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Identification of West Virginia Members of the Dentaria Complex [D. diphylla Michx., D. heterophylla Nutt., and D. laciniata Muhl. ex Willd. (Brassicaceae)] Using Above-Ground Vegetative Characters

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ABSTRACT

Long-term herb layer studies require nondestructive sampling, with species identified by above-ground characters. The purpose of this study was to determine the above-ground vegetative characters that best differentiate West Virginia members of *Dentaria diphylla*, *D. heterophylla*, and *D. laciniata*. Eleven morphological characters were measured on West Virginia herbarium specimens and data were subjected to canonical discriminant analysis and analysis of variance. Results showed that species fell into three distinct groups with length and width of basal and cauline leaflets as the most important characters for identification. *Dentaria laciniata* was identified by its lack of basal leaves and its long, narrow cauline leaflets. The basal leaflets of *D. diphylla* were similar to but larger than its cauline leaflets whereas the basal leaflets of *D. heterophylla* were much wider than its cauline leaflets. This study confirmed that these West Virginia members of the *Dentaria* complex may be identified using above-ground characters, and we provide a key to West Virginia *Dentaria* species using these characters.

INTRODUCTION

Proper identification of species is crucial to studies of forest herb layer communities. Long term and seasonal herb layer studies prefer nondestructive sampling by cover determination along transects (Graves and Monk 1982) or within plots (Gilliam and Turrill 1993, Rogers 1982, Peterson and Rolfe 1982) where species are distinguished by above-ground vegetative characteristics. Nondestructive sampling is also required with populations of rare plants or when observing reproductive patterns. In addition, identification by vegetative morphology is necessary for studies prior to or following flowering and fruiting.

Spring herb layer communities, however, often contain members of species complexes, such as *Phacelia* spp. (Levy 1991), *Vaccinium* spp. (Odell and Vander Kloet 1991), and *Pyrola* spp. (Haber 1987), that show an intergradation of char-

acters making identification by morphology alone difficult. One such complex common in eastern deciduous forests is the eastern North American Dentaria complex [D. diphylla Michx., D. heterophylla Nutt., D. incisifolia Eames ex Britt., D. laciniata Muhl. ex Willd., D. maxima (Nutt.) Gray, and D. multifida Muhl. ex Ell.]. Three of these species (D. diphylla, D. heterophylla, and D. laciniata) are found in West Virginia herb layer communities from mid-March through May (Strausbaugh and Core 1977). Members of this complex are known to be important elements of spring herb layer communities in the Great Smoky Mountains (Bratton 1976), Illinois (Bazzaz and Bliss 1971, Peterson and Rolfe 1982), the western and southern regions of the Great Lakes (Blank et al. 1980, Rogers 1982), and northern hardwood forests of high elevation regions of West Virginia (Aulick 1993).

Montgomery (1955) claimed that determining members of the Dentaria complex by vegetative morphology alone is extremely difficult due to the intergradation of characters within the complex. The three West Virginia species have been identified by rhizome morphology as stressed by Strausbaugh and Core (1977) and type descriptions [D. diphylla—dentate (Michaux 1803), D. heterophylla—concatenate (Nuttall 1818), and D. laciniata—moniliform (Nuttall 1818)]. Unfortunately, this involves sacrificing the plant and is only reliable when dealing with older populations that have well-established perennating structures. Our study intends to focus on identification by above-ground features as an aid to nondestructive sampling. The purpose of this study is to determine whether West Virginia members of the Dentaria complex may be separated with these characters by examining the morphological relationships of these species. Specific questions addressed are (1) to what degree do these species overlap in morphological similarity and (2) what vegetative characters best differentiate these species?

TAXONOMIC NOTES

Nomenclature

Dentaria spp. (toothworts) are members of the Brassicaceae (Cruciferae) family. According to Kartesz and Kartesz (1980), common synonyms are Cardamine diphylla (Michx.) A. Wood and D. incisa Small for D. diphylla, C. angustata Schulz. for D. heterophylla, and C. concatenata (Michx.) Ahles for D. laciniata. More recently, Gleason and Cronquist (1991) treated these plants as a section of Cardamine (bitter cress), separating the two groups by the shape of the principal leaves (Dentaria—palmately compound, Cardamine—pinnately compound). Since our study deals entirely with West Virginia populations, nomenclature follows Strausbaugh and Core (1977).

Morphology and Reproduction

Key descriptions show the diversity of leaf shapes found in populations of *Dentaria* spp., yet few floras describe these features quantitatively. The basal and cauline leaves of *D. diphylla* are similar with the former having lateral leaflets obliquely ovate and the central leaflet broadly ovate with coarse rounded teeth (Strausbaugh and Core 1977, Fernald 1950). The central leaflet of the cauline leaves is broadly elliptic to ovate with coarse, blunt teeth (Fernald 1950). The basal leaf of *D. heterophylla* has three rhombic-ovate or ovate-crenate or dentate or lobed leaflets; the cauline leaves have three narrowly oblong entire or toothed leaflets (Fernald 1950). *Dentaria laciniata* has three cauline leaves each with three variously cleft leaflets (Fernald 1950). These cauline leaves are sometimes simple and sharply toothed to incised; the leaflets or long segments vary from linear to oblong or oblanceolate (Strausbaugh and Core 1977, Fernald 1950). Fernald (1950) and Gleason and Cronquist (1991) report that *D. laciniata* may have basal leaves similar to its cauline leaves that are usually absent at anthesis. Strausbaugh and Core (1977), however, use the lack of basal leaves to distinguish *D. laciniata* from *D. heterophylla*.

All Dentaria spp. hybridize frequently (Harriman 1965, Fernald 1950, Strausbaugh and Core 1977) and exhibit a great degree of polyploidy (2n = 64-250) (Montgomery 1955, Easterly 1963, Harriman 1965), (n = 8) (Darlington and Janaki Ammal 1945). Dentaria spp. typically reproduce sexually (Braun 1957, Spooner 1984); yet they may form polyploid complexes with both sexual and sterile populations (Spooner 1984).

Distribution

Dentaria diphylla, D. heterophylla, and D. laciniata are sympatric and confined to rich, moist woods of the eastern one-half of North America (Gleason 1952, Fernald 1950). Dentaria heterophylla has a much more restricted range than either D. diphylla or D. laciniata (Gleason 1952, Fernald 1950) and is found primarily south of the Great Lakes to northern Alabama and Georgia and east of the Mississippi to the piedmont areas of Virginia and North Carolina. According to Strausbaugh and Core (1977), all three species are found throughout West Virginia. State distribution based on voucher specimens at Marshall University and West Virginia University support this statement with species absences most likely the result of insufficient collecting in that county (Figure 1).

MATERIALS AND METHODS

Eleven morphological characters were measured on herbarium material in Marshall University Herbarium (MUHW), Huntington, West Virginia, and West Virginia University Herbarium (WVA), Morgantown, West Virginia. All specimens (*Dentaria diphylla*—22, *D. heterophylla*—25, and *D. laciniata*—25) were collected in West Virginia. Only herbarium specimens exhibiting all of the desired characters (see Table 1) were used in our study. Through chance, relatively few specimens from the northern counties showed all of the desired characters. Thus, our analysis involved a greater proportion of specimens from southern counties (Figure 1). Appendix 1 contains a complete list of specimens used in this quantitative study.

In order to summarize the between-species variation of the measured characters and to determine which characters best separated these three species, data were subjected to canonical discriminant analysis (CDA) using the CANDISC procedure of SAS (1982), following Gittins (1985). Related to principal component analysis, CDA is especially useful when ordinating more than one data

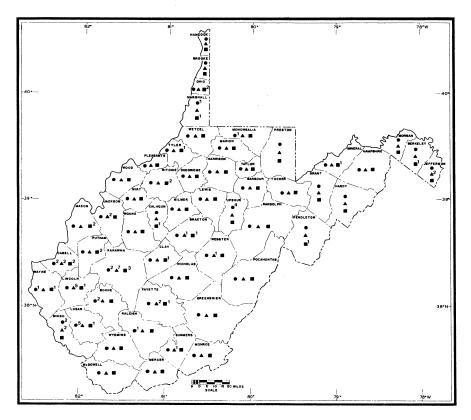


Figure 1. West Virginia distribution of *Dentaria diphylla* (\oplus) , *D. heterophylla* (\blacktriangle) , and *D. laciniata* (\blacksquare) based on observed voucher specimens in MUHW and WVA. Superscripts indicate the number of measured specimens from that county used in analyses.

matrix (Pielou 1984). In this study, there were three data matrices, one for each species. Since the data were not normally distributed, input data for this ordination were ln-transformed character measurements for each species. Mean character measurements were also subjected to analysis of variance and Duncan's Multiple Range Test using the ANOVA procedure of SAS (1982).

RESULTS AND DISCUSSION

After careful study of herbarium specimens and species descriptions by Fernald (1950) and Strausbaugh and Core (1977), the morphological characters in Table 1 were chosen for measurement. Based on these data, CDA revealed that only slight intergradation of characters existed among *Dentaria diphylla* and *D. heterophylla* and that *D. laciniata* was distinctly separate (Figure 2). The first two canonical axes accounted for 100% of the variation of the three species. The means of these groups were significantly different (P < 0.001) on both canonical axes showing that the observed specimens fell into three distinct

Character (Abbreviation)	Description	CAN1	CAN2
Basal leaf length (BL)	length (cm) of central leaflet from point of petiole attachment to tip	0.99	0.10
Basal leaf width (BW)	width (cm) of central leaflet at 50% BL	0.97	0.01
Inflorescence number (FN)	# flowers per plant	-0.18	-0.02
Cauline leaf length (LL)	length (cm) of central leaflet from point of petiole attachment to tip	-0.35	0.49
Cauline leaf width (LW)	width (cm) of central leaflet at 50% LL	-0.08	0.89
Node length (NL)	stem length (cm) from 1st node to 1st inflorescence	0.28	0.33
Petal length (PL)	petal length (mm) from pedicel to tip	-0.61	0.08
Petal width (PW)	petal width (mm) at 80% PL	-0.31	0.23
Sepal length (EL)	sepal length (mm) from pedicel to tip	0.00	0.07
Serration number (TN)	# cauline leaflet margin serrations in 2 cm at 50% LL	-0.09	0.30
Stem length (SL)	length (cm) from point of rhizome at- tachment to last inflorescence pedicel	-0.20	0.13

 Table 1. Total-sample correlation between In-transformed character measurements

 and first two canonical variables (CAN1 and CAN2)

groups based on above-ground morphology. The slight overlap in the ranges of D. diphylla and D. heterophylla (Figure 2) indicated that field separation of these two species would present the most difficulty.

The first canonical axis accounted for 93% of the variation among the species. Canonical correlations (Table 1) showed that the species were first separated by the presence or absence of a basal leaf on CAN1 (Figure 2). This caused D. laciniata to form a separate outlying group and explained the overlap of D. diphylla and D. heterophylla. Further analysis showed that the basal leaflets of D. diphylla and D. heterophylla were not significantly different in terms of width, but that the basal leaflets of D. diphylla (Table 2).

The second canonical axis further differentiated D. diphylla from D. heterophylla (Figure 2). On CAN2, canonical correlations showed that the species were separated primarily by cauline leaflet width and cauline leaflet length (Table 1). The cauline leaflets of D. heterophylla were significantly shorter than those of D. diphylla and D. laciniata (Table 2). All three species showed significant differences in cauline leaflet width with D. diphylla being the widest followed decreasingly by D. laciniata and D. heterophylla (Table 2).

CDA indicated that these species may be separated into distinct groups by comparing above-ground vegetative characters, especially basal and cauline leaflet dimensions. However, when a spring herb layer community does not contain all three species, allowing for quick comparisons, it is then best to look at ratios of basal and cauline leaflet dimensions for identification. The basal leaflets of D. diphylla were typically longer in relation to width (BL:BW = 2:1) than those of D. heterophylla (BL:BW = 1:1). Basal leaflets of D. diphylla were somewhat wider than its cauline leaflets (BW:LW = 2:1) whereas this ratio was much greater

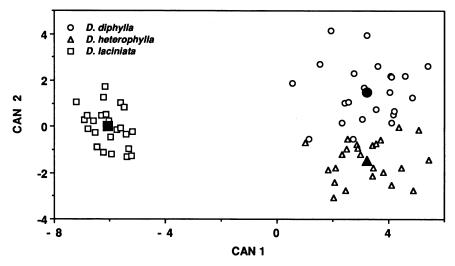


Figure 2. Canonical discriminant ordination of 72 specimens of West Virginia *Dentaria* spp. Mean score positions of each species indicated with a closed symbol.

for *D.* heterophylla (BW:LW = 4:1). Ratios of LL:LW increased from *D.* diphylla (3:1) to *D.* laciniata (4:1) to *D.* heterophylla (5:1).

In conclusion, this study shows that West Virginia Dentaria species may, indeed, be separated by above-ground vegetative characters making nondestructive field identification possible. Dentaria laciniata formed a distinctly separate group whereas slight intergradation of characters existed with D. diphylla and D. heterophylla. Dentaria laciniata was best identified by its lack of a basal leaf and a LL:LW ratio of 4:1. Dentaria diphylla had basal leaflets similar to but larger than its cauline leaflets (BW:LW = 2:1) whereas the basal leaflets of D.

Character	D. diphylla	D. heterophylla	D. laciniata
BL (cm)	4.31 ± 0.30^{a}	$3.56\pm0.23^{ ext{b}}$	
BW (cm)	$2.91 \pm 0.25^{*}$	2.78 ± 0.18^{a}	
FN (#)	9.30 ± 0.95^{a}	$8.96 \pm 0.66^{\circ}$	10.12 ± 0.61
LL (cm)	$5.91 \pm 1.30^{\circ}$	$3.31 \pm 0.21^{\text{b}}$	5.46 ± 0.19
LW (cm)	$1.97 \pm 0.18^{\circ}$	0.67 ± 0.06^{b}	1.32 ± 0.11
NL (cm)	$7.77 \pm 0.87^{\circ}$	$5.63 \pm 0.45^{\text{b}}$	5.07 ± 0.48
PL (mm)	$10.82 \pm 0.51^{\circ}$	10.42 ± 0.48 a	$14.52\pm0.51^{\circ}$
EL (mm)	$5.17 \pm 0.21^{\circ}$	5.08 ± 0.28^{a}	5.08 ± 0.18
TN (#)	$4.17 \pm 0.22^{\circ}$	3.50 ± 0.45^{a}	4.20 ± 0.37
SL (cm)	23.00 ± 1.97 a	$20.34 \pm 0.73^{\circ}$	23.39 ± 0.74

Table 2. Mean values of vegetative characters of the West Virginia Dentaria complex. Values given are means ± 1 SE. Means for a given character with different superscripts are significantly different at P < 0.05. See Table 1 for character abbreviations

heterophylla were distinctly different than its cauline leaflets (BW:LW = 4:1). Further studies should apply these characters to simplify identification throughout the range of the eastern North American *Dentaria* complex. Following is a key to West Virginia *Dentaria* which uses the above-ground vegetative characters supported by our study.

KEY TO WEST VIRGINIA DENTARIA

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1.	Basal leaves rarely present; length of cauline leaflets four times width (LW:LW
	4:1)D. laciniata
1.	Basal leaves present
	2. Basal leaflets similar to but larger than cauline leaflets; basal leaflets twice as
	wide as cauline leaflets (BW:LW 2:1); length of basal leaflets two times
	width (BL:BW 2:1); length of cauline leaflets three times width (LL:LW
	3:1) D. diphylla
	2. Basal leaflets unlike cauline leaflets; basal leaflets four times as wide as cauline
	leaflets (BW:LW = 4:1); length and width of basal leaflets similar (BL:BW
	1:1); length of cauline leaflets five times width (LL:LW 5:1) D. heterophylla

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Appendix 1. West Virginia specimens examined in MUHW and WVA and used in analysis. When more than one complete specimen was available on a herbarium sheet, each was measured separately. The number of specimens measured in such cases is shown after the herbarium acronym

Dentaria diphylla: WEST VIRGINIA. Boone County: 22 Apr 1978, Arcuri 14 (MUHW-2). Cabell County: Apr 1929, Carr s.n. (MUHW); 22 Apr 1975, Tackett 42 (MUHW). Kanawha County: 17 Apr 1976, Crews 19 (MUHW); 28 Apr 1978, Panuska 104 (MUHW). Logan County: 14 Apr 1979, Justice Ave., Adkins & Fleshman s.n. (MUHW); 14 Apr 1979, Broom Hollow, Adkins & Fleshman s.n. (MUHW); 22 Apr 1979, O'Hanlon 12 (MUHW-3). Marshall County: 19 Apr 1991, Schoene 520 (MUHW). Mingo County: 13 Apr 1979, Ferrell 50 (MUHW-2). Monongalia County: 2 May 1953, Muensher & Clovis 24020 (WVA). Raleigh County: 15 Apr 1990, Canterbury 28 (MUHW). Upshur County: 30 Apr 1963, Grose s.n. (WVA); 23 Apr 1964, Knorr s.n. (WVA); 29 Apr 1963, Rossbach 4580 (WVA); 29 Apr 1963, Rossbach 4581 (WVA). Wayne County: 2 Apr 1938, Williams s.n. (MUHW). Mont Chateau: 13 May 1909, Sheldon 3565 (WVA).

Dentaria heterophylla: WEST VIRGINIA. Braxton County: 6 Apr 1953, Boggs 20 (WVA). Cabell County: 18 Apr 1936, Gilbert & Williams 413 (MUHW); 19 Apr 1936, Smithson s.n. (WVA). Fayette County: 21 Apr 1892, Nuttall 150 (WVA); 21 Apr 1892, Nuttall 156 (WVA). Jackson County: 6 Apr 1990, O'Connor 2 (MUHW-2). Jefferson County: 21 Apr 1975, Brown s.n. (WVA-2). Kanawha County: 21 Mar 1991, King 4 (MUHW-2); 11 Apr 1978, Nugen 22 (MUHW-3); 28 Apr 1978, Panuska 105 (MUHW); 13 Apr 1979, Tysinger s.n. (MUHW). Lincoln County: 16 Apr 1981, Davis 17 (MUHW-2); 17 Apr 1979, Giles 108 (MUHW-3). Mingo County: 13 Apr 1979, Ferrell 49 (MUHW-2). Summers County: 16 Apr 1961, Boone 1174 (WVA). Webster County: 25 Apr 1953, Davis 1056 (WVA). Dentaria laciniata: WEST VIRGINIA. Berkely County: 4 Apr 1937, Shreve s.n. (WVA). Braxton County: 3 Apr 1953, Boggs 37 (WVA). Cabell County: 4 Apr 1975, Creekmore 8 (MUHW-2). Calhoun County: 19 Apr 1933, Harris s.n. (WVA). Clay County: 21 Apr 1956, Rossbach 872 (WVA). Fayette County: 16 Mar 1990, Vaughn 18 (MUHW). Kanawha County: 12 Apr 1975, Crum 109 (MUHW-2); 26 May 1933, Strickland 76 (WVA). Lincoln County: 8 Apr 1978, Messinger 115 (MUHW). Logan County: 31 Mar 1979, Adkins s.n. (MUHW). Marshall County: 19 Apr 1991, Schoene 518 (MUHW). Mason County: 6 Apr 1991, Smith 5 (MUHW); 6 Apr 1991, Turrill 5 (MUHW). Mineral County: Apr 1953, Brown s.n. (WVA). Ohio County: 11 Apr 1929, Brooks s.n. (WVA); 14 Apr 1929, Strausbaugh s.n. (WVA). Pendleton County: 7 Apr 1979, Schromm 27 (MUHW). Putnam County: 14 Apr 1980, Sauer 18 (MUHW-2). Ritchie County: 15 Apr 1978, Stephens 6 (MUHW-2). Tyler County: 19 Apr 1942, Bartholomew T-25 (WVA). Wayne County: Apr 1932, Lycan 84 (WVA).

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