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THE GENUS POLYGONATUM (SOLOMON'S SEAL) IN SOUTHERN ILLINOIS

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ABSTRACT. - The taxonomic delimitation of the *Polygonatum biflorum* -- *P. canaliculatum* complex has been a source of controversy for many years. In the present study several graphical techniques of analysis, including scatter-diagrams, hybrid indices, and radiate indicators, were used to examine the range of morphological variation in specimens of *P. biflorum* and *P. canaliculatum* collected from southern Illinois and other localities. The results show that *P. biflorum* can be distinguished from *P. canaliculatum* on the basis of its anther length, number of veins per leaf, number of flower pedicels per peduncle, and type of leaf margin, but not by any single characteristic alone. The disposition of the species "*P. commutatum*" is also dealt with.

The classification of the species of *Polygonatum* (Lily Family) native to southern Illinois has long posed a problem to the taxonomist. According to Fernald (1950) and Gleason (1952), only two species, *P. biflorum* and *P. canaliculatum*, occur in Illinois. Jones (1963), on the other hand, lists *P. commutatum* and *P. biflorum* as occurring in our area, and synonymizes *P. canaliculatum* with the latter species. *Polygonatum commutatum*, however, has been placed in synonymy with *P. canaliculatum* by Fernald (1950), and under *P. canaliculatum* (in part), and *P. biflorum* (in part) by Gleason (1952). Ownbey's (1944) treatment of *Polygonatum*, the only recent monograph of the genus, synonymizes the name *P. canaliculatum* with *P. biflorum*, and transfers all specimens previously annotated as *P. canaliculatum* to the species *P. commutatum*. Ownbey was unable to adequately separate *P. biflorum* and *P. canaliculatum* solely by their morphology, but she could distinguish two distinct populations which differed by their chromosome number.

While the nomenclatural problem will be dealt with in greater detail in a forthcoming paper, the present authors have chosen to follow Gleason's (1952) and Fernald's (1950) classification of the species of this group for reasons that will become more apparent later. The primary objective of the present work is to ascertain the limits of morphological variation within and between the taxa present in southern Illinois, and to show that these may be delimited solely on the basis of morphological criteria.

HISTORICAL REVIEW OF THE GENUS

Linnaeus (1753) listed the following three species of Polygonatum under the genus Convallaria: C. verticillata, C. Polygonatum, and C. multiflora. In 1785, Allioni transferred these to the genus Polygonatum, thus changing the name of the type species (Convallaria Polygonatum L.) to Polygonatum officinale All. (Ownbey, 1944).

Convallaria biflora, the first American species mentioned in the literature (Walter, 1788), was redescribed by Elliott (1821-1824) as Polygonatum biflorum. His brief diagnosis follows:

> Caule tereti, leavi, foliis alternis, sessilibus, elliptico-lanceolatis, trinervibus; pedunculis axillaribus, solitariis, bifloris.
>
> [Stem terete, smooth; leaves alternate, sessile, elliptic-lanceolate, 3-nerved; peduncles axillary, solitary, 2-flowered.]

In 1806, Willdenow described Convallaria pubescens and C. canaliculata Muhl. In 1814, Pursh transferred these two species to the genus Polygonatum. However, his technically poor diagnosis of the key characters of P. canaliculatum has contributed much to the difficulties encountered by taxonomists dealing with this species.

> Polygonatum canaliculatum: Caule canaliculato, foliis alternis amplexicaulibus oblongis margine pubescentibus pedunculis axillaribus bifloris.
>
> [Stem with longitudinal grooves, alternate stem-clasping oblong leaves with a pubescent margin, 2-flowered axillary peduncle.]
>
> Polygonatum pubescens: Caule teretiusculo dulco exarato, foliis alternis amplexicaulibus ovatis subtus pubescentibus, pedunculis axillaribus subbiflorus.
>
> [Cylindric stem with elevated grooves, alternate stem-clasping ovate leaves pubescent underneath, under 2-flowered axillary peduncle.]

Convallaria commutata, added to the North American flora by Schultes (1830), was transferred to Polygonatum commutatum by Dietrich in 1835, who described it as being distinguished by "the angular stem and by the pointed leaves." Dietrich (1835) also described P. giganteum from North America.

Salomonia cobrensis, the New Mexican species described by Wooten and Standley (1913), which, however, does not occur in Illinois, was recognized as Polygonatum cobrense in Gates's (1917) revision of the genus in North America. A number of other North American species, described from areas

outside Illinois, have appeared in the literature: P. latifolium (Pursh, 1814); P. multiflorum β. Americanum (Hooker, 1839); and P. cuneatum, P. virginicum, and P. boreale (Green, 1906).

Ownbey's (1944) monograph of Polygonatum in North America recognizes four species and three varieties: P. pubescens, P. cobrense, P. biflorum (P. biflorum vars. melleum, hebetifolium, and necopinum), and P. commutatum.

The key to the species of Polygonatum in Mohlenbrock's (1970) Flowering Plants -- Lilies to Orchids essentially follows Ownbey's taxonomic treatment of the genus. Jones's 1950 Flora of Illinois treats only two species, P. pubescens and P. commutatum. The latest treatments of these species for the Midwest are by Fernald (1950), Gleason (1952), and Jones (1963). Fernald's 8th edition of Gray's Manual of Botany lists four species of Polygonatum: P. pubescens, P. latifolium (introduced from Europe), P. biflorum, and P. canaliculatum. Fernald indicates that P. commutatum (R. & S.) Dietr. is synonymous with P. canaliculatum. Gleason, on the other hand, recognizes four species of Polygonatum: P. pubescens, P. canaliculatum (P. commutatum, in part; P. giganteum), P. biflorum (P. commutatum, in part), and P. melleum. In the 3rd edition of the Flora of Illinois, Jones lists only three species: P. pubescens, P. biflorum [P. canaliculatum (Muhl.) Pursh], and P. commutatum [P. giganteum Dietr.; P. canaliculatum sensu Fern.]. No other treatments are available.

MORPHOLOGY

Rhizome. All species of the genus are characterized by the presence of knotted branching rhizomes. Fernald (1950) states that the rhizome is superficial in Polygonatum pubescens and buried in P. biflorum and P. canaliculatum.

Stem. In all North American species the stem is glabrous. It may be terete, angular or channeled, but this character is not of much value in species delimitation based on herbarium material. In P. pubescens the stem is 2-11 dm tall (2-11 dm in Fernald, 1950; 5-9 dm in Gleason, 1952; and 3-9 dm in Ownbey, 1944); P. biflorum's stem is 2-9 dm tall (2-9 dm in Fernald, 1950; 4-6 dm in Gleason, 1952; up to 6 dm in Ownbey, 1944). All authors agree that P. canaliculatum is the largest plant having a stem 5-20 dm tall (6-20 dm in Fernald, 1950; 6-12 dm in Gleason, 1952; 5-20 dm in Ownbey, 1944).

Leaves. In all the North American species the leaves are alternate, and vary considerably in size and shape within each species. The leaves of P. pubescens are pubescent beneath along the veins, a character which readily distinguishes this species from P. biflorum and P. canaliculatum, which both have glabrous leaves. Ownbey (1944) states that the leaves of P. pubescens have a "fine pubescence on the minor nerves beneath." The few out-of-state specimens compared in this study were also pubescent along the major nerves, although the degree of pubescence varied from specimen to specimen. The shape of the leaves in each species is highly variable, although it is generally agreed (Fernald, 1950; Gleason, 1952; Ownbey, 1944) that the leaves of P. pubescens are elliptic-lanceolate to broadly oval, those of P. biflorum are elliptic-lanceolate (to broadly ovate according to Fernald), and those of P. canaliculatum are lance-elliptic to broadly ovate. Leaf size varies considably within each species, and the reported limits of variation differ with the various authors. It is obvious that there is so much overlap among the three species in leaf measurements, that these character states are of little taxo-

nomic worth when used as absolute values. However, if a leaf width/length ratio is calculated for each specimen, it can be used in conjunction with other characters to delimit the three species (see Fig. 2A). In P. pubescens the leaves are often, but not always, shortly petiolate; in P. biflorum and P. canaliculatum they are sessile or amplexicaulous. The state of the leaf margin provides a relatively good character for distinguishing P. canaliculatum from the other two species. In P. pubescens and P. biflorum the leaf margins are smooth, while those of P. canaliculatum are typically undulate or wavy. The nervation of the leaves presents a nearly constant character but one which is somewhat difficult to use. The leaves of P. pubescens, according to all authors, have 3-9 prominent nerves with typically only the midrib extending to the apex of the leaf; in P. biflorum there are 1-5 (rarely 9, and most typically 7) prominent nerves with only the midrib extending to the apex of the leaf. In P. canaliculatum there are many major nerves (7-22 or more) extending the length of the leaf. There is some discrepancy among the values reported for this character by the various authors, particularly those values reported by Fernald, who based his figures on all veins of the leaf, both major and minor.

Inflorescence. In P. pubescens and P. biflorum each axillary peduncle bears 1 or 2, or rarely 3, flowers. In P. canaliculatum there is great variation in the number of flowers per peduncle: 2-10 according to Fernald (1950); 1-15 according to Gleason (1952) and Ownbey (1944); and 2-9 in the specimens housed in the SIU herbarium. Pedicel/peduncle length ratios (see Fig. 2C) for all three species overlap too much to be of significant taxonomic value by themselves.

Perianth. According to Ownbey (1944) and other authors the size and color of the perianth are of some taxonomic value. However, measurements of perianth size overlapped so much among the three species that this character state was not used. Flower shape and color may be useful in living material, but not for dried specimens.

Stamens. The six stamens, inserted on the perianth tube in all species, have more or less papillose filaments and introrse anthers. Prior to this paper the anther length has not been used as a distinguishing character, however, in our opinion, it is an excellent character which does not vary greatly within each species. In P. pubescens anther length measures 2.2-2.3 mm, while in P. biflorum and P. canaliculatum it is 2.1-3.1 (rarely more than 3.1) mm and 3.9-4.8 (rarely less than 3.9) mm, respectively.

Pistil. The sessile to subsessile ovary is oblong to globose in shape, and is trilocular, having several ovules per cell. The style is filiform and shorter than the perianth (Ownbey, 1944). The style length, although more variable than the anther length, is also of some taxonomic value in separating the three species. In P. pubescens style length measures 3.8-4.8 mm, while in P. biflorum it measures 1.6-8.0 mm (rarely 10.0 mm), and in P. canaliculatum (rarely 3.0) 5.8-10.8 mm. All authors agree the stigma is capitate or obtuse, and obscurely three-lobed.

Fruit and seeds. According to all authors the fruit is a dark blue or black, globose, pulpy, several-seeded berry. The berries of P. canaliculatum are usually larger and have more seeds than those of the other two species.

GENERIC RELATIONSHIPS

Polygonatum is superficially most similar to the liliaceous genera Disporum, Streptopus, Convallaria, and Smilacina. According to Fernald (1950), the genus Disporum, which has two species, D. lanuginosum and D. maculatum, is distinguished from Polygonatum by several floral and vegetative characteristics. These include: bell-shaped flowers with perianth segments separate to the base; solitary or small umbel-like clusters of two or three flowers terminating the branches; stem dichotomously forked above the rhizome; several, sessile, reticulately veined leaves; fruit yellow or red; and anthers which are extrorse.

Streptopus, commonly called "twisted stalk," has two species, S. amplexifolius and S. roseus, both of which are distinguished from Polygonatum by the following: campanulate to rotate perianth with segments separate to the base, and recurved or spreading at the tips; fruit red; leaves cordate at the base (S. amplexifolius) or if sessile, leaves ciliate (S. roseus); and anthers which are extrorse (Fernald, 1950; Gleason, 1952).

Convallaria, the genus which included many of the earlier described species of Polygonatum, differs from the latter species by its campanulate perianth with six short, recurved lobes; stout style; triangular stigma; red berry; acaulescence; and angled scape bearing a one-sided, many-flowered raceme (Fernald, 1950).

False Solomon's-Seal, Smilacina, although vegetatively similar to Polygonatum, can be distinguished from the latter by its floral characteristics. These include: sepals and petals which are distinct rather than united, and inflorescences which are terminal and not one-sided (Fernald, 1950).

DISTRIBUTION

Polygonatum, a genus of about 50 species (Willis, 1966), is widely distributed in north temperate regions, with many more species occurring in Europe and in temperate Asia than in North America. There are discrepancies in the precise limits of distribution of two of the three species in North America as reported by Fernald (1950) and Gleason (1952). According to both Fernald and Gleason, P. pubescens occurs from southern Quebec, down along the Atlantic coast to South Carolina, west to Iowa, and north to southern Manitoba.

The range of P. biflorum, according to Fernald, extends from southern Ontario to Florida, west to Texas, and north to Nebraska, whereas Gleason restricts its range to east of the Mississippi River.

According to Fernald, P. canaliculatum ranges from southern Manitoba, down along the Atlantic coast to South Carolina, and west to Oklahoma. Gleason extends its southern boundary range to Georgia and Texas.

The Illinois distribution for each species is given in Figure 1. Open circles represent specimens of Polygonatum housed in the SIU herbarium, filled circles other sources (Pepoon, 1927; Jones, 1942; Ownbey, 1944; Jones and Fuller, 1955; Winterringer and Evers, 1960; Mohlenbrock et al., 1962, 1966; Ozment, 1967). Filled triangles represent specimens for which exact locality data is unknown.

According to Fernald (1950), all three species are found in similar habitats. Polygonatum pubescens grows in woods, along wooded bluffs, and about boulders in woods; P. biflorum occurs in dry to moist, sandy, loamy or rocky woods and thickets; and P. canaliculatum is found in rich woods, alluvial thickets, riversilts, etc. Illinois plants of P. biflorum and P. canaliculatum occur in essentially the same type of habitat, that is, moist woods, and wooded and dry bluffs. However, according to Ownbey (1944), P. canaliculatum shows greater tendency to invade open places, roadsides, fence rows, and alluvial soils than P. biflorum.

Since the ranges of the three species are sympatric and their habitats are quite similar, they must be isolated in nature by some other mechanism, such as different flowering times, different insect pollinators, etc. A comparison of the flowering times of Illinois specimens of P. biflorum and P. canaliculatum (see Fig. 1) drawn from the same climatic tension zone (Ugent and Anderson, 1969) would appear to show little difference in the flowering dates. However, if a normal curve is extrapolated for each species, it is apparent that the peak flowering times are probably separated from each other by at least 2-3 weeks.

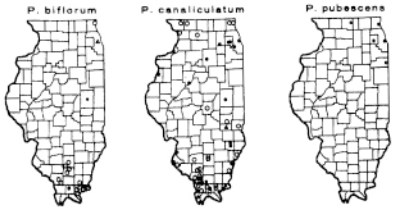
ANALYSIS OF VARIATION

Morphological variation in Polygonatum is best illustrated by graphical methods of analysis. In the present study the following techniques were used: (1) pictorialized scatter-diagrams, (2) hybrid indices, and (3) radiate indicators.

(1) Pictorialized Scatter-Diagrams. Pictorialized scatter-diagrams, a technique developed by Edgar Anderson (1949), were utilized to illustrate variation within and between the species of Polygonatum and to resolve the P. commutatum "problem."

The first and most important task in the preparation of a scatter-diagram is to obtain a variety of character measurements, and then to select for plotting those variables which most clearly isolate the species involved. The following characters were selected for evaluation:

1. Leaf width/length. The fourth leaf above the lowermost flower of the inflorescence was selected for measurement. The width was measured at the exact midpoint of the leaf.
2. Number of veins/leaf (fourth leaf above the lowermost flower of the inflorescence). Only those veins reaching or almost reaching the leaf apex were scored.
3. Leaf margin. The leaf margin was scored as follows: 0 = smooth and 1 = undulate.
4. Leaf pubescence. Scored as follows: 0 = underside of leaf glabrous and 1 = underside of leaf pubescent.
5. Maximum number of flower pedicels/peduncle.
6. Pedicel length/total peduncle length.
7. Anther length. It was felt that the absolute size of a reproductive structure could be used with confidence, since floral structures are generally considered to be genetically and environmentally conservative (Davis and Heywood, 1963).



Date	No. of Indiv.	Flowers
Apr. 15-30	4	2
May 1-15	3	3
May 16-31	1	6

o Herbarium specimens
● Specimens from other sources
▲ Exact locality unknown

FIG. 1

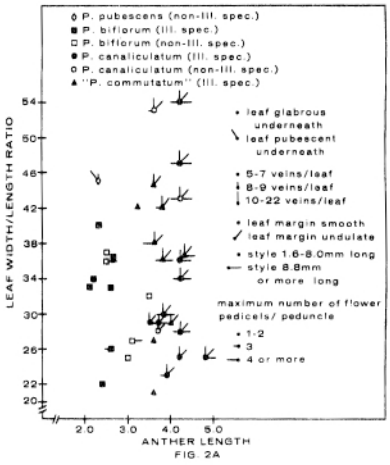


FIG. 2A

Figure 1. Geographical distribution of the species of Polygonatum native to Illinois (see text for further explanation).

Figure 2. Morphological variability in Illinois species of Polygonatum.

8. Style length. Although more variable than anther length, this character also proved to be of value.

The shape of the leaf base and position of the stamen on the perianth tube proved to be too variable in preserved specimens, therefore, these characters were discarded.

Four different scatter-diagrams were made using different character combinations on the axes. Additional characters were added as glyphs (or "cat whiskers"). If anther length versus leaf width/length is plotted on a scatter-diagram (Fig. 2A), Polygonatum biflorum and P. pubescens are readily separated from P. canaliculatum. Polygonatum pubescens is distinguishable from P. biflorum by the pubescence on the underside of its leaves. This scatter-diagram also amply illustrates the great amount of variation in the P. canaliculatum population, a topic which will be discussed in some detail later. Some of our P. commutatum specimens clearly fall within the variability limits of P. biflorum, while others fall within the limits of P. canaliculatum.

By plotting the maximum number of flower pedicels/peduncle against the anther length (Fig. 2B), a distinct separation of the three species is also obtained. This diagram illustrates that specimens of P. biflorum and P. pubescens have a much lower maximum number of pedicels/peduncle (1-3, but typically 2), that individuals of P. canaliculatum which vary from 2-5. Our specimens of P. commutatum again fall into two discrete groups.

When anther length is plotted against the pedicel length/total peduncle length (Fig. 2C), although the latter is quite variable within all the species involved, P. canaliculatum and P. biflorum are still readily separable. Within the "species" P. commutatum we again find that one group of specimens is similar to P. biflorum, while the other is like P. canaliculatum.

Since many of the specimens did not have flowers, a fourth diagram (Fig. 2D) was made plotting maximum number of veins/leaf versus leaf width/length. A separation of the three species is illustrated. Polygonatum biflorum is consistent in its possession of 7 veins/leaf, while P. pubescens, although similar to P. biflorum in many respects, is easily separated from the latter by its pubescent leaves. It is apparent that P. canaliculatum represents a much more variable species than the other two, e.g., in the maximum number of veins/leaf and the maximum number of flower pedicels/peduncle. The large number of P. commutatum specimens scored on this diagram clearly shows that this "species" is composed of entities like P. biflorum and other like P. canaliculatum.

(2) Hybrid Index. The calculation of hybrid indices, another morphological technique of analysis developed by Edgar Anderson (1949), was employed both to reflect the total amount of variation within each species and to attempt to further resolve the P. commutatum problem. Index values were calculated by scoring each character in three grades: 0 for characters like P. biflorum, 1 for intermediate characters, and 2 for characters similar to P. canaliculatum. The same characters used in the scatter-diagrams were used in calculating the hybrid index. An index value was calculated for each specimen, and these values were used in combination with scatter-diagrams. In order to indicate what characters were varying within the index, the characters were

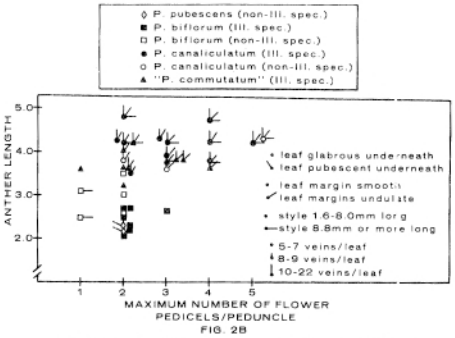


FIG. 2B

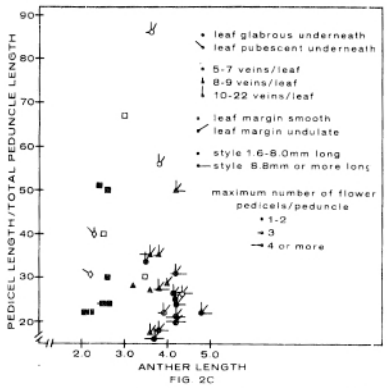


FIG. 2C

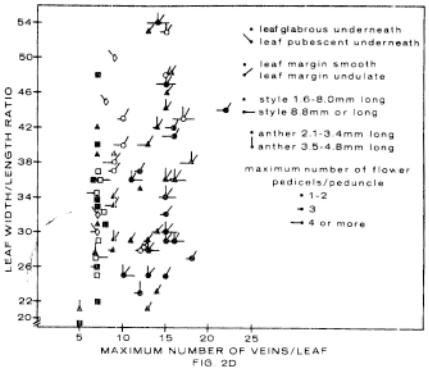


FIG. 2D

Figure 2 (continued). Morphological variability in Illinois species of Polygonatum.

added to the diagrams as glyphs. A scatter-diagram (Fig. 3A) plotting a leaf index number (based on the number of veins/leaf and the type of leaf margin) against the maximum number of flower pedicels/peduncle clearly indicates that P. biflorum and P. canaliculatum represent valid taxa. Specimens in our herbarium identified as P. commutatum, on the other hand, either fall within the limits of P. biflorum or P. canaliculatum.

In Figure 3B, anther length is plotted against a composite index number composed of summed indices for all characters except anther length. This diagram again clearly shows P. biflorum and P. canaliculatum as distinct species, and our P. commutatum specimens as a mixture of specimens of both species.

By plotting a floral index (based on the anther length and the style length) against a leaf index (Fig. 3C), the results obtained are similar to those of the other two scatter-diagrams, except the separation between P. biflorum and P. canaliculatum is greater.

(3) Radiate Indicators. Two types of polygonal graphs were used. First, to study variation within each species, the numerical values of each individual specimen's characters were plotted on a single graph. And secondly, to delimit P. biflorum, P. canaliculatum, and P. commutatum, the maximum, minimum, and averages of their respective characters were plotted on separate graphs. Five characters were used: leaf width/length, maximum number of veins/leaf, maximum number of flower pedicels/peduncle, anther length and style length. The characters, which were recorded by a variety of methods, were graphed as percentages of the maximum value obtained for each character. Figure 4, A and B, in which the mean, minimum and maximum values of each character were plotted, illustrates again the clear separation between P. biflorum and P. canaliculatum. The graph of P. commutatum (Fig. 4C) reveals minimum values like those of P. biflorum, maximum values very similar to those of P. canaliculatum, and mean values almost half-way between the latter two species. This graph adds more evidence to the supposition that P. commutatum specimens at the SIU herbarium were really a mixture of mislabelled P. biflorum and P. canaliculatum specimens. Figure 4D, showing the range of variability of each character analyzed in P. biflorum, illustrates that the leaf margin, maximum number of veins/leaf, maximum number of flower pedicels/peduncle, and the anther length are the most stable characters in this species. The polygonal graph of variability in P. canaliculatum (Fig. 4E), on the other hand, illustrates that all except the leaf margin, show a greater range of variability than in P. biflorum. Our specimens of P. commutatum (Fig. 4F) again fall within the variability limits of P. biflorum or P. canaliculatum.

DISCUSSION AND SUMMARY

The application of graphical techniques of analyses, such as pictorialized scatter-diagrams, hybrid indices, and polygonal graphs, suggests the following conclusions about the species studied:

1. Polygonatum pubescens is similar to P. biflorum in most characters studied, except in anther length and pubescence on the lower leaf surface.
2. Polygonatum biflorum seems to be a genetically stable species.

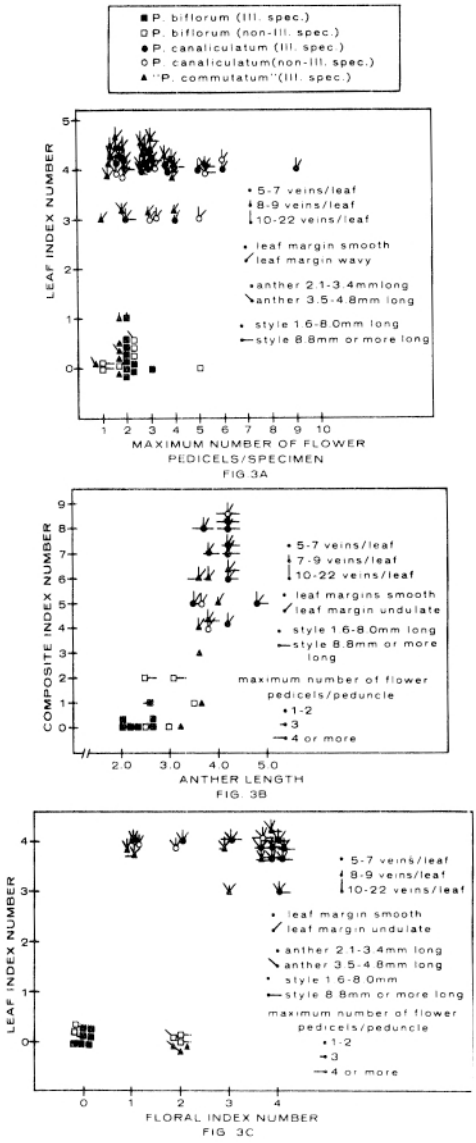


Figure 3. Scatter-diagrams employing hybrid indices based upon leaf characteristics, floral characteristics, and/or leaf and floral characteristics.

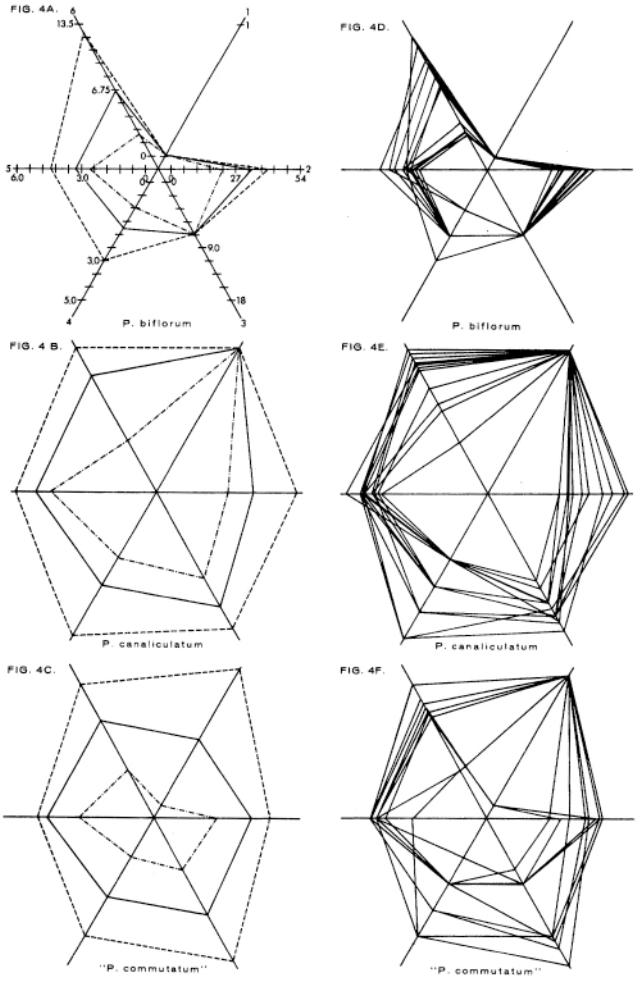


Figure 4. Polygonal graphs. In all diagrams arm 1 equals the type of leaf margin; arm 2, leaf width/length; arm 3, maximum number of veins/leaf; arm 4, maximum number of flower pedicels/peduncle; arm 5, anther length in mm; arm 6, style length in mm. Solid lines on graphs A, B, and C denote the mean value of each character; broken lines, the maximum value; and dots-and-dashes, the minimum value. Each solid line on graphs D-F represents the character values of individual specimens.

3. Polygonatum canaliculatum shows a great amount of variability for almost all characters examined. It is distinct morphologically from P. biflorum in every character investigated, and, would therefore appear to be a valid species.

The P. commutatum-canaliculatum problem is not a simple matter to resolve because it is tied up in a nomenclatural "Gordian knot." Fernald (1950) indicates that P. commutatum is synonymous with P. canaliculatum, whereas Gleason (1952) states that P. commutatum is partly synonymous with P. biflorum and partly with P. canaliculatum. Ownbey (1944), on the other hand, is convinced that P. canaliculatum should be put in synonymy with P. biflorum. Thus, according to Ownbey, all specimens identified as P. canaliculatum should be reannotated as P. commutatum. In our opinion, since Ownbey did not examine the type specimens of either P. canaliculatum or P. commutatum, her justification for synonymizing P. canaliculatum with P. biflorum on the basis of the original description alone is inadequate. Until the type specimens of P. canaliculatum and P. commutatum can be examined and compared with other herbarium specimens, it seems logical to retain the older of the two species names, P. canaliculatum. We maintain this view because the original descriptions of all the species involved are technically poor and, therefore, should not be used as the sole basis for synonymy.

The variability of P. canaliculatum as compared to the relative constancy of P. biflorum has been noted repeatedly throughout this study. Cytological studies of the North American species of Polygonatum have been conducted by various researchers (Eigsti, 1942; Ownbey, 1944; Therman, 1950, 1956; Kawano and Iltis, 1963). While Therman (1956) has shown that a polyploid series from diploid to hexaploid exists in P. canaliculatum, which, if true, would perhaps explain the variability observed in this species, at least in part, the actual taxonomic identity of the species used in this investigation, as pointed out by Kawano and Iltis (1963), is open to question. All plants cytologically examined by Therman were said to be first identified by Ownbey on the basis of their morphology. Yet, in her monograph of the genus Polygonatum, Ownbey (1944) clearly states that P. biflorum and P. canaliculatum (= P. commutatum sensu Ownbey) cannot be separated on the basis of their morphology alone, as is evidenced by the fact her key to the species relies primarily on the chromosome number. According to Kawano and Iltis (1963) little may be done with this problem until the present confused situation is resolved. We, therefore, feel that until cytological work can be done on morphologically authenticated specimens, little reliance can be placed on the chromosome number of the species as reported in the literature. Nevertheless, cytological work does indicate that a polyploid series exists within the genus Polygonatum. Many specimens of P. canaliculatum, for example, exhibit an enhancement of character states typical of the greater vigor which often accompanies higher degrees of polyploidy. These include: a stouter stem; greater number of leaves, flowers, and fruits; larger leaves, flowers, and fruits; broader, thicker many-nerved leaves; and larger anthers.

While it is not known for certain whether or not our smaller plants of P. canaliculatum are diploid, they share certain characteristics in common with the larger plants, and both are readily distinguishable from P. biflorum on the basis of morphology. Ownbey (1944), whose classification of this group relies primarily upon cytological evidence, may be wrong in assuming

all specimens of P. biflorum are diploid and those of P. canaliculatum (= P. commutatum sensu Ownbey) are tetraploid. From a floristic point of view it is not feasible in any event to construct keys based primarily upon chromosome numbers, which, of course, may not be obtained from dried herbarium specimens in the first place. Our study does show, however, that P. biflorum and P. canaliculatum can be separated on the basis of morphology alone.

SYSTEMATIC TREATMENT

Key to the Species

A. Anther length 2.1-3.1 mm (rarely larger) at anthesis; 1-9 veins/leaf leaf margin smooth; 1-2 (rarely 3) flower pedicels/peduncle

1. Leaves pubescent beneath; 3-9 veins/leaf ..... P. pubescens
1. Leaves glabrous beneath; 1-7 (rarely 9, typically 7) veins/leaf ..... P. biflorum

A. Anther length 3.9-4.8 mm (rarely smaller) at anthesis; 7-22 or more veins/leaf; leaf margin undulate; 2-5 flower pedicels/peduncle, typically 3 or more ..... P. canaliculatum

1. Polygonatum pubescens (Willd.) Pursh, Fl. Am. Sept. 1: 234, 1814.

Perennial herb, usually 2-6, but occasionally as much as 9 dm high; rhizome slender, not buried in the soil; stem slender, glabrous, erect or slightly arched at top; leaves alternate, elliptic-lanceolate to elliptic or broadly ovate, narrowed at the base to a short petiole or occasionally sessile, 3.5 to 15 cm long, 1.0 to 7.5 cm broad, glabrous above, pubescent on minor nerves and along major veins beneath, 3 to 9 (typically 7 or 8) prominent nerves running to or almost to the leaf apex; cauline bract subulate, papery, caducous; peduncles axillary, solitary, slender, glabrous, strongly and sharply deflexed, usually 2 (occasionally 1-5)-flowered; pedicels slender, glabrous; filaments densely papillose, inserted near top of perianth tube; anthers 2.2-2.3 mm long; style variable from 3.8-4.8 mm in length; berry dark blue, usually between 7 and 10 mm in diameter.

Representative Specimens: MASSACHUSETTS: HAMPSHIRE CO. Amherst, 17 May 1896, Shepardson 2. MICHIGAN: ST. CLAIR CO. Near Sanilac Co. line, near Jeddo, moist woods, 30 June 1937, Anderson and Peck, s.n. MINNESOTA: STEARNS CO. St. Joseph, May 1964, Sister Remberta, s.n. NORTH CAROLINA: WATAUGA CO. 3.5 mi se of US 421 on Junalaska Road, e slope of Rich Mtn., roadcut through deciduous forest, 9 July 1967, Bozeman, Radford & Culwell 10698. WISCONSIN: DANE CO. 22 May 1957, Ugent, s.n.

2. Polygonatum biflorum (Walt.) Elliott, Sketch Bot. S.C. & Ga. 1: 393, 1817.

Perennial herb 2-9 dm high; rhizome slender, buried in the soil; stem slender, glabrous, erect or arching; leaves alternate, sessile or amplexicaulous , elliptic-lanceolate or ovate, 4 to 15 cm long, 0.9 to 6.0 cm broad, glabrous on both sides, with 1 to 8 (typically 7) prominent nerves running to or almost to the leaf apex; cauline bract green, leaf-like, persistent; peduncles axillary, solitary, slender, glabrous, arcuate, typically 2 (rarely 1-5)-flowered; pedicels slender, glabrous; filaments minutely papillose, inserted

near middle of perianth tube; anthers 2.1-3.5 mm long (typically 2.4-3.1 mm long); style length varies from 1.7-10.0 mm (typically less than 8.0 mm long); berry dark blue, usually less than 8 mm in diameter.

Representative Specimens: ALABAMA: LEE CO. Wet woodlands, 4 Apr 1963, Hayes 142. ILLINOIS: FRANKLIN CO. 3 mi w of Benton, oak-hickory woods, April 1972, Adams, s.n.; 2 mi n, 1/2 mi e of Ewing, Robinson farm, wooded hillside, 24 Apr 1972, Harmon 27. HARDIN CO. Rock Creek Valley, T11S, R9E, "closed" woods on lower slopes of valley and open dry woods on n slope, 3 May 1949, Bailey & Swayne 673. JACKSON CO. Giant City State Park, rich mesophytic woods, 18 Apr 1954, Mohlenbrock 2092; between Murphysboro and Etherton, along roadside, 23 May 1954, Mohlenbrock 2138; Giant City State Park, sandstone bluff, 25 Apr 1959, Sands 535. JEFFERSON CO. 5 mi sw of Mt Vernon, 1 mi w of State Hwy 148, slight w slope, under oak and hickory, 7 May 1972, Agee 20; 3 mi n and 2 mi w of Sesser, rich, moist, oak-hickory woods, 6 May 1972, Williams 46. JOHNSON CO. Ferne Clyffe, bluff top, w-facing slope, 27 June 1963, Bollwinkel & Windler FC 1; Ferne Clyffe, bluff top, dry, rocky outcrop, w-facing, 25 June 1963, Bollwinkel & Windler FC 46. POPE CO. Belle Smith Springs, e slope, dense woods, 27 May 1956, Carter 33; Lusk Cr, moist woods, 21 May 1966, Hopkins 130; Dixon Springs, rich woods, 16 Apr 1954, Mohlenbrock 2099; near Martha's woods along Little Lusk Cr, very dry, sandy upland woods, 11 May 1968, Schwegman 1666. KENTUCKY: MARSHALL CO. Near e fork of Clarks River, e of Benton, moist woods, 29 Jul 1963, O'Dell & Windler 1233. NEW JERSEY: GLOUCESTER CO. Along streamlet tributary to South Branch Timber Creek, loamy, wooded w slope, 7 May 1921, Long 24003. NORTH CAROLINA: FORSYTH CO. 4.4 mi n of Kernersville, wooded slope, 17 May 1958, Ahles & Britt 40732. WAKE CO. Little River, Mitchells Mill, 2 mi ne of Rolesville, 22 Sept 1966, Windler 1603. VIRGINIA: BEDFORD CO. No locality data, 20 May 1872, Curtiss, s.n.

3. Polygonatum canaliculatum (Muhl.) Pursh, Fl Am. Sept. 1: 234, 1814.

Perennial herb, 5-20 dm high; rhizome stout, often branched, deeply buried; stem usually stout and arching, glabrous; leaves alternate, amplexicaulous, varied in shape, ovate-lanceolate, elliptic-lanceolate, oblong-lanceolate, or broadly oval, 6 to 25 cm long, 1.5 to 13 cm broad, glabrous on both sides, with 7 to 22 or more major nerves prominent the full length of the leaf, the major nerves alternating with other fainter but distinct nerves, leaf margin undulate or "puckered"; cauline bract green, leaf-like, persistent; peduncles coarse, flattened, often stiff and wiry, usually long and arched, glabrous, 1- to 15-flowered (typically 3 or more); pedicels flattened, glabrous; filaments smooth to densely papillose, inserted near the middle of perianth tube; anthers 3.4-4.8 mm long (usually 3.9-4.2 mm long); style length variable from 3.0-10.8 mm (typically 8.8-10.8 mm); berry dark blue, 8 to 12 mm in diameter.

Representative Specimens: CONNECTICUT: NEW HAVEN CO. Middlebury, Hop Swamp, 27 June 1896, Shepardson, s.n. ILLINOIS: CARROLL CO. T24N, R5E, sect 5, roadside, edge of woods, 13 Aug 1963, Verts 109. CLARK CO. Rocky Branch Nature Preserve, T12N, R12W, sects 29 & 30, 12 Jul 1969, Ebinger 8623. COLES CO. Fox Ridge State Park, T11N, R9E, sect 13, steep wooded slope, 7 June 1968, Mohlenbrock 15016. CUMBERLAND CO. Hazel Dell, extreme se corner, dry oak-

hickory woods, 12 Aug 1964, DeFilipps & Ozment 1509. HARDIN CO. Blind Hollow, 24 Apr 1954, Voigt & Mohlenbrock 2222. JACKSON CO. Fern Rocks, June 1971, French, s.n.; Hickory Ridge, w side of hill, dry woods, 15 May 1956, Gotway 38; near Boskeydell, woods, 14 Aug 1941, Hall 1033; Little Grand Canyon, mesic lowland woods and canyon ledges, 7 Aug 1967, Johnson 436; Giant City State Park, woods, 25 June 1953, Mohlenbrock 356; s of Murphysboro, GMORR, moist shaded soil, 23 Apr 1954, Mohlenbrock 2138; Lake Murphysboro, wet low woods, 18 May 1954, Mohlenbrock 2441; Lake Murphysboro, rich moist woods, 19 May 1955, Mohlenbrock 5315; Big Muddy River, 3.5 mi n of Carbondale, rich moist woods, 5 May 1956, Sands 63; Botany Preserve, Southern Illinois University, Carbondale, shaded moist woods, 27 May 1952, Voigt, s.n. JEFFERSON CO. 6 mi n of Mt Vernon, Casey Fork Bottoms, Idlewood Rd, 28 Apr 1964, Estes 87; 5 mi n of Mt Vernon, moist woodland, 30 May 1965, Estes 248. JO DAVIESS CO. Apple River Canyon State Park, 30 May 1965, Hinkley, s.n. JOHNSON CO. Heron Pond, 3 mi s of Vienna, moist woods, 30 Apr 1969, White 965. LAKE CO. Illinois Beach State Park, shaded grass covered dunes, 12 June 1966, Brouillard 1; Miltmore Lake, moist shoreline, 16 June 1966, Moran 8. MACON CO. e shore of Lake Decatur, about 250 m n of NWRR, rich leaf mold in woods, 30 May 1972, Shildneck C-3720. MONROE CO. s of Fults, T4S, R10W, talus, base of limestone bluff, 11 May 1952, Bailey & Swayne 2248A. OGLE CO. Lowden State Park, moist low woods, 18 July 1964, DeFilipps & Ozment 210. PERRY CO. United Electric Fidelity Coal Co., w of DuQuoin, black locust plot, 21 May 1963, Baker, s.n.; near Matthews along "Old Mud Line," 9 May 1954, Mohlenbrock 2388. POPE CO. Bay Bottoms, T12S, R5E, sect 9, rich mesic woods, 27 Aug 1952, Bailey & Swayne 2861; Jackson Hollow, T11S, R5E, sect 31, closed beech-maple woods, 17 Aug 1950, Swayne & Bailey 1278. ST. CLAIR CO. Vic of 3-Forks, rich shaded soil, 10 Sept 1960, Neill 15286; vic of Imbs Station, edge of woods, 8 July 1967, Neill 15716; STEPHENSON CO. Lake Le-Aqua-Na State Park, moist woods, 19 July 1964, DeFilipps & Ozment 293. UNION CO. Union Co.-Johnson Co. line, Drapers Bluff, T11S, R2-3E, sects 31-36, oak-hickory woods, top of bluff, 29 May 1952, Bailey & Swayne 2421; Hanging Rocks, e of McClure, T13S, R2W, sect 31, chert bluff, 19 June 1952, Bailey & Swayne 2556; Pine Hills, Mar 1953, Mohlenbrock s.n. WABASH CO. n of Mt Carmel, T1N, R12W, oak-hickory woods on hilltop, 16 Aug 1951, Bailey & Swayne 1728. WASHINGTON CO. Near nashville, wooded hillside, 12 May 1951, Bailey & Swayne 1393. WHITE CO. 1 mi n of Emma, low woods, 20 June 1958, Voigt & Weber 2021. IOWA: DES MOINES CO. 3 mi nw of jct of Hwys 34 & 406, wooded country lane, 26 Aug 1967, Johnson, s.n. KENTUCKY: LYON CO. Along roadside to Sugar Bay, moist woods, 22 Apr 1967, Riggs & DeVillez 62. MARSHALL CO. e fork of Clarks River, e of Benton, woods, 29 July 1962, O'Dell & Windler 1237. MICHIGAN: KALAMAZOO CO. Schoolcraft Twp, T45, R11W, sw 1/4 sect 18, beech-maple woods, 6 May 1971, Krusel, s.n. MISSOURI: CHRISTIAN CO. Near Garrison, rocky wooded banks of Swan Cr, 20 Apr 1956, E J Palmer 62021A, 62021B. JASPER CO. 1 mi ne of Joplin, along Turkey Cr, steep rocky n-facing hillside, 10 June 1964, E J Palmer 57780. POLK CO. 6 mi ne of Rondo, along creek, rocky wooded bluffs, 23 May 1956, E J Palmer 62519.

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