PHYLOGENETIC RELATIONSHIPS WITHIN *UVULARIA* (COLCHICACEAE) BASED ON MORPHOLOGY

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Abstract: The five species of bellworts in the genus *Uvularia* are common woodland herbs endemic to eastern North America. Two previous studies conducted phylogenetic analyses of *Uvularia* based on *matK* and *rbcL* gene sequences. The objective of this study was to create a phylogeny for *Uvularia* based on 18 qualitative morphological characters and 14 quantitative characters. Two phylogenetic analyses were performed, one including all 32 characters and one excluding the 14 quantitative characters. Strict consensus trees from the two analyses had the same topology and were congruent with published molecular phylogenies, supporting two sections of the genus.

Key Words: *Uvularia*; morphological phylogenetics; quantitative characters; Colchicaceae.

INTRODUCTION

Uvularia L. (Colchicaceae) is a genus of woodland herbs comprising five species endemic to eastern North America, from Nova Scotia and Quebec southward to Florida and Texas (Soper 1953; Wilbur 1963; Utech & Kawano 1999, 2003). All five species are understory perennials with bell-shaped flowers that bloom from April to mid-June (Kawano and Iltis 1964) and are stoloniferous, growing in dense clumps (McCall and Primack 1987). *Uvularia* grows in well-drained or mesic upland forests or in swampy alluvial bottomlands and rarely in xeric coniferous woodlands (Hayashi et al. 1998). Seeds are ant-dispersed in late summer (Whigham 1974).

Uvularia was divided into two genera based on morphological characteristics, *Oakesia* Watson (later renamed *Oakesiella* by Small 1913) comprising three sessile-leaved species (*U. puberula*, *U. floridana* and *U. sessilifolia*), and *Uvularia*, comprising two perfoliate species (*U. grandiflora* and *U. perfoliata*; Watson 1897). Wilbur (1963) later reunited all five species into *Uvularia* on the basis of morphological characteristics such as branching pattern and inflorescence structure, and still recognized the two groups as sections [Section *Oakesiella* (Small) Wilbur and Section *Uvularia*].

Two phylogenetic studies of *Uvularia* based upon molecular data (Shinwari 1988; Hayashi et al. 1998) used *rbcL* and *matK* sequence data. The results of both studies supported *Uvularia* as a monophyletic group as

well as Wilbur's (1963) division of *Uvularia* into two sections as described above.

We present here a phylogenetic study of *Uvularia* based upon morphological characters. The objectives of this study were (1) to analyze the morphology of the five species in *Uvularia* and construct a phylogeny based on shared morphological characteristics, and (2) to compare the morphological phylogeny to previous studies based on molecular data (Hayashi et al. 1998).

METHODS

Taxon sampling. All five species of *Uvularia* were included in the study. We selected *Prosartes lanuginosa* (Michx.) D. Don as our outgroup based on Hayashi et al. (1998). Herbarium specimens of *U. puberula* Michx., *U. sessilifolia* L., *U. grandiflora* Smith, and *U. perfoliata* L., and the outgroup, *P. lanuginosa* (Michx.) D. Don, were borrowed from the herbaria listed in the acknowledgments and below. Both fruiting and flowering specimens of all six species were obtained for evaluation of characters pertaining to both life stages.

Specimens examined: *Uvularia floridana*: FLAS: S. Daniel 8571, A. Gholson Jr. 11578, S.L. Orzell 38-16159, D.B. Ward 38; TENN: R. Kral 26212, 57408.

Uvularia grandiflora: BOON: Carpenter 3967, T.R. Fisher 119, S. Hearn 39, B. Kallenbach 35, Love 4019, D. Morrison 9, S. Perry 12-607, T.P. Taylor; TENN: R. Boner 47719, E.M. Browne 4034, E.A. Burdo 28-343, T. Koyama 13081, P. Marx 34306, V.E. McNellus no #, G.W. Ramsey 373.

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Table 1. Characters and character states used in the analysis of *Uvularia*. All multistate characters were treated as unordered. Consistency index (CI) and retention index (RI) are given for each character.

	Character	Character States	CI	RI
1.	Leaf attachment	0 = sessile, 1 = perfoliate.	1	1
2.	Leaf margin	0 = ciliate, 1 = entire, 2 = papillose.	1	1
3.	Leaf indumenta	0 = lanulose, 1 = glabrous, 2 = pubescent	0.67	0
4.	Leaf width	0 = ≥ 14 mm, 1 = < 14 mm	0.33	0
5.	Leaf length	0 = ≥ 54 mm, 1 = < 54 mm	0.5	0.5
6.	Stem cross-section	0 = terete; 1 = distally angled	1	1
7.	Stem pith	0 = hollow; 1 = solid	1	1
8.	Stem length	0 = ≥ 600 mm; 1 = 350–600 mm; 2 = < 350 mm	0.67	0
9.	Internode length	0 = ≥ 30 mm; 1 = < 30 mm	1	1
10.	Number of nodes on sterile branch	0 = no sterile branch; 1 = < 6 nodes; 2 = ≥ 6 nodes	0.5	0
11.	Number of flowers per shoot	0 = 2–25; 1 = 1–3; 2 = 1–2; 3 = 1	1	1
12.	Bract	0 = absent; 1 = present, perfoliate; 2 = present, sessile	1	1
13.	Pedicle length	0 = ≥ 10 mm; 1 = < 10 mm	0.5	0.67
14.	Tepal length	0 = < 23 mm; 1 = ≥ 23 mm	0.5	0.67
15.	Tepal width	0 = < 4.75 mm; 1 = ≥ 4.75 mm	0.5	0.5
16.	Stamen length	0 = < 14.5 mm; 1 = ≥ 14.5 mm	1	1
17.	Filament length	0 = < 4.5 mm; 1 = ≥ 4.5 mm	1	1
18.	Anther length	0 = < 6 mm; 1 = 6–9 mm; 2 = ≥ 9 mm	0.5	0
19.	Length of connective protrusion on anther	0 = < 0.5 mm; 1 = ≥ 0.5 mm	1	1
20.	Location of stamen attachment	0 = receptacle; 1 = tepal	1	1
21.	Stigmatic lobe length	0 = < 4.25 mm; 1 = ≥ 4.25 mm	0.5	0.5
22.	Style length	0 = < 10 mm; 1 = ≥ 10 mm	0.33	0.33
23.	Length of stigmatic exertion beyond stamen	0 = < -1 mm; 1 = -1 to 4 mm; 2 = ≥ 4 mm	0.67	0
24.	Ovary attachment	0 = sessile; 1 = stipitate	1	1
25.	Ovary profile	0 = round; 1 = ovate; 2 = rhombic (apex acute); 3 = obovoid	1	1
26.	Fruit shape	0 = round; 1 = obpyramidal; 2 = ovate	1	1
27.	Fruit cross section	0 = entire; 1 = lobed; 2 = sharply angled	1	1
28.	Lobes of fruit	0 = nonbifid; 1 = bifid	1	1
29.	Fruit apex shape	0 = round; 1 = truncate; 2 = rostrate; 3 = acute	1	1
30.	Aril type	0 = basal; 1 = crested; 2 = membranous	1	1
31.	Rhizome length	0 = ≥ 10 mm; 1 = < 10 m	0.5	0.5
32.	Anther attachment	0 = dorsifixed; 1 = linear	1	1

Uvularia perfoliata: BOON: L.W. Carpenter 3050, M. Hicks 8931, D.B. Pointdexter 05-256; TENN: J.G. Allawos 60, D. Dixon 2920, E. Edward 3098, D. Estes 08754, C.J. Hansen 2001-32, P. Kotter no #, R. Kral 34252, D. Lashlee no #, L. Lipps no #, V.E. McNellus 93-408, B.T. Mounts no #, H.L. Sherman 089.

Uvularia puberula: BOON: Carrigan 34-5200, M. Livengood 20-6503, W. Miller 3905, D.B. Pointdexter 81-17476, Roberson 79-3860, A. Rodgers 23, Dot Simpson 1975; TENN: P. DePriest 85, M.A. Feist 406. 2892, E.L. Green 1120, R.L. James 18904, L. R. Phillippe 30221, 33343, R.E. Shanks 15210, R.D. Thomas 33354, L.J. Uttal 6998; WWC: C. Blaine no #, L. Laufer no #, B. Sharp no #.

Uvularia sessilifolia: BOON: R. Kral 34251, D.W. Woods 1795; TENN: D.E. Boufford 23324, J.M. Coleman 46331, D. Estes 01825, R. Kral 16401, 34393, 42385, V.E. McNellus 89-244, 90-13, P.A. Schmalzer 562, R.D. Thomas 70311, no #, D.H. Webb 734, R.D. Thomas 70311; WWC: M. Heller no #.

Prosartes lanuginosa: BOON: E. Croon 12-491, C.A. Flemming 17080, D.I. Glasco 12-669, E. Gillespie 16640, W. Hester 11-159, Hicks 8936; M. Monroe

15708, R.C. Patton 5015, D.B. Pointdexter 05-121, A. Rodgers 6873, R. Ruis 5017, Stanberry 112, T.P. Taylor 10-046.

Characters. Thirty-two morphological characters were selected (Table 1): 18 qualitative and 14 quantitative characters, based upon observation and from the literature (e.g., Wilbur 1963; Radford et al. 1968). All characters were analyzed in at least 15 specimens of each species, except *U. floridana* (6 specimens). All quantitative characters were measured with a digital caliper with repeatability to 0.01 mm. These characters (characters 4, 5, 8, 9, 13–15, 16–19, and 21–23) were coded using break points established by visual inspection of ranges plotted for individual species. Selected character states were non-overlapping at the 95% confidence interval; taxa that were polymorphic were assigned multiple character states.

Data analysis. The character by taxon matrix (Table 2) was assembled using MacClade 4.08 software (Maddison and Maddison 2005). All character states for polymorphic taxa were entered, and polymorphic characters were treated as polymorphic in the phylogenetic analysis (corresponding to method #6 for treating polymorphic

Table 2. Distribution of character states among taxa. Characters are numbered as in Table 1. The presence of more than one character state indicates that taxa are polymorphic for that character.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>Uvularia puberula</i> Michaux	0	1	1/2	1	0	1	1	2	0/1	1	3	0	0/1	0/1	0/1	0
<i>U. sessilifolia</i> L.	0	1	2	0/1	0	1	1	2	1	1/2	1	0	0/1	0	0	0
<i>U. floridana</i> Chapman	0	1	2	0	0	1	1	2	1	1/2	1	2	1	1	0	0
<i>U. perfoliata</i> L.	1	2	2	0/1	0/1	0	0	1/2	0/1	1	2	1	0/1	0/1	0/1	0
<i>U. grandiflora</i> Smith	1	2	1/2	0	1	0	0	1	1	1/2	2	1	0	1	1	1
<i>Prosartes lanuginosa</i> (Michaux) D. Don	0	0	0	0	0/1	0	0	0	0	0	0	0	0	0	0	0
Taxon	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
<i>Uvularia puberula</i> Michaux	1	1/2	0	0	1	0	1	0	1	2	2	0	2	1	1	1
<i>U. sessilifolia</i> L.	1	1	0	0	0	0/1	1/2	1	1	2	2	0	2	1	0	1
<i>U. floridana</i> Chapman	1	1	0	0	0	0	1/2	0	2	2	2	0	3	1	0	1
<i>U. perfoliata</i> L.	1	1/2	1	1	0/1	0/1	1	0	1	1	1	1	1	2	1	1
<i>U. grandiflora</i> Smith	0/1	2	0/1	0	1	1	0/1	0	3	1	1	0	1	2	1	1
<i>Prosartes lanuginosa</i> (Michaux) D. Don	0	0	0	0	0	0/1	1	0	0	0	0	0	0	0	0	0

characters in Kornet and Turner 1999). Maximum parsimony analyses and bootstrap analyses were performed in PAUP* 4.0b10 (Swofford 2003). All characters were unordered and equally weighted, and tree construction was conducted using an exhaustive search. Clade support was estimated using bootstrap analyses (Felsenstein 1985; Hillis and Bull 1993), with 1,000 bootstrap replicates, as well as decay indices generated via constraint trees. Consistency index, retention index, and rescaled consistency index were obtained from MacClade for each tree.

We initially performed two phylogenetic analyses: the first including all 32 characters, and the second restricted to the 18 qualitative characters. We performed this second analysis because the size of structures of the same species varied depending on the time of year and growth stage. In general, specimens of the same species collected later in the growing season had larger structures (such as leaves, flowers, and stem lengths) than specimens collected earlier in the growing season. Quantitative characters were eliminated in the second analysis for the purpose of minimizing this temporal variation within the same species.

To evaluate the phylogenetic utility of the various characters in the data set, we calculated consistency index (CI) and retention index (RI) for each character. We then repeated the phylogenetic analyses, reweighting the characters based upon these values, to determine if this would give us better phylogenetic resolution and/or better clade support.

In addition to the phylogenetic analysis, we also performed a principal components analysis on the quantitative character data using JMP® statistical analysis software (version 8), to examine the way in which variation in size of these characters may or may not distinguish different taxa from one another.

RESULTS

Parsimony analysis of the complete data set yielded six most-parsimonious trees of 45 steps (CI = 0.96, RI = 0.87, RC = 0.83; Fig. 1). The strict consensus of these six trees is shown in Figure 1, with branches labeled with bootstrap values above 50% and decay indices above 1. Parsimony analysis of the qualitative character data yielded three most parsimonious trees of 30 steps (CI = 0.97, RI = 0.93, RC = 0.90; Fig. 2). The strict consensus of these three trees is given in Figure 2, with branches labeled with bootstrap values above 50% and decay indices above 1.

Both the qualitative data phylogeny and the complete data phylogeny contain a clade composed of *U. grandiflora* + *U. perfoliata*, supported by high bootstrap values of 96 in both. In addition, both phylogenies include a clade consisting of a polytomy of the remaining three species (*U. puberula*, *U. sessilifolia*, *U. floridana*), with bootstrap values of 51 (unsupported; we base our interpretation of bootstrap values upon Hillis and Bull 1993) in the complete data phylogeny and 69 (weak support) in the qualitative data phylogeny.

Character states supporting the monophyly of *Uvularia* include lanulose leaf indumenta (character 3) and dorsifixed anther (character 32). Character states supporting the monophyly of Section *Oakesiella* include sessile leaves (character 1), papillose leaf margins (character 2), distally angled stems in cross section (character 6), and ovate, sharply-angled fruits (characters 26 and 27), and crested arils (character 30). Character states supporting the monophyly of Section *Uvularia* include perfoliate leaves (character 1), entire leaf margins (character 2), terete stems in cross section (character 6), solid stem pith (character 7), obpyramidal lobed fruits (characters 26 and 27), and membranous arils (character 30). Morphological synapomorphies are

FIG. 1. Strict consensus of six most-parsimonious trees describing phylogenetic relationships within the genus *Uvularia* based on parsimony analysis of all 32 morphological characters (length = 46, consistency index (CI) = 0.96, retention index (RI) = 0.87, rescaled consistency index (RC) = 0.83). Bootstrap support values (%) greater than or equal to 50 are shown above branches. Decay indices were all = 1 (not shown).

mapped upon the consensus tree in Figure 3. CI and RI for individual characters (Table 1) show that the most phylogenetically informative characters include those named above.

When the phylogenetic analyses were repeated with characters reweighted based upon CI and RI values, resulting tree topologies were the same as the initial analyses, but in the analysis of qualitative data, bootstrap values for the sessile-leaved clade (Section *Oakesiella*) were much stronger (85 using CI for weighting; 84 using RI for weighting; Fig. 4).

Principal components analysis (PCA) of the quantitative character data clearly separated *U. grandiflora* from the other *Uvularia* species in the first two dimensions, but all other species overlap substantially (Fig. 5). The first principal component (PC1), accounting for 37% of the variation in the data set, has eight eigenvectors between 0.28 and 0.40, representing size of

FIG. 2. Strict consensus of three most-parsimonious trees describing phylogenetic relationships within the genus *Uvularia* based upon parsimony analysis of 18 qualitative morphological characters (length = 30, consistency index (CI) = 0.97, retention index (RI) = 0.93, rescaled consistency index (RC) = 0.90). Bootstrap support values (%) greater than or equal to 50 are shown above branches. Decay indices were all = 1 (not shown).

FIG. 3. Strict consensus of three most-parsimonious trees obtained from analysis of qualitative morphological characters in the genus *Uvularia* with state changes mapped for significant characters (see discussion). Numbers for characters and character states are as listed in Table 1.

floral structures and stem lengths/internode lengths. All of these are positive except for filament length, which appears to vary inversely with anther length, as well as stem length and internode length. PC1 has low eigenvectors for characters involving leaf size and style length. Therefore, PC1 generally represents floral size (except style length). *U. grandiflora* has higher values for PC1 than *U. sessilifolia* and *U. floridana*, but overlaps with *U. puberula* and *U. perfoliata* on this axis. PC1 also distinguishes *U. puberula* from *U. sessilifolia*, with *U. puberula* having higher values for PC1; this is notable because these two taxa are sister taxa on the phylogeny and have many similarities otherwise.

The second principal component (PC2) accounts for an additional 28% of the variation in the data. PC2 has highest eigenvectors for leaf size measurements, stem length, and a few measurements of floral size such as stamen length and tepal length, all of which are positive. Lowest eigenvectors for PC2 include style lobe length, style exertion, and anther length. Therefore, PC2 represents another indicator of plant size with emphasis on leaf size, stem length, and corolla length. PC2 separates *U. grandiflora* even more strongly from the other taxa than does PC1, while the other taxa overlap substantially on this axis.

Principal Component 3 (PC3) accounts for an additional 10% of the variation, and has highest eigenvectors for style length and style exertion. However, this axis when graphed (not shown) does not separate the species from one another and therefore is not a useful variable for us here.

DISCUSSION

Results of both phylogenetic analyses support *U. grandiflora* and *U. perfoliata* as sister taxa with several synapomorphies including: perfoliate leaves (character 1); entire leaf margins (character 2); obpyramidal, lobed

Table 3. Eigenvectors and eigenvalues for the first three principal components from analysis of quantitative characters, together explaining 75% of the variation in the data set. Characters are listed in descending order of PC1 loadings.

Character	PC1	PC2	PC3
Anther length	0.4008	0.1568	0.0149
Style lobe length	0.3653	0.1038	0.1590
Filament length	-0.3417	0.2463	-0.0660
Tepal width	0.3325	0.2451	-0.0213
Stem length	-0.3200	0.3143	-0.0351
Length of connective protrusion on anther	0.2963	-0.0745	-0.2774
Tepal length	0.2948	0.2969	-0.1317
Internode length	-0.2751	0.2080	-0.1867
Stamen length	0.2443	0.3801	-0.0179
Leaf width	-0.2265	0.3303	-0.0965
Leaf length	-0.0801	0.4125	-0.0112
Length of style exertion past stamen	-0.0683	-0.1789	0.6616
Pedicle length	-0.0474	0.2918	0.3209
Style length	0.0390	0.2583	0.5375
Eigenvalues	5.19	3.90	1.43
% variance explained	37.09	27.85	10.20

fruit shape (characters 26 and 27); and membranous aril (character 30). The close relationship between these two species has also been supported by molecular data (Shinwari 1994; Hayashi 1998) and was recognized in early morphological studies as well (Wilbur 1963). This concordance of data from various sources leaves little doubt of this systematic relationship. These two taxa, in fact, are difficult to distinguish in the field. However, there are a few distinguishing characteristics, including some that were used in our analysis: stamen attachment location (on the receptacle in *U. perfoliata*; on the tepals in *U. grandiflora*), ovary profile shape (ovate in *U. perfoliata*; obovoid in *U. grandiflora*), and fruit lobe structure (bifid in *U. perfoliata*; non-bifid in *U. grandiflora*).

Both complete and qualitative data phylogenies show a polytomy of the remaining three species (*U. puberula*, *U. sessilifolia*, and *U. floridana*). A clade comprising these species was found in molecular studies (Shinwari

1994; Hayashi 1998), and Hayashi (1998) showed better resolution within the clade with *U. sessilifolia* and *U. floridana* as sister taxa, and *U. puberula* as their basal group.

The division of the genus into distinct clades matches Wilbur's (1963) delineation of two sections within the genus, section *Uvularia* (*U. grandiflora* and *U. perfoliata*) and section *Oakesiella* (including the remaining three species). These sections have also been supported by molecular studies of the genus (Shinwari 1994; Hayashi 1998). The complete data and qualitative data analyses yielded identical phylogenies, although bootstrap values supporting the *U. puberula* + *U. sessilifolia* + *U. floridana* clade differed. This suggests that morphological structure size may not have been a confounding variable in determining relatedness between species as initially suspected. However, the fact that the *U. puberula* + *U. sessilifolia* + *U. floridana* clade, a clade strongly supported by molecular studies (Shinwari 1994; Hayashi 1998), is

FIG. 4. Strict consensus of three most-parsimonious trees obtained from analysis of qualitative morphological characters in the genus *Uvularia*, with characters weighted according to consistency indices (length = 31, consistency index (CI) = 0.98, retention index (RI) = 0.96). Bootstrap support values (%) greater than or equal to 50 are shown above branches. Decay indices were all = 1 (not shown). Weighting characters according to retention indices resulted in identical topology and comparable support.

FIG. 5. First two principal components (PC1 and PC2) from PCA analysis of quantitative character data. Symbols indicate species of *Uvularia*.

supported by a bootstrap value of 69 (weak support) in the qualitative data phylogeny and is not supported by a bootstrap value of 51 in the complete data phylogeny suggest that varying structure size may affect statistical analysis of phylogeny accuracy. In addition, when characters were weighted according to their phylogenetic usefulness (using CI and RI values), support for this clade became quite strong, with a bootstrap value of 85.

Our observations suggest that the size of structures does vary between specimens of the same species of *Uvularia* depending on the time of year they were collected. Principal components analysis also demonstrated that the quantitative characters in general failed to separate the species into distinct groups, and only distinguished between *U. grandiflora* and the other four species. For these reasons, and because of congruence with molecular studies and higher bootstrap values, we place more confidence in the relationships delineated by the qualitative data phylogeny in Figure 4.

This phylogenetic analysis of the morphology of the five species in *Uvularia* produced a hypothesis of relatedness supporting phylogenies based on molecular data (Shinwari 1994; Hayashi 1998). Analyses of morphology indicate two clades within the genus: *U. grandiflora* + *U. perfoliata* and *U. puberula* + *U. sessilifolia* + *U. floridana*. These two clades match the division of *Uvularia* into two sections proposed by Wilbur (1963).

Acknowledgments: This research was supported by grants from the North Carolina Academy of Sciences and Warren Wilson College. Gratitude is given to the curators of the herbaria at Appalachian State University (BOON), University of Tennessee, Knoxville (TENN), the University of Florida, Gainesville (FLAS), and Warren Wilson College (WWC), who loaned *Uvularia* specimens crucial to completing this study.

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