

A MONOGRAPH OF THE GENUS *PHYSOSTEGIA* (LABIATAE)

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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*.

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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.

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| <ul style="list-style-type: none"> 1. Habit <ul style="list-style-type: none"> a. Perennial b. Annual 2. Stem Pubescence <ul style="list-style-type: none"> a. Glabrous or nearly so below inflorescence b. Pubescent throughout much of its length 3. Leaf Texture <ul style="list-style-type: none"> a. Firm b. Membranaceous 4. Leaves Conspicuously Glandular-punctate <ul style="list-style-type: none"> a. Yes b. No 5. Leaf Pubescence <ul style="list-style-type: none"> a. Glabrous or at most ciliate on margins b. Pubescent on both surfaces 6. Petioles <ul style="list-style-type: none"> a. Only lower leaves petiolate b. All leaves petiolate 7. Inflorescences <ul style="list-style-type: none"> 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 <ul style="list-style-type: none"> 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 | <ul style="list-style-type: none"> d. Absent (i.e., flowers borne in axils of normal foliage leaves) 9. Shape of Calyx <ul style="list-style-type: none"> 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 <ul style="list-style-type: none"> a. Obscurely veined b. Conspicuously veined 11. Flower Color <ul style="list-style-type: none"> a. White to shades of pink and purple b. Yellowish 12. Anthers Bearded <ul style="list-style-type: none"> a. No (although may be slightly pubescent) b. Yes 13. Anther Coherence <ul style="list-style-type: none"> a. Anthers free from one another b. Upper anthers coherent 14. Nutlet Shape <ul style="list-style-type: none"> 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 <ul style="list-style-type: none"> a. Glabrous b. Puberulent 16. Nutlet Sculpturing <ul style="list-style-type: none"> a. Smooth b. With many irregular ribs running parallel to long axis of nutlet c. Verrucose |
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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 Melitteae, 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,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.

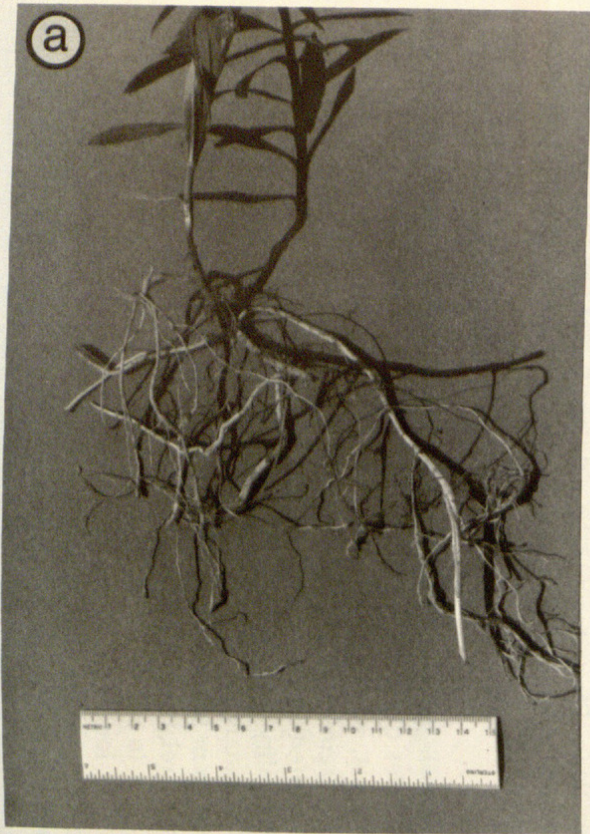


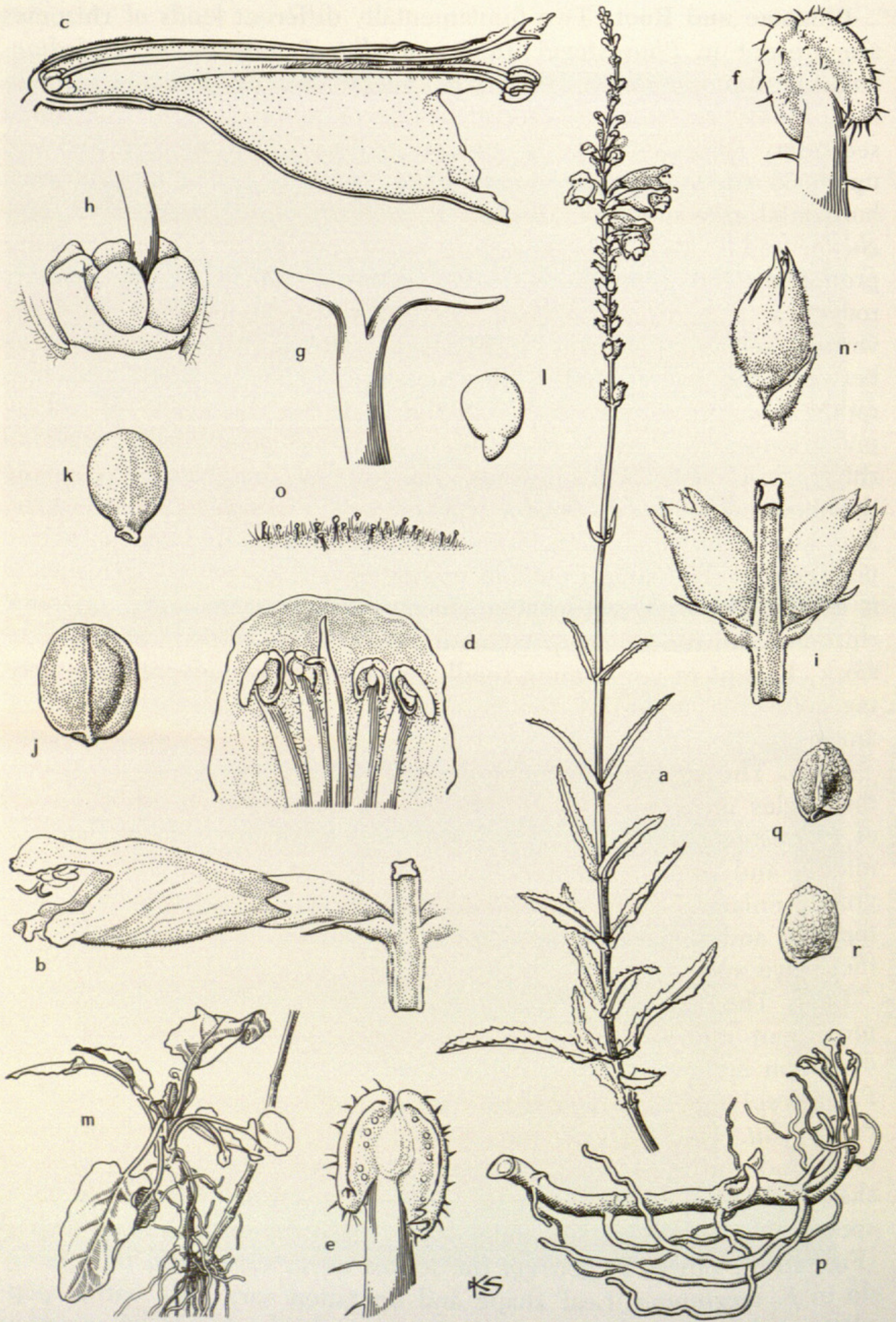
FIG. 1. Rhizome morphology of *Physostegia virginiana* ssp. *virginiana* (a) and ssp. *praemorsa* (b).

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 μ . 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 μ dia.) has a cap composed of 4–8 cells, with the cell walls all situated perpendicular to the pe-

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, vesture 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.

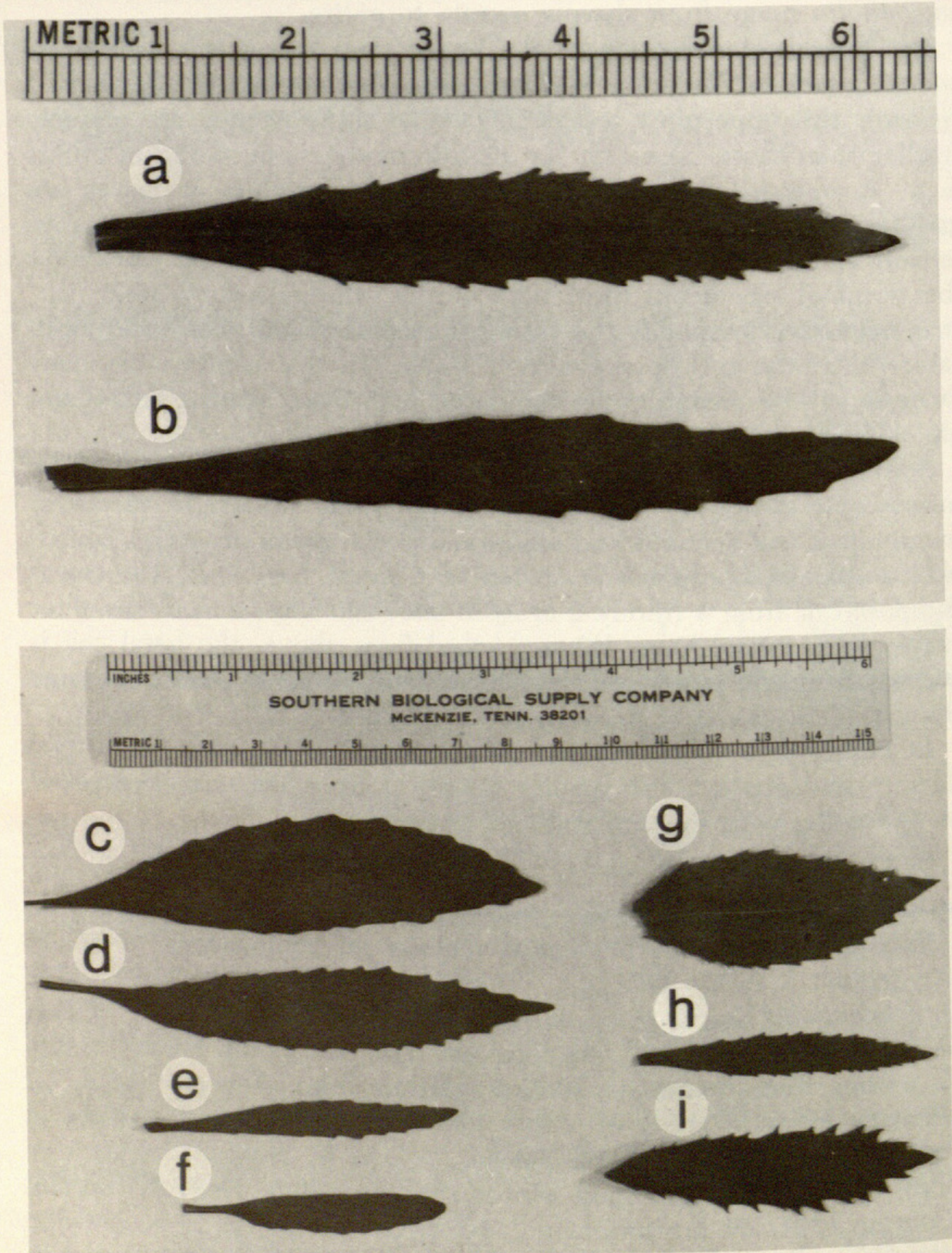
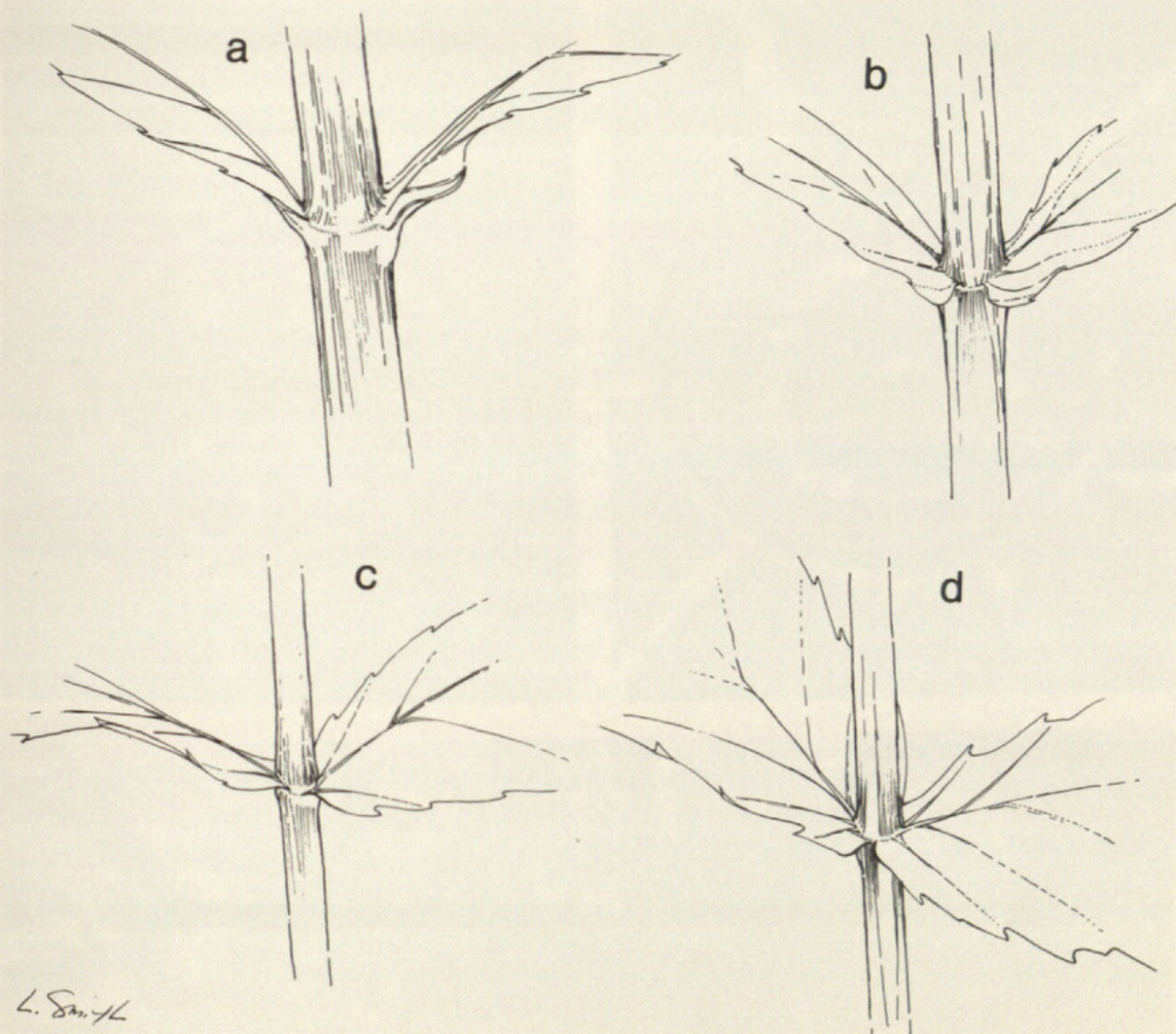


FIG. 3. Variation in leaf margin. A, *Physostegia virginiana* ssp. *praemorsa* (Cantino 918). B, *P. purpurea* (Cantino 1004). C and D, *P. leptophylla* (Cantino 973 and 970). E, *P. purpurea* (Cantino 1004). F, *P. intermedia* (Cantino 1065). G, *P. correllii* (Cantino 1064). H and I, *P. virginiana*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



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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 μ 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 μ , 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

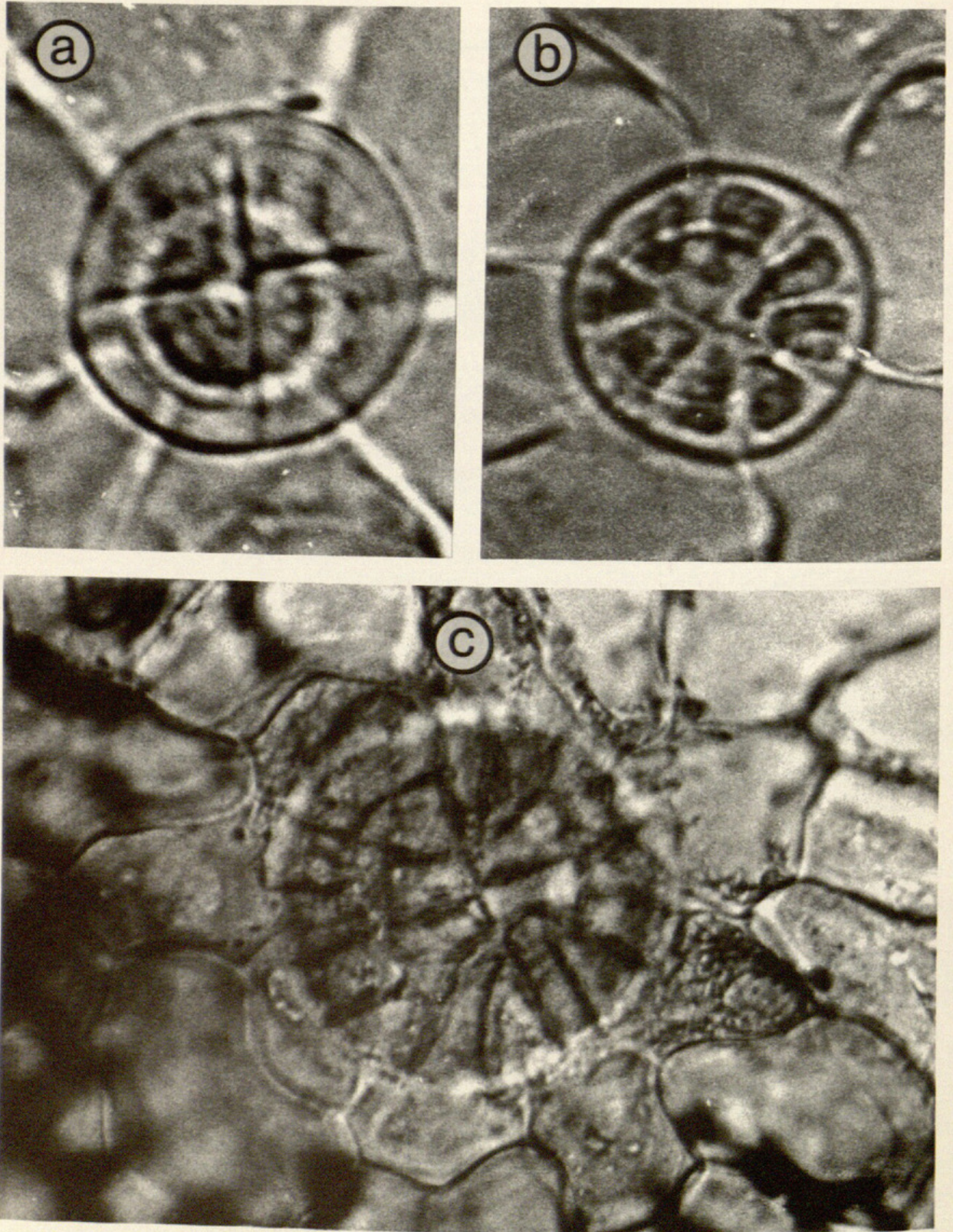


FIG. 5. Glands on leaf surface in *Physostegia virginiana*. A, small gland with four-celled cap, $\times 1150$ (Cantino 944). Note circular outline of basal cell visible through cap. B, small gland with eight-celled cap, $\times 850$ (Cantino 946). C, large gland, $\times 700$ (Cantino 877). Note that 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,

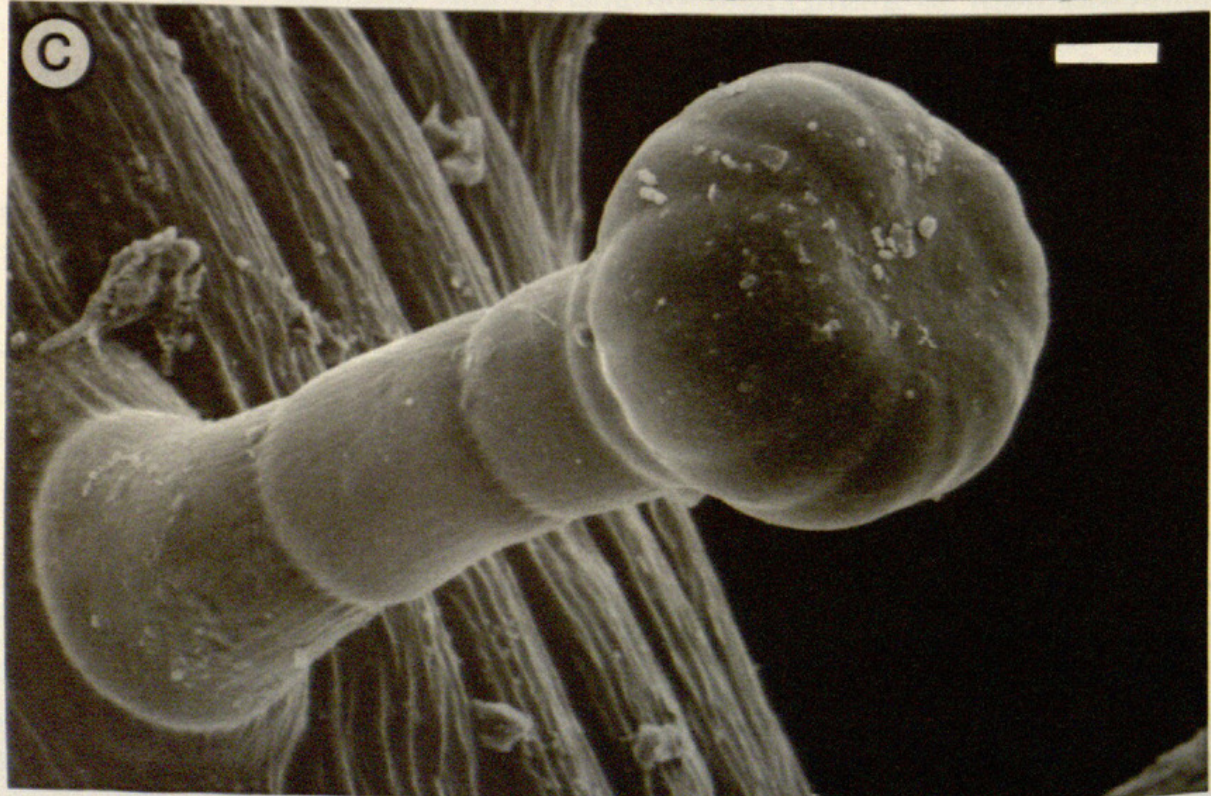
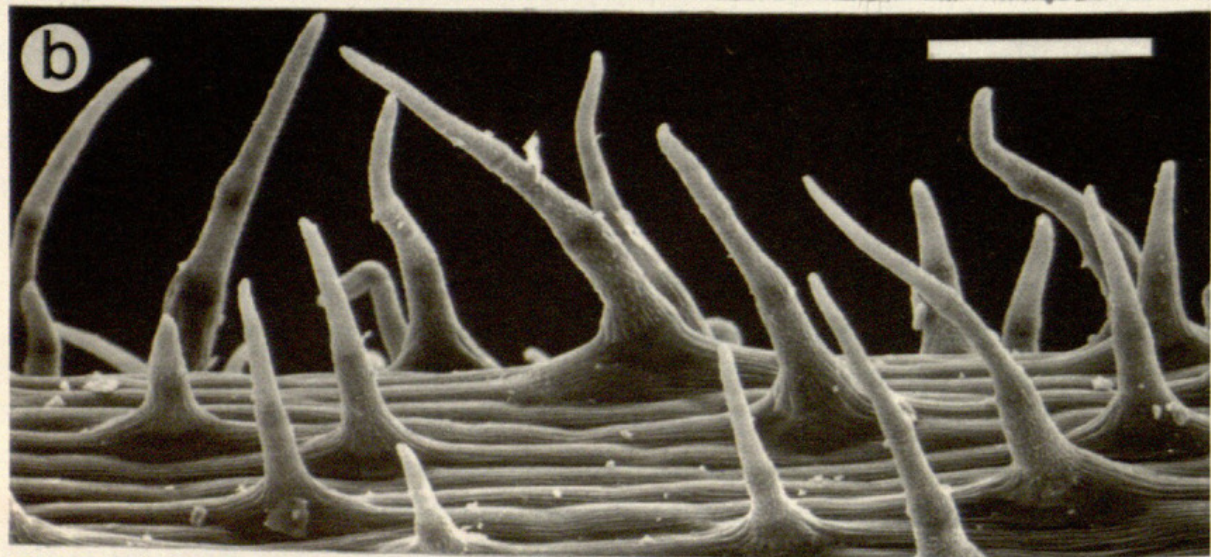
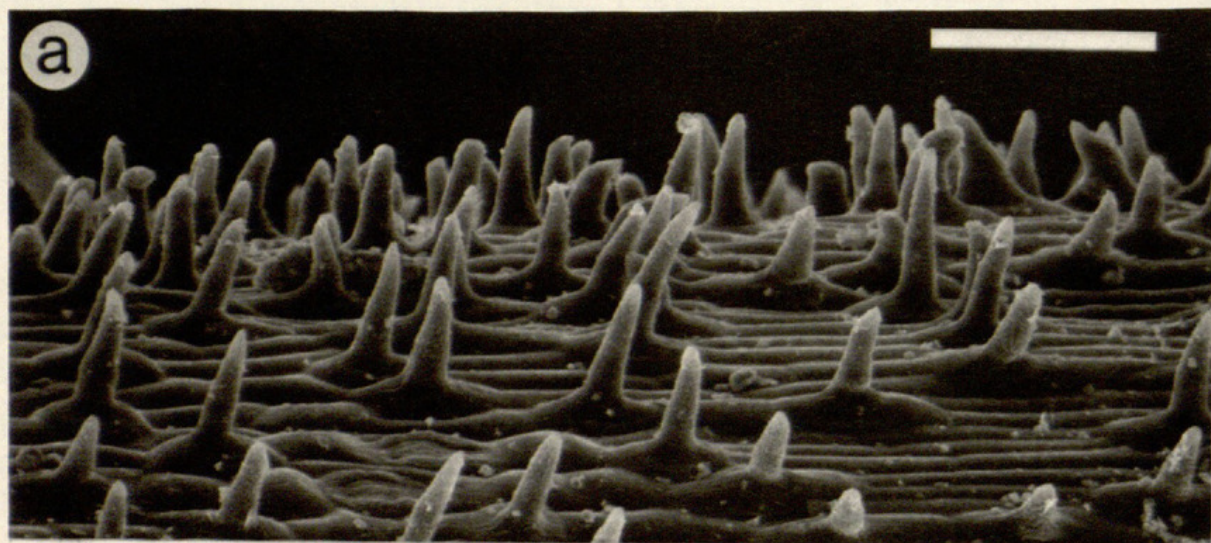
there being one ovule per ovary lobe. The embryo sac is unusual in shape, composed of two expanded regions, a downward-directed micropylar lobe and an upper lobe in which the endosperm later develops, with the two lobes separated by a constriction.

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 μ long and 29–59 μ wide; the polar diameter ranged from 38 to 58 μ .

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 μ . B, *P. angustifolia* (Cantino 1057), white bar = 100 μ . C, *P. godfreyi* (Cantino 1054), white bar = 10 μ . Plants grown from rhizomes collected in same natural population as voucher. Vouchers at GH.

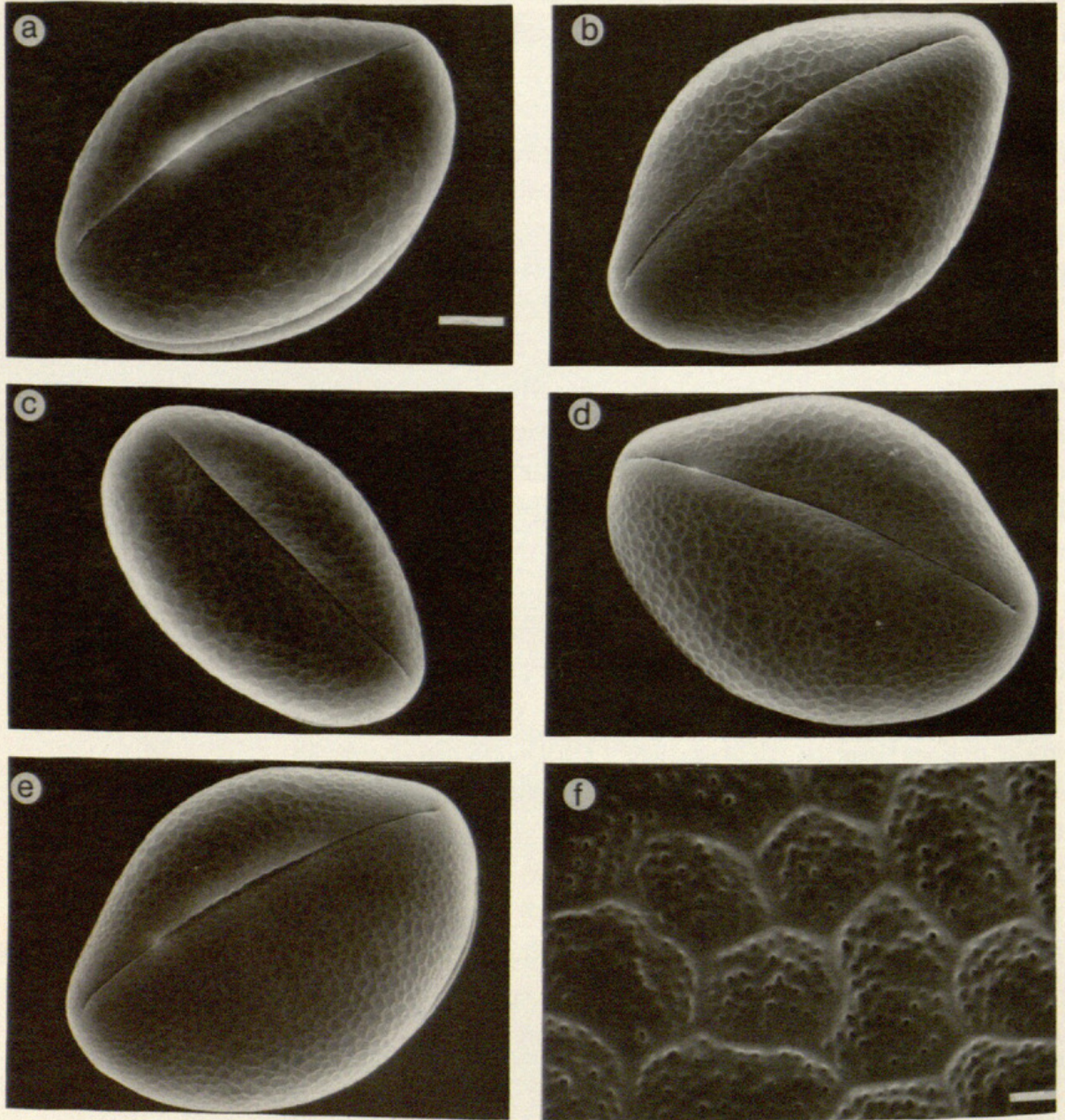


FIG. 7. Pollen grains of *Physostegia*. A, *P. virginiana* ssp. *praemorsa* (Cantino 882). B, *P. correllii* (Cantino 1137). C, *P. parviflora* (Eastham s.n, DAO 16106). D, *P. digitalis* (Cantino 1068). E, *P. godfreyi* (Cantino 1054). A-E, white bar = 10 μ . F, *P. leptophylla* (Cantino 970), white 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 (μ)	Width (μ)
<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 & 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-

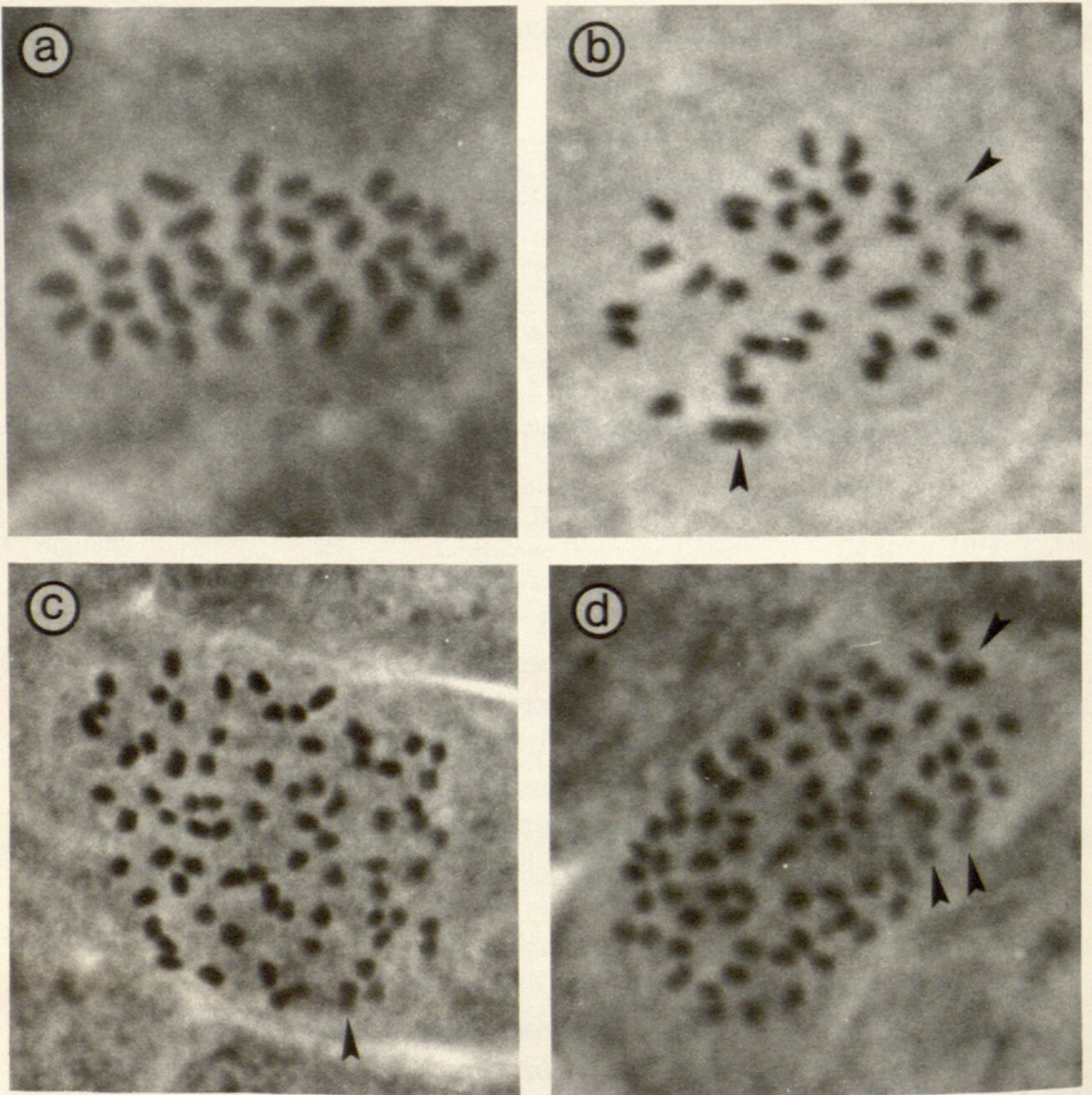


FIG. 8. Chromosomes of root tip cells. Magnifications are approximate. Vouchers at GH. A, *Physostegia godfreyi*, $2n = 38$, $\times 3250$ (Cantino 1138). B, *P. pulchella*, $2n = 38$, $\times 2700$ (Mahler 8520): upper arrow—chromosome lying partly outside the plane of focus; lower arrow—two overlapping 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
	8-Hour Photoperiod	
<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%)
	12-Hour Photoperiod	
<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%)
	16-Hour Photoperiod	
<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.

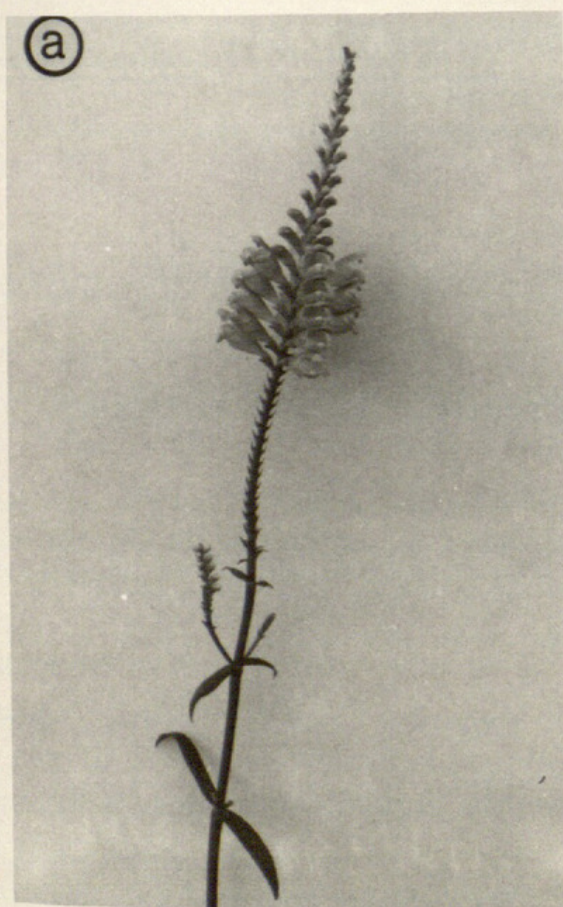


TABLE 8. SEED GERMINATION WITHOUT PRETREATMENT.

<u>Taxon and Voucher*</u>	<u>No. of seeds</u>	<u>% germination after 30 days</u>
<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

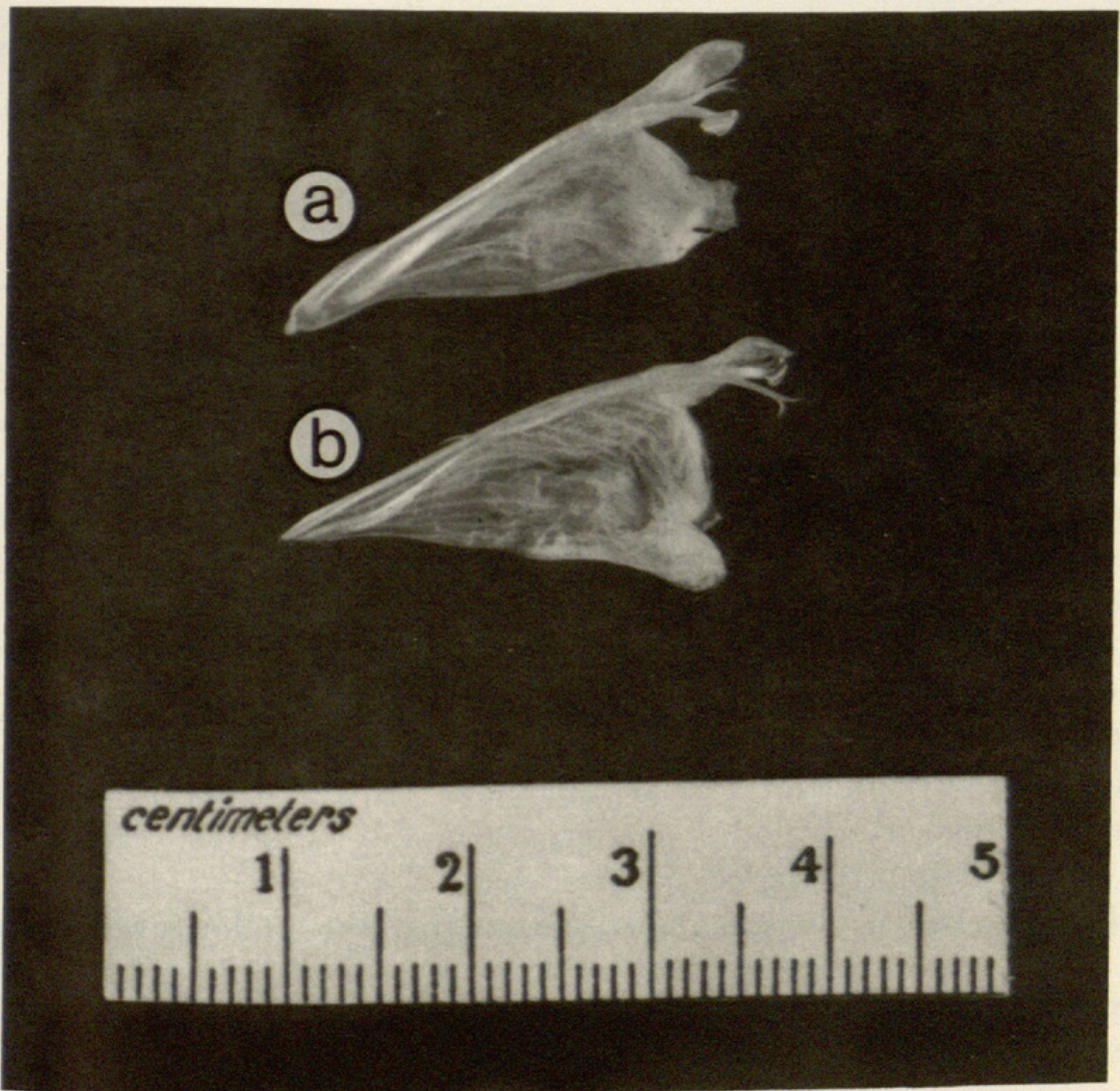


FIG 10. Stages of protandry in *Physostegia virginiana*. A, functionally staminate stage. B, functionally carpellate stage.

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. longispala*; 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 emasculating 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.

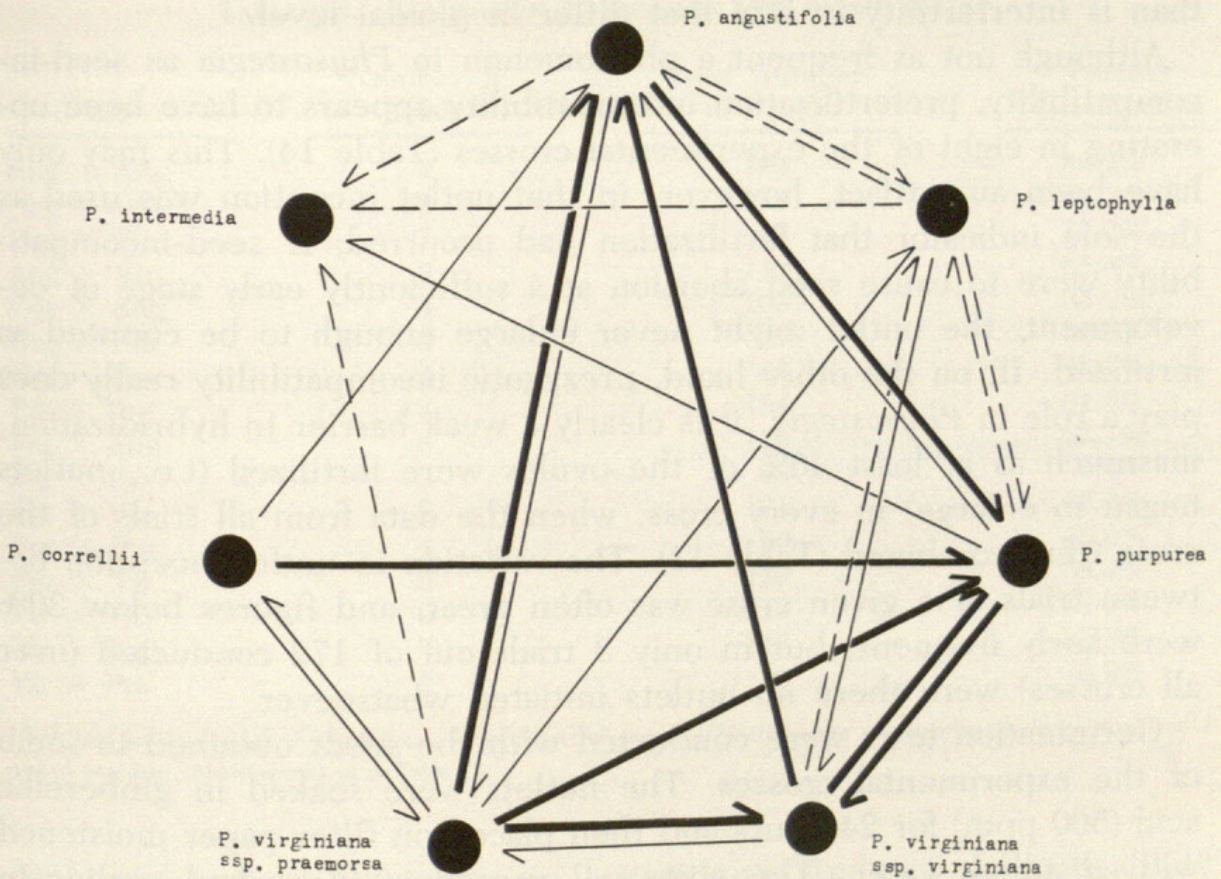


FIG. 11. Interfertility in *Physostegia*. Broken line—seed yield 10% or less of maximum possible. Thin solid line—seed yield greater than 10% but significantly less than control crosses. Heavy solid line—no significant difference between seed yield of experimental hybridizations and control crosses. No line signifies no cross attempted. Arrows indicate direction of pollen transfer.

and $\text{Vir} \times \text{Pra}$) 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* × *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* × *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 F₁ generation of the crosses listed in Table 15 were grown to anthesis. The incidence of grossly abnormal plants among the F₁s 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 pre-mating 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 pre-mating 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 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 autoployploid 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"> 1. One or more leaves widest below middle of blade: 0, no; 1, yes. 2. At least one leaf widest near base of blade: 0, no; 1, yes. 3. Majority of larger leaves bluntly toothed to entire, 0; sharply serrate, 1. 4. One or more leaves clasp stem: 0, yes; 1, no. 5. One or more petiolate leaves present at anthesis: 0, no; 1, yes. 6. Empty bracts produced below flowers: 0, no; 1, yes. 7. Base of stem conspicuously swollen: 0, no; 1, yes. 8. Flowers crowded, adjacent calyces overlapping half or more of their lengths: 0, yes; 1, no. 9. Horizontal rhizomes produced, 0; all rhizomes vertical, 1. 10. Stalked glands present on calyx: 0, yes; 1, no. 11. Stalked glands present on corolla: 0, no; 1, yes. 12. Glandular dots on calyx inconspicuous, few, or absent, 0; abundant and conspicuous, 1. 13. Calyx lobes all acute to attenuate, 0; some cuspidate, 1. 14. One or more pairs of weak primary veins (besides midrib) at base of blade: 0, no; 1, yes. 15. Nutlet surface smooth, 0; verrucose, 1.
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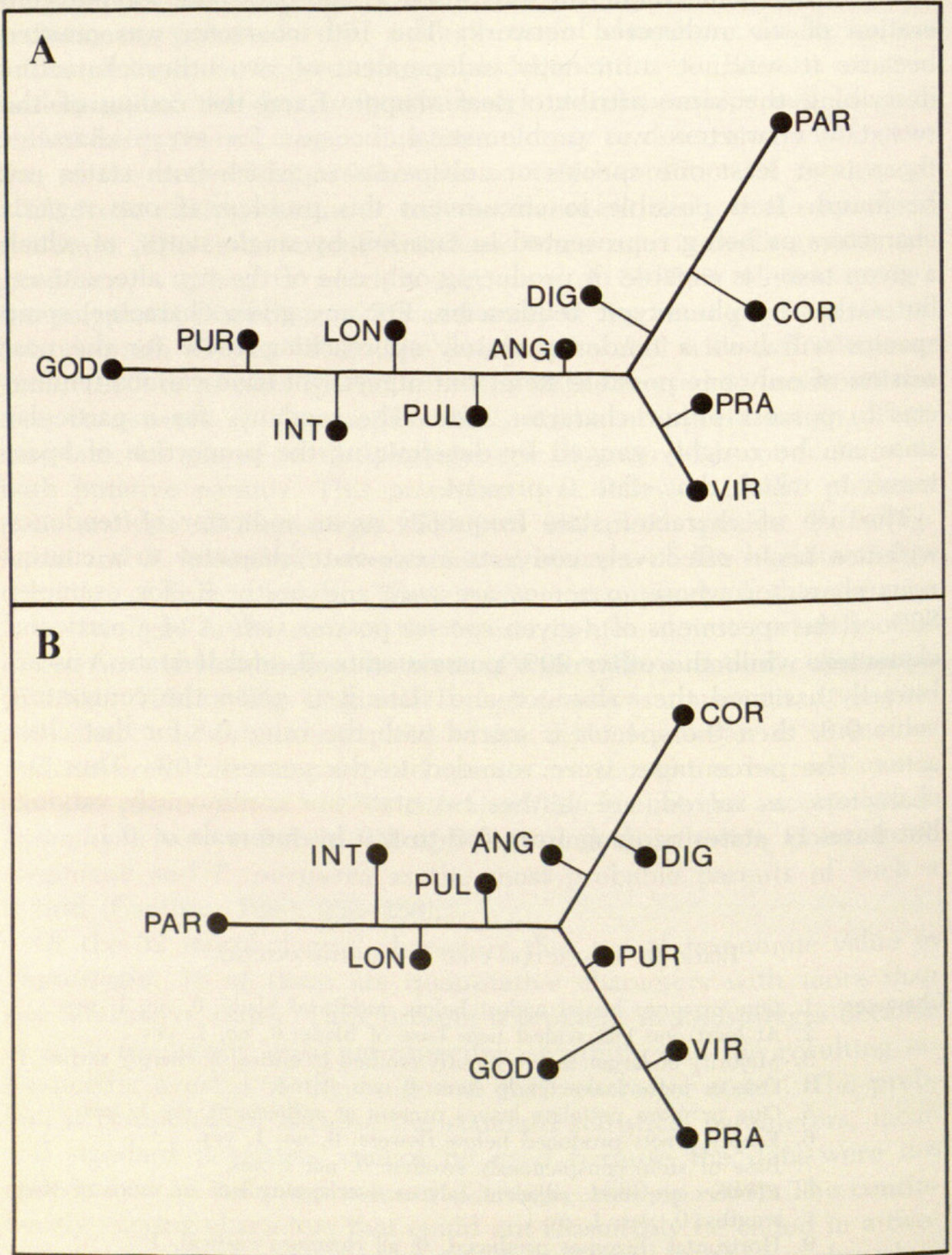


FIG. 12. Undirected networks for *Physostegia*. A, network based on entire 15-character data set. B, network based on data set lacking character no. 3. Taxon abbreviations as in Table 17.

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).

NOMENCLATRURAL 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 Breyne (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 Breyne 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 Bentham, a more likely explanation was hinted at by Shinners (1949), although he incorrectly attributed the reversal of Bentham'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 Bentham'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 vesture 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 (Fig. 4b, d), inconspicuously clasping (Fig. 4c), not clasping (Fig. 4a); 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 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 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.** Clarendon 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.

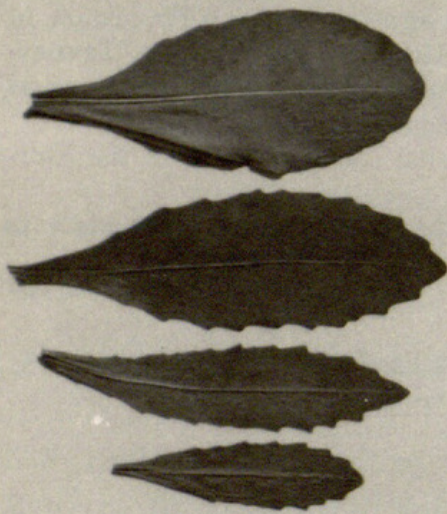
NOMENCLATURAL NOTES: The application of the epithets *purpurea* and *denticulata* to this species is discussed elsewhere (Cantino, 1981b).

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.

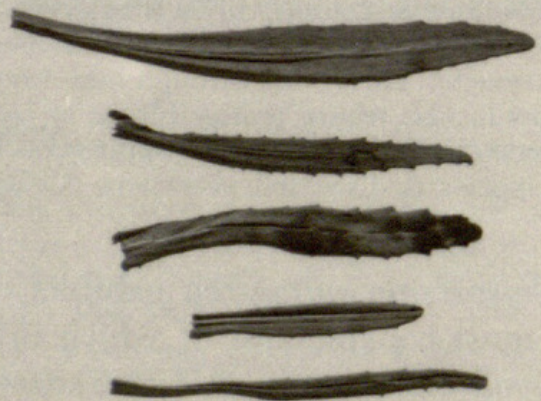
Another character that varies clinally in *Physostegia purpurea* is the degree of crowding of the flowers. In southern Florida, the flowers are always loosely spaced, adjacent calyces overlapping little if at all. More tightly packed flowers occur with increasing frequency as one moves northward through 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

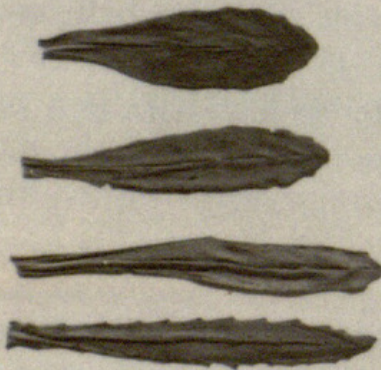
PHYSOSTEGIA PURPUREA



N. CAROLINA



GEORGIA



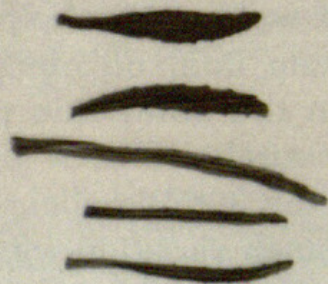
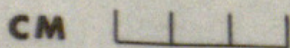
N. CAROLINA



S. FLORIDA



GEORGIA



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 intrapopulation 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).

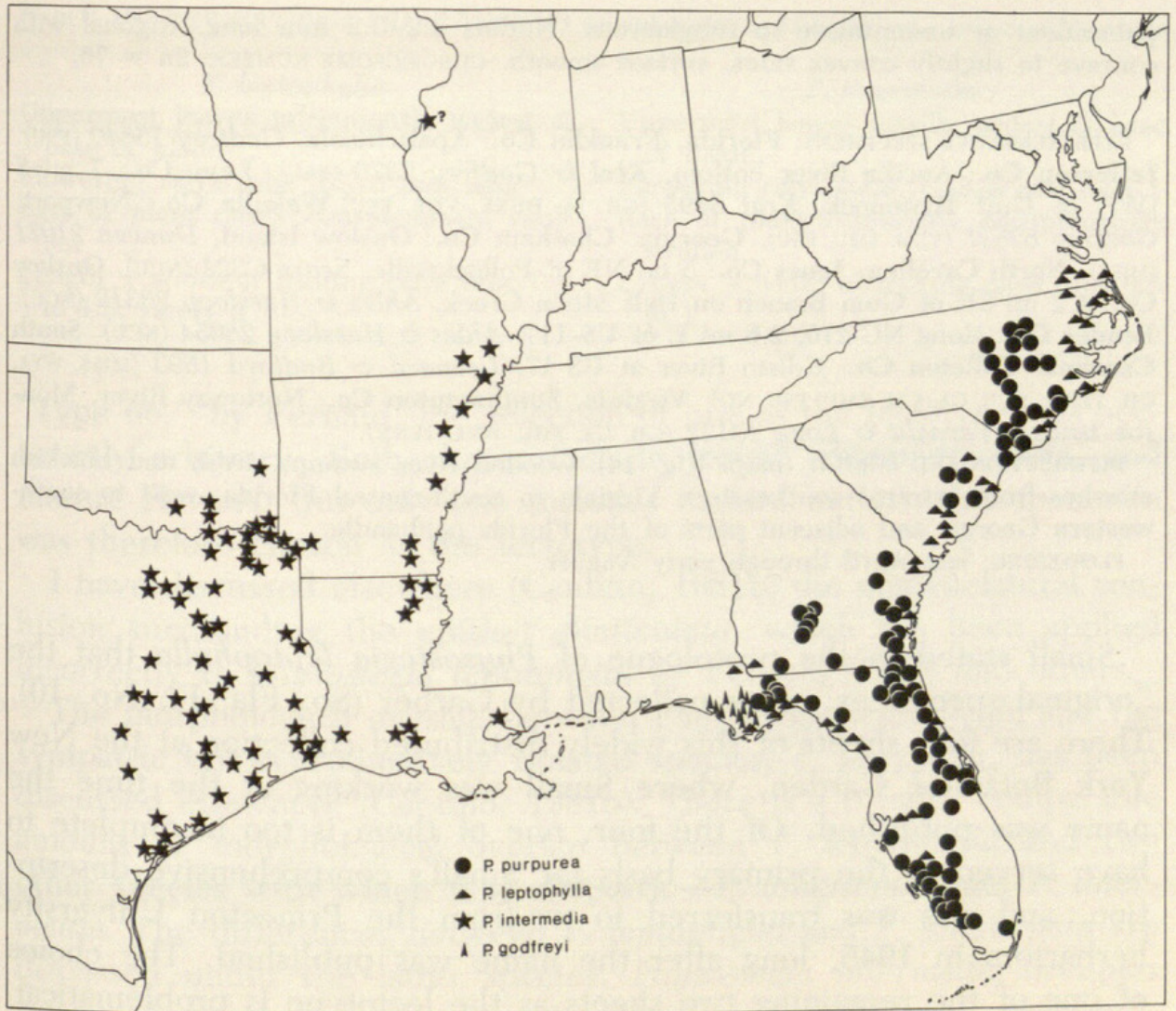


FIG. 14. Distribution map of *Physostegia purpurea*, *P. leptophylla*, *P. godfreyi*, and *P. intermedia*.

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) Engelman & 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* (NLU). **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 infima 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 sessilia, 5–12 cm longa, 0.5–1.7 cm lata, oblanceolata, elliptica vel lanceolata, base attenuata, cuneata, rotundata vel auriculata, pro parte maxima amplectenti, apice plerumque acuto vel attenuato, marginibus repandis, obtusi-dentatis, vel serratis (raro integris). Folia caulina superna magnopere vel modice diminuta, lanceolata vel elliptica, saepe prope basem laminae amplectem 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. HOLOTYPUS: Louisiana, Calcasieu Parish, 2 miles north of Edgerly, 18-V-1968, J. W. Thieret 28876 (SMU). ISOTYPUS: 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;

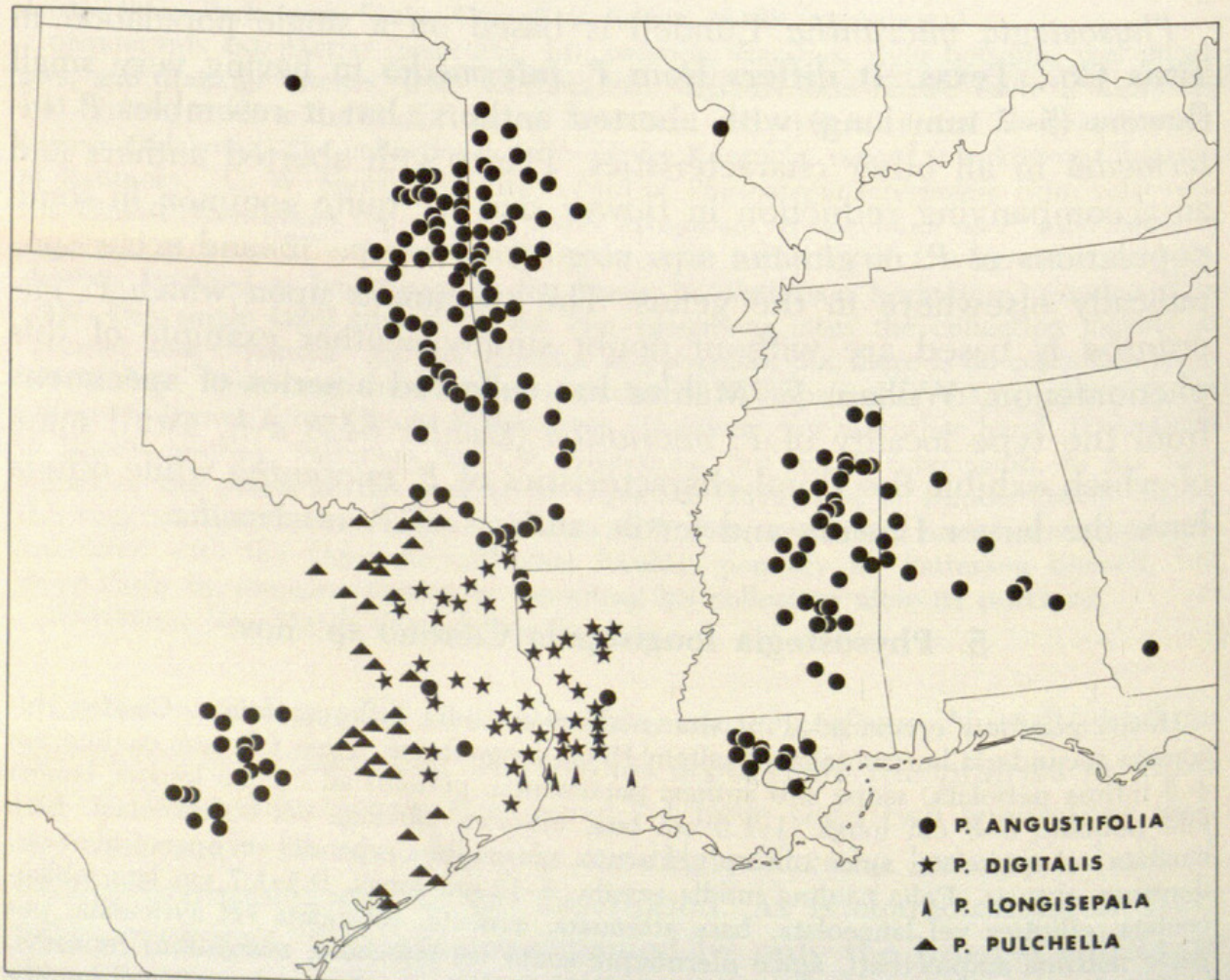


FIG. 15. Distribution map of *Physostegia angustifolia*, *P. digitalis*, *P. longisepala*, and *P. pulchella*.

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

<p><i>P. longisepala</i></p> <p>Longest calyx lobes 2.5–3.5 mm long; frequently cuspidate</p> <p>Longest trichomes on raceme axis 0.2–0.25 mm long</p> <p>Lower stem leaves usually oblanceolate</p> <p>Stem leaves commonly sharply serrate</p>	<p><i>P. leptophylla</i></p> <p>Calyx lobes rarely over 2.5 mm long; infrequently cuspidate</p> <p>Longest trichomes on raceme axis 0.1–0.13 mm long</p> <p>Lower stem leaves elliptical to lanceolate (rarely oblanceolate)</p> <p>Leaves bluntly toothed, repand, or entire (rarely sharply serrate)</p>
<p><i>P. longisepala</i></p> <p>Longest calyx lobes 2.5–3.5 mm long; frequently cuspidate</p> <p>Horizontal secondary rhizomes produced</p> <p>Lowest 4–8 stem nodes bear petiolate leaves</p> <p>Stem with (9–)11–15 leafy nodes below inflorescence</p>	<p><i>P. pulchella</i></p> <p>Calyx lobes rarely over 2.2(–2.5) mm long; infrequently cuspidate</p> <p>Horizontal secondary rhizomes never produced; rhizomes short and vertical</p> <p>Lowest 1–4 stem nodes bear petiolate leaves</p> <p>Stem with 7–10(–12) leafy nodes below inflorescence</p>
<p><i>P. longisepala</i></p> <p>Corolla deep lavender to reddish violet</p> <p>Horizontal secondary rhizomes produced</p> <p>Lowest 4–8 stem nodes bear petiolate leaves; some usually persistent through anthesis</p>	<p><i>P. angustifolia</i></p> <p>Corolla usually very pale lavender to white</p> <p>Horizontal secondary rhizomes rarely produced</p> <p>Lowest 1–4 stem nodes bear petiolate leaves; these usually deciduous by anthesis</p>

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* (VPI, 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. Shinnery (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

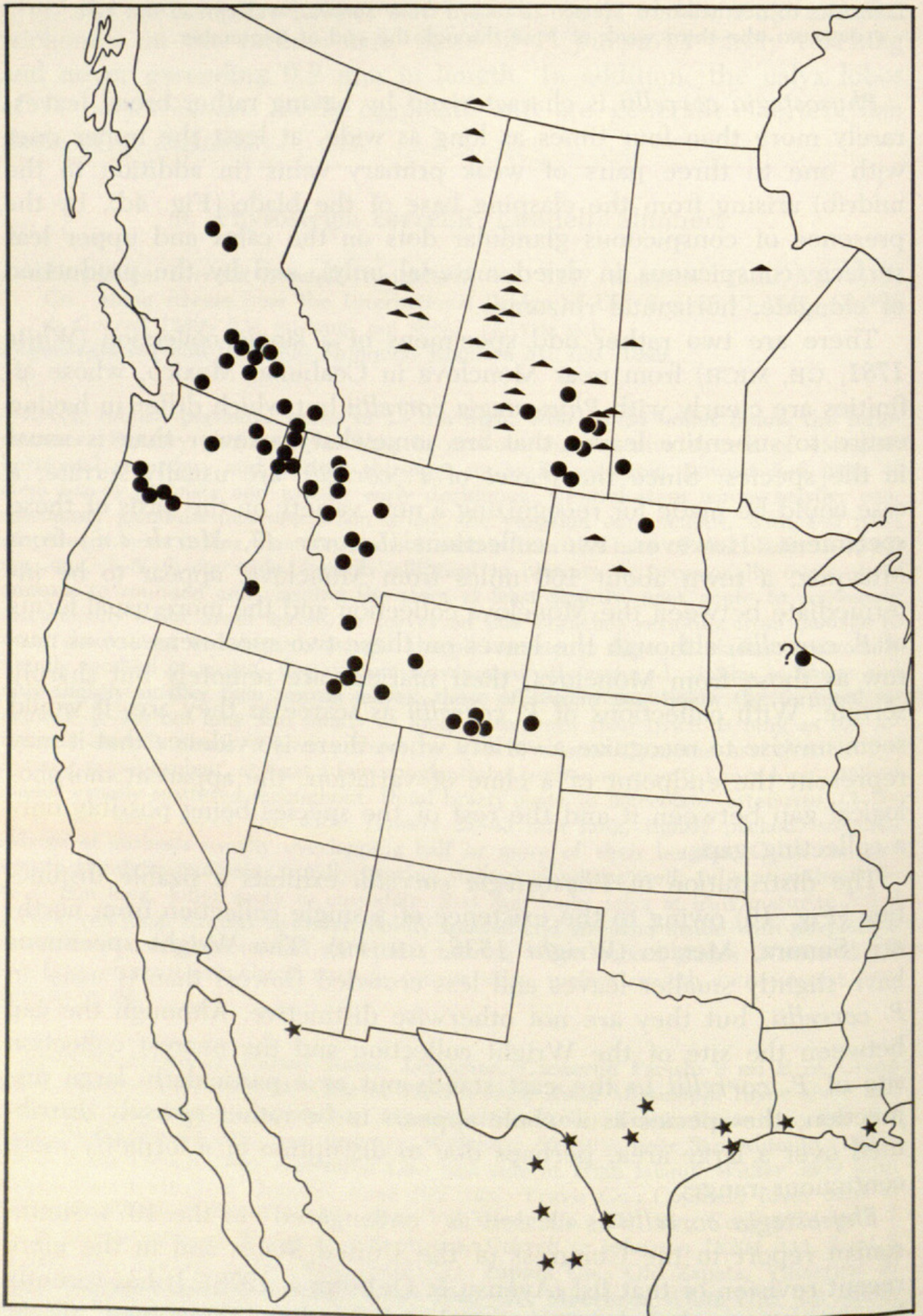


FIG. 16. Distribution map of *Physostegia correllii* (stars), *P. parviflora* (circles), and *P. ledinghamii* (triangles).

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, triangular 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, *Muenschler & Muenschler 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, Cabri, "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 interspecific 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, *Glownke 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, *Muenschler, 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

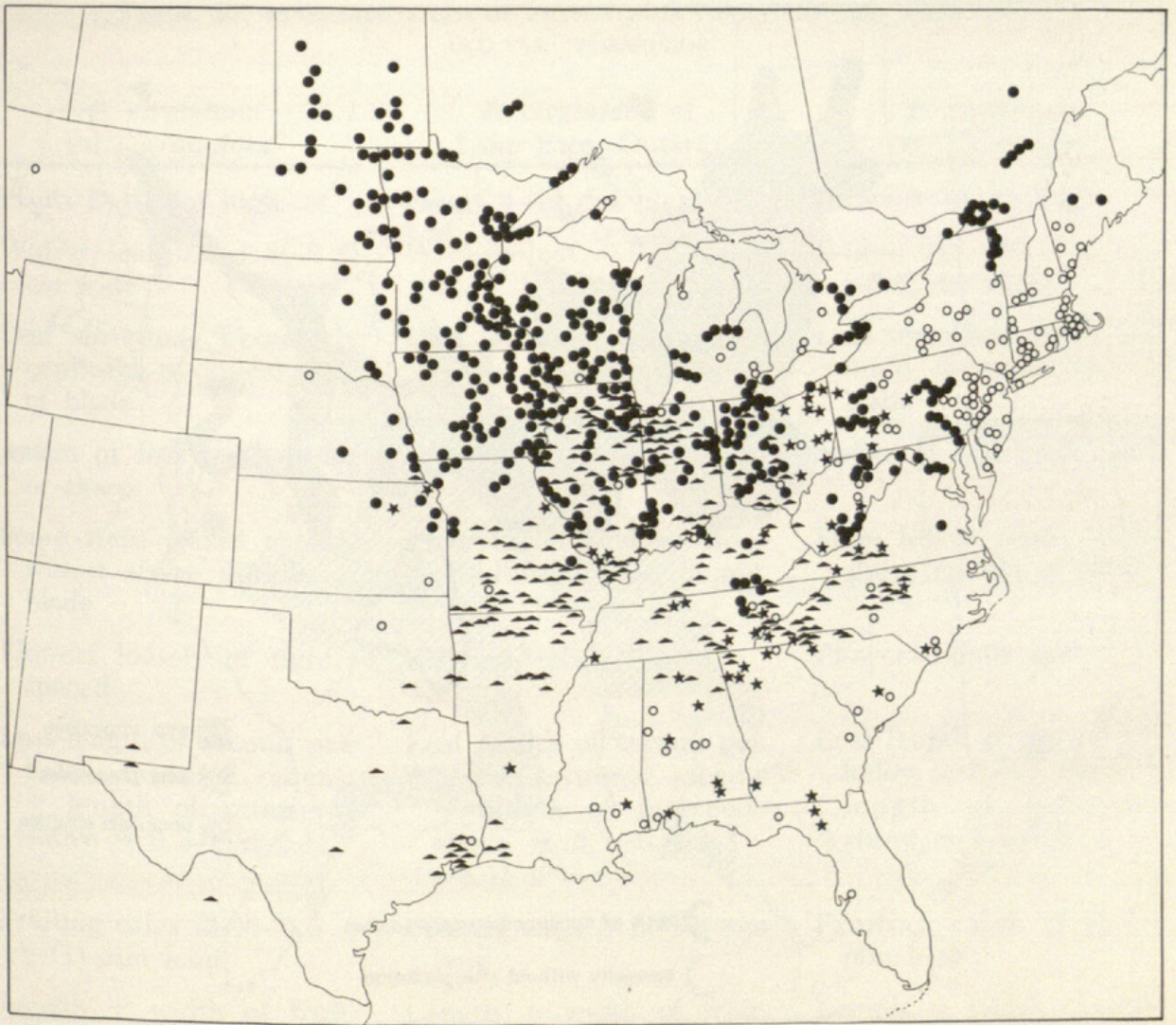


FIG. 17. Distribution map of *Physostegia virginiana*. Ssp. *virginiana* (closed circles); ssp. *praemorsa* (triangles); garden escapes (open circles); uncertain subspecific affinities, probably mostly garden escapes (stars).

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

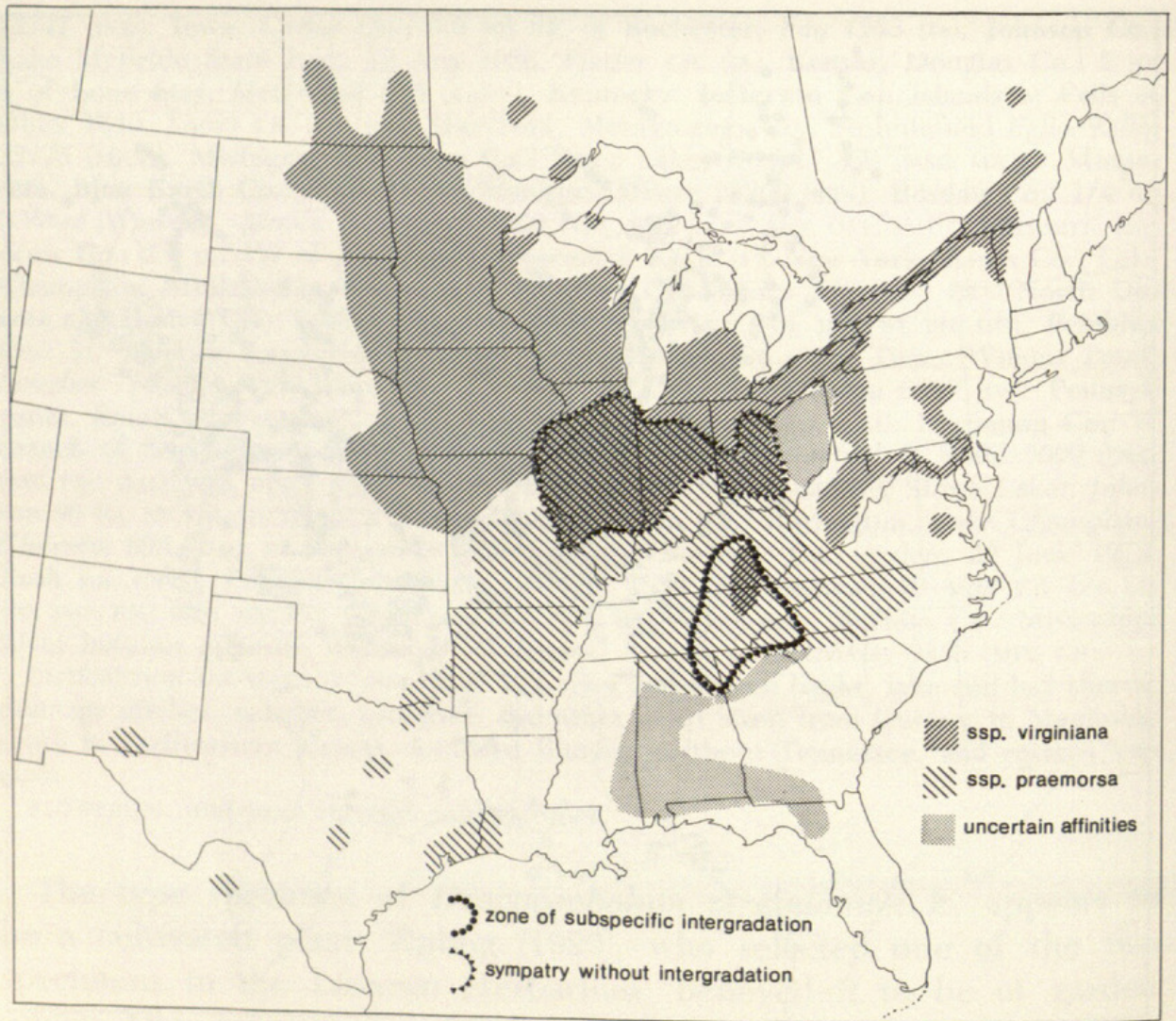


FIG. 18. Subspecific sympatry and intergradation in *Physostegia virginiana*. Plants of "uncertain affinities" are probably garden escapes (see text). Definite garden escapes have been omitted.

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 intrapopulation 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. "granulosa"	<i>P. virginiana</i> of Lake Erie, Ontario	<i>P. virginiana</i> var. "formosior"
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 con- fined 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 fruit- ing calyx = 1-2	Length ÷ width of fruit- ing calyx = 0.8-1.7	Length ÷ width of fruit- ing 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.** Mcpo. 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* SPP. *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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