile or with a short gynophore up to 1 mm. long; styles subclavate, 1–2 mm. long; stigmas slightly bilobed with the lobes over the replum margin; seeds oblong, wingless, 1.5–2 mm. long, ca. 1 mm. wide; cotyledons incumbent. *n* = 11 (Rollins and Rüdénberg, 1977).

**DISTRIBUTION**: eastern Utah: Carbon, Emery, Garfield, Grand, San Juan, and Wayne counties.

**FLOWERING**: April–June.

**HOLOTYPE**: Utah, San Juan County, about 75 miles west of Blanding and 10 miles east of Hite, T34S, R14E, 16 May 1961, Arthur Cronquist 9033 (GH!).

**REPRESENTATIVE SPECIMENS**: Utah. Emery Co.: 10 mi. E of Huntington, 30 Apr 1968, Higgins & Reveal 1256 (GH); Clawson, 2 Jun 1944, Ripley & Barneby 4735 (GH); off U.S. Hwy. 6, 48 mi. SE of Price, 29 May 1979, R. C. & K. W. Rollins 79108 (GH);

off U.S. Hwy. 6, 28.8 mi. SE of Price, 29 May 1979, R. C. & K. W. Rollins 79111 (GH); ca. 3 mi. ESE of Castledale, 20 May 1979, Welsh & Neese 18379 (BRY); 13 mi. NNW from Green River, 29 Jun 1977, Welsh & Taylor 15217 (BRY); W base of Assembly Hall Peak, San Rafael Swell, 10 June 1979, J. & M. Harris 395 (BRY); San Rafael Swell, 6.5 mi. SE of Ferron, 20 May 1979, N. H. Holmgren et al. 9103 (GH). **Grand Co.:** Westwater, 6 May 1891, M. E. Jones s.n. (GH); 3 mi. E of Caineville, 5 May 1949, Harrison 11437 (BRY); Grand River near Moab, 3 Jun 1915, M. E. Jones s.n. (GH); 9.9 mi. E of Green River, 29 May 1979, R. C. & K. W. Rollins 79107 (GH). **Garfield Co.:** SE of Mt. Hillers, junction between Starr Spring road and Utah Hwy. 276, 30 May 1976, Neese 1502 (BRY); Cave Flat road, W side of Henry Mts., 15 May 1970, Welsh 9815 (BRY); crossing, Bull Frog Creek, 5 mi. W of turnoff from Utah Hwy. 276, 29 Apr 1977, Neese & White 2736 (BRY). **Wayne Co.:** 5 mi. W of Hanksville, 3 May 1973, Albee 1286 (GH); 1 mi. S of junction Utah Hwy. 24 and Notom Road, 7 Apr 1968, Atwood 1255 (GH); ca. 29 mi. SW of Hanksville, 29 Apr 1961, Cronquist 8934 (GH); summit of North Cainville Mesa, 18 May 1976, Welsh et al. 13098 (BRY); Flint Trail, Maze Overlook road, 19 Apr 1970, Welsh 9600 (BRY).

Field work during the spring of 1979 gave me an opportunity to study populations of *Thelypodopsis divaricata*. Near Green River, Utah, we found a population mostly in fruit but with one flowering individual having sterile siliques that appeared to be a hybrid between *T. divaricata* and *T. elegans*. Both species are known to occur in this area although we did not find a truly mixed population of the two. The sterile plant had flowers with petals somewhat similar to those of *T. elegans* while the sepals were erect and formed an urn-like calyx similar to that of *T. divaricata*. The putative hybrid is documented by R. C. & K. W. Rollins 79107a (GH).

Although *Thelypodopsis divaricata* has a "caulanthoid" flower, i.e., an urn-shaped connivent calyx and petals with a broader claw than blade with a stricture between the blade and claw and a crisped blade, other characters are so similar to *T. elegans* that it seems best to follow Welsh and Reveal (1977) in removing this species from *Caulanthus*. Indeed, Jones made mixed collections of these two species and for some time specimens of *T. divaricata* were identified as *T. elegans* (Rollins, 1971). The evidence cited above, suggesting interspecific hybridization, further supports the placement of this species in *Thelypodopsis*.

7. *Thelypodopsis wootonii* (Robins.) Rollins, based on *Sisymbrium wootonii* Robinson, Bot. Gaz. 30: 59, 1900. *Thelypodopsis wootonii* (Robins.) Rollins, Contrib. Gray Herb. 206: 12, 1976.

Biennial or perennial, glabrous throughout, branched, up to 6 dm. tall; stems leafy, terete; rosette leaves formed a season before flowering occurs not seen; cauline leaves oblong, acuminate to acute or the lower slightly obtuse, auriculate and clasping, strongly 1-nerved, entire or obscurely denticulate, overlapping, 6–10(–14) cm. long, 6–20(–25) mm. wide; inflorescences dense, greatly elongating in fruit; buds whitish; sepals white, inner pair non-saccate, outer pair boat-shaped and slightly saccate, (4)–5–6 mm. long, easily shed; petals white, spatulate to obovate, not unguiculate, gradually tapered from rounded blade to point of insertion, (6)–8–10 mm. long; (2)–3.5–4.5 mm. wide; paired stamens erect, single stamens curved upward at base; filaments slightly petaloid or terete; anthers 1.2–1.5 mm. long; stigma bilobed with

lobes over replum margin; fruiting pedicels slender, divaricately ascending to more widely spreading, curved upward, 1.5–2 cm. long, abruptly expanded at summit or slightly so; siliques terete, sessile or with a short stout gynophore, erect to ascending, torulose, narrowed below and above, nerved from base to apex, 3–5 cm. long, ca. 1 mm. in diameter; styles slender, 0.5–1 mm. long; stigmas persistent, distinctly lobed, sharply expanded over the styles; seeds plump, broadly oblong, 1.2–1.5 mm. long, ca. 1 mm. in diameter; cotyledons incumbent.

## KEY TO THE VARIETIES

- Petals obovate, 8–10 mm. long, 3.5–4.5 mm. wide ..... 7a. var. *wootonii*.  
 Petals spatulate, ca. 6 mm. long, ca. 2 mm. wide ..... 7b. var. *parviflora*.

7a. **T. wootonii** (Robins.) Rollins var. **wootonii**.

DISTRIBUTION: known only from the type collection.

FLOWERING: July–August.

HOLOTYPE: Mexico, state of Chihuahua, 16 km. southeast of Colonia Garcia, Sierra Madre, 7600 ft., 27 Jul 1899, C. H. T. Townsend & C. M. Barber 176 (GH!). Isotypes (GH!, US!).

7b. **T. wootonii** var. **parviflora** Rollins, var. nov.

Herba perennis, floribus parvis, sepalis albis ca. 4 mm. longis, petalis spathulatis albis ca. 6 mm. longis, siliquis teretibus, 3–5 cm. longis.

DISTRIBUTION: Mpio. de Bocoyna, Chihuahua, Mexico.

FLOWERING: August–November.

HOLOTYPE: Mexico, state of Chihuahua, Gonogochic, E of Creel, Mpio. de Bocoyna, open flat of pine-oak forest, ca. 7,400 ft., 16 Oct. 1975, Robert A. Bye, Jr. 7128 (GH).

OTHER SPECIMENS STUDIED: Mexico. Chihuahua. Mpio. de Bocoyna: W of Gonogochic, 13 Aug 1977, Bye 7994 (GH); E of Gonogochic, 12 Aug 1977, Bye 7935 (GH); same locality, different dates, Bye 4287, 4775, 5479 (GH).

The difference in flower size between the collections of Dr. Bye and the type collection of *Thelypodopsis wootonii* are substantial and indicate that two taxa are represented. The difficulty of interpreting their proper relationship arises from the limited available material of var. *wootonii* and by the fact that only very young siliques are present on the specimens. From most features of the specimens we have studied, the similarity of the two populations from which they came is readily inferred. However, the mature seeds and fruits of var. *wootonii* may ultimately turn out to be different enough to suggest a higher rank for var. *parviflora*. Our present treatment must be considered tentative, but at the same time it serves to point up the differences between the two presently known populations without obscuring the fact that they are undoubtedly very closely related.

8. **Thelypodopsis alpina** (Standl. & Steyermark.) Rollins, based on *Romanschulzia alpina* Standley & Steyermark, Fieldiana, Bot. 24, pt. 4: 377, 1946. *Thelypodopsis alpina* (Standl. & Steyermark.) Rollins, Con-

trib. Gray Herb. 206: 12-13, 1976. *Sisymbrium standleyi* Rollins, Rhodora 58: 156, 1956, based on *Romanschulzia alpina*, not *Sisymbrium alpinum* Fourn., Recherch. Crucif. 131, 1865.

Annual or possibly biennial, glabrous throughout or with a few simple trichomes on the margins of the lower petiole; stems one or few, simple to sparingly branched, 3-7 dm. tall; strictly basal leaves absent; lowest cauline leaves petiolate, narrowly lanceolate; cauline leaves scarcely reduced upward, remote, glaucous, lanceolate, acuminate, auriculate, clasping the stem, remotely denticulate, 3-7 cm. long, 6-12 mm. wide; inflorescences lax, few-flowered; sepals erect, oblong, purplish, scariously-margined, 3-3.5 mm. long; petals purplish, lingulate, narrowed near insertion, 5-6 mm. long; stamens erect; anthers 1 mm. or less long; fruiting pedicels divaricately ascending, slender, 7-12 mm. long; siliques erect, nearly terete to slightly compressed contrary to septum, slightly torulose, subsessile, 4-5.5 cm. long, ca. 1.5 mm. wide; styles 1 mm. or less long; stigma larger in diameter than style, faintly bilobed, the lobes apparently over the valves; immature seeds oblong, wingless, ca. 1.2 mm. long.

DISTRIBUTION: Guatemala, Departments of Huehuetenango and Quezaltenango.

FLOWERING: July-August.

HOLOTYPE: Guatemala, Dept. of Huehuetenango, between Tojquiá and Caxín bluff, summit of Sierra de Los Cuchumatanes, 6 Aug. 1942, Julian A. Steyermark 50144 (F).

OTHER SPECIMENS STUDIED: Guatemala. Huehuetenango: near Tunima, Sierra de los Cuchumatanes, 6 Jul 1942, Steyermark 48923 (F). Quezaltenango: Volcán Santa Maria, 27 Jul 1934, Skutch 864 (GH).

This species is imperfectly known. Only three collections have been available for study. None of these have fully mature siliques. The abrupt transition from the lowermost two or three leaves that are petiolate to the sessile and fully auriculate leaves only three or four leaves up from the base is very unusual. On the specimens seen there is no suggestion of a basal rosette. Usually in the Cruciferae, if there are dimorphic leaves, the petiolate type is characteristic of the basal rosette or are at least clustered at the base of the stem where the internodes between the leaves are extremely short. In the case of *Thelypodopsis alpina*, where all of the leaves are truly cauline, the internodes are one to several centimeters long even in the lowermost leaves which are petiolate. The petiole is very slender. The third or fourth leaf up the stem is abruptly sessile and auriculate. The situation in *T. shinniersii* is not far different from this except that the petioles are winged with small auricles at the base and the lower leaves are broadly obovate.

9. *Thelypodopsis shinniersii* (M. C. Johnst.) Rollins, based on *Sisymbrium shinniersii* M. C. Johnston, Southw. Nat. 2: 129, 1957, which in turn was based on *Thelypodium vaseyi* Coulter, Contrib. U.S. Nat. Herb. 1: 30, 1890, not *Sisymbrium vaseyi* S. Watson ex Robinson in Gray, Synop. Fl. N. Amer. 1: 138, 1895. *Thelypodopsis shinniersii* (M. C. Johnston) Rollins, Contrib. Gray Herb. 206: 13, 1976.

Annual, glabrous throughout; stems erect, branched beginning just above base or less frequently simple, 4–8 dm. tall; lowest cauline leaves with a winged petiole, thin, glaucous, obovate, 5–10 cm. long, up to 3 cm. wide, with a prominent broad central vein; cauline leaves gradually changing upward from pandurate-obovate to obovate, ovate, then oblong and from rounded to obtuse then broadly acute, auriculate, mostly overlapping below but becoming remote and reduced above; inflorescences elongating in fruit; flower parts quickly shed; sepals erect, oblong, pale purplish, non-saccate, 3–3.5 mm. long; petals white, sublingulate, not unguiculate, 4–5 mm. long; fruiting pedicels divaricately ascending to more widely spreading, straight, 6–12 mm. long; siliques terete, divaricately ascending, straight to slightly in-curved, subsessile, 4–6 cm. long, ca. 1 mm. wide, not torulose; styles less than 1 mm. long; stigmas nearly entire, slightly larger in diameter than style; seeds plump, oblong, wingless, less than 1 mm. long; cotyledons incumbent or obliquely so.

**DISTRIBUTION:** Mexico, State of Tamaulipas, and the lower Rio Grande Valley of Texas, USA.

**FLOWERING:** July–April.

**HOLOTYPE:** near Rio Grande City, Texas, 1889, *G. C. Neally* 188 (US!). Tracing of holotype in (GH!).

**OTHER SPECIMENS STUDIED:** **Mexico. Tamaulipas:** region of Rancho Las Yucas, ca. 40 km. NNW of Aldamia, Mpio. de Aldamia, 25 Jul 1957, *Dressler* 2014 (GH); same locality, 16 Oct 1957, *Dressler* 2427 (GH); 9 mi. S of Ciudad Victoria, 9 Feb 1961, *McGregor* 16296 (GH); along route 70, ca. 6 mi. S of Ciudad Victoria, 6 Apr 1961, *King* 4510 (US). **USA. Texas. Cameron Co.:** Olmito, 15 Apr 1905, *Tracy* 9197 (GH); 6 mi. NE of Olmito, 20 Apr 1959, *Rollins & Correll* 5953 (GH, TEX-LL); road to Boca Chica from Brownsville, 15 Dec 1967, *Correll* 35502 (GH); Barreda Tract, Barreda, 11 Apr 1941, *Runyon* 2521 (GH); just S of Harlingen, 21 Apr 1959, *Rollins & Correll* 5956 (GH, TEX-LL); near San Benito, 20 Apr 1959, *Rollins & Correll* 5954 (GH, TEX-LL); along Arroyo Colorado, Harlingen brushlands, 13 Mar 1964, *Correll* 28953 (GH).

Recent acquisitions from Mexico and Cameron County, Texas, have helped to clarify this species which was known from only two or three collections for many years. The flowers are very small and although the infructescences are considerably elongated, reaching three decimeters or more in some plants, the dense little cluster of flowers is always at the very top of the inflorescence. This is because the floral parts are shed very quickly after anthesis and the developing young siliques just below the pollinated flowers are devoid of the remnants of any flowers.

The nomenclatural situation is fairly complicated but without ambiguities. This has been discussed previously (Rollins, 1960).

# 10. *Thelypodopsis byerii* Rollins, sp. nov.

Annual; stems single, erect, branched beginning near base or above, 2–5 dm. tall, lower hirsute with simple spreading trichomes, becoming glabrate upwards, upper glabrous; basal rosette not formed; leaves petiolate, very thin, sparsely hirsute with simple acerose trichomes especially on midribs and petioles, lowest broadly obovate to nearly orbicular, shallowly crenate, repand or nearly entire, middle and upper leaves lobed to sharply incised and irregularly dentate, middle leaves largest, 4–10 cm. long, 2–4 cm. wide, ovate to broadly oblong, apex rounded or obtuse, the upper acute, petioles slender; inflorescences becoming a loose raceme as development proceeds; flowering pedicels slender, divaricately ascending, glabrous, longest up to 1 cm. long; buds purplish; sepals oblong, glabrous, purplish, 3.5–4.5 mm. long, ca. 2 mm. wide, inner pair non-saccate, outer pair slightly saccate, petals purplish to nearly

white, obovate to broadly spatulate, gradually narrowing to point of insertion, 7–9 mm. long, 4–5 mm. wide; stamens erect, included, filaments slender, straight, anthers erect at anthesis, ca. 1.2 mm. long; stigmas capitate, scarcely lobed at flowering; infructescences lax; fruiting pedicels widely spreading to slightly descending, slender; siliques immature, terete, widely spreading, glabrous, 3–5 cm. long, less than 1 mm. in diameter, sessile or with a short gynophore less than 1 mm. long; styles slender, 2 mm. or less long; stigmas slightly lobed, lobes over the replum; seeds numerous, apparently small and plump without wing margins.

Herba annua; caulibus erectis, ramosis, 2–5 dm. altis; inferne pilosis; superne glabris; foliis petiolatis, inferne sparse pilosis, repandis vel lobatis, obtusis vel acuminatis, 4–10 cm. longis, 2–4 cm. latis; pedicellis anguste ca. 1 cm. longis patentibus; sepalis oblongis, purpureis, glabris, 3.5–4.5 mm. longis, ca. 2 mm. latis; petalis purpureis vel albis, obovatis vel late spatulatis, 7–9 mm. longis, 4–5 mm. latis; infructescentiis laxis; siliquis immaturis, teretibus, patentibus, 3–5 cm. longis.

DISTRIBUTION: western Chihuahua, Mexico.

FLOWERING: February–April.

HOLOTYPE: in the Gray Herbarium, collected along Arroyo Wimivo (= Arroyo Samachique) between Wimivo and Rio Batopilas on N side of Barranca de Batopilas, Sierra Madre Occidentale, Mpio. Batopilas, Chihuahua, Mexico, 28 Feb 1973, *Robert A. Bye* 3433.

OTHER SPECIMENS STUDIED: **Mexico. Mpio. Batopilas:** Sierra Madre Occidentale, Barranca de Batopilas, in moist shaded rock area with large boulders, near seepage area, above burro trail along Arroyo Wimivo, 28 Feb 1973, *Bye* 3436 (GH); vicinity of Wimivo, Feb 1973, *Bye* 9904 (GH); between La Bufa and Bacosiachi, Mar 1973, *Bye* 9902 (GH); same locality, Feb 1973, *Bye* 9903 (GH).

*Thelypodiopsis byeei* is unlike any other species of the genus in that it has cauline leaves that are petiolate and very thin. These typically have broad, lobed to dentate blades and very slender petioles. In texture of the leaves and slenderness of the siliques it simulates *T. shinneryi* to some extent. But that species has entire auriculate leaves and siliques that are erect rather than widely spreading as in *T. byeei*. In habit and general appearance, *T. byeei* resembles *Dryopetalon runcinatum* Gray var. *laxiflorum* Roll. but the petals are absolutely entire which precludes its being placed in the genus *Dryopetalon*. If the petal character were to be ignored and the species placed in *Dryopetalon*, it would still be an undescribed species. However, if it were placed in that genus, the entire genus *Thelypodiopsis* would have to disappear into *Dryopetalon*, it being the older of the two generic names. There is no justification for such an action.

*Thelypodiopsis byeei* grows in open areas, or in the shade of rocks and boulders, in a short tree and thorn forest at about 1,000 meters elevation. According to Dr. Bye, for whom the species is named, the plants are cooked and eaten by the native Tarahumara people who populate the area where it grows.

11. *Thelypodiopsis arcuata* (Roll.) Rollins, based on *Sisymbrium arcuatum* Rollins, *Rhodora* 62: 58, 1960. *Thelypodiopsis arcuata* Rollins, *Contrib. Gray Herb.* 206: 14, 1976.

Annual, glabrous throughout; stems single from base, weak, usually branched at each node, occasionally simple, 5–10 dm. tall; leaves all cauline, sessile, auriculate, entire, sometimes with minute teeth, lower nearly pandurate, rounded above, gradually ovate to broadly oblong upward, glaucous beneath, greenish above, 2–8 cm. long, 1–4 cm. wide; inflorescences few-flowered, elongating into a lax elongated infructescence; flower parts quickly shed; sepals erect, purplish, narrowly oblong, non-saccate, 3–4 mm. long, ca. 1 mm. wide; petals white, spatulate with a slender claw, 5–6 mm. long, nearly equal on all six stamens; fruiting pedicels widely spreading to gently recurved, 8–11 mm. long; siliques terete, slender, pendulous, slightly arched, 7–10 cm. long, slightly exceeding 1 mm. in diameter; styles 1–1.5 mm. long; stigmas unexpanded; immature seeds oblong, wingless, ca. 1 mm. long.

**DISTRIBUTION:** in the states of Nuevo León and San Luis Potosí, Mexico.

**FLOWERING:** July–October.

**HOLOTYPE:** 1–2 miles SW of Páblillo, Nuevo León, Mexico, 21 Jul 1958, D. S. Correll & I. M. Johnston 19941 (GH!).

**OTHER SPECIMENS STUDIED:** Mexico. San Luis Potosí: Sierra de Alvarez, cerca del Punta Huerta, 27 Oct 1954, Rzedowski 5211 (GH).

Only the above two cited collections of *Thelypodiopsis arcuata* are known to me and neither of these has mature seeds. Evidently the plants of this species are quite weak-stemmed and, according to the collectors, tend to sprawl. In the type collection, the lowermost leaves have been shed and there are no petiolate leaves present but on the specimen from San Luis Potosí, where new growth has started on a broken-off stem, the lowest leaves have winged petioles and at least one or two leaves are scarcely auriculate. This suggests that the very lowermost cauline leaves in *T. arcuata* are wing-petioled and probably similar to those of *T. shinnersii*. The inflorescence of this species behaves very much like that of *T. shinnersii* in the early shedding of flower parts but the resulting infructescence is very different except in the most general features.

12. *Thelypodiopsis purpusii* (Brandege) Rollins, based on *Thelypodium purpusii* Brandege, Zoe 5: 232, 1906. *Sisymbrium purpusii* (Brandeg.) O. E. Schulz, Pflanze nr. 86 (IV, 105) 58, 1924. *Thelypodiopsis purpusii* (Brandeg.) Rollins, Contrib. Gray Herb. 206: 14, 1976. *Thelypodium vernale* Wootton & Standley, Contrib. U.S. Nat. Herb. 16: 128, 1913. [Holotype: low mountains west of San Antonio, Socorro County, New Mexico, Wootton 3847 (us, not seen; apparently lost, cf. Al-Shehbaz 1973, p. 141)]. *Sisymbrium vernale* (Woot. & Standl.) O. E. Schulz, loc. cit., p. 57. *Sisymbrium kearneyi* Rollins, Leafl. West. Bot. 7: 15, 1953.

Annual, glabrous throughout; stems single from base, branched, often purplish and leafy below, variable in height, fruiting plants 3–7 dm. tall; basal and lowest stem leaves oblanceolate in outline to oblong, narrowed to a winged petiole, with a strong central nerve, not auriculate, lowest leaves nearly rosulate or with evident internodes between them, 4–12 cm. long, 1–3 cm. wide; cauline leaves sessile, auriculate except

the lowest one or two in some plants, reduced upward and becoming lanceolate with rounded clasping lobes, lower pinnatifid to somewhat lobed, upper entire; inflorescence lax, remaining few-flowered as the fruiting axis elongates; sepals oblong, non-saccate, purplish or greenish, scarious-margined, 3.5–5 mm. long; petals white to light lavender, spatulate narrowing to a slender base, 4–6 mm. long; paired stamens slightly exerted; fruiting pedicels divaricately ascending to nearly erect, straight, 1–1.5 cm. long; siliques terete, narrowly linear, divaricate to ascending, sessile to subsessile, 3–6 cm. long, ca. 1 mm. wide; styles ca. 1 mm. long; seeds oblong, wingless, plump, less than 1 mm. long; cotyledons incumbent.

**DISTRIBUTION:** Grand Canyon of Arizona to New Mexico, Texas, south to Coahuila, Mexico.

**FLOWERING:** February–May.

**HOLOTYPE:** Sierra de Parras, Coahuila, Mexico, March 1905, C. A. Purpus 1392 (UC!). **Isotype** (GH).

**OTHER SPECIMENS STUDIED:** **Mexico. Coahuila:** Sierra Pata Galena, Feb 1905, Purpus 1329A (GH). **USA. Arizona. Mohave Co.:** along trail into S.B. Canyon, Grand Canyon National Park, 8 May 1952, McClintock 481a (holotype of *Sisymbrium kearneyi*, GH!); same locality and date, McClintock 53-481 (GH). **New Mexico. Dona Ana Co.:** southern end of the San Andres Mts., on NE side of Black Mountain, 7 May 1980, Spellenberg & Todsén 5497 (GH, NMC). **Luna Co.:** N side of Tres Hermanas Mts., about halfway up the North Sister, S of Deming, 13 Apr 1973, Spellenberg 3002 (GH). **Otero Co.:** about 3.5 mi. due E of U.S. Hwy. 70 through Alamogordo, in Marble Canyon, 11 May 1980, R. & M. Spellenberg 5501 (GH). **Socorro Co.:** Sevilleta Grant, west slope of Los Pinos Mts., directly E of Nunn-Burris Ranch headquarters, 2 May 1980, Spellenberg & Ward 5485 (GH, NMC). **Texas. Hudspeth Co.:** canyon, S end of Hueco Mts., 18 Mar 1979, Worthington 4012 (GH); same locality, 12 May 1979, Worthington 7474 (GH). **Presidio Co.:** McCormick Ranch, near Fresno Canyon, 1 Mar 1959, Johnston & Warnock 3734, 3735, 3736 (GH); head of Fresno Canyon, Big Bend Ranch, 20 Apr 1961, Rollins & Correll 61174 (GH).

The unfolding of the nature and distribution of *Thelypodopsis purpusii* has taken many decades. Only the original two collections of Purpus from Mexico were known to me when *Sisymbrium kearneyi* was described from the Grand Canyon of Arizona in 1953, and these were the only specimens for comparison. At that time, the Grand Canyon specimens were thought to be sufficiently distinct from the Coahuila material of Purpus to represent a distinct taxon. Then came specimens from Fresno Canyon of western Texas in 1959, later material from southern New Mexico (1973), and more recently (1979) specimens from the Hueco Mountains of extreme northwestern Texas. In addition, specimens from the general area where *Thelypodium vernale* was originally collected have permitted us to interpret the application of that name. As indicated above, the holotype of *T. vernale* has apparently been lost and there are no known isotypes so that the name has been accepted without anyone knowing for sure to what taxon it applied. Now, it is clear that specimens from Socorro County, New Mexico, do fit the protologue of this name and they in turn are very similar to the collections from the Hueco Mountains of Texas. These populations represent a minor deviant from the other material of *Thelypodopsis purpusii* in that a definite rosulate cluster of leaves



is developed and there is a sharp distinction between these leaves and the strictly cauline leaves. In other populations, such as those of the Grand Canyon, there is a weakly developed rosette of basal leaves. Otherwise, internodes do develop between the first formed leaves and there is a gradual transition from the lowest petiolate to the sessile auriculate leaves further up the stem. But these differences are only a matter of degree. They hardly represent the basis for defining separately recognizeable taxa.

The present interpretation of *Thelypodiopsis purpusii* includes what appear to be disjunct populations, quite far from each other, in six localities. In all of these, the species occupies similar shady habitats, either at the base of cliffs, near large boulders, or in the shade of trees or shrubs. A number of distinctive features characterize plants of all populations. Aside from the lobed or deeply pinnatifid lowest leaves, the ascending siliques are very narrow and the seeds are extremely small in a single row. The anthers of the paired stamens are exserted and are relatively short, ca. 1 mm. long. Minor trends toward discrete populations are recognizable even though there appears to be no solid basis for dividing the species into infraspecific taxa. Given the history of exploration involving *S. purpusii*, it is likely that the future will see at least some of the geographic gaps filled.

13. *Thelypodiopsis incisa* Rollins, Contrib. Gray Herb. 206: 13. 1976.

Annual or biennial, sparsely pubescent with simple spreading trichomes below, glabrous above; stems erect, one to several from base, branched, 4–6 dm. tall; strictly basal rosette not formed; lower cauline leaves with erect simple trichomes, deeply pinnatifid or incised, up to 1 dm. long, terminal lobe larger than lateral; petioles winged, lobed and those of lowermost leaves with small auricles at base; lower middle, middle and upper cauline leaves strongly auricled and clasping, incised or uppermost entire, glabrous, narrowly ovate to broadly oblong or lanceolate, acute, 3–5 cm. long, with a strong central nerve; inflorescences racemose, terminating each branch; sepals purplish, oblong, 4–5 mm. long, ca. 1–5 mm. wide, outer pair saccate, boat-shaped, narrowed above, inner pair flat, blunt at apex; petals lavender, narrowly lingulate, 8–10 mm. long, 3–4 mm. wide, not differentiated into blade and claw; stamens strongly tetradynamous, paired stamens erect, 6–7 mm. long, single stamens curved upward, 4–5 mm. long; anthers ca. 1.5 mm. long, straight; fruiting pedicels 6–9 mm. long; divaricate, not expanded toward apex, straight; siliques erect to divaricately ascending, nearly terete to slightly flattened parallel to septum, not nerved, tapering above and below, somewhat torulose, 3.3–5 cm. long; styles ca. 2 mm. long; stigma scarcely cleft, very slightly lobed over replum margin; immature seeds wingless, oblong, occupying full width of silique, 1.75–2 mm. long.

DISTRIBUTION: known only from the type collection.

FLOWERING: March.

HOLOTYPE: ca. 80 miles north of Saltillo along Highway 57, Coahuila, Mexico, 13 Mar 1970, *Larry C. Higgins* 2717 (WTS!). Isotype (ENCB!).

One of the most distinctive features of *Thelypodiopsis incisa* is the definite sterile beak narrowing to the apex of the silique. It is nearest

in its relationship to *T. purpusii* but differs from that species in having much larger flowers, torulose instead of plane siliques, a beak tipped with a prominent style about 2 mm. long instead of no beak and a style about 1 mm. long as in *T. purpusii*. The latter also has narrower nearly terete instead of slightly flattened siliques, as in *T. incisa*, and usually white instead of the lavender petals.

**14. *Thelypodiopsis versicolor*** (Brandege) Rollins, based on *Thelypodium versicolor* Brandege, Univ. of Calif. Publ. Bot. 4: 178, 1911. *Sisymbrium versicolor* (Brandeg.) O. E. Schulz, Pflanzenr. 86 (IV, 104) 57, 1924. *Thelypodiopsis versicolor* (Brandeg.) Rollins, Contrib. Gray Herb. 206: 12, 1976.

Biennial or perennial, usually with a few simple trichomes at base of stems and along petiole margins of basal leaves, otherwise glabrous throughout, glaucous; stems single or few from the base, branched, slender, 4–12(–15) dm. tall; basal leaves with a winged petiole, entire or shallowly dentate, often denticulate with minute teeth, obovate to oblanceolate, obtuse, up to 4 cm. long; cauline leaves auriculate, glabrous, lower obovate, denticulate with minute teeth, middle oblong, entire or denticulate; upper entire, ovate to ovate-lanceolate, acute; inflorescences few-flowered at the apex of narrow, greatly elongated infructescences; sepals erect, oblong, purplish, ca. 3 mm. long, nearly 2 mm. wide; petals white, broadly spatulate to obovate, ca. 5 mm. long, blade abruptly narrowed to a slender claw; stamens included; anthers less than 1 mm. long; fruiting pedicels erect to slightly spreading, often appressed to the rachis, slender, straight, 7–10 mm. long; siliques erect to slightly divergent, terete, torulose, sessile or subsessile, blunt or tapered above and below, 1.5–3 cm. long, ca. 1 mm. in diameter; styles nearly obsolete to 1 mm. long; seeds oblong, wingless, plump, ca. 1.5 mm. long, ca. 1 mm. in diameter; cotyledons incumbent.

**DISTRIBUTION:** Coahuila and San Luis Potosí, Mexico.

**FLOWERING:** June–October.

**HOLOTYPE:** Sierra de Parras, Coahuila, Mexico, Oct 1910, C. A. Purpus 4978 (UC!). **Isotypes** (GH!, US).

**OTHER SPECIMENS STUDIED:** **Mexico. Coahuila:** 26 km. N of Fraile, 16 Jul 1941, *Stanford et al.* 438 (ARIZ, GH, NY, UC); summit of Mt. Jimulco, 13 km. E of Jimulco, 29 Jun 1941, *Stanford et al.* 98 (ARIZ, GH); 26 (air) mi. SW of Torreon in Sierra de Jimulco, 18 Sep 1973, *Henrickson* 13173 (GH); higher part and N slope of Sierra de la Madera, SE and SSE of Rancho Cerro de la Madera, 20 Sep 1972, *Chiang et al.* 9420 (GH); 9 km. S of Parras on Sierra Negras, 3 Jul 1941, *Stanford et al.* 216 (ARIZ, GH, NY). **San Luis Potosí:** 12 km. al W de Estacion Berrendo, Mpio. de Charcas, 11 Sep 1955, *Rzedowski* 6590 (GH, ENCB).

*Thelypodiopsis versicolor* is distinctive because of the erect appressed pedicels and strictly erect siliques that are shorter than those of its nearest relatives. The infructescences are narrower than in most other species. The cauline leaves are strongly auricled with the auricles fully clasping the stem in most plants. Variation between specimens of the few collections known suggest that future collecting may show up correlations of characters that are taxonomically significant. If this happens, more than one taxon may be present in the material we have referred to this species.

15. *Thelypodopsis vaseyi* (S. Wats.) Rollins, based on *Sisymbrium vaseyi* S. Wats. ex Robinson in Gray, Syn. Fl. N. Amer. 1: 138, 1895. *Sisymbrium watsonii* Payson, Univ. Wyo. Publ. Bot. 1: 16, 1922, based on *S. vaseyi* S. Wats. *Thelypodopsis vaseyi* (S. Wats.) Rollins, Contrib. Gray Herb. 206: 12, 1976.

Annual, glabrous throughout, somewhat glaucous; stems single, highly branched beginning above base, 4–10 dm. tall; basal rosette not formed; lower cauline leaves narrowly oblong to lanceolate or slightly oblanceolate, sometimes auriculate with small auricles not fully clasping the stem, entire or rarely denticulate with minute teeth, 4–6 cm. long, up to 1.5 cm. wide but usually much narrower, upper leaves cuneate at base, lanceolate to narrowly linear, acute; inflorescences few-flowered, terminating each slender branch, not elongating greatly in fruit; infructescences narrow, usually less than 1 dm. long; sepals spreading at anthesis, oblong, white to purplish, 2–2.5 mm. long; petals white, broadly spatulate to obovate, abruptly narrowed from blade to claw, unguiculate, 3–3.5 mm. long; filaments relatively stout, white or purplish; anthers small, ca. 0.5 mm. long; fruiting pedicels very slender, spreading nearly at right angles to rachis to slightly ascending, straight, 8–11 mm. long; siliques erect, subsessile to sessile, tapered both above and below, strongly torulose, 1.5–2.5 cm. long; styles ca. 0.5 mm. long; stigmas inconspicuously 2-lobed with the lobes over the replum margin; seeds plump, slightly narrowed at distal end, wingless, oblong, 1.2–1.5 mm. long, less than 1 mm. wide; cotyledons incumbent.

DISTRIBUTION: mountains of central New Mexico.

FLOWERING: July–August.

LECTOHOLOTYPE: Las Vegas (probably in the mountains to the west of Las Vegas), New Mexico, 1881, *G. R. Vasey s.n.* (GH!).

OTHER SPECIMENS STUDIED: New Mexico. San Miguel Co.: Windsor's Ranch, Pecos River Nat. Forest, 3 Aug 1908, *Standley 4741* (GH); Lion Head trail above Cowles, 3 Aug 1934, *Goodwin 942* (GH); mts. W of Las Vegas, 1881, *Vasey 41* (GH). Otero Co.: Clouderoft, 19 Aug 1968, *D. S. & H. B. Correll 36129* (GH, TEX-LL); James Canyon, Sacramento Mts., 5 Aug 1905, *Wootton s.n.* (NMC); Mescalero Reservation, 21 Jul 1905, *Wootton s.n.* (NMC).

The flowers of *Thelypodopsis vaseyi* are the smallest in the genus and both sepals and petals flare during anthesis. The plants are highly ramified with the numerous branches being much more slender than the main axis. The habit is very distinctive. The lower cauline leaves are quickly shed and I have not seen any specimens with all of the lower leaves present. On the holotype, the middle and below middle leaves have small auricles but in several other specimens leaves in this position on the plant are merely sessile and are truncate at the base without auricles being present. It appears that this is a variable feature of the species.

The substitution of the name *Sisymbrium watsonii* for *S. vaseyi* by Payson was a mistake as pointed out several years ago (Rollins, 1960). A detailed discussion of the nomenclatural situation will be found in that publication.

16. *Thelypodopsis retrofracta* (Roll.) Rollins, based on *Sisymbrium retrofractum* Rollins, Rhodora 59: 66, 1957. *Thelypodopsis retrofracta* (Roll.) Rollins, Contrib. Gray Herb. 206: 15, 1976.

Annual or possibly biennial, glabrous throughout, strictly basal leaves not known, basal rosettes not formed; stems single from base, branched above, 5-8 dm. tall; lower cauline leaves petiolate-lanceolate to linear-lanceolate, coarsely dentate to somewhat lobed, 4-6 cm. long; upper cauline leaves cuneate at base, entire to sparsely and shallowly dentate, nearly linear; inflorescence few-flowered; flowers erect or ascending on slender ascending pedicels which reflex shortly after anthesis; sepals purplish, oblong, 3.5-4 mm. long, ca. 1 mm. wide, outer pair slightly saccate; petals spatulate with a slender claw, white, 6-8 mm. long; fruiting pedicels strictly reflexed, straight, slender, 9-11 mm. long; siliques terete or nearly so, not torulose, pendulous, 4-6 cm. long, ca. 1 mm. wide; valves 1-nerved nearly full length; styles 1.5-2 mm. long; stigmas weakly lobed over the replum margin; seeds plump, slightly longer than broad, ca. 1.2 mm. long, ca. 1 mm. wide, with a narrow distal wing; cotyledons accumbent.

DISTRIBUTION: known from only two collections, one each from Coahuila (?) and Zacatecas, Mexico.

**FLOWERING:** July–August.

HOLOTYPE: 18 km. west of Concepcion del Oro, Coahuila (?), Mexico, 22 Jul 1941, L. R. Stanford, K. L. Retherford & R. D. Northcraft 570 (GH!). Although the printed label reads State of Coahuila, it is difficult to accept that a point 18 km. W of Concepcion del Oro, which is in the state of Zacatecas, would be other than in Zacatecas. More likely the wrong label form was inadvertently used by the collectors.

OTHER SPECIMENS STUDIED: **Mexico. Zacatecas:** Aranzazu, Sierra Madre Oriental, 19 Jul 1934, *Pennell* 17443 (GH).

Fortunately, specimens of the second collection seen of *Thelypodopsis retrofracta* (Pennell 17443) have mature seeds. It was surprising to find that these are distally winged and that the cotyledons are nearly accumbent. Both of these features are characteristic of *Arabis* and together with the reflexed siliques make a fairly strong case for placing the species in that genus. However, the siliques are terete and the seeds are plump, features not characteristic of *Arabis*. Until the species is better known, it is perhaps best to leave it in *Thelypodopsis* where it does not violently disturb the integrity of that genus. The species is certainly not with its congeners in *Sisymbrium*, the genus to which I originally referred it.

# SCHOENOCRAMBE

**Schoenocrambe** Greene, *Pittonia* 3: 124-126. 1896.

*Hesperidanthus* Rydberg, Bull. Torr. Bot. Club 34: 433. 1907.

Perennials with ligneous caudices and roots, sometimes rhizomatous, old stems often present, glabrous or with simple trichomes; stems one to several, usually rigid, erect to somewhat decumbent, simple or branching from caudex, simple or branched above; leaves monomorphic on mature plants, linear, lanceolate or oblanceolate, petioled to sessile, entire to somewhat pinnatifid, thickish; flowers in a lax raceme terete at base; entire to somewhat pinnatifid, thickish; sepals glabrous, plane or with subapical callosities on inner pair in *Schoenocrambe linearifolia*; petals yellow or purplish, spatulate to oblong, erect to widely spreading; siliques terete, narrowly linear, erect to widely spreading, sessile or rarely subsessile; styles evident, up to 2 mm.

long; stigmas bifid or conical with lobes over the replum margins; seeds plump, oblong, wingless; cotyledons incumbent to obliquely incumbent. Type species: *Schoenocrambe linifolia* (Nutt.) Greene.

## KEY TO THE SPECIES

- A. Petals not differentiated into blade and claw, gradually tapered from apex toward base; sepals plane, without a callose just below apex.
  - B. Petals yellow, without purple veins; filaments more than twice the length of the anthers; plants branched above, usually rhizomatous ..... 1. *S. linifolia*.
  - B. Petals purplish, purple veined; filaments less than twice the length of the anthers; plants usually not branched above, not rhizomatous.
    - C. Leaves linear, non-petiolate; flowers pale purple ..... 2. *S. argillacea*.
    - C. Leaves oblanceolate, petiolate; flowers deep purple ..... 3. *S. barnebyi*.
- A. Petals strongly differentiated into blade and claw, abruptly narrowed from blade to claw; inner sepals with a prominent callose just below apex... 4. *S. linearifolia*.

1. *Schoenocrambe linifolia* (Nutt.) Greene, based on *Nasturtium linifolium* Nuttall, Journ. Acad. Nat. Sci. Philad. 7: 12, 1834. *Sisymbrium linifolium* (Nutt.) Nuttall in Torrey & Gray, Fl. N. Amer. 1: 91, 1838. *Erysimum linifolium* (Nutt.) Jones, Proc. Calif. Acad. Sci. 5: 622, 1895. *Schoenocrambe linifolia* (Nutt.) Greene, Pittonia 3: 124-128, 1896. *Nasturtium pumilum* Nuttall, Journ. Acad. Nat. Sci. Philad. 7: 12, 1834. *Sisymbrium pygmaeum* Nuttall in Torrey & Gray, Fl. N. Amer. 1: 91, 1838. *Schoenocrambe pygmaea* (Nutt.) Greene, Pittonia 3: 128, 1896. *Erysimum glaberrimum* Hooker & Arnott, Bot. Beechey's Voy. 323, 1840. *Schoenocrambe pinnata* Greene, Pittonia 3: 127, 1896. *S. linifolia pinnata* (Greene) A. Nelson in Coulter & Nelson, Manual Bot. Central Rocky Mts., 209, 1909. *Sisymbrium linifolium* Nutt. var. *pinnata* (Greene) O. E. Schulz, Das Pflanzenr. 86, IV, 105: 104, 1924. *Schoenocrambe decumbens* Rydberg, Bull. Torr. Bot. Club 31: 409, 1904. *Sisymbrium decumbens* (Rydb.) Blankinship, Mont. Agric. Coll. Sci. Studies Bot. 1: 60, 1905. *Sisymbrium linifolium* Nutt. var. *decumbens* (Rydb.) O. E. Schulz, Das Pflanzenr. 86, IV, 105: 104, 1924.

Perennial, rhizomatous, glabrous to sparsely pilose with simple trichomes below, glabrous above, glaucous; rhizome usually vertical; stems erect to somewhat decumbent, one to several (sometimes numerous), stiff, simple or with few branches above, 3-7 dm. tall; strictly basal leaves not present, lower cauline leaves entire to pinnatifid, fleshy, thick when dry, linear to linear-oblanceolate, 3-7 cm. long, blade or main axis of pinnatifid leaves up to 8 mm. wide; middle and upper leaves entire, smaller and narrower than lower, upper leaves terete or nearly so; inflorescences few to many-flowered, racemose with a bud cluster at apex; sepals yellowish, erect to slightly spreading, oblong, non-saccate, 5-6 mm. long; petals yellow, spatulate, narrowed gradually from widest point, 8-11 mm. long, 2.5-3.5 mm. wide, not differentiated into blade and claw; stamens tetradynamous; anthers not apiculate, 2.5-3 mm. long; stigma lobed, lobes over replum margin; pedicels straight, strongly ascending to divaricately ascending, 6-12 mm. long, expanded at summit; siliques terete, erect to slightly divergent, sessile or nearly so, 3-6 cm. long, ca. 1 mm. in diameter; styles stout, nearly same diameter as siliques, up to 1 mm. long; stigma cleft evident, persistent; seeds oblong, plump, slightly over 1 mm. long, ca. 0.5 mm. in diameter, cotyledons incumbent.

**DISTRIBUTION:** British Columbia and Montana to northern New Mexico west to eastern Nevada. It has been reported from northern Arizona but I have not seen specimens from that state.

**FLOWERING:** April–August.

**HOLOTYPE:** “sources of the Salmon River, Columbia,” [probably Idaho] *Wyeth* (PH!).

**REPRESENTATIVE SPECIMENS:** **Canada. British Columbia:** Thompson River Canyon near Spences Bridge, 29 May 1938, *J. W. & E. M. Thompson* 29 (GH); within 5 mi. of Lillooet, 2 Jul 1916, *Macoun* s.n. (GH); about 9 mi. SW of Clinton on Loon Lake Road, 11 Jul 1956, *Calder et al.* 18657 (GH); Fraser River Valley, 19 May 1875, *Macoun* 146 (GH); Oliver, 5 May 1960, *Beamish & Vrugtman* 60128 (us); 1 mi. S of Osoyoos, 20 May 1953, *Calder & Savile* 7975 (us). **USA.** Head of the Missouri, *Wyeth* (holotype of *Sisymbrium pygmaeum* Nutt., PH!). Snake country [probably Idaho], *Tolmie* (isotype of *Erysimum glaberrimum* H & A, GH!). **Colorado. Archuleta Co.:** 5 mi. NE of Arboles, 15 May 1981, *R. C. & K. W. Rollins* 8117 (GH); **Eagle Co.:** Gypsum, 6 Aug 1894, *Crandall* 65 (GH). **Gunnison Co.:** 4 mi. E of Gunnison, 22 May 1938, *Rollins* 2097 (GH); 2 mi. E of Sapinero, Jul 1957, *Beaman & Erbsich* 1186 (GH); Gunnison Canyon, 7.6 mi. W of Gunnison, 27 May 1979, *R. C. & K. W. Rollins* 7968 (GH). **La Plata Co.:** Arboles, Jun 1899, *Baker* 357 (GH). **Montezuma Co.:** just E of Cortez, 25 May 1934, *McKelvey* 4647 (GH). **Montrose Co.:** Paradox, 17 Jun 1912, *Walker* 98 (GH, us); Naturita, 18 May 1914, *Payson* 317 (GH). **San Miguel Co.:** 16 mi. N of junction, Colo. Hwy. 141 and U.S. Hwy. 666, 16 May 1981, *R. C. & K. W. Rollins* 8130 (GH). **Idaho. Blaine Co.:** Martin, 5 Jul 1916, *Macbride & Payson* 3048 (GH); Picabo, 1 Jul 1916, *Macbride & Payson* 2973 (GH). **Butte Co.:** along Hwy. 88, 8 mi. N of its junction with Hwy. 20/26, 22 May 1967, *Atwood* 819 (GH); 1 mi. N Midway, 13 Jun 1941, *Cronquist* 2334 (GH). **Cassia Co.:** near City of Rocks, 11 mi. N of Idaho-Utah line, 12 Jun 1981, *R. C. & K. W. Rollins* 81293 (GH). **Custer Co.:** hills across river from Challis, 14 Jun 1944, *Hitchcock & Muhlick* 8977 (GH); Mackay (Pass Creek), 30 Jul 1911, *Nelson & Macbride* 1418 (GH). **Lemhi Co.:** Salmon, 26 Jun 1920, *E. B. & L. B. Payson* 1790 (GH). **Twin Falls Co.:** Shoshone Falls, 24 Jun 1912, *Nelson & Macbride* 1719 (GH). **Montana.** Melrose, 6 Jul 1895, *Rydberg* 2671 (holotype of *Schoenocrambe decumbens* Rydb., NY! isotype NY!). **Deer Lodge Co.:** Deer Lodge, 8 Jun 1938, *Barkley* 2511 (GH); Anaconda, 11 Jul 1906, *Blankinship* 660 (us). **Lewis & Clark Co.:** about 1 mi. N of airport, Helena, 25 May 1956, *Don Scharff* s.n. (GH). **Wheatland Co.:** 13 mi. W of Shawmut, 29 May 1956, *Don Scharff* s.n. (GH). **Nevada. Elko Co.:** ca. 3/4 mi. NW of Pecoup-Spruce Mt. Pass, Pecoup Mts., 9 Jun 1981, *Pinzl* 4108 (GH). **Pershing Co.:** East Humboldt Mts., Aug 1868, *Watson* 96 (GH, us). **White Pine Co.:** E side of Schellbourne Pass, 25 Jun 1979, *Tiehm et al.* 5287 (GH); 5 mi. SE of summit on road from Tippet to Pleasant, Kern Mts., 25 Jun 1979, *Tiehm et al.* 5292 (GH); Purple, Long Valley, W of Butte Mts., T20N, R59E, Sec. 5, 21 Jul 1980, *Williams* 80-235-3 (GH). **Utah.** 1875, *L. F. Ward* s.n. (holotype of *Schoenocrambe pinnata* and *Tiehm* (GH)). **Carbon Co.:** between Soldier's Summit and Helper, 10 May 1934, *Greene*, us). **Maguire 18548 (GH). **Daggett Co.:** Sheep Creek Canyon, 6 Jun 1932, *Williams* 546 (GH); 6 mi. S of Manila, 16 Aug 1935, *Maguire* 12654 (GH). **Duchesne Co.:** near Myton, 13 May 1935, *Graham* 8838 (GH); 1 mi. up side canyon of Indian Canyon, 3 Jun 1965, *N. H. Holmgren et al.* 1767 (GH). **Emery Co.:** ca. 3 mi. S of San Raphael River bridge, 25 May 1968, *Higgins* 1316 (GH). **Juab Co.:** Johnson's Canyon, Deep Creek Mts., 29 May 1937, *Cottam* 7202 (GH). **Kane Co.:** 38 mi. E of Kanab, 19 Apr 1967, *Rollins* 6785 (GH); about 77 mi. E of Kanab, 4 May 1965, *Cronquist* 10018 (GH). **Rich Co.:** 4 mi. SE of Lake City, 17 Jun 1946, *Rollins* 3069 (GH). **San Juan Co.:** 19 Apr 1935, *Maguire* 16008 (GH); north of Bluff, 9 May 1944, *A. H. Holmgren* 3162 (GH). **Uintah Co.:** 26 mi. S of Ouray, 31 May 1979, *R. C. & K. W. Rollins* 79122 (GH); near Willow Creek, 5 mi. N Thorne's Ranch, 19 Jun 1946, *Rollins* 3085 (GH); 10 mi. NW of Vernal, 26 Jun 1931, *Graham* 6392 (GH). **Washington Co.:** Red Creek, 1877, *Palmer* 20 (GH, us). **Washington. Grant Co.:** junction of Crab and Wilson creeks, 30 May 1936, *Thompson* 13714 (GH, us); Dry**

Falls near Coulee City, 2 May 1931, *Thompson 6153* (GH, US). **Kittitas Co.:** side canyon of Columbia River, Spring, 1978, *Richard Old s.n.* (GH). **Klickitat Co.:** rocks, 11 Jun 1981, *Suksdorf 3* (GH); near Bingen, 27 Apr 1935, *Thompson 11413* (GH, US). **Wyoming.** **Albany Co.:** near Wyo. Hwy. 34, 22 mi. E of Laramie, 24 Jun 1951, *Rollins & Porter 5113* (GH, RM); Laramie, 20 Jun 1900, *Nelson 7277* (GH, NY, RM, US). **Carbon Co.:** 1 mi. S of Baggs, 22 May 1979, *Reed C. & Richard C. Rollins 7935* (GH). **Fremont Co.:** 32 mi. NE of Farson, 25 Jun 1979, *R. C. & M. L. Rollins 79322* (GH). **Lincoln Co.:** 9 mi. N of Kemmerer, 21 Jun 1979, *R. C. & K. W. Rollins 79305* (GH). **Natrona Co.:** 13.5 mi. NE of Muddy Gap, 21 May 1979, *Reed C. & Richard C. Rollins 7924* (GH). **Sweetwater Co.:** 48 mi. S of Rock Springs, 19 Jun 1981, *R. C. & K. W. Rollins 81357* (GH). **Uinta Co.:** near Lyman, 21 Jun 1937, *R. C. Rollins 1773* (GH, US).

As one of the two most widespread species of *Schoenocrambe*, *S. linifolia* is also one of the most polymorphic. In that respect, it rivals *S. linearifolia*. The rhizomatous habit of *S. linifolia* is distinctive but it is not certain that every population is exclusively made up of plants with rhizomes. At several different locations, I have attempted to determine the extent to which identifiable rhizomes are present. Whenever the rhizomes are elongated, they are easily seen as such. However, many plants have close branching just below the caudex and it is difficult to tell in the field whether the branches are coming off a vertical rhizome or whether this is merely an underground branching system. In any case, there are many plants that are hardly rhizomatous as usually understood. The type of caudex branching is very similar to that of the other three species of *Schoenocrambe*.

Many populations of *Schoenocrambe linifolia* have at least a few plants with pinnatifid lower leaves. In a few, pinnatifid lower leaves predominate but in most populations the leaves are entire. I agree with Payson (1922) that pinnatifid leaves cannot be made the basis for a distinct taxon as was done by Greene when he described *S. pinnata*.

There is a rather wide range of flower size in *Schoenocrambe linifolia*. Relatively large-flowered plants occur especially in southwestern Colorado and southern Utah but other characters are very similar to those of populations in the more northerly areas of the species range. I was surprised to find a population in central Wyoming where each plant had six siliques or less when the usual number per fruiting branch is more than twelve. The siliques of specimens from northern Washington and southern British Columbia are narrower than in material from most of the species range. These types of variations appear to be characteristic of the species and illustrate the polymorphism mentioned above.

**2. *Schoenocrambe argillacea*** (Welsh & Atwood) Rollins, comb. nov., based on *Thelypodopsis argillacea* Welsh & Atwood, Great Basin Nat. 37: 95–96, 1977.

Perennial, wholly glabrous; stems several from a stout, ligneous, elongated, usually vertical underground caudex which also supports old broken stem-stubs; stems rigid, unbranched, purplish toward base, greenish above, lax to erect, 1.5–3 dm. tall; leaves

all cauline, sessile or rarely with a short petiole, overlapping, linear, occasionally oblanceolate, thick, slightly fleshy, entire or rarely obscurely dentate, 1–2.5(–3.5) cm. long, usually less than 2 mm. wide (sometimes up to 6 mm. wide), widest leaves cuneate at base; inflorescences few to about 20-flowered, elongating in fruit; sepals oblong, purplish, spreading at anthesis, non-saccate, 5–7 mm. long, 2–3 mm. wide; petals pale lavender to whitish, prominently purple-veined, broadly spatulate to lingulate, tapered gradually from outer blade to point of insertion, not unguiculate, 9–11 mm. long, 3.5–4.5 mm. wide; stamens erect, included; filaments of paired stamens erect, 2.5–3 mm. long, filaments of single stamens slightly curved, 1.5–2 mm. long; anthers straight, erect, 2.5–3 mm. long; glandular tissue poorly developed, mainly above petal insertions; fruiting pedicels widely spreading to divaricately ascending, 8–12 mm. long, abruptly expanded at apex; siliques sessile, terete, nearly straight to curved outward, slightly torulose, 4–7 cm. long, 1.5–2 mm. in diameter, narrowed toward apex; styles subclavate, 1–2 mm. long; stigma slightly lobed with lobes overreplum margins; seeds oblong, plump, marginless, ca. 2 mm. long, ca. 1 mm. in diameter; cotyledons obliquely incumbent.

**DISTRIBUTION:** apparently endemic to the Uinta Basin of eastern Utah.

**FLOWERING:** April–June.

**HOLOTYPE:** hills west of Willow Creek, on east slope of Big Pack Mountain, T10S, R20E, Sec. 33, at 5,000 ft. elevation, on Green River shale, Uintah County, Utah, 11 May 1976, *N. D. Atwood 6627* (BRY!). Isotypes (GH!, NY!, US!).

**OTHER SPECIMENS STUDIED:** **Utah.** **Uintah Co.:** 25 mi. due S of Ouray, between Hill and Willow Creeks, 26 May 1978, *Neese 4962, 4972* (BRY); Uinta Formation, steep N facing slope, Big Pack Mountain, 1 mi. W of Willow Creek, 27 Apr 1978, *Neese & England 4284* (BRY); rocky slopes above Green River, below Uinta Formation, Moon Bottom, mouth of King's Canyon in Wild Horse Bench area, S of Ouray, 9 Jun 1979, *Schulz 3345* (GH, UTC); ridges on N end of Big Pack Mountain, on and below red sandstone of Uinta Formation, 14 May 1979, *Schulz et al. 3168* (UTC); N side of Big Pack Mountain, T11S, R20E, Sec. 23, 14 May 1979, *Schulz & Schulz 3172* (GH, UTC); Big Pack Mountain, W of Willow Creek, 16 May 1978, *Neese & Peterson 4620* (BRY).

Juvenile leaves of *Schoenocrambe argillacea* are very much like mature leaves of *S. barnebyi*, being oblanceolate to obovate and petiolate. These leaves are formed on retoños of old stems or caudex branches that secondarily have been covered with soil. At exposed places several new branches are produced on these old stems that will become independent plants after the connection with the mother plant has been severed. The juvenile leaves are quite different from the narrowly linear leaves on most mature plants. But there are mature individuals with flattened leaves that are somewhat transitional between the usual very narrow nearly terete leaves and the broader juvenile leaves found on the occasional retoños. The case for recognizing *S. barnebyi* as a distinct species is weakened by the fact that there are branches and some plants of *S. argillacea* with leaves approaching those of *S. barnebyi* in size and shape. The differences between the narrowly linear leaves of *S. argillacea* and the broadened petiolate leaves of *S. barnebyi* are one of the bases for keeping these species apart. However, a more complete set of material of *S. bar-*



*nebyi* is needed to be sure whether one taxon or two actually exist.

*Schoenocrambe argillacea* appears to be restricted to the Uinta and Green River formations and is local in the Big Pack Mountain area of the Uinta Basin. Another crucifer, *Glaucocarpum suffrutescens* is restricted to the same general area. *Schoenocrambe argillacea* is distinctive because of its narrow, usually nearly terete leaves. The closest species is the recently described *S. barnebyi* which is similar in most respects. As compared to *S. linearifolia*, which is purple-flowered, usually single-stemmed and much taller, these species are closer to *S. linifolia* in habit. But *S. linifolia* has bright golden yellow flowers instead of purplish flowers as in *S. argillacea* and *S. barnebyi*. As pointed out above, the buds and young flowers of *S. linearifolia* always show a prominent callose or short horn just below the apex of the inner pair of sepals. There is no such structure on the sepals of either *S. argillacea* or *S. barnebyi*. In these, the filaments are equal to or shorter than the anthers while in *S. linearifolia* the filaments are at least twice as long as the anthers. The stigmas, too, are different. In *S. linearifolia* the stigmatic surface extends over the entire apex and down the sides of the style, remaining larger than the style diameter in mature fruit. Whereas in *S. argillacea* and *S. barnebyi* the stigma is only at the very apex of the style and recedes to an area smaller than the style apex as the fruit matures.

3. *Schoenocrambe barnebyi* (Welsh & Atwood) Rollins, comb. nov., based on *Thelypodopsis barnebyi* Welsh & Atwood, *Brittonia* 33: 300-301, 1981.

Perennial, glabrous throughout, glaucous; stems several from a ligneous vertical underground caudex which also supports old broken stem-stubs, stems unbranched, 2.5-3.5 dm. tall; leaves all cauline, petiolate, oblanceolate, entire or nearly so, 1.5-5 cm. long, 0.5-2.5 cm. wide, thickish; inflorescence racemose, elongating in fruit, 2-8 flowered or more; pedicels straight, divaricately ascending to more widely spreading, 1-2 cm. long; sepals oblong, purplish green, scarious margined, outer pair somewhat saccate, ca. 7-8 mm. long; petals spatulate to lingulate, tapered gradually from outer blade to point of insertion, not unguiculate, purplish, prominently purple-veined, ca. 12 mm. long; siliques subsessile, terete, 3.5-6.4 cm. long, 1.5-2 mm. in diameter, ascending to widely spreading; styles subclavate, 1-1.5 mm. long; seeds not known.

DISTRIBUTION: known only from the type area in Utah.

HOLOTYPE: Utah, N-facing slope, Sye's Butte, Emery County, 27 Apr 1981, S. L. Welsh 20345 (BRY, not seen). Isotype (GH!).

OTHER SPECIMENS STUDIED: Utah. Emery Co.: San Rafael Reef, ca. 18 mi. due NW of Hanksville, 21 Jul 1980, Harris 1007, 1008 (GH).

This species is quite closely related to *Schoenocrambe argillacea* differing mainly in leaf-shape and intensity of flower color. The leaves of *S. barnebyi* are definitely petiolate whereas those of *S. argillacea* are at most cuneate at base. There may be other character differences that will show up when specimens with mature seeds and fruits that have not fully shed are available for examination.

4. *Schoenocrambe linearifolia* (Gray) Rollins, comb. nov., based on *Streptanthus linearifolius* Gray, Mem. Amer. Acad. 4: 7, 1849. *Thelypodium linearifolium* (Gray) S. Watson, Bot. King's Exped. 25, 1871. *Hesperidanthus linearifolius* (Gray) Rydb., Bull. Torr. Bot. Club 34: 434, 1907. *Sisymbrium linearifolium* (Gray) Payson, Univ. Wyo. Publ. Bot. 1: 19, 1922. *Thelypodopsis linearifolia* (Gray) Al-Shehbaz, Contrib. Gray Herb. 204: 140, 1973. *Streptanthus stenophyllus* Rollins, Contrib. Dudley Herb. 3: 175, 1941 [holotype: Sierra de Parras, Coahuila, Mexico, 5 Sep 1950, Shreve & Tinkham 9886 (GH)].

Perennial, glabrous throughout, glaucous; stems one or few from base, erect, stiff, branched upward, up to 15 dm. tall; leaves of first year's rosette obovate, dentate to entire, petiolate, shed before plants mature; lower cauline leaves oblanceolate to narrower, short petiolate to cuneate, entire or rarely weakly dentate, 5–10 cm. long; middle and upper cauline leaves reduced upwards, entire, thickish, linear to linear-lanceolate, narrowed at base and acute to acuminate at apex; inflorescences few-flowered, racemose, elongating in fruit but not greatly so; sepals erect, purplish, 5–7 mm. long, outer pair saccate, inner pair with a prominent callose just below apex, non-saccate; petals broadly spatulate or narrower, differentiated into blade and claw, purple, veiny, 1.2–1.6(–2.2) cm. long, up to 7 mm. wide, claw slender; pedicels divaricately ascending, straight, slender, expanded at apex, 1–2 cm. long; siliques terete, erect to widely spreading, sessile to subsessile, 4–10 cm. long, 1–1.5 mm. in diameter; styles 0.5–1.5(–2) mm. long; stigmas elongated, conical; seeds plump, angular, ca. 1 mm. long; cotyledons obliquely incumbent.  $n = 11, \pm 20$  (Rollins, 1966; Rollins and Rüdénberg, 1977; Rodman, 1978).

DISTRIBUTION: Colorado and Arizona to Texas, southward to San Luis Potosí and westward to Durango and Sonora.

FLOWERING: July–November.

HOLOTYPE: New Mexico, mountainous regions from Santa Fe to Las Vegas, July–Aug. 1847, Fendler 24 (GH!).

REPRESENTATIVE SPECIMENS: for specimens from Mexico, given under the name *Thelypodopsis linearifolia*, see Contrib. Gray Herb. no. 206, p. 15, 1976. **USA. Arizona.** **Cochise Co.:** 1 mi. N of Rustler's Park, Chiricahua Mts., 21 Oct 1974, Rollins & Roby 74198 (GH); 2.4 mi. down Pinery Canyon from Pinery Campground, Chiracahua Mts., 22 Nov 1974, Rollins et al. 74199 (GH). **Coconino Co.:** Cape Royal, Kaibab Forest, 19 Jul 1930, Goodman & Hitchcock 1636 (GH); N rim of the Grand Canyon, 12 Aug 1957, Rollins 57331 (GH). **Gila Co.:** Workman Creek rd., above end of car road, Sierra Ancha Mts., 11 Aug 1946, Gould 3646 (GH). **Pima Co.:** South Canyon, Baboquivari Mts., 15 Sep 1931, Gilman 41 (GH). **Santa Cruz Co.:** Wicherscheims Cabin, Huachuca Mts., 6 Aug 1909, Goodding 360 (GH); Ramsey Canyon, Huachuca Mts., 29 Sep 1929, Jones 24837 (GH). **Colorado.** **Fremont Co.:** Cañon City, 1873, Greene s.n. (GH); near Big Cottonwood Cr., ca. 4 mi. above Nat. Forest boundary, Sangre de Cristo Range, 3 Jul 1936, Rollins 1313 (GH, US). **Las Animas Co.:** 1 mi. S of Mosley, 4 Jul 1937, Rollins 1818 (GH). **Rio Grande Co.:** Del Norte, 1 Jul 1921, Bethel et al. 4138 (US). **New Mexico.** **Catron Co.:** Beaverhead, Datil Forest, 29–30 Jul 1924, Eggleston 20438 (GH). **Colfax Co.:** 2 mi. N of Raton, 1 Jul 1938, Rollins 2409 (GH). **Dona Ana Co.:** mouth of canyon, S end of Organ Mts., 9 Sep 1930, Fosberg S3711 (GH). **Grant Co.:** Burro Mts., 20 Jun 1903, Metcalfe 204 (GH); Fort Bayard Watershed, 27 Nov 1905, Blumer 191 (GH). **Lincoln Co.:** Sierra Blanca Peak, 1 Jul 1934, Hodgdon & Rossbach 10 (GH); along Ruidoso Cr., White Mts., 3 Jul 1895, Wootton s.n. (GH). **McKinley Co.:** between Gallup and Zuni, 5 Jul 1934, Hodgdon & Rossbach 8 (GH). **Quay Co.:** 10 mi. S of San Jon, Sep 1942, Kirk Bryan s.n. (GH). **Santa Fe Co.:** 8 mi. E of Santa Fe, 29 Aug 1934, Goodman 2304 (GH); Canoncito, 18 Jun 1897, A. A. & E. G. Heller 3729 (GH). **Socorro Co.:** 31,000 ft. from crater fence, Hees et al. 574 (GH). **Texas.** **Brewster Co.:** 9-point

Mesa, 60 mi. S of Alpine, 22 Sep 1966, *Correll* 33817 (GH); Chaney Ranch, ca. 25 mi. SE of Marathon, 16 Apr 1961, *Rollins & Correll* 6168 (GH); Boot Spring, Chisos Mts., 21 Jul 1957, *Correll & Johnston* 18300 (GH). **Crockett Co.:** divide between forks of the Llano, May 1885, *Reverchon* 3 (GH). **Culberson Co.:** Pine Springs Canyon, Guadalupe Mts., 7 Sep 1961, *Correll & Johnston* 24243 (GH); 6.5 mi. NW of Van Horn, Beach Mt., 14 Jul 1943, *Waterfall* 5075 (GH). **El Paso Co.:** McKelligon Canyon, Franklin Mts., 2 May 1970, *D. S. & H. B. Correll* 38599 (GH); 4.5 mi. N of El Paso, 13 May 1946, *Cory* 52958 (GH). **Hudspeth Co.:** 12 mi. S of Sierra Blanca, 25 Apr 1961, *Rollins & Correll* 61133 (GH); N peaks of Eagle Mts., ca. 7 mi. WSW of Hot Wells, 17 Jul 1943, *Waterfall* 5154 (GH). **Jeff Davis Co.:** upper slopes of Sawtooth Mts., Davis Mts., 13 Oct 1952, *Correll* 15012 (GH); Mt. Locke, Davis Mts., 12 Aug 1934, *Cory* 9426 (GH). **Pecos Co.:** 30.5 mi. S of Ft. Stockton, 5 Sep 1933, *Cory* 6862 (GH). **Presidio Co.:** above Capote Falls, 3 Nov 1966, *Correll* 34122 (GH); Fresno Canyon, ca. 50 mi. E of Presidio, 20 Apr 1961, *Rollins & Correll* 61175 (GH); below San Estaban Lake, Marfa, 18 Aug 1940, *Hinckley* s.n. (GH).

As far as present records show it, *Schoenocrambe linearifolia* is the most widespread species of the genus. Its flowering period, which stretches from April to November, is unusually long. Part of this is due to the substantial elevational range the species is able to tolerate but also the flowering period is very much affected by the large differences in climate taking the total geographical range into account.

When *Schoenocrambe linearifolia* grows in the open, the stems are erect, stiff, and reed-like. In the shade of small trees or bushes and on shady cliffs, the stems are much weaker and tend to be less erect. The plants are usually scattered rather than in dense colonies, most often in open pine forests or oak woods. The species is taxonomically distinctive. The flowers are relatively large and reminiscent of *Streptanthus* where Gray originally described it. Unfortunately, I was misled in the same way when I described *Streptanthus stenophyllus* as new. But there is still some possibility of the latter being a species distinct from *S. linearifolia*. If this proves to be the case when more material is available for study, it will certainly belong to *Schoenocrambe* rather than *Streptanthus*. For the present, the evidence suggests that *Streptanthus stenophyllus* is to be synonymized under *Schoenocrambe linearifolia*.

The nomenclatural history of *Schoenocrambe linearifolia* shows not only that the placement of this species as to genus has been uncertain and difficult but that it is also a very distinctive species. In setting up the monotypic *Hesperidanthus*, Rydberg (1907) based his decision, in part, on the fact that Robinson (1895) had already set *Schoenocrambe linearifolia* aside from the main group of *Thelypodium* in its own section *Hesperidanthus*. Two features are unique to *S. linearifolia*: the conical decumbent stigmas, which are often considerably elongated, and the presence of a prominent callose (almost a small horn in some individuals) just below the tip on each of the inner pair of sepals. Payson (1922) called these sepals hooded. It could be argued that these differences are sufficient to justify placing *S. linear-*

*ifolia* in a genus of its own. However, the recent discovery of *S. argillacea* and *S. barnebyi*, which are certainly close relatives and which do not have the stigma and sepal characters mentioned, provide a connecting link to *Schoenocrambe* that cannot be overlooked.

An unusual individual plant of *Schoenocrambe linearifolia* was found in Pinery Canyon of the Chiricahua Mountains in southern Arizona. This proved to be a polyploid with much larger petals and other floral structures than is normal for the species as a whole. It was cited as an example of a naturally occurring polyploid showing gigas features (Rollins, 1979) but with these having no known taxonomic significance. Populations of plants with these features apparently have not become established.

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# STUDIES ON ARABIS (CRUCIFERAE) OF WESTERN NORTH AMERICA II<sup>1</sup>

REED C. ROLLINS

The present paper continues the results of a restudy of *Arabis*, building on my former monograph (Rollins 1941) of the genus for western North America. New collections of rare and little known taxa now permit a better assessment of their status in the genus, both as to relationship with other taxa and as to the nature of the variability present.

## THE ARABIS DEMISSA-A. OXYLOBULA-A. PENDULINA GROUP

At the time of my previous study of *Arabis oxylobula* Greene and related taxa, there were only two collections of this species available for study that could, with confidence, be associated with the name. Because it was considered rare and possibly endangered, *A. oxylobula* was sought at its type locality near Glenwood Springs, Colorado, and was rediscovered by Barry C. Johnston and Pete Lucas in 1978. Since then, typical material has been collected at several additional localities in Colorado. The new material now makes it possible to see some of the variation present in this species and to better assess its relationships and taxonomic position in the genus. Of particular interest was whether a fuller knowledge of *A. oxylobula* would now dictate that populations previously recognized as *A. demissa* Greene be incorporated in a more broadly defined and widespread *A. oxylobula*. At the same time, the position of *A. pendulina* with respect to these taxa has received attention together with several large collections of new material belonging to this alliance.

In the original material of *Arabis oxylobula*, the erect basal leaves are nearly glabrous with only a few ciliate trichomes on the slender petioles. New material from the type area shows that the cilia may extend fully around the blade as well as on the petioles. Material away from the type area, for example in northwestern Colorado, northern Utah and Wyoming, has similar trichomes occurring sparsely on the narrow leaf-blades as well. These trichomes are large with a broadened base and mostly simple. Occasionally a few forked trichomes are present and these are as large as those of the rest of the trichome complement. In contrast, the trichomes of *A. demissa* are much smaller and mostly branched. Those on the leaf-blade are at least forked and in many cases 3- to 5-branched dendritic trichomes occur there. Larger simple trichomes sometimes form cilia along the petiole margins but rarely extend to the blade area of the leaf.

<sup>1</sup>The first paper in this series was published in *Systematic Botany* (1981) 6(1): 55-64.

Typical *Arabis oxylobula* has acute siliques that are less than 2.5 cm long and they are borne on very slender pedicels that vary from spreading nearly at right angles to the infructescence rachis to arching downward. The siliques themselves are at right angles to loosely pendulous. In typical *A. demissa*, the siliques are obtuse, loosely pendulous and the lower limit of their length is 2.5 cm. They range up to 4 cm. The style is obsolete in *A. demissa*, whereas there is a short but definite style present in *A. oxylobula*.

Except for the sharp differences in the trichomes, the distinctions between *Arabis demissa* and *A. oxylobula* are rather weak. What tips the balance in favor of recognizing both of these taxa as species is a consideration of the populations that occur outside of the type areas. It has always been uncomfortable for me to recognize as var. *languida* and var. *russeola* plants which possess the same different trichome types as *A. demissa* and *A. oxylobula*. Both varieties occur in the same areas of Colorado, Wyoming, and Utah, yet they are not in mixed populations and the distinctions between them are sharp. There is no evidence of hybridization or introgression. When var. *russeola* is associated with *A. pendulina* and var. *languida* with *A. demissa*, as given below, then the geography is no longer at variance with the general phytogeographic patterns of the region.

#### KEY TO THE TAXA

- A. Basal leaves with predominately large simple ascicular trichomes, these sometimes restricted to petiole margins, rarely glabrous.
  - B. Siliques acute, less than 2.5 cm long, straight, at right angles to rachis to loosely descending; pedicels filiform, 3–6 mm long; stems numerous . . . 1. *A. oxylobula*.
  - B. Siliques obtuse, 2.5–4 cm long, slightly incurved, pendulous; pedicels stouter, 5–8 mm long . . . 2. *A. pendulina*.
    - C. Seeds in two definite rows, narrowly winged at least distally, forked trichomes present on leaf-blade surfaces; basal leaves broadly oblanceolate . . . 2a. *A. pendulina* var. *pendulina*.
    - C. Seeds in one irregular row, wingless, only simple trichomes on leaf-blade surfaces; basal leaves linear to narrowly oblanceolate . . . 2b. *A. pendulina* var. *russeola*.
- A. Basal leaves with much smaller, predominately branched trichomes on the leaf-blades, sometimes with simple ciliate trichomes on the petioles; pubescence dense to sparse on basal leaves, never glabrous.
  - D. Siliques arcuate, widely spreading, 4–6 cm long; pedicels at right angles to rachis . . . 3. *A. falcatoria*.
  - D. Siliques straight or nearly so, if slightly curved then pendulous, less than 3 cm long; pedicels at right angles to rachis to strongly curved downward.
    - E. Siliques acuminate, widely spreading at right angles to rachis to slightly ascending, plain, ca. 2 mm wide; pedicels 2–3 mm long . . . 4. *A. pusilla*.
    - E. Siliques obtuse to acute, pendulous, often constricted between seeds, ca. 1.5 mm wide; pedicels 3–6 mm long . . . 5. *A. demissa*.
      - F. Basal leaves linear; cauline leaves non-auriculate; siliques constricted between seeds; seeds winged or wingless . . . 5a. *A. demissa* var. *demissa*.
      - F. Basal leaves oblanceolate; cauline leaves auriculate; siliques plain; seeds wingless . . . 5b. *A. demissa* var. *languida*.

1. *Arabis oxylobula* Greene, *Pittonia* 4: 195. 1900.

This species is presently known from Garfield, Gunnison, and Montrose counties, Colorado. It occurs in rock crevices and tiny cracks of limestone on ridges, cliff edges, and mesa tops. Its nearest relative is *Arabis pendulina* var. *russeola* which occurs farther north and west in Colorado, Wyoming, and Utah.

**SPECIMENS STUDIED.** **Colorado.** **Garfield Co.:** Glenwood Springs, 18 Jun 1899, *Osterhout* 1942 (holotype ND; isotype RM; photo of holotype GH); same locality, 6 Jun 1902, *Osterhout* 2575 (COLO, NY, RM 2 sheets); Glenwood Canyon, rimrock of uppermost "breaks" in canyon wall, N of head of Hanging Lake Trail, 29 Jun 1978, *Johnston and Lucas* 1763 (COLO, RM); very top of exposed breaks, Leadville Limestone, uppermost breaks of Glenwood Canyon, 29 Jun 1979, *Johnston et al.* 2137 (COLO). **Gunnison Co.:** 1/4 mile W of Blue Mesa Dam, Black Canyon, 6 Jun 1979, *Ratzloff* 1645 (COLO); same general locality, 17 May 1978, *Ratzloff* 1329 (COLO). **Montrose Co.:** Black Canyon National Monument, 21 May 1962, *Weber* 11340 (COLO).

2. *Arabis pendulina* Greene, *Leaflets* 2: 81. 1910.

2a. *Arabis pendulina* var. *pendulina*

Specimens of *Arabis pendulina* from the type area in southwestern Nevada are varietally distinct from the material we have from middle elevations of southern Utah north to Colorado and Wyoming. New collections from the type locality north of Vernal, Utah, clearly demonstrate that var. *russeola*, which was described from that area, should be associated with *A. pendulina* rather than *A. demissa* as in my former treatment (Rollins 1941). It is not necessary to cite specimens of var. *pendulina* since a number were previously listed.

2b. *Arabis pendulina* var. *russeola* (Roll.), comb. nov., based on *A. demissa* Greene var. *russeola* Roll., *Rhodora* 43: 398. 1941. *A. setulosa* Greene, *Leaflets* 2: 81. 1910.

The geographic range of this variety has been much expanded by recent collections. It is now known from extreme northwestern Utah as well as from central Wyoming, and from much farther south in Utah than was previously recognized.

**SPECIMENS STUDIED.** **Colorado.** **Moffat Co.:** terraces above Yampa River, between Maybell and Sunbeam, 13 Jun 1967, *Weber s.n.* (COLO); summit of Round Top Mt., Dinosaur National Monument, 27 Jun-1 Jul 1948, *Wolf and Dever* 5192 (COLO); same locality, 1 Jun 1956, *Weber and Welsh* 9618 (COLO). **Wyoming.** **Albany Co.:** Laramie Hills, 4 Jun 1899, *E. Nelson* 212 (GH); E of Laramie, 1 Jun 1902, *Sellon* 15 (RM). **Carbon Co.:** 8.5 miles N of Rawlins, 27 Jun 1979, *R. C. and M. L. Rollins* 79349 (GH). **Fremont Co.:** east of the Continental Divide, 36.5 miles E of Farson, 26 Jun 1979, *R. C. and M. L. Rollins* 79325 (GH); ca. 1 mile SSE of highway crossing Continental Divide, 15 Jun 1978, *Johnston and Lucas* 1689X (COLO, RM). **Natrona Co.:** 2 miles NE of Alcova, off Wyo. Hwy. 220, 21 May 1979, *Reed C. and Richard C. Rollins* 7915 (GH). **Sweetwater Co.:** Cedar Mountain, 28 Jun 1951, *Rollins and Porter* 5134 (GH); high windswept ridge, 31.8 miles south of Rock Springs, 19 Jun 1981, *R. C. and K. W. Rollins* 81360 (GH, duplicates to be distributed). **Utah.** **Box Elder Co.:** summit of ridge in mineralized chip rock, 4 miles S of Lynn, 12 Jun 1981, *R. C. and K. W. Rollins* 81283 (GH, duplicates to be distributed). **Dagget Co.:** vicinity of Flaming Gorge, 3 Jun 1938, *Rollins* 2272 (GH, RM); same locality, 31 May 1932, *Williams* 459



(GH, RM). **Garfield Co.:** about 4 miles SW of Cannonville, 4 Jun 1967, *J. L. Reveal et al.* 776 (COLO, GH, RM); between Bryce Canyon and Red Canyon, 6 Jun 1979, *R. C. and K. W. Rollins* 79172 (GH); 1 mile S of Cannonville, 6 Jun 1979, *R. C. and K. W. Rollins* 79171 (GH). **Kane Co.:** 4 miles south of Cannonville, 12 May 1965, *Cronquist* 10080 (COLO, GH, RM). **Millard Co.:** windswept rock ridge, near Oak City, 15 Jul 1980, *Goodrich* 14363 (GH). **Uintah Co.:** 18 miles N of Vernal, 17 Jun 1937, *Rollins* 1757 (GH, holotype); 12 miles N of Maeser, 21 Jun 1979, *Neese and Moore* 7783 (RM). **Washington Co.:** Horse Pasture Plateau, Zion National Park, 22 Jun 1965, *N. H. Holmgren et al.* 1986 (GH).

The distinctions between var. *pendulina* and var. *russeola* tend to break down to some extent in the area of overlap in Utah. The southwestern populations, including those in most of Nevada, are clearly separable from the northeastern populations of Colorado and Wyoming. Some populations of var. *russeola* take on aspects of *A. oxylobula* showing a definite relationship in that direction. For example, plants of the population in Box Elder County, Utah, have on the average, shorter siliques than most populations of var. *russeola* and in this respect, they approach *A. oxylobula*.

### 3. *Arabis falcatoria* Roll., sp. nov.

Herba perennis, caespitosa; caulibus erectis vel decumbentibus, 1-2(-3) dm altis; foliis radicalibus integris, linearibus vel linear-oblancoelatis, hispidulis, acutis, 1-2(-2.5) cm longis, 2-4(-5) mm latis; foliis caulinis sessilibus, 1-1.5(-2) cm longis; sepalis purpureis, nonsaccatis, sparse pubescentibus vel glabris; petalis albis vel purpureis, spatulatis, rectis; pedicellis fructiferis rectis divaricatis, glabris vel sparse pubescentibus, 3-6(-8) mm longis; siliquis arcuatis, divaricatis, glabris, acutis, 4-6 cm longis, ca. 2 mm latis; seminibus late oblongis, compressis, anguste alatis; cotyledonibus accumbentibus.

Perennial; caespitose; caudex simple; stems few to several, arising below terminal cluster of erect leaves, simple or branched above, decumbent or sometimes erect; hirsute with simple or forked trichomes below, sparsely pubescent to glabrous above, 1-2(-3) dm tall; outer basal leaves oblanceolate, widely spreading; inner basal leaves linear to linear-oblancoelate, erect, entire, densely hirsute with forked or branched erect trichomes, 1-2(-2.5) cm long, 2-4(-5) mm wide; cauline leaves sessile, oblong, usually few, 1-1.5(-2) cm long, lower densely pubescent and nonauriculate, upper sparsely pubescent to glabrous and with small auricles; flowers few; sepals erect, nonsaccate, oblong, purplish, sparsely pubescent, scarious-margined, 2.5-3.5 mm long, ca. 1 mm wide; petals spatulate to narrowly lingulate, white to pale lavender, erect, 5-6 mm long, ca. 2 mm wide; fruiting pedicels widely spreading, nearly at right angles to rachis, straight, glabrous or occasionally with a few trichomes near apex, 3-6(-8) mm long, markedly expanded at apex; siliques widely spreading, arcuate, glabrous, 1-nerved below, 4-6 cm long, ca. 2 mm wide, styles barely evident; seeds broadly oblong to nearly orbicular, compressed, narrowly winged, 1.8-2 mm long, ca. 1.5 mm wide, uniseriate; cotyledons accumbent, radicle equalling cotyledons.

TYPE: Utah, Box Elder County, in marble chip rock, 3.7 miles north of Grouse Creek (on road to Oakley, Idaho), 9 Jun 1981, *Reed C. and Kathryn W. Rollins* 81259 (holotype: GH; isotypes: to be distributed).

OTHER COLLECTIONS STUDIED. **Utah. Box Elder Co.:** summit of ridge in highly mineralized chip rock, 4 miles S of Lynn, 12 Jun 1981, *R. C. and K. W. Rollins* 81282 (GH); growing in crevices and partial shade of large rocks, same locality, 12 Jun 1981, *R. C. and K. W. Rollins* 81288 (GH). **Nevada. Elko Co.:** 3.2 air miles S of Cass House Peak, Ruby Mts., 26 Jun 1981, *Tiehm and Williams* 6661 (GH).

The coarse forked to few-branched trichomes on the basal leaves of *Arabis falcatoria* are similar to those of *A. demissa* but the widely

spreading, much longer, bow-shaped siliques are radically different from the pendulous, narrow and straight siliques of that species. The siliques are closer in shape to *A. cusickii* or *A. sparsiflora* var. *sparsiflora* than to most other species of the genus. But in *A. falcatoria* the caudex is simple, the cauline leaves few and mostly remote, and the pubescence while coarse, is not hispid as in *A. cusickii* where the caudex is branched and the cauline leaves are many and overlapping. *Arabis sparsiflora* var. *sparsiflora* is tall and scarcely caespitose while *A. falcatoria* is mostly low-growing and definitely caespitose. Neither *A. sparsiflora* nor *A. cusickii* are closely related to *A. falcatoria*. Rather, they belong to another group of species in the genus. In general habit, *A. falcatoria* is closest to *A. pendulina* var. *russeola* but the trichomes are completely unlike in these two taxa and the siliques of the latter are shorter and pendulous instead of widely spreading as in *A. falcatoria*.

There is considerable difference in the size and amount of branching in different plants of *Arabis falcatoria*, depending on the site where they are growing. In open undisturbed marble chip rock, the plants are mostly 1 dm tall or less, the stems few, unbranched and slender, and the cauline leaves small and remote. In another area, where there was disturbance of the chip rock as a result of its being mined, plants of the disturbed places grew taller, had many more robust, often branched, stems and cauline leaves that were more ample than in plants from undisturbed sites. Larger plants were also found in partially shaded crevices of large rocks. In spite of the rather large range of quantitative differences in plants from the different sites, the essential distinctive features of *A. falcatoria* were retained and the individual plants readily fit within the total spectrum of size differences.

In the collection from Nevada, *Tiehm and Williams 6661*, the pubescence is not quite as coarse as in the material from northwestern Utah. However, in most features, the plants of the two areas are very similar. *Arabis falcatoria* has stamens noticeably exceeding the calyx in length. This is unusual among species of the *demissa-oxyllobulapendulina* group. The exerted anther feature in this species deserves further study in relation to the mechanisms of pollination.

#### 4. *Arabis pusilla* Rollins, sp. nov.

Herba perennis; caulibus filiformibus, erectis vel decumbentibus, 6–12 cm altis; foliis radicalibus erectis, linearibus vel lineari-oblongatis, 1–1.5 cm longis, 1.5–2 mm latis, foliis caulinis 3–5, sessilibus, oblongis, remotis; sepalis oblongis, erectis, nonsaccatis, purpureis, ca. 2 mm longis; petalis spathulatis, roseis, 3.5–4.5 mm longis; pedicellis fructiferis divaricatis, rectis, glabris, 2–3 mm longis; siliquis divaricatis, acuminatis, glabris, 1–1.5 cm longis, ca. 2 mm latis; seminibus oblongis, exalatis, ca. 2 mm longis, ca. 1 mm latis; cotyledonibus accumbentibus.

Perennial with a simple, thickened, mostly nonbranching caudex; stems one or few, slender, slightly decumbent toward base, 6–12 cm tall; basal leaves erect, linear to

linear-oblongeolate, petiolate, entire, acute to acuminate, 1–1.5 cm long, 1.5–2 mm wide; sparsely pubescent with erect 2–3 branched trichomes, rarely ciliate on the margins with simple or forked trichomes; petioles usually ciliate on the margins with simple or forked trichomes; cauline leaves 3–5, remote, sessile, nonauriculate, 4–8 mm long; sepals oblong, nonsaccate, erect, purplish, scarious-margined, glabrous or with a few trichomes, 2–2.5 mm long; petals spatulate, erect, light lavender, 3.5–4.5 mm long; fruiting pedicels widely spreading, straight, glabrous, 2–3 mm long; siliques widely spreading to slightly ascending, glabrous, acuminate, nearly straight but with slightly undulating margins, 1–1.5 cm long, ca. 2 mm wide; styles nearly obsolete; seeds oblong, slightly compressed, wingless or occasionally with a slight distal margin, ca. 2 mm long, ca. 1 mm wide; radical pointed, slightly exceeding cotyledons; cotyledons accumbent.

TYPE: Wyoming, Fremont County, in cracks and crevices of huge metamorphosed rocks, off Wyoming State Highway 28, 39 miles SW of Lander, 20 Jun 1981, *Reed C. and Kathryn W. Rollins 81366* (holotype: GH; isotypes: to be distributed).

In general appearance, *Arabis pusilla* is more like *A. oxylobula* than any other species. The very slender stems, few cauline leaves and widely spreading siliques are features they share in common. But the seeds of *A. oxylobula* are winged all around and are in a single row in each silique whereas the seeds of *A. pusilla* are wingless and are disposed in a double row. The siliques of *A. pusilla* are nearly twice as wide as those of *A. oxylobula* and the margins are slightly wavy, not straight as in the latter. Most importantly, the trichomes of the two species are vastly different. Those of *A. pusilla* are small, mostly forked or 3-branched and only a few along the petiole margins are simple. In contrast, the trichomes of *A. oxylobula* are large, ascicular and simple; often the plants are completely glabrous. *Arabis oxylobula* is restricted to west central Colorado, where it overlaps to some extent with *A. demissa* var. *demissa* and is wholly separated geographically from *A. pusilla*.

Both *Arabis pendulina* var. *russeola* and *A. demissa* var. *languida* grow in west central Wyoming, but they are comprised of more robust individuals with much longer and narrower siliques than *A. pusilla*. Both have pendulous siliques and arched pedicels while those of *A. pusilla* are at right angles to the infructescence rachis to slightly ascending.

5. *Arabis demissa* Greene, Pl. Baker. 3: 8. 1901. *A. rugocarpa* Osterhout, Bull. Torr. Bot. Club 31: 357. 1904. *A. aprica* Osterhout ex Nelson in Coulter and Nelson, New Man. Bot. Rky. Mts. 228. 1909.

#### 5a. *Arabis demissa* var. *demissa*

The typical variety of *Arabis demissa* occurs in west central Colorado. The plants are definitely caespitose with several to many upright stems, arched pedicels and pendulous siliques. There is a strong tendency for the mature siliques to be constricted between the seeds which are in a single row. The coarse pubescence on the basal leaves consists of large simple trichomes on the petiole margins, sometimes

but rarely extending somewhat up the leaf-blade, and smaller, more abundant trichomes on the leaf-blades and margins. In addition to those specimens previously cited (Rollins 1941), the following are representative.

**Colorado.** **Garfield Co.:** flat limestone ridge overlooking Colorado River to the E and Glenwood Canyon to the S, 29 Jun 1978, *Johnston and Lucas 1756* (COLO). **Gunnison Co.:** 1.6 mi. E of U.S. Hwy. 50, 17.2 mi. W of Gunnison, 27 May 1979, *R. C. and K. W. Rollins 7974* (GH); near Woods Gulch road, E of Gunnison, 19 Jun 1979, *Ratzloff 1648* (COLO); 1 mi. SW of Powderhorn store, 22 Jun 1979, *Ratzloff s.n.* (COLO). **Hinsdale Co.:** 3 mi. S of Lake City, 26 Jun 1957, *Beaman and Erbsch 1117* (COLO, GH). **Lake Co.:** Twin Lakes, 1903, *Juday B108* (COLO). **Ouray Co.:** Ouray, *E. Bethel s.n.* (RM). **Pitkin Co.:** Aspen, *E. Bethel s.n.* (RM). **Saguache Co.:** E of Cochetopa Creek, 20 Jun 1979, *Ratzloff s.n.* (COLO).

**5b. *Arabis demissa* var. *languida* Rollins, *Rhodora* 43: 388. 1941.**

Although definitely caespitose, as in var. *demissa*, var. *languida* is taller, coarser, and with more spreading siliques. The upper cauline leaves of var. *languida* have auricles while in var. *demissa* all cauline leaves are sessile and without auricles. Some populations of var. *languida*, in unusually favorable sites, come close to attaining the size of the most depauperate populations of *A. fendleri*. However, the habitats of the two species are quite different. *Arabis fendleri* tends to occur on slopes, cliffs, and rocky places in woodland areas while *A. demissa* var. *languida* is found in open, often windswept ridges, calcareous slopes and benches. Some previously uncited collections of var. *languida* are as follows.

**Colorado.** **Gunnison Co.:** dike just west of and parallel to "the Dike," S ridge of Ruby Peak, 16 Jul 1980, *B. C. Johnston 2832* (COLO, GH). **Moffat Co.:** Douglas Mountain, 4.5 air km S of Graystone, 24 May 1978, *Peterson 492* (COLO). **Wyoming.** **Albany Co.:** ca. 2-1/2 mi. SE of Laramie, T15N, R73W, S13, 23 May 1980, *Dorn 2631* (RM); 8 mi. E of Laramie, 10 May 1936, *M. Ownbey 1019* (GH). **Sweetwater Co.:** Aspen Mt., T17N, R104W, S17, 3 Jun 1980, *Dorn 3440* (RM); *Lichvar 2758* (RM). **Utah.** **Uintah Co.:** 10 mi. W of Vernal, 11 Jun 1965, *Despain 59* (RM). **Duchesne Co.:** ca. 3.5 mi. WNW of Duchesne, 16 Jun 1980, *Neese and Welsh 8900* (GH). **Emery Co.:** ca. 9 mi. E of Huntington, 30 Apr 1968, *Higgins and Reveal 1249* (GH).

**ARABIS PLATYSPERMA AND RELATED SPECIES**

The previously presumed distributional range of *Arabis platysperma* Gray, for which there has been vouchered evidence, centers in the Sierra Nevada extending north into southern Oregon and southward to the San Jacinto Mountains of southern California. In Nevada, it has been known from the Mount Rose area, which is part of the Sierra Nevada system. Recent collections extend this species to the White Mountains of Mono County, California, and Esmeralda County, Nevada. The White Mountain material, although usually with narrower siliques, is referable to var. *platysperma*, not var. *howellii* which occurs at higher elevations in the Sierra Nevada and northward. The

Nevada populations were found by Ann Pinzl of the Nevada State Museum in Carson City. She has also discovered a new species of *Arabis*, related to *A. platysperma*, growing in the same area. Both species grow mostly above 10,000 feet in a bowl on the northeastern side of Boundary Peak. The new species is named as follows.

***Arabis pinzlae* Rollins, sp. nov.**

Herba perennis; caulibus tenuibus, erectis, 3–8 cm longis; foliis lanceolatis, dense pubescentibus; foliis caulinis oblongis erectis, pubescentibus vel superne glabris; sepalis oblongis, purpureis, sparse pubescentibus; petalis anguste spatulatis, erectis, purpureis; pedicellis erectis vel adscendentibus, tenuis, glabris vel pubescentibus, 3–7 mm longis; siliquis erectis vel adscendentibus, linearis, acuminatis, glabris, 2–4 cm longis, 2–3 mm latis; stigmatibus sessilibus; seminibus late oblongis vel orbicularibus alatis, ca. 2.5 mm longis, ca. 2 mm latis, cotyledonibus accumbentibus.

Perennial; stems simple, slender, one or few from a simple or branched caudex, 3–8 cm tall, densely pubescent below, sparsely pubescent to glabrous above; basal leaves erect, greyish, tufted, linear-lanceolate mostly inrolled, densely pubescent with to narrower, tapering to an acute tip, thickish, 1–2 mm wide; cauline leaves 3–5, with minute dendritic trichomes, 6–10 mm long, densely pubescent, upper pubescent sessile, narrowly oblong, non-auriculate, lower to nearly glabrous, 4–6 mm long, 1.5–2 mm wide; sepals non-saccate, oblong, purple, scarious-margined, ca. 3 mm long, ca. 1 mm wide; petals purple-tipped, whitish below, spatulate, erect, ca. 5 mm long; pedicels erect to divaricately ascending, straight, sparsely pubescent to glabrous, 3–5 mm long; siliques erect to ascending, linear with uneven margins, acuminate, glabrous, purplish at maturity, 2–4 cm long, 2–3 mm wide; seeds in a single row filling width of silique, widely winged all around, compressed, broadly oblong to nearly orbicular, ca. 2.5 mm long, ca. 2 mm wide not including wings; wings varying in width, narrower on the sides than distally, up to 0.5 mm wide; radical exceeding cotyledons; cotyledons is accumbent.

TYPE: Nevada, Esmeralda County, near center of bowl, approximately 11,200 feet, northeast side of Boundary Peak, White Mountains, 12 July 1981, *Ann Pinzl 4442* (holotype: Gray Herbarium; isotypes: to be distributed from the Nevada State Museum).

OTHER SPECIMENS STUDIED. **Nevada.** Esmeralda Co.: White Mts., northeast side of Boundary Peak, 10,400 ft., 7 Jul 1979, *Ann Pinzl 2397*, *J. Pinzl* (GH); bowl on NE side of Boundary Peak, one-third of the way down the middle, approx. 11,300 ft., 20 Jul 1981, *George T. Austin s.n.* (GH); central bowl, NE side of Boundary Peak, 10,800 ft., 21 Jul 1981, *Ann Pinzl 4448* (GH).

In habit, *Arabis pinzlae* is more like *A. pygmaea* Roll. than *A. platysperma*, although all three species are closely related. The one to three erect or ascending siliques of *A. pinzlae* are narrower than in either of the other species. The seeds of *A. pinzlae* are smaller, less flattened and more narrowly winged than in either *A. platysperma* or *A. pygmaea*. But the most fundamental difference that marks *A. pinzlae* as a distinct species is in the nature of the trichomes. The trichomes on the leaves of *A. pygmaea* are comparatively very coarse and simple or merely forked. Both *A. platysperma* and *A. pinzlae* have dendritically branched trichomes but in *A. platysperma* they have but 3 to 5 branches, are relatively coarse, and are noticeably spaced from each other, while in *A. pinzlae* the trichomes are fine, have many branches, and are densely packed on the leaf surface. The pubescence

is dense and abundant, extending from basal leaves to the cauline leaves, upper stems and even occurring sparsely on the pedicels and sepals in *A. pinzlae* whereas at least the upper parts of the plants in the other two species are glabrous. Typically, the caudex of *A. pinzlae* is branched below the ground surface and the elongated tap root appears to be adapted to moving soil. Remnants of old basal leaves are often present on the caudex branches that show evidence of having been buried beneath the soil.

*Arabis platysperma*, *A. pygmaea*, and *A. pinzlae* form a distinctive group in *Arabis*. They share features such as erect to divaricately ascending siliques, relatively widely winged seeds, broad siliques, and small sessile non-auriculate cauline leaves. The nearest relative of these species is *A. suffrutescens* but that species has reflexed siliques.

At the time of my former treatment, *Arabis pygmaea* was known from only two collections. Since then, it has been collected several times but always in a relatively restricted area of the southern Sierra Nevada, and so far, not outside of Tulare County, California. I have seen only three flowers of this species. The sepals are erect, nonsaccate, broadly oblong and sparsely pubescent. The petals are white, erect, more lingulate than spatulate, ca. 4 mm long, and less than twice as long as the sepals. There are minor differences between some of the five collections at my disposal. The importance of these differences cannot be assessed without a fuller sampling of the species as a whole.

#### SPECIES RELATED TO *ARABIS COBRENSIS*

Aside from the loose branching habit, narrow entire basal leaves densely pubescent with fine dendritic trichomes characteristic of *Arabis cobrensis* M. E. Jones, the nearly orbicular substantially winged seeds are a distinctive feature of this species. Although somewhat related to *A. puberula* Nutt., *A. cobrensis* has, in the past, stood alone as a relatively uniform, easily distinguished species. Material from the Bodie Hills of eastern Mono County, California, collected in 1945 (Rollins 1946), might have cast doubts on the singularity in *Arabis* if *A. cobrensis* had the appropriate connection been made at that time. But the specimens then referred to as possible hybrids between *A. sparsiflora* var. *subvillosa* and *A. fernaldiana* var. *stylosa* were so different from *A. cobrensis* that the chance of their being a related species, not hybrids at all, did not surface. New material of still a third taxon of this alliance from Elko and Washoe counties, Nevada, has sparked the necessary study to clarify the situation. Many new collections of *A. fernaldiana* var. *stylosa* (Rollins 1981) are available and that taxon is much better understood than previously. I do not

now believe var. *stylosa* is present in eastern California as previously indicated (Rollins 1946). It appears to be common but restricted, as far as our present information shows it, to the mountains of central and northern Nevada.

Thus delimited, var. *stylosa* cannot logically be considered parental to putative hybrids in the Bodie Hills area of Mono County, California, as was presumed to be the case earlier. Furthermore, an extensive sampling of *Arabis* populations of the Bodie Hills by Tim Messick has shown that what we name *A. bodiensis* below is consistent in its characters and is present on many appropriate sites throughout the area. This adds up to the necessity of recognizing the Bodie Hills material as an undescribed species.

The following key gives the readily seen distinctions between *Arabis cobrensis* and the two related new species, *A. bodiensis* and *A. falcifructa*.

#### KEY TO THE SPECIES

- A. Siliques strongly descending, straight or nearly so; pedicels strongly recurved but not geniculate; seeds nearly orbicular, compressed, prominently winged all around; wing at least 0.25 mm wide ..... 1. *A. cobrensis*.
- A. Siliques widely spreading, curved; pedicels divaricately ascending to widely curved downward; seeds oblong to somewhat orbicular, plump, narrowly winged to winged only distally, wing less than 0.05 mm wide.
  - B. Pedicels widely arched downward, 6–10 mm long; siliques widely arched downward, acuminate; styles evident ..... 2. *A. falcifructa*.
  - B. Pedicels divaricately ascending, 3–6 mm long; siliques widely spreading at right angles to rachis to divaricately ascending, acute; styles obscure ..... 3. *A. bodiensis*.

#### 1. *Arabis cobrensis* M. E. Jones.

The known geographic range of this species has changed but little since my earlier treatment. It has been found in eastern California (Rollins 1946) but otherwise no significant extensions of range have been reported. It is surprising that it has not been found in Utah. Evidently the sweep of occurrence is northward from Mono County, California, across Nevada to eastern Oregon, then eastward through southern Idaho to south central Wyoming.

#### 2. *Arabis falcifructa* Rollins, sp. nov.

Herba perennis multicaulis; caudicibus ramosis; caulibus simplicibus vel sparse ramosis, erectis, 2–4.5 dm altis, inferne dense pubescentibus, superne sparse pubescentibus vel glabris; foliis radicalibus petiolatis integris, linearis vel lineari-oblongatis, canescentibus, 1.5–2.5 cm longis, 2–3.5 mm latis; foliis caulinis oblongis, remotis, sessilibus, auriculatis, 8–15 mm longis, 1.5–3 mm latis; sepalis erectis, oblongis, non-saccatis, ca. 3 mm longis; petalis albo-purpureis, anguste spathulatis, 5–7 mm longis; pedicellis fructiferis patentibus vel recurvatis, sparse pubescentibus, 7–10 mm longis; siliquis falciformis, glabris, patentibus, 4–6 cm longis, ca. 1.5 mm latis; seminibus oblongis vel late oblongis, anguste alatis vel exalatis, ca. 1.5 mm longis; cotyledonibus accumbentibus.

Perennial with numerous stems and many branched caudices; stems erect, numerous, mostly simple, occasionally branched above, densely pubescent below, sparsely pubescent to glabrate above, 2–4.5 dm tall; basal leaves numerous, erect, entire, linear to linear-oblongate, acuminate, densely pubescent with minute dendritically branched trichomes, 1.5–2.5 cm long, 2–3.5 mm wide; cauline leaves oblong, acute, sessile, auriculate, few and remote, 8–15 mm long, 1.5–3 mm wide; sepals erect, oblong, nonsaccate, sparsely pubescent, scarious-margined above, ca. 3 mm long; petals erect, narrowly spatulate, not differentiated into blade and claw, pale purplish, 5–7 mm long; stamens exserted above calyx; fruiting pedicels widely arched downward, slender, pubescent, sparsely so or glabrate, 7–10 mm long, slightly swollen toward apex; siliques widely arched downward, gently curved inward, acuminate, 1-nerved below middle, glabrous, 4–6 cm long; ca. 1.5 mm wide; valves not constricted between seeds, plain; styles ca. 1 mm long; seeds oblong to broadly oblong, narrowly winged mainly distally or the wings obsolete, ca. 1.5 mm long, ca. 1.2 mm wide; cotyledons accumbent.

TYPE: Nevada, Elko County, in crevices of rocks, sagebrush area on slope of a high ridge, near U.S. Hwy. 93 between Thousand Springs and Jackpot, 37 miles south of Jackpot, 18 Jun 1979, *Reed C. and Kathryn W. Rollins* 79267 (holotype: GH; isotypes: distributed as *A. cobrensis*).

OTHER COLLECTIONS STUDIED. Nevada. Elko Co.: 1 mile N of San Jacinto, 30 May 1945, *Ripley and Barneby* 6465 (GH). Lander Co.: Shoshone Mts., ca. 18 mi. and 315° from Austin, 18 Jun 1979, *S. Goodrich* 12746 (GH).

Material of *Arabis falcifructa* was at first identified as *A. cobrensis* even though the siliques were longer, bowed instead of straight, and both pedicels and siliques were gently and widely bent downward instead of being strongly recurved as in *A. cobrensis*. Had we looked at the seeds, such an identification would have been difficult to make because the seeds of *A. cobrensis* are substantially winged all around whereas those of *A. falcifructa* are only winged distally and with the barest suggestion of wings along the lateral margins, or they are scarcely winged at all. The amount of winging present on the seeds of *Arabis*, taken generally, is somewhat variable and this character must be used with care. But when the differences are substantial, as in the case of *A. cobrensis* vs. *A. falcifructa*, this can be decisive in correlation with other characters in pointing to taxa that should be recognized. The siliques of *A. falcifructa* are acuminate and tipped with a style nearly 1 mm long while the siliques of *A. cobrensis* are blunt or at most acute and there is either no style at all or if one is present, it is so short that it can scarcely be seen without considerable magnification.

### 3. *Arabis bodiensis* Rollins, sp. nov.

Herba perennis, multicaulis; caulibus erectis, inferne dense pubescentibus, superne sparse pubescentibus vel glabratis, 1.5–3.5 dm altis; foliis radicaulibus petiolatis, integris, lineari-oblongatis, canescentibus, 1–3 cm longis, 1.5–3 mm latis; foliis caulinis sessilibus, oblongis, auriculatis, pubescentibus, 1–2.5 cm longis; pedicellis fructiferis, divaricatis, sparse pubescentibus vel glabris, 3–6 mm longis; siliquis falcatis, divaricatis, glabris, 3–5 cm longis, ca. 2 mm latis; seminibus anguste-alatis, oblongis vel obicularibus, ca. 1.5 mm longis; cotyledonibus accumbentibus.

Perennial; caudex usually with many branches; stems several to numerous, erect, usually branched above but sometimes simple, densely pubescent below, sparsely pubescent to glabrate above, 1.5–3.5 dm tall; basal leaves whitish with a dense covering



of minute dendritically branched trichomes, usually with a few large simple or forked trichomes near base of petiole, entire, linear to linear-oblongate, acute to acuminate, petiolate, 1-3 cm long, 1.5-3 mm wide; cauline leaves sessile, auriculate, oblong, acute, reduced upward, 1-2.5 cm long, 1.5-3 mm wide, lower densely pubescent, upper less so; fruiting pedicels divaricately ascending, straight, pubescent to glabrous or nearly so, expanded toward apex, 3-6 mm long; siliques widely spreading to slightly ascending, gently curved to nearly straight, glabrous, faintly 1-nerved below, acute at apex, 3-5 cm long, ca. 2 mm wide; seeds broadly oblong to nearly orbicular, narrowly winged, ca. 1.5 mm long; cotyledons accumbent.

TYPE: California, Mono County, in loose soil of old mine, 2 miles northwest of Masonic, 5.9 miles from Bridgeport-Sweetwater highway, 3 Aug 1945, *Ira L. Wiggins and Reed C. Rollins* 536 (holotype: GH; isotype: DS).

OTHER SPECIMENS STUDIED. **California. Mono Co.:** small hill adjacent to Masonic Peak and on Masonic Peak, 4 Aug 1945, *Wiggins and Rollins* 553 (DS, GH); 2 mi. NW of Masonic, 5.9 mi. from Bridgeport-Sweetwater hwy., 3 Aug 1945, *Wiggins and Rollins* 537 (DS, GH); NE slope of Masonic Peak, ca. 8 mi. NE of Bridgeport-Sweetwater hwy., 4 Aug 1945, *Wiggins and Rollins* 559 (DS, GH); top of cliff across Clearwater Creek, road to Bodie from hwy. 395, Bodie quadrangle, 27 Jun 1979, *Messick* 645 (HSC); near summit of Mt. Biedeman, 18 Jun 1979, *Messick* 515 (HSC); 5.1 mi. S of Bodie, 20 Jun 1980, *Messick* 992 (HSC); between New York Hill and Masonic Mt., 25 Jun 1980, *Messick* 1062 (HSC); near W summit of Masonic Mt., 24 Jul 1981, *Messick* 1726 (HSC). **Nevada. Mineral Co.:** Big Indian Mine road, road to Cory Canyon, 9,500 ft, 12 Jul 1945, *Alexander and Kellogg* 4449 (GH).

Although *Arabis bodiensis* is most closely related to *A. cobrensis* on the basis of similarity of pubescence, basal leaves and the remoteness of the cauline leaves, it also has some features in common with *A. inyoensis*. Upward spreading pedicels and widely spreading siliques are characters shared by *A. bodiensis* and *A. inyoensis*. The trichomes of *A. inyoensis* are coarser than those of *A. bodiensis* and the siliques are straight instead of being curved as in the latter species. Characters given in the key readily separate *A. bodiensis* from *A. cobrensis*. It is probable that *A. bodiensis* is relatively local in its occurrence, following somewhat the pattern of *Draba quadricostata* and *Streptanthus oliganthus* which also have a limited distribution in the same general area.

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