

TAXONOMIC STUDY OF THE *CLEMATIS RETICULATA* SPECIES COMPLEX  
(RANUNCULACEAE: SUBGENUS *VIORNA*)

By

Thomas H. Murphy

A Thesis Submitted in Partial Fulfillment  
of the Requirements for the Degree of  
Master of Science in Biology

Austin Peay State University  
August 2020

Thesis Committee:

Dr. L. Dwayne Estes, Committee Chair

Dr. Don Dailey

Dr. Rebecca Johansen

TAXONOMIC STUDY OF THE *CLEMATIS RETICULATA* SPECIES COMPLEX  
(RANUNCULACEAE: SUBGENUS *VIORNA*)

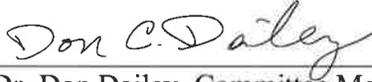
Thomas H. Murphy

Approved:



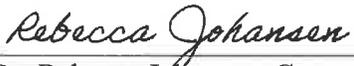
---

Dr. L. Dwayne Estes, Committee Chair



---

Dr. Don Dailey, Committee Member



---

Dr. Rebecca Johansen, Committee Member



---

Dr. Chad Brooks, Associate Provost and Dean, College of Graduate Studies

## Statement of Permission to Use

In presenting this thesis in partial fulfillment of the requirements for the Master of Science in Biology at Austin Peay State University, I agree that the library shall make it available to borrowers under the rules of the library. Brief quotations from this thesis are allowable without special permission, provided that accurate acknowledgement of the source is made. Permissions for extensive quotation or reproduction of this thesis may be granted by my major professor, or in his absence, by the Head of the Interlibrary Services when, in the opinion of either, the proposed use of the material is for scholarly purposes. Any copying or use of the material in this thesis for financial gain shall not be allowed without my written permission



---

Thomas H. Murphy

07/01/2020

I dedicate this research to my family.

## ACKNOWLEDGMENTS

I would like to acknowledge and thank my advisor and mentor Dr. Dwayne Estes for giving me the opportunity to undertake this study for my graduate research, as well as providing guidance during my time at Austin Peay State University (APSU). I thank Dr. Johansen and Dr. Dailey, my committee members, for providing guidance and helpful comments for my manuscript. I would like to thank Mt. Cuba Center for funding the majority of this study and the broader revisionary systematics research of North American *Clematis* subgenus *Viorna* with the Mt. Cuba Center Graduate Fellowship in Eastern North American Botany. I would also like to thank the British Clematis Society for funding additional fieldwork and supplies to complete our research, Lyndy Broder for funding fieldwork, and APSU Center of Excellence for Field Biology for allowing the use of field vehicles. I am grateful to Zach Irick, Mason Brock, Joseph Aroh, Dr. Brian Keener, Kevin England, Jesse Harris, Kate Love, Glen Dale Bryant, and Steve Scarborough for assistance and guidance during fieldwork. I thank Dr. Jared Barnes, Sonnia Hill, and Theo Witsell for sending herbarium specimens and/or living plants to include in our study. I would like to thank Claire Ciafre and Annie Lindsey for generously caring for common garden plants while I was travelling for fieldwork. I thank Dr. Aaron Floden for discussing and providing valuable insight into *Clematis* taxonomy. I am appreciative of Dr. Kanchi Gandhi for expertise and helpful comments in regard to the Shenzhen Code. I am grateful to Alan Cressler for allowing me to use his photograph from Pine Mountain, Georgia. I also thank the curatorial staff of all herbaria that generously sent specimen loans to APSC, as well as MO for allowing me to visit. I would like to thank my parents for their unwavering support of me. Lastly, I would like to thank my partner, Kate, for always being supportive, encouraging, and understanding while we worked towards our degrees from a distance.

## ABSTRACT

Chapter 1 is a literature review of the taxonomic history of *Clematis* subg. *Viorna*. Chapter 2 is a morphometric study and taxonomic treatment of the *Clematis reticulata* species complex. *Clematis* subgenus *Viorna* of North America currently consists of 21 species, most of which are distributed in the southeastern United States. Past taxonomic treatments of subg. *Viorna* have varied greatly, which has led to unclear species limits. Often recognized as a single, polymorphic species with a high degree of ecological amplitude, variation in *C. reticulata* s.l. species complex is typically attributed to phenotypic plasticity. A combination of herbarium specimen examination and extensive fieldwork led to formation of seven *a priori* morphological groups, or hypothesized taxa, in the *C. reticulata* species complex based on previously used and novel morphological characters. A total of 16 morphological characters, quantitative and qualitative, were measured to generate two datasets from herbarium specimens and a common garden experiment which were subjected to the same statistical analyses. To visualize morphological separation in multivariate space, data were subjected to factor analysis of mixed data. To infer if hypothesized taxa were diagnosable, partial least squares discriminant analysis models were used to assess classification accuracy based on *a priori* groups. Morphological characters were subjected to non-parametric univariate analyses. Of the seven hypothesized taxa, six were supported by evidence from morphology, biogeography, and ecology. Four new species are recognized: *C. arenicola* sp. nov., *C. cumberlandensis* sp. nov., *C. ouachitensis* sp. nov., and *C. terminalis* sp. nov. *Viorna subreticulata* is given a new combination in *Clematis* and the newly defined *C. reticulata* s.s. is re-circumscribed. An updated dichotomous key, species descriptions, ecological notes, and distribution maps are provided.

## TABLE OF CONTENTS

CHAPTER I: A Review of the Systematics and Taxonomy of <i>Clematis</i> subgenus <i>Viorna</i> A. Gray (Ranunculaceae) .....	1
Introduction .....	1
Nomenclatural History .....	2
Taxonomic Treatments .....	3
Palynological Studies .....	6
Leaf Surface .....	6
Seedling Phyllotaxy .....	7
Cytological Studies .....	8
Chemotaxonomic Studies .....	9
Molecular Methods .....	9
Conclusion .....	10
Literature Cited .....	12
CHAPTER II: A Morphometric Approach to Delimiting Species in the <i>Clematis reticulata</i> Species Complex (Ranunculaceae: Subgenus <i>Viorna</i> ) .....	16
Introduction .....	16
Materials and Methods .....	20
Herbarium specimen sampling .....	20
Common garden sampling .....	20

Common garden experiment .....	21
Character selection.....	22
Data subsetting .....	23
Multivariate analyses .....	24
Univariate analyses .....	25
Comparison of herbarium specimens and common garden datasets .....	26
Results.....	27
Herbarium specimens.....	27
Common garden experiment .....	28
FAMD .....	28
PLS-DA.....	30
Univariate analysis of quantitative and ordinal characters.....	31
Nominal characters .....	34
Comparison of herbarium specimens and common garden datasets .....	35
Discussion .....	35
Utility of common garden .....	36
Species delimitation .....	37
Taxonomic diversity in the southeastern United States .....	44
Future taxonomic work .....	45
Taxonomic Treatment.....	45
Key to the <i>Clematis reticulata</i> Species Complex.....	92
Literature Cited.....	94

Appendices .....	99
Appendix A. Character collection methods, guidelines, and calculations. ....	99
Appendix B. Sample size summary of specimens measured for multivariate and univariate analyses of herbarium specimens and common garden datasets, subset by flowering and fruiting individuals.....	100
Appendix C. Pairwise comparisons of hypothesized taxa of herbarium specimens dataset .....	101
Appendix D. Pairwise comparisons of hypothesized taxa of common garden dataset .....	102

## LIST OF TABLES

<b>Table 1.</b> Geographic centers of distribution of <i>Clematis reticulata</i> s.l., serving as a priori morphological groups, or taxonomic hypotheses, for this study.....	19
<b>Table 2.</b> Morphological characters hypothesized to delimit groups in the <i>Clematis reticulata</i> species complex, measured from herbarium specimens and common garden individuals.....	27
<b>Table 3.</b> Confusion matrices from LOOCV of PLS-DA models of herbarium specimens, subset by bract placement and reproductive stage.....	31
<b>Table 4.</b> Confusion matrices from LOOCV of PLS-DA models of common garden individuals, subset by bract placement .....	32
<b>Table 5.</b> Summary statistics and comparisons of morphological characters between hypothesized taxa for herbarium specimen and common garden dataset.....	33
<b>Table 6.</b> Statistical significance of characters within hypothesized taxa between herbarium specimen and common garden datasets .....	36

## LIST OF FIGURES

<b>Figure 1.</b> Geographic sampling of herbarium specimens for univariate and multivariate analyses for the <i>Clematis reticulata</i> species complex .....	22
<b>Figure 2.</b> Geographic sampling of common garden individuals for univariate and multivariate analyses for the <i>Clematis reticulata</i> species complex .....	23
<b>Figure 3.</b> Scatterplot of first and second axes of FAMD of the herbarium specimen datasets....	28
<b>Figure 4.</b> Scatterplot of first and second axes of FAMD of common garden datasets .....	29
<b>Figure 5.</b> Proportional histogram plots of leaf thickness of <i>a priori</i> groups.....	34
<b>Figure 6.</b> Diagnostic characters of <i>Clematis arenicola</i> .....	47
<b>Figure 7.</b> Generalized range map of <i>Clematis arenicola</i> .....	49
<b>Figure 8.</b> Diagnostic characters of <i>Clematis cumberlandensis</i> .....	54
<b>Figure 9.</b> Generalized range map of <i>Clematis cumberlandensis</i> .....	57
<b>Figure 10.</b> Diagnostic characters of <i>Clematis ouachitensis</i> .....	61
<b>Figure 11.</b> Generalized range map of <i>Clematis ouachitensis</i> .....	63
<b>Figure 12.</b> Diagnostic characters of <i>Clematis reticulata</i> s.s.....	68
<b>Figure 13.</b> Generalized range map of <i>Clematis reticulata</i> s.s. ....	69
<b>Figure 14.</b> Diagnostic characters of <i>Clematis subreticulata</i> .....	80
<b>Figure 15.</b> Generalized range map of <i>Clematis subreticulata</i> .....	83
<b>Figure 16.</b> Diagnostic characters of <i>Clematis terminalis</i> .....	89

## CHAPTER I: A Review of the Systematics and Taxonomy of *Clematis* subgenus *Viorna* A. Gray (Ranunculaceae)

### Introduction

The genus *Clematis* L. is large and diverse, consisting of approximately 300-350 species, mostly native to temperate, subarctic, subalpine, and tropical climates (Johnson 2001). Members of the genus are distinguished from other genera in Ranunculaceae by climbing vine or erect herbaceous perennial habit, opposite leaf arrangement, usually compound leaves, petaloid sepals, absence of petals, and aggregate of achenes as fruit (Pringle 1997; Johnson 2001; Wang and Li 2005). *Clematis* has been widely cultivated for hundreds of years as an ornamental garden plant and used for cut flowers. Species have also been hybridized within the horticulture trade to create thousands of cultivated varieties (Johnson 2001). Twenty-six *Clematis* species have been used in traditional medicine and 35 species have been analyzed chemically to serve as a source of phytochemicals (Chawla et al. 2012).

The use of names for various infrageneric ranks has made *Clematis* confusing from nomenclatural, taxonomic, and horticultural perspectives (Lehtonen et al. 2016). Subgenus *Viorna* A.Gray has received considerable taxonomic attention since its conception (Keener and Dennis 1982). A plethora of research has been conducted, but few of the classifications are comparable due to differences of rank, treatment, and geography.

Subgenus *Viorna* and lower ranks have been subjected to multiple taxonomic treatments and systematics studies pertaining to nomenclature, taxonomy, numerical studies, and DNA sequencing. The objective of this review is to provide a systematic literature review of the history of taxonomy and systematics of *Clematis* subg. *Viorna* A.Gray. *Clematis* subg. *Viorna* or subg. *Viorna* are reference to the name with the authority of A.Gray; any use of the name

“Viorna” to groups, sections, subsections, etc. that are different from the concept of subg. *Viorna* sensu Gray (1895) will be noted.

### Nomenclatural History

Keener and Dennis (1982) described subg. *Viorna* as a group that has undergone the most taxonomic and nomenclature scrutiny within *Clematis*. The following discussion and historical description are partly adapted from Keener and Dennis (1982) with added treatments of the subgenus since 1982.

The name “Viorna” was first applied to *Atragene* subg. *Viorna* Pers. to include *Atragene balearica* Pers. and *A. cirrhosa* Pers. (Persoon 1806) and was later elevated to genus rank, *Viorna* (Pers.) Rchb. by Reichenbach (1837). Consequently, the genus *Viorna* and *Atragene* subg. *Viorna* were recognized as taxonomically synonymous (Reichenbach 1837). In a treatment of tribe *Clematideae* DC., Spach (1839) cited the genus “*Viorna* Reichenb.”. Although Spach (1839) placed *Viorna cylindrica* Spach ex Dippel, *V. urnigera* Spach, and *V. integrifolia* (L.) Spach in his treatment of the genus and maintained Reichenbach as the authority, it is evident from his misapplied citation that he assumed *V. urnigera* (= *Clematis viorna* L.) should be intuitively placed in the genus *Viorna*. Small (1933) cited Spach as the authority of the genus *Viorna*, as *Viorna* Spach.

Prantl’s (1888) treatment was the first known treatment to establish a sectional rank for *Viorna* under *Clematis* and named himself as authority (Prantl 1887). Keener and Dennis (1982) stated that *Clematis* sect. *Tubulosae* Decainse is synonymous with Prantl’s sect. *Viorna*. However, sect. *Tubulosae* was described to encompass distantly related species such as *C. stans* Siebold & Zucc. and *C. tubulosa* Turcz. (Decainse 1881).

Gray (1895) was the first to name sect. *Viorna* sensu Prantl (1888) at the subgeneric level as *Clematis* subg. *Viorna* A.Gray. Because *Clematis* subg. *Viorna* A.Gray is typified by *C. viorna*, there is no ambiguity to the application of this name. Gray's classification of subg. *Viorna* has been accepted in most treatments and floras since but has included conflicting infrageneric and interspecific classifications (Keener and Dennis 1982; Pringle 1997; Yang and Moore 1999). *Clematis* subg. *Viorna* Rchb. has been incorrectly applied since Gray's treatment (1908). The misapplication and confusion of nomenclature has confounded and obscured the name "Viorna".

### **Taxonomic Treatments**

Major revisions of the "Viorna" group sensu Prantl (1888) have included treatments confined to higher taxonomic ranks such as genus, subgenus, section, subsection, and series (James 1838; Kuntze 1885; Prantl 1888; Gray 1895; Small 1933; Erickson 1943; Keener and Dennis 1982; Tamura 1987; Pringle 1997; Johnson 2001; Wang and Li 2005). These treatments would be considered to be intuitive taxonomic studies per Henderson (2005), as they employ a philosophical view to delineate taxa.

The earliest infrageneric classifications of *Clematis* were based on the artificial character of growth habit; "Scandentes" and "Erectae" were two groups recognized within sect. *Clematis* (James 1838; Torrey and Gray 1838). Kuntze (1885) further subdivided these artificial groups and employed an ambiguous taxonomic hierarchy, with many of his described taxa treated as probable synonyms by Keener and Dennis (1982). Several of the taxa described by Kuntze (1885) lacked thorough descriptions, some of which were based solely on cultivated material from botanical gardens.

Spach (1839) recognized three species in the genus *Viorna*. The only other major treatment that recognized *Viorna* at the generic level included 13 species from the southeastern US and included species such as *Viorna flaccida* (Small) Small, *V. gattingeri* Small, *V. obliqua* Small, and *V. subreticulata* Harb. ex Small (Small 1933), which have been synonymized with other species in modern day treatments of subg. *Viorna* (Dennis 1976; Keener and Dennis 1982; Yang and Moore 1999).

The first treatment of sect. *Viorna* included four subsections and 45 species from North America and Eurasia: *Crispae*, *Tubulosae*, *Atragenae*, *Cirrhosae* (Prantl 1888). Prantl's treatment (1888) is the only known publication to include subsect. *Atragenae* and *Cirrhosae*, which are morphologically distant and not considered closely related to sect. or subg. *Viorna* in other major treatments (Torrey and Gray 1838; Keener and Dennis 1982; Yang and Moore 1999; Wang and Li 2005). Erickson (1943) defined sect. *Viorna* to be confined to the North American species of subg. *Viorna*, in which 18 species and five subsections were included: *Euviornae* R.O.Erickson, *Viticellae* R.O.Erickson, *Integrifoliae* R.O.Erickson, *Baldwinianae* R.O.Erickson, *Hirsuttissimae* R.O.Erickson. Although, two Eurasian species, *C. integrifolia* L. and *C. fusca* Turcz., are discussed as potentially belonging to sect. *Viorna*. Erickson (1943) did not provide Latin diagnoses (Keener and Dennis 1982), but his names were later validated by Johnson (2001) with Latin descriptions and including *C. integrifolia* and *C. fusca* as part of the circumscription of sect. *Viorna*.

Taxonomic treatments of "Viorna" as a subgenus have also been variable (Gray 1895; Pringle 1997; Wang and Li 2005). Gray (1895) included 10 species in subg. *Viorna*, restricted to North America. Pringle (1997) recognized 18 species in North America and stated subg. *Viorna* includes 25 species when Eurasian congeners are considered. Wang and Li's (2005) broader

interpretation of the subgenus included 71 species, 2 sections, 3 subsections, and 11 series.

Within subg. *Viorna sensu* Wang and Li (2005), species from subg. *Viorna sensu* Gray (1895) were placed in multiple series, which were similar to subsectional treatments of section *Viorna* by Erickson (1943) and Johnson (2001), in sect. *Viorna* subsect. *Crispae*. Wang and Li's (2005) treatment remains to be the only comprehensive treatment of subg. *Viorna* in the broadest sense.

### **Numerical Taxonomy**

With the development of statistical methods and computing technology, numerical taxonomy has contributed to the classification of species and higher taxa (Sokal 1963). Keener (1967) included seven multi-state quantitative vegetative and floral characters along with pollen, stomata, and ecological amplitude traits to infer evolutionary relationships between species in subsect. *Integrifoliae*. A similar study on the subsect. *Viornae* used nine binary morphological characters and flavonoid compounds for ordination analyses to infer evolutionary relationships and morphological differences (Dennis 1976). Like Dennis (1976), Yang and Moore (1999) also employed ordination, but rather, a combination of multi-state and binary characters were used to analyze subgeneric relationships in a study of what they referred to as the “*Viorna* Group”. Subgenera *Campanella*, *Integrifolia*, *Tubulosa*, and *Viorna* and several sectional classifications and new sectional ranks were established, many of which were rank changes from Erickson's sectional treatment (1943). While multivariate analyses have been applied within several taxonomic studies within subg. *Viorna*, the statistical methods employed were not used to inform species-level taxonomy; rather, the numerical studies listed above sought to infer phenetic distance and hypothesized evolutionary relationships of existing taxa.

### **Palynological Studies**

Pollen morphology of angiosperms has been effective in the classification of orders, families, genera, species, and hybrids (Erdtman 1969) and has provided insight on phylogenetic relationships (Van Campo 1976). Efforts to distinguish *Clematis* from other genera in Ranunculaceae have been attempted (Wodehouse 1936), but single couplets in the proposed dichotomous key lead to multiple genera, making generic delimitation solely on pollen grains problematic. At the interspecific level, Keener (1967) found that *C. integrifolia* had tricolpate pollen while pollen of other species in subsect. *Integrifoliae* had a polycolpate structure, corroborating the geographic separation between Eurasian *C. integrifolia* and North American species. A similar study of subsect. *Viornae*, to examine the taxonomic significance of pollen morphology on an interspecific level, did not find differences between species (Dennis 1976). A recent study on pollen morphology of the genus found sect. *Viorna* to be closely allied with sect. *Viticella*, as they both exhibited heteromorphic aperture types (Xie and Li 2012) which is largely aligned with the findings from a molecular phylogenetic study of *Clematis* (Xie et al. 2011). The taxonomic utility of pollen morphology in *Clematis* has shown to clarify sectional relationships and few species level classifications, making it a classification tool with limited use. As suggested by Tobe (1974), pollen morphology in *Clematis* would be best examined alongside other morphological features.

### **Leaf Surface**

A number of studies have examined leaf surface characters of *Clematis* subg. *Viorna* members with scanning electron microscopy and have resolved few species level relationships within the subg. *Viorna* (Keener 1967; Dennis 1976; Shi and Li 2003). Yang and Huang (1992)

examined 14 leaf surface traits, including measurements of trichomes, epidermal cells, and stomata but found none of these characters to be taxonomically informative.

In a study on subsect. *Viornae*, Dennis (1976) separated the subsection into artificial groups. *Clematis pitcheri* Torr. & A.Gray, *C. reticulata* Walter, and *C. viorna* were characterized by absence of epicuticular wax, presence of trichomes, and presence of parallel striations perpendicular to stomata. *Clematis addisonii* Britton, *C. glaucophylla* Small, *C. texensis* Buckley, and *C. versicolor* Small ex Rydb. were characterized by the presence of epicuticular wax and absence of trichomes. The latter group plus the newly described *C. carrizoensis* D.Estes was later acknowledged as comprising the *C. glaucophylla* species complex (Estes 2006) based on the characters that delimit the group by Dennis (1976).

In subsect. *Integrifoliae*, *C. albicoma* Wherry, *C. fremontii* S.Watson, *C. viticaulis* E.S.Steele were possessed amphistomatic leaves while *C. integrifolia*, *C. ochroleuca* Aiton, and *C. coactilis* (Fernald) Keener possessed hypostomatic leaves (Keener 1967). Yang and Moore (1999) included *Clematis fremontii* in the subsect. *Integrifoliae* and found the same stomatal pattern. In a study on leaf epidermal features of the entire genus, amphistomatic leaves were detected in multiple subgenera but not in the 11 species of *Clematis* subg. *Viorna* from China (Shi and Li 2003). A thorough examination of stomatal patterns in subsect. *Viornae* is needed, as Dennis (1976) did not indicate whether adaxial sides of leaves were examined in addition to abaxial surfaces.

### **Seedling Phyllotaxy**

Seedling phyllotaxy has been considered an effective character in classifying *Clematis* into subgeneric or sectional groups (Tamura 1980, 1987; Essig 1991; Yang and Moore 1999;

Johnson 2001; Wang and Li 2005; Cheng et al. 2016). A greenhouse study showed that 11 species from subg. *Viorna* exhibit opposite, or type 2, phyllotaxy. Results also suggested subg. *Viorna* and subg. *Viticella* to be closely allied (Essig 1991), which was corroborated in molecular phylogenetic studies (Miikeda et al. 2006; Xie et al. 2011; Lehtonen et al. 2016). However, seed for the study by Essig (1991) was collected from cultivated material and is therefore at risk of confounding results through interspecific hybridization. This seedling phyllotaxy character was adopted by Johnson (2001) in a dichotomous key to the sections of *Clematis*. Yang and Moore (2005) reported the seedling phyllotaxy in their treatment of subg. *Viorna*. A recent study of seedling morphology used *C. integrifolia* as the representative of subg. *Viorna* and found the same phyllotaxy as in previous studies (Cheng et al. 2016) but emphasized that less than 25% of the genus has been studied, in regard to seedling phyllotaxy, making any classification with the character premature.

### **Cytological Studies**

Cytological comparisons have been useful in resolving relationships between species and higher taxonomic ranks (Anderson 1937). *Clematis* subg. *Viorna* species have exhibited a stable haploid number ( $n=8$ ) and have all been classified as diploids ( $2n=16$ ; Meurman and Therman 1939; Dennis 1975; Keener 1967, 1975). Meurman and Therman (1939) reported structural hybridity in *C. texensis* and *C. integrifolia* but was not found in later subsectional studies study (Dennis 1975; Keener 1967); these conflicted findings may be attributed to the use of cultivated plant material of unknown origin by Meurman and Therman (1939) versus material collected from known wild origin by Dennis (1975) and Keener (1967). Studies of species outside of subg. *Viorna* have shown *C. ispanica* Boiss., *C. flammula* L., and *C. manschurica* Rupr. to be

tetraploids and *C. paniculata* J.F.Gmel to be hexaploid (Meurman and Therman 1939; Sheidai et al. 2009). Polyploidy has not been reported in subg. *Viorna* (Keener 1967; Dennis 1975), but it should be noted that most chromosome counts were obtained from small sample sizes.

### **Chemotaxonomic Studies**

Two studies have utilized chemotaxonomic methods in attempt to resolve interspecific relationships within subsections *Integrifoliae* and *Viornae* (Keener 1967; Dennis and Bierner 1980). Keener (1967) examined 51 phenolic compounds in subsect. *Integrifoliae*. All species had unique phenolic compound profiles, but compound identities were unknown. Keener (1967) concluded that all members of the subsect. *Integrifoliae* are closely related based on group-affinity values, but this experiment lacked an outgroup for comparison. Dennis and Bierner (1980) conducted a similar study with subsect. *Viornae*, in which 15 known and 2 unknown flavonoid compounds were examined. All taxa except *C. versicolor* and *C. glaucophylla* contained distinct flavonoid profiles, inferring that the two species are of recent origin. Keener (1967) and Dennis and Bierner (1980) did not report localities of sampled material.

### **Molecular Methods**

Molecular phylogenetics research in *Clematis* has focused primarily on elucidating subgeneric and sectional classifications with DNA sequence data from coding and non-coding regions of the plastome and nuclear ribosomal internal transcribed spacer (nrITS) regions. Miikeda et al. (2006) sampled two taxa in subg. *Viorna*, which formed a monophyletic clade, sister to subg. *Viticella*. Xie et al. (2011), with a broader sampling and use of three non-coding chloroplast regions, found subg. *Viorna* to be not monophyletic, forming a monophyletic group

with subg. *Viticella*. Lehtonen et al. (2016), with a further broadened sampling, revealed that subg. *Viorna* is strongly supported to be nested within the same clade as subg. *Viticella*, which is supported by palynological and seedling morphology studies (Essig 1991; Xie and Li. 2012).

The use of nrITS for infraspecific research on *C. fremontii* revealed high rates of polymorphism and was unreliable to resolve phylogenetic relationships (Montgomery 2009). The recent development and accessibility of next-generation sequencing (NGS) has allowed for the identification of two plastid regions from the small single copy region of the chloroplast, *ycfI* and *ndhF*, to be variable across several whole genome sequences of *Clematis* species (Liu et al. 2018). However, the actual utility of these two coding regions is unknown until employed in a broader phylogenetic context.

### **Conclusion**

Nomenclatural instability of the name “*Viorna*” has undoubtedly led to confusion within the systematics and taxonomy of *Clematis*. A majority of systematics and taxonomic research has focused on infrageneric relationships. Macromorphology, palynology, seedling phyllotaxy, and molecular methods have proven to be successful in delimiting infrageneric groups, such as subgenera, sections, and subsections.

Those studies that investigated interspecific and intraspecific variation within *Clematis* subg. *Viorna* have emphasized relationships between existing taxa (Keener 1967; Dennis 1976) but have not employed rigorous sampling techniques to characterize variation between individual populations within species. Macromorphological studies have shown to be the most employed and useful method to delimit species within subg. *Viorna*. By sampling many populations and

employing statistically rigorous morphometric methods, a better understanding of taxonomic diversity in subg. *Viorna* could be achieved.

### Literature Cited

- Anderson, E. 1937. Cytology in its relation to taxonomy. *Botanical Review* 3:335–350.
- Chawla, R., S. Kumar, and A. Sharma. 2012. The genus *Clematis* (Ranunculaceae): chemical and pharmacological perspectives. *Journal of Ethnopharmacology* 143:116–150.
- Cheng, J., S. X. Yan, H. J. Liu, L. Le Lin, J. Y. Li, S. Liao, L. Q. Li, and L. Xie. 2016. Reconsidering the phyllotaxy significance of seedlings in *Clematis*. *Phytotaxa* 265:131–138.
- Decainse, M. J. 1881. Revision des Clématites du groupe des Tubuleuses cultivées au muséum. *Nouvelles archives du Muséum d'histoire naturelle* 2:195–214.
- Dennis, W. M. 1976. A Biosystematic Study of *Clematis* Section *Viorna* Subsection *Viornae*. University of Tennessee, Knoxville.
- Dennis, W. M. and M. W. Bierner. 1980. Distribution of flavonoids and their systematic significance in *Clematis* subsection *Viornae*. *Biochemical Systematics and Ecology* 8:65–67.
- Erdtman, G. 1969. *Handbook of Palynology, An Introduction to the Study of Pollen Grains and Spores*. Hafner Publishing Co., Munksgaard, Copenhagen.
- Erickson, R. O. 1943. Taxonomy of *Clematis* section *Viorna*. *Annals of the Missouri Botanical Garden* 30:1–62.
- Essig, F. B. 1991. Seedling morphology in *Clematis* (Ranunculaceae) and its taxonomic implications. *SIDA* 14:377–390.
- Estes, D. 2006. A new narrowly endemic species of *Clematis* (Ranunculaceae: subgenus *Viorna*) from northeastern Texas. *SIDA* 22:65–77.
- Gray, A. 1895. Ranunculaceae. B. L. Robinson, editor. *Synoptical Flora of North America* Vol. I. - Part II. American Book Company, New York. Pages 5–9.
- Gray, A. 1908. *Gray's New Manual of Botany*. Page (M. L. Fernald and B. L. Robinson, Eds.). Seventh edition. American Book Company, New York.
- Henderson, A. 2005. The methods of herbarium taxonomy. *Systematic Botany* 30:456–459.
- James, J. F. 1838. A revision of the genus *Clematis* of the United States. *Cincinnati Society of Natural History*:118–135.
- Johnson M. 2001. *The genus Clematis*. Södertälje: Magnus Johnsons Plantskola AB.
- Keener, C. S. 1967. A biosystematic study of *Clematis* subsection *Integrifoliae* (Ranunculaceae). *Journal of the Elisha Mitchell Scientific Society* 83:1–41.

- Keener, C. S. 1975. Studies in the Ranunculaceae of the southeastern United States. III *Clematis* L. SIDA 6(1): 33–47.
- Keener, C. S. and M. W. Dennis. 1982. The subgeneric classification of *Clematis* (Ranunculaceae) in temperate North America north of Mexico. Taxon 31:37–44.
- Kuntze, O. 1885. Monographie der gattung *Clematis*. Verhandlungen des Botanischen Vereins für die Provinz Brandenburg 86:83–202.
- Lehtonen, S., M. J. M. Christenhusz, and D. Falck. 2016. Sensitive phylogenetics of *Clematis* and its position in Ranunculaceae. Botanical Journal of the Linnean Society 182: 825–867.
- Liu, H. J., C. H. Ding, J. He, J. Cheng, L. Y. Pei, and L. Xie. 2018. Complete chloroplast genomes of *Archiclematis*, *Naravelia* and *Clematis* (Ranunculaceae), and their phylogenetic implications. Phytotaxa 343:214–226.
- Meurman, O. and E. Therman. 1939. Studies on the Chromosome Morphology and Structural Hybridity in the Genus *Clematis*. Cytologia 10:1–14.
- Miikeda, O., K. Kita, T. Handa, and T. Yukawa. 2006. Phylogenetic relationships of *Clematis* (Ranunculaceae) based on chloroplast and nuclear DNA sequences. Botanical Journal of the Linnaean Society 152:153–168.
- Montgomery, M. C. 2009. Incomplete concerted evolution in the non-hybrid diploid *Clematis fremontii* S. Watson (Ranunculaceae). The University of Tennessee Chattanooga.
- Persoon, C. H. 1806. *Synopsis plantarum, seu Enchiridium botanicum, complectens enumerationem systematicam specierum hucusque cognitarum*. Second edition. Parisiis Lutetiorum, Paris, France.
- Prantl, K. 1887. Ranunculaceae in A. Engler and K. Prantl, editors. *Die natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigeren Arten insbesondere den Nutzpflanzen unter Mitwirkung zahlreicher hervorragender Fachgelehrten*. Wilhelm Engelmann, Leipzig. Pages 43–66
- Prantl, K. 1888. Beiträge zur morphologie und systematik der Ranunculaceen. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 9:225–273.
- Pringle, J. S.. 1997. *Clematis*. In: Flora of North America Editorial Committee, eds. 1993+. Flora of North America North of Mexico. 19+ vols. New York and Oxford. Vol. 3.
- Reichenbach, H. G. L. 1837. Handbuch des Natürlichen Pflanzensystems Nach Allen Seinen Classen, Ordnungen und Familien : nebst naturgemässer Gruppierung der Gattungen, oder Stamm und Verzweigung des Gewächsreiches : enthaltend eine vollständige Charakteristik und Ausführung der natur. Arnoldischen Buchhandlung, Dresden.

- Sheidai, M., M. Habibi, D. Azizian, and M. Khatamsaz. 2009. Cytology and palynology of the *Clematis* L. species (Ranunculaceae) in Iran. *Acta Botanica Croatica* 68:67–77.
- Shi, J.-H. and L.-Q. Li. 2003. Leaf epidermal feature in *Clematis* (Ranunculaceae) with reference to its systematic significance. *Acta Botanica Sinica* 45:257–268.
- Small, J. K. 1933. Ranunculaceae. *Manual of the Southeastern Flora*. University of North Carolina Press, Chapel Hill, NC. Pages 525–528.
- Sokal, R. R. 1963. The principles and practice of numerical taxonomy. *Taxon* 12:190–199.
- Spach, E. 1839. *Histoire naturelle des végétaux. Phanérogames*. Librairie encyclopédique de Roret, Paris, France.
- Tamura, M. 1980. Change of phyllotaxis in *Clematis lasiandra* Maxim. *Journal of Japanese Botany* 55:257–265.
- Tamura, M. 1987. A classification of genus *Clematis*. *Acta Phytotaxonomica et Geobotanica* 38:33–44.
- Tobe, H. 1974. Morphological studies on the genus *Clematis* Linn. I. Pollen grains. *Sci. Rep. Tohoku Univ. Ser. IV (Biol.)* 37:47–53.
- Torrey, J. and A. Gray. 1838. Order I. Ranunculaceae. Juss. *A Flora of North America*. Wiley & Putnam, New York City. Pages 7–11
- Van Campo, M. 1976. Patterns of pollen morphological variation within taxa. I. K. Ferguson and J. Muller, editors. *The Evolutionary Significance of the Exine*. Linnean Society of London, London. Pages 125–135
- Wang, W. T. and L.-Q. Li. 2005. A new system of classification of the genus *Clematis* (Ranunculaceae). *Acta Phytotaxonomica Sinica* 43:431–488.
- Wodehouse, R. P. 1936. Pollen grains in the identification and classification of plants . VII . The Ranunculaceae. *Bulletin of the Torrey Botanical Club* 63:495–514.
- Xie, L. and L. Q. Li. 2012. Variation of pollen morphology, and its implications in the phylogeny of *Clematis* (Ranunculaceae). *Plant Systematics and Evolution* 298:1437–1453.
- Xie, L., J. Wen, and L.-Q. Li. 2011. Phylogenetic analyses of *Clematis* (Ranunculaceae) based on sequences of nuclear ribosomal ITS and three plastid regions. *Systematic Botany* 36:907–921.
- Yang, T. Y. A. and D. M. Moore. 1999. A revision of the Viorna group of species (section Viorna sensu Prantl) in the genus *Clematis* (Ranunculaceae). *Systematics and Geography of Plants* 38:281–303.

Yang, A. T. Y. and T.-C. Huang. 1992. Additional remarks of Ranunculaceae in Taiwan. (3)  
*Clematis* section *Viorna* (Reichb.) Prantl. *Taiwania* 37:19–53.

## CHAPTER II: A Morphometric Approach to Delimiting Species in the *Clematis reticulata* Species Complex (Ranunculaceae: Subgenus *Viorna*)

This chapter is formatted, in part, for publication in *Systematic Botany*

### Introduction

*Clematis* L. subgenus *Viorna* A.Gray, in the broadest sense, consists of approximately 70 species worldwide and is distributed in North America and East Asia (Wang and Li 2005). Twenty-one of these species are native to North America, many of which are native to the southeastern United States with disjunctions in the south-central, southwestern, and midwestern regions (Pringle 1997; Estes 2006; Floden 2013). The past 40 years of *Clematis* subg. *Viorna* alpha taxonomy in the southeastern United States has offered a glimpse into the group's species diversity and endemic tendencies. *Clematis morefieldii* Kral, *C. socialis* Kral, *C. carrizoensis* D.Estes, and *C. vinacea* Floden are recently described taxa, each narrowly endemic to four counties at most, all distinguished based on morphology (Kral 1982, 1987; Estes 2006; Floden 2013). These four taxa were not detected until recently due, in part, morphological traits obscured by drying and pressing of specimens, with potentially informative characters such as flower color and shape being lost (Estes 2006; Floden 2013). This demonstrates the problematic nature of relying solely on herbarium specimens to inform species limits in subg. *Viorna*. When considered with Ridge and Valley (of Virginia and West Virginia) endemics, *C. addisonii* Britton, *C. albicoma* Wherry, *C. coactalis* (Fernald) Keener, and *C. viticaulis* E.S.Steele, endemism within North American subg. *Viorna* is undoubtedly high. This recently realized diversity within North American subg. *Viorna*, from taxonomic study, along with obscured morphology, from pressing and drying, suggests that the species diversity within subg. *Viorna* could be widely underestimated.

*Clematis reticulata* Walter is separated from other North American members of subg. *Viorna* by the combination of its raised-reticulate leaf venation, climbing habit, non-glaucous foliage, stems, and flowers, spreading plumose achene tails, and habitat consisting of sandy soils in thickets, pine-oak savannas, sandhills, or open woodlands (Erickson 1943; Dennis 1976; Keener & Dennis 1982; Pringle 1997). *Clematis reticulata* is distributed in the southeastern United States with several centers of distribution (Table 1) that we have interpreted through examination of herbarium specimens and fieldwork. Records of *C. reticulata* shown in Kartesz (2015) in the Ozark Mountains region are treated as part of an upcoming revision of the *C. viorna* species complex by Irick and Estes (in prep.) and is therefore not included in *C. reticulata* s.l. here. The name, *Clematis reticulata*, has appeared in molecular phylogenetics studies conducted by Xie et al. (2011) and subsequently represented by a GenBank accession in Lehtonen et al. (2016). Upon examination, of the herbarium specimen (*Wen 9780*, US) corresponding to the GenBank accession, the plant collected is decidedly *C. pitcheri* Torr. & A.Gray and possesses a label showing so. Therefore, it should be noted that the phylogenetic placement cannot be inferred for *C. reticulata* in relation to other taxa in subg. *Viorna* until appropriate measures are taken to ensure correct identification of material sampled.

*Clematis reticulata* has often been considered a single, variable species (Erickson 1943; Keener 1975; Dennis 1976; Pringle 1997), but this has not always been the case. Small (1933) distinguished *Viorna* (= *Clematis* subg. *Viorna*) *subreticulata* Harbison ex Small by its thinner and larger leaflets, less pronounced vein reticulation, and thinly pubescent sepals. All subsequent treatments placed *V. subreticulata* into synonymy with *C. reticulata* (Erickson 1943; Keener 1975; Dennis 1976; Keener and Dennis 1982; Yang and Moore 1999). Erickson (1943) attributed

this taxonomic inclusion to natural variation of leaf thickness and sepal pubescence in *C. reticulata*, especially in the northeastern part of its range, as well as in Texas. Similarly, Dennis (1976) stated that *V. subreticulata* “fits into the broader concept” of *C. reticulata*. While Keener (1975) followed a similar treatment to Dennis (1976) and Erickson (1943), he did acknowledge the need for further study at the population level. Small (1933) also recognized *V. beadleii* Small (= *Clematis beadleii* [Small] Erickson), distinguishing it from *V. reticulata* (= *C. reticulata*) and *V. subreticulata* by being more conspicuously reticulate on the abaxial leaf surface than the adaxial surface. Erickson (1943) recognized and designated a rank change to *C. beadleii*, maintaining it as a distinct species that is closely related to *C. reticulata* but “clearly outside the range of variation” with scattered distribution from Georgia to Texas. Johnson (2001) and Yang and Moore (1999) maintained *C. beadleii* as a distinct taxon. Correll and Johnston (1979) included *C. beadleii* in the Texas flora, but no reference to specimens makes their reference to the taxon problematic to interpret. Keener (1975) included *C. beadleii* within *C. reticulata* while Dennis (1976) and Keener and Dennis (1982) placed it in synonymy with *C. viorna* L. Since the treatments of Small (1933) and Erickson (1943), The Tennessee Flora Committee (2015) is the only known treatment to suggest that *C. reticulata* consists of more than a single taxon, stating that *C. reticulata* of the Cumberland Plateau of Tennessee represents a distinct entity due to differences in flower color, flower size, and bract placement.

Phenotypic plasticity has been hypothesized to explain morphological variation within *C. reticulata* s.l. by Mohr (1892), emphasizing geographic correlation to morphological differences in proximal and mid-stem leaflets, as well as the shape and size of foliaceous bracts. This difference in morphology was attributed to disparity in rainfall between the Southern Atlantic Coastal Plain regions, West Gulf Coastal Plain of Texas, and Alabama and eastern Mississippi

(Mohr 1892). While this claim does offer a logical explanation for observed variation within the *C. reticulata* species complex, no known research has tested whether these variable morphologies are maintained within a common garden.

**Table 1.** Geographic centers of distribution of *Clematis reticulata* s.l., serving as *a priori* morphological groups, or taxonomic hypotheses, for this study.

<b>Code</b>	<b>General Geographic Center</b>	<b>Previously recognized as</b>
AGCP	Atlantic and East Gulf Coastal Plains	<i>Clematis reticulata</i> Walter, 1788
CPTN	Interior Low and Appalachian Plateaus of Tennessee	Undescribed in Tennessee Flora Committee, 2015
NOAL	Northern Alabama	<i>Viorna subreticulata</i> Harbison <i>ex</i> Small, 1933
OUMT	Ouachita Mountains of Arkansas and Oklahoma	Undescribed
PMGA	Pine Mountain Ridges of Georgia	Undescribed
TMAL	Talladega Mountains of Alabama	Undescribed
WGCP	West Gulf Coastal Plain	Undescribed

*Clematis reticulata* s.l. has been the subject of several taxonomic opinions in regard to its species limits and intraspecific variation. Additionally, its geography and ecology are highly variable (Mohr 1892; Kartesz 2015). While *C. reticulata* s.l. has been included in several taxonomic and systematics studies of subg. *Viorna*, no research has attempted to quantify whether variation is explained by unclear species limits, phenotypic plasticity, or a combination of the two. We hypothesize what has been called *C. reticulata* historically, may consist of multiple unrecognized taxa based on morphology, ecology, and biogeography, that forms a species complex. In order to ensure that morphological differences represent evolutionarily divergent groups, and are not an artifact of the environmental conditions in which they grow, a common garden experiment was used in conjunction with herbarium specimens and field observations to make taxonomic inferences. The unified species concept (De Quieroz 2007) is employed in this study, similar to Nery and Fiaschi (2019), hypothesizing lineage separation

between species when morphological discontinuity is detected in correlation with biogeography and ecology.

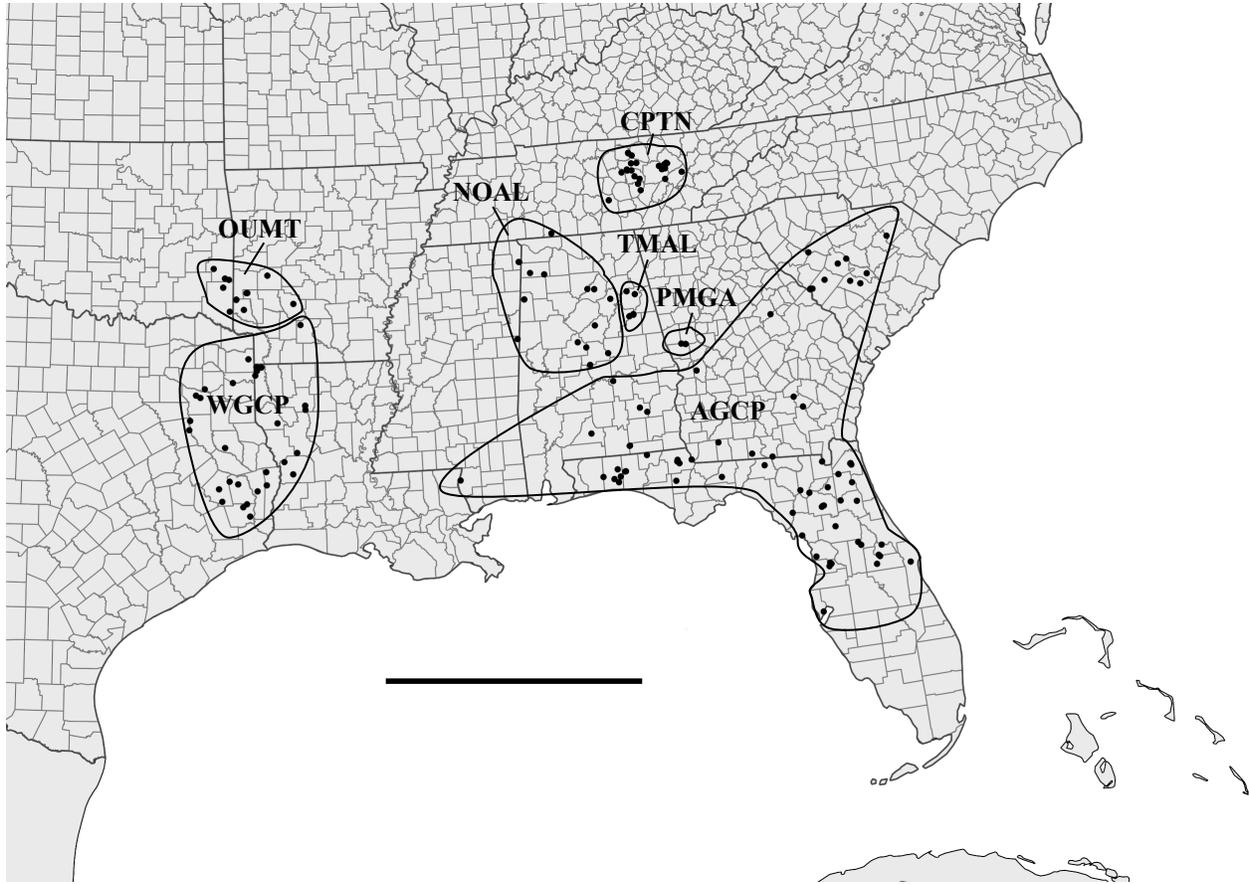
## Materials and Methods

**Herbarium specimen sampling**— A total of 401 herbarium specimens of *C. reticulata* s.l. were examined from the following herbaria, acronyms from Thiers (2016): AA, ALNHS, ANHC, APSC, BRIT, CLEMS, FLAS, GH, HTTU, JSU, LL, MO, NCU, NO, NY, OKL, TENN, TEX, UARK, UCHT, USC, USF, and VDB. Sampling efforts of herbarium specimens focused on covering the broadest possible geographic extent (Fig. 1) and extremes of morphological variation of *C. reticulata* s.l. Seven *a priori* groups were identified to serve as hypothesized taxa (Table 1). These were based on the authors' observations of morphology, habitat, and biogeographic patterns. Sampling also included the neotype of *C. reticulata* (*Wherry* s.n., GH) and the holotype of *V. subreticulata* (*Biltmore Herbarium 15011*, NY), which we hypothesized to belong to the AGCP and NOAL groups, respectively, based on the morphology and locality of the type specimens. When possible, specimens were selected to represent unique collections and localities, but for the *a priori* groups that are geographically restricted and rare (*e.g.* PMGA), multiple individuals from the same locality were, at times, sampled to both increase statistical power and ability to capture morphological variation. Forty-nine characters, both quantitative and qualitative, of vegetative and reproductive structures were selected to measure for preliminary analysis.

**Common garden sampling**— To assess morphological variation within and between *a priori* defined groups in a fixed environment and across homologous developmental stages, a common garden experiment was implemented. Fieldwork took place from 2017 to 2019.

Herbarium specimens, local expertise, and habitat sighting were utilized to locate populations of *C. reticulata* s.l. throughout the entirety of its range (Fig. 2). If a population was successfully located, one to three individuals were vouchered (included in herbarium specimen sampling) from above-ground material while the root systems were transplanted, labeled, and placed into a sealable plastic bag with adequate moisture. Transplants were only collected if the population consisted of over 20 individual plants. Scientific collecting permits for all public land and permissions from private land owners were obtained for collecting.

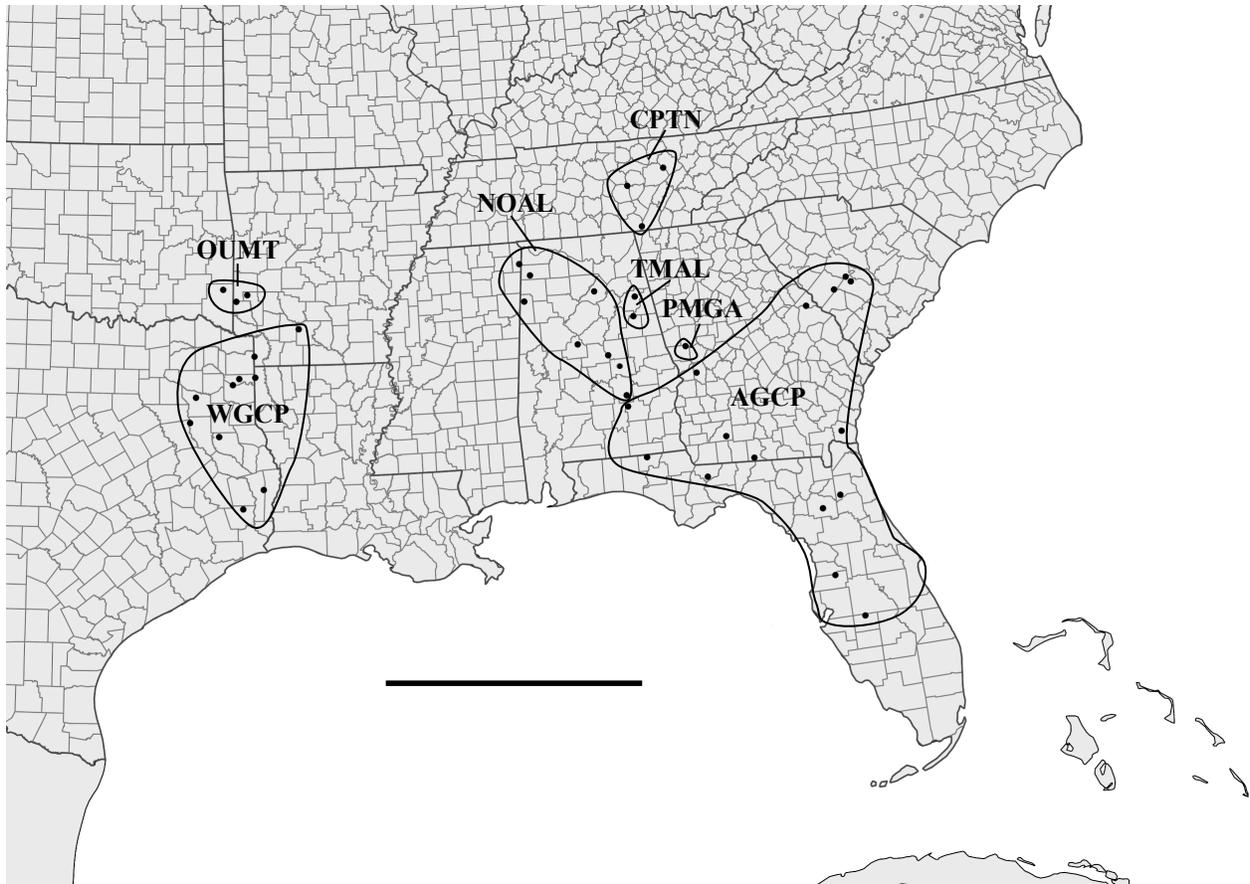
**Common garden experiment**— Upon return from fieldwork, rootstock was washed of any remaining soil and transplanted into 6.6 liter (= 1.75 gallon) containers with a growing medium composed of 3:2:1, peat: sand: perlite. On 11 October 2019, 94 transplants were transferred into the Austin Peay State University greenhouse and arranged in a completely randomized design among five benches. Equal amounts of pellet 10-10-10 (N-P-K) fertilizer were applied to each container on 18 October 2019. To ensure release of nutrients into the growing potting mix, plants were watered until soil moisture reached total saturation. Moisture of the potting mix was monitored bi-weekly with a General Tools DSMM500 Precision Digital Soil Moisture Meter (Cincinnati, Ohio). When soil moisture was detected to be below 9% in a given container, that plant was watered until soil moisture reached total saturation. Two days after the second fertile node reached anthesis, plants were photographed and entire vines were pressed in sections, dried, and processed as herbarium specimens to be deposited at APSC.



**Figure 1.** Geographic sampling of herbarium specimens for univariate and multivariate analyses for the *Clematis reticulata* species complex. Outlines of populations sampled indicate hypothesized taxa. Scale bar represents 500 km.

**Character selection**— Characters were screened for potential taxonomic utility with boxplots and distribution plots with a smaller preliminary dataset derived from herbarium specimens. After visual inspection, differences between hypothesized taxa for morphological characters were detected in the preliminary dataset with Welch’s one-way analysis of variance (ANOVA) or a Kruskal-Wallis test, depending on the measurement scale. A  $p$ -value cutoff of 0.05 was used to determine significance. The percentage of missing values were also considered when selecting for characters. Sixteen characters were maintained for multivariate and univariate analyses (Table 2). Abbreviated codes from Table 2 are herein used to reference morphological characters. Characters used for multivariate analyses in the herbarium specimens dataset were also measured on vouchered plants grown in the common garden. One additional character that

can only be readily detected with living material, INFHAB, was recorded for each plant before pressing. Fruit characters were not collected from common garden accessions due to the destructive nature of vouchering plants, as well as time considerations. Guidelines for measuring morphological characters can be found in Appendix A.



**Figure 2.** Geographic sampling of common garden individuals for univariate and multivariate analyses for the *Clematis reticulata* species complex. Outlines of populations sampled indicate hypothesized taxa. Scale bars represent 500 km.

**Data subsetting**— Three datasets in total were generated: two from herbarium specimens, flowering and fruiting, and one from flowering plants of the common garden. Due to the number of hypothesized taxa and our predictions that certain characters represented taxonomically meaningful variation across some groups more so than others, all datasets (flowering herbarium specimens, fruiting herbarium specimens, and common garden individuals)

were subset into two groups each based on bract placement: the basal bract group (BBG) and the elevated bract group (EBG). The BBG consists of hypothesized taxa, CPTN, OUMT, and WGCP and consistently possess a peduncle length to combined peduncle and pedicel length ratio of  $< 0.20$ ; the EBG consists of hypothesized taxa AGCP, NOAL, PMGA, and TMAL and possess a peduncle length to combined peduncle and pedicel length ratio of  $> 0.20$ . We felt this was justified because bract placement has been used to delimit *Clematis* species in the past— *C. morefieldii* from other North American subg. *Viorna* (Kral 1982; Pringle 1997; Johnson 2001), as well as numerous species across the genus in China (Wencai and Bartholomew 1997). While specimens representing the hypothesized taxon, PMGA, tends to solely possess terminal ebracteate inflorescences, we included these specimens in the EBG due to its ability to produce elevated bracts on axillary inflorescences in the late season. Additionally, it is within close geographic proximity to other hypothesized taxa of the EBG. This subsetting of data meant that all multivariate analyses (see below) were conducted on all six data subsets. The characters used for each subset of data can be found in Table 2.

**Multivariate analyses**— Multivariate analyses of morphological data were partially adapted from Aquino et al. (2019). To avoid character loading, all quantitative characters were screened for collinearity with Pearson's correlation coefficient (PCC). If PCC correlation values found two characters to be highly correlated ( $\geq 0.85$ ), the character with lesser discriminatory power was removed from the analysis. No characters were found to be correlated and were therefore not removed. Individuals sampled that contained missing values were removed from the multivariate analyses. Factor analysis of mixed data (FAMD) was used to visualize morphological data in multivariate space to assess distinctiveness between hypothesized taxa with R package FactoMineR's (Le et al. 2008) function 'FAMD'. To infer the degree to which

the hypothesized taxa were diagnosable, a second analysis was conducted to assess classification accuracy with constrained ordination. Partial least squares discriminant analysis (PLS-DA) was performed to classify samples within their respective data subsets. The performance of the PLS-DA model was evaluated with leave-one-out cross-validation (LOOCV). This validation method was chosen due to it being more suitable for datasets with small sample sizes. Two components were maintained; this was based on an initial PLS-DA with 10 components. Classification error rate was lowest with two components with additional components showing no change in error rate. A confusion matrix was generated with true classes as the *a priori* groups and the predicted classes from the PLS-DA LOOCV. All constrained ordination analyses were conducted with the R package *mixomics* (Rohart et al. 2017) with functions ‘*plsda*’, ‘*perf*’, and ‘*get.confusion\_matrix*’. Balanced error rate (BER) was calculated with the function ‘*get.BER*’. When BERs were found to be relatively high, we considered alternative classifications and reran the model and cross-validation. In this study, this only applies to NOAL and TMAL groups (see Results and Discussion). An additional PLS-DA LOOCV was run for the common garden dataset of the BBG, in addition to one with the same characters from flowering herbarium specimens, with an added qualitative character, INFHAB. Both FAMD and PLS-DA were chosen due to the importance of both quantitative and qualitative characters in delimiting hypothesized taxa, as our dataset applied to other commonly used ordination methods (i.e. principal component analysis, linear discriminant analysis) would violate statistical assumptions.

**Univariate analyses**— If results from multivariate analyses supported an alternative classification (combining multiple hypothesized taxa), groups were combined for univariate comparisons. Due to the unequal sample sizes between groups, Welch’s ANOVA was used to test whether quantitative characters originate from the same distribution with function

‘oneway.test’ from the R package stats (R Core Team 2019). Pairwise comparisons were made for quantitative characters with a Games-Howell post-hoc test, with the function ‘gamesHowellTest’ from the package PMCMRplus (Pohlert 2020). The ordinal character, LFTH, was compared between groups with a Kruskal-Wallis test with function ‘kruskal.test’ from the R package stats (R Core Team 2019). Pairwise comparisons for LFTH were made with a Dwass-Steel test with function ‘dscfAllPairsTest’ from the R package PMCMRplus (Pohlert 2020). Because missing data did not allow for the inclusion of the entire dataset in the multivariate analysis, all samples were included in the univariate analysis if a given character was present. For characters that were represented in both the flowering and fruiting herbarium datasets, they were combined in the univariate analysis to better represent overall variation across and increase statistical power. A  $p$ -value cutoff of 0.05 was used to infer differences as statistically significant when groups being compared had a sample size of  $n \geq 5$ . In the case that  $n < 5$ , summary statistics were still reported and examined for trends.

**Comparison of herbarium specimens and common garden datasets**— To test for the phenotypically plasticity in morphological characters, Welch’s ANOVA tests were used to compare quantitative morphological characters within hypothesized taxa, based on groups identified by the multivariate analyses, between herbarium specimen and common garden datasets. For the ordinal character, LFTH, Kruskal-Wallis tests were used to compare between datasets within each hypothesized taxon. A  $p$ -value cutoff of 0.05 was used to infer differences as statistically significant. Groups with  $n < 5$  were not included in this analysis. The same protocol to execute this analysis as the univariate analyses (see above) was followed.

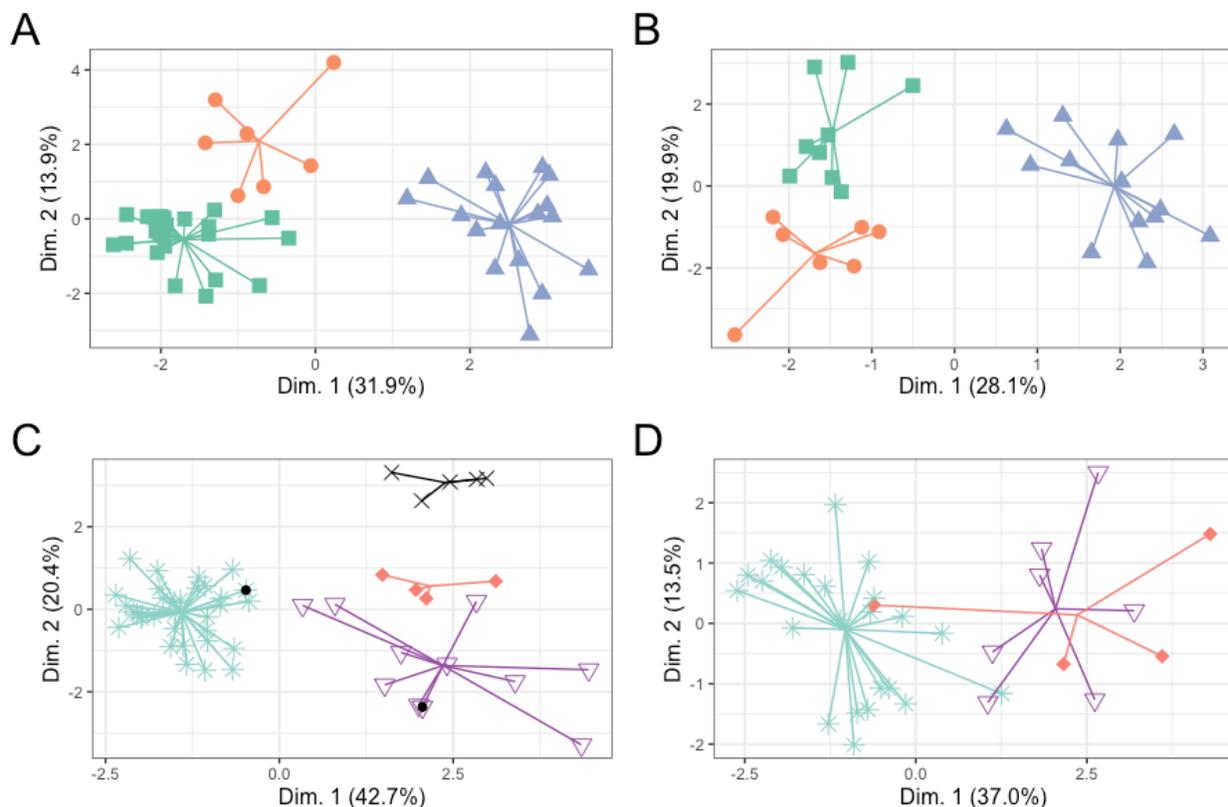
## Results

**Herbarium specimens**— The flowering and fruiting datasets consisted of a total of 204 specimens for univariate analyses. After individuals of the herbarium specimen dataset with missing value were removed, 160 specimens remained for multivariate analyses. Two specimens included in the analyses contained both flowering and fruiting material (*Charles M. Allen 8999*, NCU and *Thomas H. Murphy 371*, APSC) and were therefore represented in flowering and fruiting datasets. Specimens measured are shown in Taxonomic Treatment. See Appendix B for a detailed summary of sample sizes in the herbarium specimens dataset.

**Table 2.** Morphological characters hypothesized to delimit groups in the *Clematis reticulata* species complex, measured from herbarium specimens and common garden individuals. BBFL= basal bract flowering specimens, BBFR= basal bract fruiting specimens, EBFL= elevated bract flowering specimens, EBFR= elevated bract fruiting specimens. All characters for BBFL and EBFL were used in the common garden experiment. \* indicates a character only measured on common garden specimens. \*\* indicates bract position character that subsets specimens into basal and elevated bract groups and is therefore excluded from multivariate analyses.

Character	Code	Data subset(s) characters used for
Achene body length : achene body width at widest point (ratio)	ACLW	BBFR
Achene rim thickness at midpoint : achene body width at widest point (ratio)	ACRT	BBFR, EBFR
Achene tail length (mm)	ACTL	BBFR
Anther connective length (mm)	ANCOL	BBFL
Average areole area (mm <sup>2</sup> )	AREAR	BBFL, BBFR, EBFL, EBFR
Inflorescence habit (0 = erect/ ascending, 1 = pendulous/ hanging below node)	INFHAB	BBFL*
Inflorescence position (0 = axillary, 1 = terminal)	INFPOS	EBFL, EBFR
Leaflet thickness (0 to 5, from membranaceous to coriaceous)	LFTH	BBFL, BBFR, EBFL, EBFR BBFL, BBFR, EBFL,
Pedicle length : primary peduncle length (ratio)	BRPL	EBFR**
Petiolule length (mm)	PTLU	EBFL
Pedicle length + peduncle length : stem width (ratio)	PDLST	BBFL, BBFR
Sepal length: sepal width at widest point (ratio)	SPLW	EBFL
Trichome length on leaf abaxial (mm)	TLLF	BBFL, BBFR, EBFL, EBFR
Trichome length on proximal half of sepal (mm)	TLSP	BBFL, EBFL
Vein width (mm)	VNWD	BBFL, BBFR, EBFL, EBFR
Width at 90% leaflet length : total leaflet length (ratio)	W90LL	BBFL, BBFR, EBFL, EBFR

**Common garden experiment**— Of the 95 individuals of *Clematis reticulata* s.l., 71 plants, 29 of the BBG and 41 of the EBG, representing 40 populations flowered and were measured. For a detailed summary of sample sizes in the common garden experiment, see Appendix B. Because PMGA was represented by a single individual, it was excluded from multivariate and univariate analyses.

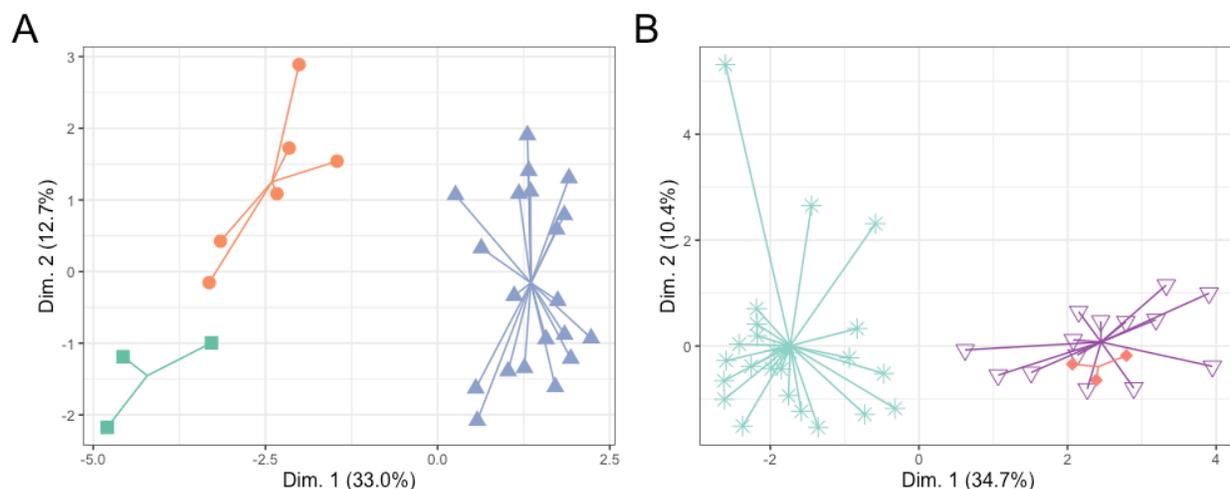


**Figure 3.** Scatterplot of first and second axes of FAMD of the herbarium specimen datasets. A) flowering specimens and B) fruiting specimens of the BBG; C) flowering specimens and D) fruiting specimens of the EBG. Each point represents an individual specimen. Acronyms for putative taxa defined in Table 1. For A and B— CPTN= solid green squares, OUMT= solid orange circles, and WGCP= solid blue triangles. For C and D— AGCP= teal asterisks, NOAL= hollow purple upside down triangles, PMGA = black X's (only C), and TMAL= solid red diamonds. For C, the solid black dots in the middle of AGCP and NOAL symbols indicate the neotype of *Clematis reticulata* and the holotype of *Viorna subreticulata*, respectively.

**FAMD**— The FAMD of flowering herbarium specimens of the BBG with two dimensions retained explained 45.8% of variation between individuals, 31.9% and 13.9% for the first and second axes, respectively (Fig. 3A). The FAMD of fruiting herbarium specimens of the basal bract group with two dimensions retained explained 48.0% of variation between

individuals, 28.1% and 19.9% for the first and second axes, respectively (Fig. 3B). Of the three hypothesized taxa in the basal bract group, the FAMD scatterplot of both flowering and fruiting herbarium specimen datasets showed that the three hypothesized groups do not overlap (Fig. 3A and B).

The FAMD of flowering herbarium specimens of the EBG with two dimensions retained explained 63.1% of variation between individuals, 42.7% and 20.4% for the first and second axes, respectively. AGCP and PMGA formed discrete groups with no overlap while NOAL and TMAL show slight overlap (Fig. 3C). The FAMD of the fruiting herbarium specimens of the EBG with two dimensions retained explained 50.5% of variation between individuals, 37.0% and 13.5% for the first and second axes respectively. AGCP and NOAL show minimal overlap. TMAL does overlap with both AGCP and NOAL (Fig. 3D).



**Figure 4.** Scatterplot of first and second axes of FAMD of common garden datasets. A) BBG and B) EBG. Each point represents an individual specimen. For A, CPTN= solid green squares, OUMT= solid orange circles, and WGCP= solid blue triangles. For B, AGCP = teal asterisks, NOAL = hollow purple upside down triangles, and TMAL = solid red diamonds

The FAMD of common garden individuals of the BBG with two dimensions retained explained 45.8% of variation between individuals, 33.0% and 12.7% for the first and second dimensions, respectively. Of the three hypothesized taxa in the basal bract group, FAMD of the flowering herbarium specimen dataset contained three discrete groups with no overlap,

corresponding to our hypotheses (Fig. 4A). The FAMD of common garden plants of the EBG with two dimensions retained explained 45.1% of variation between individuals, 34.7 % and 10.4% for the first and second dimension, respectively. Of the three hypothesized taxa in the elevated bract group, subjected to this analysis, individuals from AGCP and NOAL form obviously discrete and separate groups while individuals from TMAL appear to overlap with NOAL individuals (Fig. 4B).

**PLS-DA**— The PLS-DA LOOCV of flowering herbarium specimens of the BBG had a BER of 0.01 for individuals representing CPTN, OUMT, and WGCP with a single misclassification of an OUMT specimen as CPTN (Table 3A). For fruiting herbarium specimens of the BBG, there was a BER of 0 with no specimens assigned to groups different from their original assignment (Table 3B). Flowering herbarium specimens of the EBG from four groups, AGCP, NOAL, TMAL, and PMGA, had a BER of 0.12 (Table 3C). When NOAL and TMAL were combined into a single group, the BER was reduced to 0.01, with two NOAL specimens assigned to AGCP. Fruiting herbarium specimens of EBG from three groups, AGCP, NOAL, and TMAL, had a BER of 0.22 (Table 3D). When NOAL and TMAL were combined into a single group, the BER was reduced to 0.02, with two AGCP specimens assigned to NOAL and one NOAL assigned to AGCP.

The PLS-DA LOOCV of the common garden plants of the BBG had a BER of 0.04, with a single CPTN specimen assigned to OUMT (Table 4A). When the character, INFHAB was added into the model, this reduced the BER to 0 with no specimens predicted as different from their original assigned group. The EBG, with AGCP, NOAL, and TMAL represented, has a BER of 0.125 (Table 4B). When TMAL and NOAL were combined, the BER was reduced to 0, with all individuals predicted as originally assigned.

**Table 3.** Confusion matrices from LOOCV of PLS-DA models of herbarium specimens, subset by bract placement and reproductive stage. A= flowering specimens of BBG, B= fruiting specimens of BBG, C= flowering specimens of EBG, and D= fruiting herbarium specimens of EBG.

<b>A)</b>					
	Predicted as CPTN	Predicted as OUMT	Predicted as WGCP		Model Accuracy
CPTN	22	0	0		22/22
OUMT	1	6	0		6/7
WGCP	0	0	17		17/17
			<b>Total</b>		<b>45/46</b>

<b>B)</b>					
	Predicted as CPTN	Predicted as OUMT	Predicted as WGCP		Model Accuracy
CPTN	9	0	0		9/9
OUMT	0	7	0		7/7
WGCP	0	0	13		13/13
			<b>Total</b>		<b>29/29</b>

<b>C)</b>					
	Predicted as AGCP	Predicted as NOAL	Predicted as TMAL	Predicted as PMGA	Model Accuracy
AGCP	33	0	0	0	33/33
NOAL	2	9	0	0	9/11
TMAL	0	4	0	0	0/4
PMGA	0	0	0	5	5/5
				<b>Total</b>	<b>47/53</b>

<b>D)</b>					
	Predicted as AGCP	Predicted as NOAL	Predicted as TMAL	Predicted as PMGA	Model Accuracy
AGCP	22	1	0	—	22/23
NOAL	4	2	1	—	2/7
TMAL	1	3	0	—	0/4
PMGA	—	—	—	—	—
				<b>Total</b>	<b>27/34</b>

**Univariate analysis of quantitative and ordinal characters**— Because the PLS-DA LOOCV supported the combination of NOAL and TMAL, they were combined for the univariate analyses and is herein referred to as NOAL+TMAL. Similar to the results from the multivariate analyses, the Welch's ANOVA and Games-Howell tests showed that means of all quantitative

characters were significantly different between hypothesized taxa for both the herbarium and common garden datasets, except for PTLU for the common garden dataset which was not found to be significant from the Welch's ANOVA. Pairwise comparisons showed unique combinations of morphological characters differentiated each taxon (Table 5, Appendices C and D). For the hypothesized taxa with  $n < 5$  (CPTN and PMGA) directional differences in means were maintained (Table 5).

The ordinal character, LFTH, had some overlap between all hypothesized taxa in both the herbarium specimen and common garden datasets, but median differences are evident. Common garden individuals generally had thinner leaflets, or lower median values, when compared to herbarium specimens of the same hypothesized group (Figure 5; Table 6). *A priori* groups AGCP and WGCP generally had the thickest leaflets, whereas CPTN and OUMT had thinner leaflets. Samples representing NOAL+TMAL and PMGA appear to exhibit some degree of intermediacy in herbarium specimens but are most similar to groups with thinner leaflets in the common garden experiment.

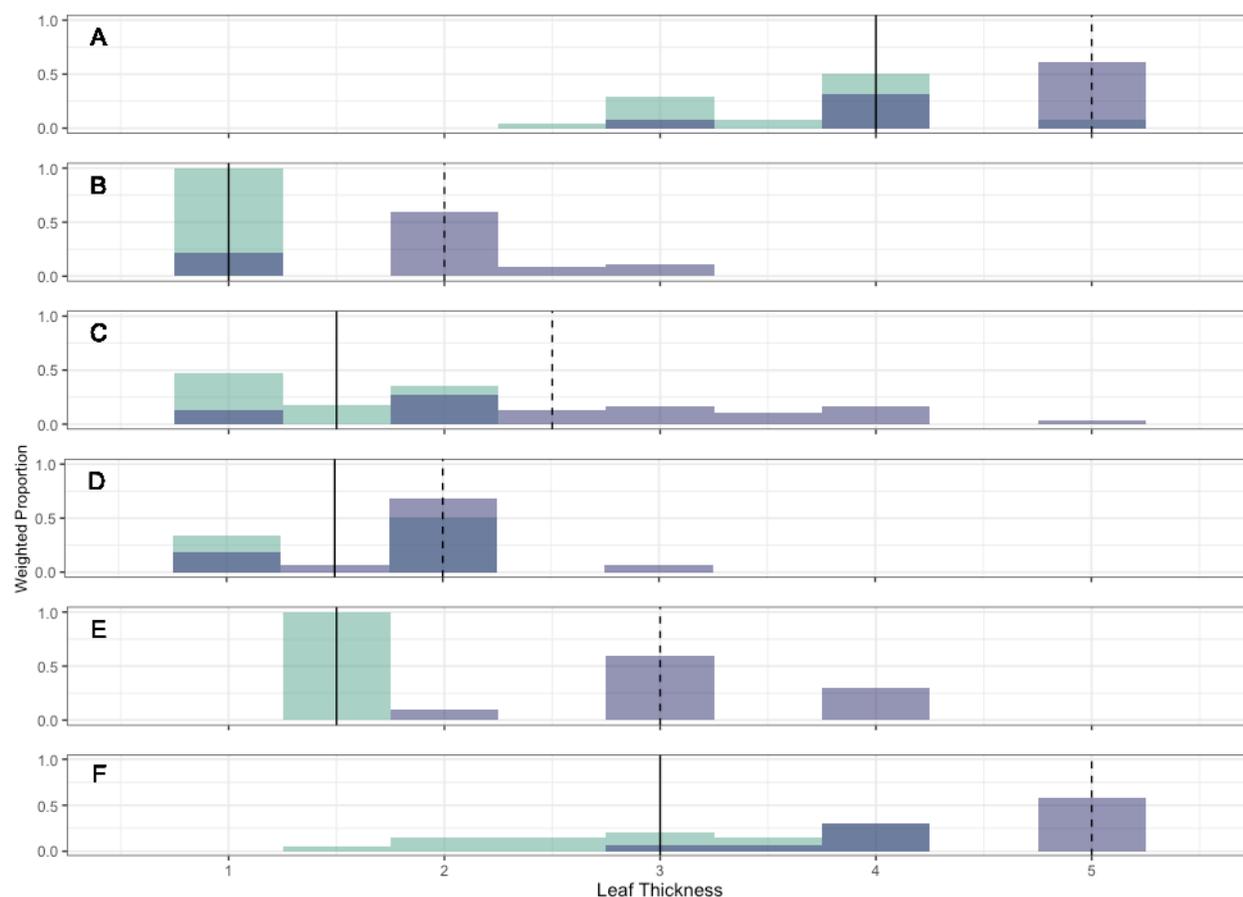
**Table 4.** Confusion matrices from LOOCV of PLS-DA models of common garden individuals, subset by bract placement. A= flowering specimens of BBG, B= flowering specimens of EBG.

<b>A)</b>				
	<b>Predicted as CPTN</b>	<b>Predicted as OUMT</b>	<b>Predicted as WGCP</b>	<b>Model Accuracy</b>
<b>CPTN</b>	2	1	0	2/3
<b>OUMT</b>	0	6	0	6/6
<b>WGCP</b>	0	0	20	20/20
			<b>Total</b>	<b>28/29</b>
<b>B)</b>				
	<b>Predicted as AGCP</b>	<b>Predicted as NOAL</b>	<b>Predicted as TMAL</b>	<b>Model Accuracy</b>
<b>AGCP</b>	24	0	0	24/24
<b>NOAL</b>	0	14	0	14/14
<b>TMAL</b>	0	3	0	0/3
			<b>Total</b>	<b>38/41</b>

**Table 5.** Summary statistics and comparisons of morphological characters between hypothesized taxa for herbarium specimens and common garden datasets. Means and standard deviation are listed for all characters except LFTH, which lists only median values, due to its ordinal scale. Hypothesized taxa that do not share a letter in common are significantly different at  $p < 0.05$ . Sample sizes with a ‘\*’ indicate hypothesized taxa that were not subjected to univariate analysis due to low sample size. All characters except for LFTH were subjected to Welch’s ANOVA and Games-Howell tests. LFTH was subjected to Kruskal-Wallis and Dwass-Steel tests. For the common garden dataset PTLU does not have significance letters listed because the Welch’s ANOVA of was not statistically significant and was therefore not subjected to a Games-Howell test.

Herbarium specimens						
	AGCP	CPTN	NOAL+ TMAL	OUMT	PMGA	WGCP
ACLW	1.38 (0.18) <i>n</i> = 27 a	1.38 (0.22) <i>n</i> = 9 ab	1.39 (0.12) <i>n</i> = 12 a	1.13 (0.08) <i>n</i> = 9 b	1.60 * <i>n</i> = 2	1.29 (0.22) <i>n</i> = 15 ab
ACRW	0.15 (0.02) <i>n</i> = 24 a	0.14 (0.02) <i>n</i> = 9 a	0.19 (0.03) <i>n</i> = 12 b	0.15 (0.02) <i>n</i> = 8 a	0.22 * <i>n</i> = 2	0.17 (0.03) <i>n</i> = 14 ab
ACTL	49.6 (9.09) <i>n</i> = 29 a	47.6 (6.95) <i>n</i> = 10 a	48.1 (7.48) <i>n</i> = 12 a	37.7 (6.71) <i>n</i> = 9 b	51.7 * <i>n</i> = 2	45.1 (4.33) <i>n</i> = 16 ab
ANCOL	0.80 (0.26) <i>n</i> = 40 abc	0.90 (0.19) <i>n</i> = 23 ad	0.90 (0.29) <i>n</i> = 18 abd	0.72 (0.09) <i>n</i> = 7 bc	0.58 (0.17) <i>n</i> = 6 c	1.09 (0.24) <i>n</i> = 18 d
AREAR	0.43 (0.14) <i>n</i> = 75 a	1.14 (0.33) <i>n</i> = 36 b	0.90 (0.52) <i>n</i> = 28 b	1.16 (0.46) <i>n</i> = 15 b	0.93 (0.58) <i>n</i> = 10 ab	0.45 (0.21) <i>n</i> = 33 a
LFTH	5 <i>n</i> = 77 a	2 <i>n</i> = 36 b	2.5 <i>n</i> = 30 c	2 <i>n</i> = 15 b	3 <i>n</i> = 10 c	5 <i>n</i> = 33 a
PDLST	45.4 (16.7) <i>n</i> = 67 a	31.8 (8.9) <i>n</i> = 36 b	34.4 (7.3) <i>n</i> = 30 b	13.4 (3.9) <i>n</i> = 16 c	NA	39.1 (12.9) <i>n</i> = 32 ab
PTLU	19.3 (7.7) <i>n</i> = 69 a	19.7 (7.6) <i>n</i> = 36 a	23.5 (10.7) <i>n</i> = 30 a	21.1 (6.9) <i>n</i> = 15 a	6.5 (4.1) <i>n</i> = 11 b	19.7 (7.8) <i>n</i> = 32 a
SPLW	2.87 (0.46) <i>n</i> = 38 a	2.36 (0.46) <i>n</i> = 17 b	3.29 (0.62) <i>n</i> = 17 a	2.59 (0.46) <i>n</i> = 6 ab	3.25 (0.63) <i>n</i> = 9 a	2.46 (0.44) <i>n</i> = 16 b
TLLF	0.41 (0.09) <i>n</i> = 73 a	0.45 (0.10) <i>n</i> = 31 a	0.60 (0.09) <i>n</i> = 30 b	0.64 (0.11) <i>n</i> = 15 b	0.65 (0.11) <i>n</i> = 10 b	0.62 (0.06) <i>n</i> = 33 b
TLSP	0.36 (0.06) <i>n</i> = 40 a	0.35 (0.07) <i>n</i> = 23 a	0.59 (0.11) <i>n</i> = 18 b	0.58 (0.06) <i>n</i> = 8 b	0.63 (0.12) <i>n</i> = 6 b	0.60 (0.05) <i>n</i> = 18 b
VNWD	0.144 (0.033) <i>n</i> = 74 a	0.068 (0.018) <i>n</i> = 36 b	0.084 (0.023) <i>n</i> = 28 c	0.074 (0.018) <i>n</i> = 15 bc	0.084 (0.022) <i>n</i> = 10 bc	0.121 (0.034) <i>n</i> = 33 d
W90LL	0.23 (0.07) <i>n</i> = 68 a	0.12 (0.04) <i>n</i> = 36 b	0.16 (0.07) <i>n</i> = 29 bc	0.16 (0.06) <i>n</i> = 15 bc	0.21 (0.06) <i>n</i> = 11 ac	0.26 (0.06) <i>n</i> = 32 a
Common garden						
	AGCP	CPTN	NOAL+ TMAL	OUMT	PMGA	WGCP
ANCOL	0.81 (0.30) <i>n</i> = 24 ab	0.89 (0.15) <i>n</i> = 3 *	0.94 (0.29) <i>n</i> = 17 a	0.65 (0.14) <i>n</i> = 6 b	0.65 <i>n</i> = 1 *	1.20 (0.23) <i>n</i> = 20 c
AREAR	0.588 (0.219) <i>n</i> = 24 a	2.790 (1.130) <i>n</i> = 3 *	1.540 (0.732) <i>n</i> = 17 b	1.63 (0.452) <i>n</i> = 6 b	1.415 <i>n</i> = 1 *	0.691 (0.231) <i>n</i> = 20 a
LFTH	4 <i>n</i> = 24 a	1 <i>n</i> = 3 *	1.5 <i>n</i> = 17 b	1.5 <i>n</i> = 6 b	1.5 <i>n</i> = 1 *	3 <i>n</i> = 20 a
PDLST	46.1 (22.7) <i>n</i> = 24 a	30.4 (15.7) <i>n</i> = 3 *	33.7 (24.7) <i>n</i> = 17 a	11.6 (3.55) <i>n</i> = 6 b	31.3 <i>n</i> = 1 *	46.0 (15.2) <i>n</i> = 20 a
PTLU	20.8 (12.2) <i>n</i> = 24	22.8 (6.67) <i>n</i> = 3 *	16.4 (6.4) <i>n</i> = 17	17.9 (14) <i>n</i> = 6	1.9 <i>n</i> = 1 *	19.2 (4.78) <i>n</i> = 20
SPLW	2.98 (0.43) <i>n</i> = 24 a	2.62 (0.26) <i>n</i> = 3 *	3.54 (0.57) <i>n</i> = 17 b	2.77 (0.30) <i>n</i> = 6 a	3.51 <i>n</i> = 1 *	2.80 (0.39) <i>n</i> = 20 a
TLLF	0.42 (0.09) <i>n</i> = 24 a	0.42 (0.08) <i>n</i> = 3 *	0.61 (0.07) <i>n</i> = 17 bc	0.56 (0.03) <i>n</i> = 6 b	0.59 <i>n</i> = 1 *	0.67 (0.09) <i>n</i> = 20 c
TLSP	0.38 (0.06) <i>n</i> = 24 a	0.38 (0.06) <i>n</i> = 3 *	0.57 (0.07) <i>n</i> = 17 b	0.58 (0.06) <i>n</i> = 6 b	0.66 <i>n</i> = 1 *	0.60 (0.07) <i>n</i> = 20 b
VNWD	0.097 (0.013) <i>n</i> = 24 a	0.048 (0.006) <i>n</i> = 3 *	0.055 (0.010) <i>n</i> = 17 b	0.051 (0.007) <i>n</i> = 6 b	0.063 <i>n</i> = 1 *	0.083 (0.014) <i>n</i> = 20 c
W90LL	0.25 (0.07) <i>n</i> = 24 a	0.08 (0.06) <i>n</i> = 3 *	0.13 (0.06) <i>n</i> = 17 b	0.12 (0.03) <i>n</i> = 6 b	0.08 <i>n</i> = 1 *	0.22 (0.05) <i>n</i> = 20 a

**Nominal characters**— INFPOS readily separated specimens designated in the PMGA group from the remaining hypothesized taxa in the elevated bract group with a terminal inflorescence position (vs. axillary). The single individual from PMGA in the common garden experiment exhibited the same terminal INFPOS. In the common garden individuals of the BBG, INFHAB readily separated OUMT individuals, with pendulous pedicels, from those of CPTN and WGCP with erect pedicels. Additional qualitative characters, not included in the morphometric analyses, that are of taxonomic utility to varying degrees are addressed in the Discussion (see below).



**Figure 5.** Proportional histogram plots of leaf thickness of *a priori* groups. The x-axis shows weighted proportion of hypothesized taxon, blue and green indicating herbarium specimens and common garden datasets, respectively. Dashed and solid lines indicate median values for herbarium specimens and common garden datasets, respectively. A= AGCP, B= CPTN, C= NOAL+TMAL, D= OUMT, E= PMGA, F= WGCP. Sample sizes are in Table 5.

**Comparison of herbarium specimens and common garden datasets**— Similar to the univariate analyses of quantitative and nominal characters, NOAL and TMAL were combined into a single group. AREAR, LFTH, PTLU, SPLW, TLLF, VNWD, and W90LL differed significantly between the herbarium specimens and common garden datasets for at least one hypothesized taxon. AREAR, LFTH (Fig. 5), VNWD, and W90LL were found to be significantly different between herbarium specimens and common garden datasets for more than one hypothesized taxon (Table 6). General trends between herbarium specimens and common garden datasets between taxa include larger AREAR, lesser LFTH, narrower VNWD, and lesser W90LL (Table 5).

### **Discussion**

The goal of this study was to test whether *C. reticulata* s.l. consisted of more than a single taxon with morphological evidence from herbarium specimens and a common garden experiment with supporting evidence from biogeographic and ecological factors. Subgenus *Viorna* presents several challenges when assessing morphological variation with herbarium specimens, which include 1) small sample sizes due to endemism and rarity, 2) ontogenetic differences across individual vines, and 3) loss of potentially informative characters when pressed and dried. This study demonstrates that these challenges can be overcome with a complementary common garden experiment. While drawing conclusions from any one standalone dataset used in our analyses would be suspect, use of several datasets (flowering herbarium specimens, fruiting herbarium specimens, and common garden experiment), plus extensive *in situ* examination, greatly reduces the probability of drawing erroneous conclusions. This study demonstrates support, in part, for our hypotheses of morphological separation

between *a priori* defined groups, which correlate with geographic structure and ecological preference of the *C. reticulata* s.l.

**Table 6.** Statistical significance of characters within hypothesized taxa between herbarium specimens and common garden datasets. ‘\*’ indicates characters significantly different between herbarium specimens and common garden at  $p < 0.05$ ; ‘ns’ indicates characters that are not significantly different at  $p < 0.05$ . All characters except LFTH were subjected to Welch’s ANOVA. LFTH was subjected to Kruskal-Wallis test. Note that only hypothesized taxa with  $n \geq 5$  in both datasets were included.

	NOAL+			
	AGCP	TMAL	OUMT	WGCP
ANCOL	ns	ns	ns	ns
AREAR	*	*	ns	*
LFTH	*	*	ns	*
PDLST	ns	ns	ns	ns
PTLU	ns	*	ns	ns
SPLW	ns	ns	ns	*
TLLF	ns	ns	ns	*
TLSP	*	ns	ns	ns
VNWD	*	*	*	*
W90LL	ns	ns	*	*

This study presents the second comprehensive investigation to quantify the morphological variation within *Clematis* subg. *Viorna* at a population level and in a taxonomic context with Keener’s morphometric analysis of varieties of *C. fremontii* in his broader study of *Clematis* subsect. *Integrifoliae* R.O.Erickson (1967). When considered across the entire genus, this study represents the third morphometric investigation to assess species limits at the population level in *Clematis* with a morphometric study of subg. *Atragene* (L.) Torr. & A.Gray by Yang et al. (2009).

**Utility of common garden**— This study represents the first taxonomic study of *Clematis* to employ a common garden. The shift in quantitative measures, such as AREAR, LFTH, VNWD, and W90LL (Table 6) may suggest that these characters are sensitive to environmental conditions including, but not limited to, sunlight exposure, soil moisture, or humidity. Still,

hypothesized taxa maintained directional differences in all morphological characters (Table 5). Similar to a study of *Myosotis* L. by Prebble et al. (2018), characters found to be plastic in the common garden still differentiated hypothesized groups in both herbarium and common garden datasets (Table 5; Appendices C and D). Rather than removing these characters from analyses or disregarding their taxonomic utility, it would be better to use them, but with caution, when differentiating taxa. It should be noted that this study did not quantify the potential direct environmental drivers or limits of plasticity, which would be better tested with a reciprocal transplant experiment. Rather, this study just deduced whether or not plasticity confounds our taxonomic hypotheses.

In addition to identifying potentially plastic characters, we were able to use the common garden to capture INFHAB, a character which is lost in herbarium specimens. When added to the PLS-DA LOOCV, our BER decreased, demonstrating the utility of common garden experiments when quantifying species limits. Because the character states of INHAB in the common garden matches what we observed in the field, we are confident that our decision to employ INFAB as a character to delimit species is not confounded by phenotypic plasticity.

The common garden also allowed us to control for ontogenetic differences, which is an obvious downfall to relying strictly on herbarium specimens for plants that do not completely fit on a standard herbarium sheet. This study highlights the need for common garden experiments to better understand potentially plastic characters between and within species and account for variation that may be explained by ontogeny.

**Species delimitation**— While species limits within the BBG are clearly corroborated between herbarium and common garden datasets, the EBG is less straightforward. The common garden data supports the presence of two (out of three groups tested) distinct morphological

entities. This may be attributed to its ability to control for ontogenetic variation. Another possible reason for different results between common garden and herbarium datasets could be an artifact of sampling, which could make a single polymorphic taxon appear to be two morphological entities if geographically intermediate populations are not included in sampling. Because our common garden sampling does not contain any obvious geographical gaps (see Fig. 2), we are inclined to reject the reasoning that differing results between herbarium and common garden results of the elevated bract group are an artifact of sampling.

Multiple characters employed in our morphometric analyses have previously been used to delimit other species and groups of species in both subg. *Viorna* and *Clematis* in general. Bract placement (basal vs. elevated) has been used to separate *C. morefieldii* (Kral 1982; Pringle 1997; Johnson 2001) from other species of the North American subg. *Viorna*. This study found bract placement to be the most reliable character to subset hypothesized taxa for further analyses. Inflorescence position (terminal vs. axillary) has been utilized to separate several species of North American subg. *Viorna*, such as *C. addisonii*, *C. albicoma*, *C. bigelovii* Torrey, *C. crispa* L., *C. fremontii* S. Watson, *C. hirsutissima* Pursh, *C. socialis*, *C. vinacea*, and *C. viticaulis* (Pringle 1997; Floden 2013) from taxa with mainly axillary inflorescences. In this study, inflorescence position readily separated PMGA specimens from all other hypothesized taxa in the *C. reticulata* species complex. ACTL has been used to separate *C. socialis* from *C. baldwinii* (Pringle 1997). Our analyses indicate that OUMT specimens can be differentiated from AGCP, CPTN, and NOAL+TMAL specimens by their distinctly shorter achene tails. Petiolule length has not been previously utilized to delimit species in North American subg. *Viorna* but has been used to separate *C. nukiangensis* M. Y. Fang from other *Clematis* species in China (Wencai and Bartholomew 1997). Our analyses show that PMGA are distinctly sessile or shorter than other

hypothesized taxa. Wencai and Bartholomew (1997) used leaf thickness to delimit species (e.g. *C. sinii* W.T. Wang vs. *C. meyeniana* Walpers). We demonstrated that leaf thickness can be used to delimit specimens assigned to AGCP and WGCP from CPTN, NOAL+TMAL, and OUMT (Fig. 5; Table 5).

Characters quantified in this study that are novel to the genus, to the best of our knowledge, include ACLW, ANCOL, AREAR, SPLW, TLLF, TLSP, and VNWD. While AREAR and VNWD present obvious challenges for differentiating taxa in the field, they serve as reliable ways to quantify overall degree of vein reticulation, more so than areole length, as used by Dennis (1976) and Pringle (1997) to separate *C. reticulata* s.l. from *C. pitcheri*.

All groups tested in this study that were identified as morphologically diagnosable are proposed to be treated as distinct species. This includes AGCP, CPTN, NOAL+TMAL, OUMT, PMGA, and WGCP. Despite morphological overlap being present in most individual characters between *a priori* groups, differences in morphology are unique when examined in combination (Appendices C and D) in both the herbarium specimens and common garden datasets, emphasizing the importance of multivariate methods when delimiting species. *A priori* groups that were supported as morphologically distinct by our multivariate analyses are discussed below with discussion of geographic distribution. For further information of distribution and habitat, see Taxonomic Treatment.

1) The AGCP group (Fig. 12) has long been recognized as *C. reticulata*, but in a much broader sense, widespread in distribution throughout the southeastern US (Erickson 1943; Keener 1975; Dennis 1976; Pringle 1997). Even after the segregation of numerous taxa in the *C. reticulata* species complex, *C. reticulata* s.s., defined by this study, still exhibits a considerable degree of morphological variation in leaflet lobing (Fig 12D; 12E), leaflet shape, and flower

color (Fig. 12B; 12C). If morphological characters were examined with phylogenetic data, these variants could show to be worthy of taxonomic recognition. Future research with geometric morphometrics of leaflets may prove useful for species delimitation. While traditional morphometrics was successful at capturing morphological variation overall, we feel that it does not adequately capture variation in leaflet lobing. Also, there have been numerous collections of *C. reticulata* in northeastern Florida and southeastern Georgia with completely cream white sepals. Considering that flower color delimits taxa, in part, in the *C. glaucophylla* species complex (*sensu* Estes 2006), investigation of sepal color further may elucidate additional variation, some of which may be of taxonomic utility. Still, sepal color should be used with caution, as we observed remarkable variation in color within individuals and between years. The AGCP group is treated as *C. reticulata* s.s.

2) The NOAL+TMAL group (Fig. 14) was first noted by Small (1933), who recognized this group as *Viorna subreticulata*. Small (1933) differentiated *V. subreticulata* from *V. reticulata* (= *C. reticulata*) by its less coarse veins, larger leaflets, and larger foliaceous bracts. Small (1933) described the distribution of *V. subreticulata* as occurring from Alabama to East Texas and Arkansas. The only cited specimen is the holotype, making Small's broader *V. subreticulata* concept impossible to interpret without extrapolating due to lack of reference to specimens from the other listed localities. If Small (1933) was referring to the *a priori* groups OUMT or WGCP from Arkansas and East Texas, respectively, this study demonstrates several characters that differentiate OUMT and WGCP from NOAL+TMAL populations from both herbarium specimens and common garden individuals (Table 5; Appendices C and D; see Taxonomic Treatment). Our data support the morphological differences in the thin leaflets and lesser degree of reticulate venation (inferred by areole area and vein width) of populations

assigned to NOAL+TMAL. More specifically, our common garden data suggest that these differences remain when environmental conditions are controlled (Appendices C and D). Small's (1933) leaflet size character to separate *V. subreticulata* from *V. reticulata*, while not included in the analysis, was too variable to be used as a reliable character to separate AGCP and NOAL+TMAL specimens. Small (1933) also noted that *V. subreticulata* had larger foliaceous bracts, but we found bracts to also be highly variable and often developmentally aborted in NOAL+TMAL specimens, as well as all other hypothesized groups tested in this study.

Populations of the *C. reticulata* species complex found in the Talladega Mountains of the Piedmont in Alabama (TMAL) are ecologically distinct, in that they are found in relatively high elevation areas (~735 m at highest). Our morphological investigation of populations assigned to TMAL showed them to be most similar to populations assigned to NOAL based on our FAMD scatterplots (Fig. 3C; Fig. 3D; Fig. 4B) and the reduction in BER when combined with NOAL in the PLS-DA LOOCV. Because of its morphological similarity to populations assigned to NOAL, it seems best to treat TMAL and NOAL as conspecific. Characters that the authors originally thought separated TMAL populations from others included densely pilose abaxial leaflet and sepal abaxial surfaces. Fieldwork and examination of herbarium specimens revealed that these characters are highly variable within and between populations of both NOAL and TMAL, with opposing extremes of trichome type and density found on two individuals from the same population. We observed that common garden individuals exhibited a unique flower morphology, with elongated, cylindric sepal bodies, but we did not observe these same differences consistently in the field. Populations from TMAL may represent a weakly diverged geographic variant, but it is not diagnosable in this study and should not be recognized at any

taxonomic rank. Future research may be warranted, with further sampling at the population level. The NOAL+TMAL group is given a new combination below, *C. subreticulata* comb. nov.

**3)** The PMGA group (Fig. 16) is perhaps the most readily separated taxon within the *C. reticulata* species complex due to its terminal INFPOS, shorter PTLU, and erect-herbaceous habit. While the nature of its narrow endemism did not allow us to include as many samples as other groups, the FAMD shows it to be a distinct group (Fig. 3C). The five specimens subjected to the PLS-DA LOOCV were all predicted to the same group to which they were originally assigned (PMGA). We only included a single individual in the common garden, which did not allow use to subject it to multivariate or univariate analyses. Still, the morphological characters used to delimit this group in herbarium specimens remained the same in the common garden.

PMGA specimens are restricted to the Pine Mountain Ridges (PMR), which are the southernmost mountains of eastern continental North America, with an east-west orientation. Located in the extreme southern portion of the Piedmont, PMR is known for its unique assemblage of taxa with a combination of Appalachian and Coastal Plain species (Jones 1974). Currently, there are no known published species endemic to the PMR, making *C. terminalis* sp. nov. the first published PMR endemic. There is an undescribed *Clinopodium* L., apparently endemic to the PMR (Weakley 2015).

**4)** The CPTN group (Fig. 8) has long been mistaken for several species of subg. *Viorna*, including *C. viorna*, *C. beadlei*, and *C. reticulata*. While a single individual from the common garden experiment was assigned to OUMT in the PLS-DA LOOCV, we attribute this to our low number of samples ( $n = 3$ ) based on the substantially higher standard deviation present in characters like PDLST. Still, PDLST of CPTN common garden individuals had a similar mean to that of our herbarium specimens dataset (Table 6). Additionally, when we added the character

INFHAB to our PLS-DA model, there was no discrepancy between our group designations and the model predictions.

Populations assigned to CPTN also consistently possess achene tail hairs that are yellow-brown to golden-brown in color (Fig. 8C), with few exceptions, which differs from other hypothesized taxa, in that they have white to downy yellow achene tail hairs. We chose not to include this character in the analysis, as it was discovered after obtaining initial results.

Erickson (1943) cited two specimens as *C. beadlei* from White County (*Biltmore Herbarium H/2689*, US) and Warren County (*Biltmore Herb. s.n.*, US), Tennessee. While the taxonomic status of *C. beadlei* was not assessed in this study, examination of type material of *C. beadlei* (*Small s.n.*, NY) revealed that specimens assigned to this name have elevated bract placement and are also better placed in the *C. viorna* species complex. CPTN populations have also been previously assigned to *C. viorna* and *C. versicolor*. This undescribed taxon is recognized as *C. cumberlandensis* sp. nov.

5) The OUMT group's (Fig. 10) pendulous INFHAB is perhaps its most diagnostic character, but this can only be observed from living plants. The distribution of the OUMT group is confined to the southern portion of the Ouachita Mountains Region of Arkansas and Oklahoma (Fig. 11). The Ouachita Mountains is part of the Interior Highlands region, which has been previously recognized as an area to harbor numerous endemic plant species (Zollner et al. 2005). The OUMT group is treated as *C. ouachitensis* sp. nov., which joins the 28 percent of the endemic flora that are found primarily in riparian habitats of the Ouachita and Ozark Mountains (Zollner et al. 2005). This habitat would fall under the Ozark-Ouachita Riparian ecological system as described by NatureServe (2020).

6) The WGCP group (Fig. 6) occupies the West Gulf Coastal Plain region of southwestern Arkansas, western Louisiana, and eastern Texas (Fig. 7). The range of this taxon fits into the phytogeographic pattern of the West Gulf Coastal Plain, previously identified as a center of endemic plant species (Sorrie and Weakley 2001; MacRoberts et al. 2002). The WGCP group is treated as *C. arenicola* sp. nov.

**Taxonomic diversity in the southeastern United States**— While the increase in taxa recognized in the *C. reticulata* species complex, from one to six species, may be a surprise to some, recent investigations into various plant groups in the southeastern United States have led to similar revisionary work that recognizes greater species diversity than previously accepted. Genera that have undergone this type of revisionary work include, but are not limited to, *Carex* L. (Naczi 1997; Naczi et al. 1998; Naczi et al. 2001; Naczi and Ford 2001; Naczi et al. 2002), *Opuntia* (L.) Mill. (Majure et al. 2017), *Stachys* L. (Fleming et al. 2011; Floden 2016; Keener and Davenport 2016; Nelson 2008; Nelson and Rayner 2014; Poindexter and Nelson 2011), and *Trillium* L. (Schilling et al. 2013; Schilling et al. 2017; Schilling et al. 2019). Phytogeographic investigations into taxonomic groups in the southeastern United States have led to the understanding the degree of endemism of plant species in multiple areas (Estill and Cruzan 1999; Sorrie and Weakley 2001; MacRoberts et al. 2002; Zollner et al. 2005). Most notably, the North American Coastal Plain (NACP) was recognized as a global biodiversity hotspot by Noss et al. (2015), in part, due to the high number of endemic species found in the region. The NACP, as defined by Noss et al. (2015), contains three of the species of the *C. reticulata* complex that are at least partially distributed within its boundaries. Given that all members of the *C. reticulata* species complex are found in open habitats that require some level of natural disturbance (see Taxonomic Treatment), the increase of diversity in North American subg. *Viorna* highlights the

importance of grassland habitats in harboring biodiversity in the southeastern U.S., as discussed by Noss et al. (2015). This study is further testament to the need for ongoing taxonomic research, even in regions where biodiversity is considered well-documented.

**Future taxonomic work**— While this study makes substantial progress towards clarifying species limits in the *C. reticulata* species complex and the North American subg. *Viorna*, there are remaining populations of the *C. reticulata* species complex that could not be readily placed, nor had enough specimens available to include in morphometric analyses. One of these populations is from Elmore County, Alabama and grows along the banks of the Tallapoosa River (e.g. *T. Wayne Barger SP# 3212*, ALNH). Specimens from the Elmore County population contains plants with weakly glaucous stems, short trichomes on the sepal abaxial surfaces, flowers that are faded purple on the exterior and interior, and short sepal apices that are sharply reflexed. A collection from Autauga County, Alabama (*S. C. Gunn 545*, UNA) shares several the noted morphological characters with the Elmore County population, but flower color cannot be known until fresh material is seen. Whether or not these populations are conspecific, separate undescribed taxa, or are hybrids, remains to be known. More fieldwork along the Alabama and Tallapoosa Rivers, as well as including samples in an ongoing phylogenetic study (Harris and Smith, in prep.) may elucidate the taxonomic status of these populations.

### **Taxonomic Treatment**

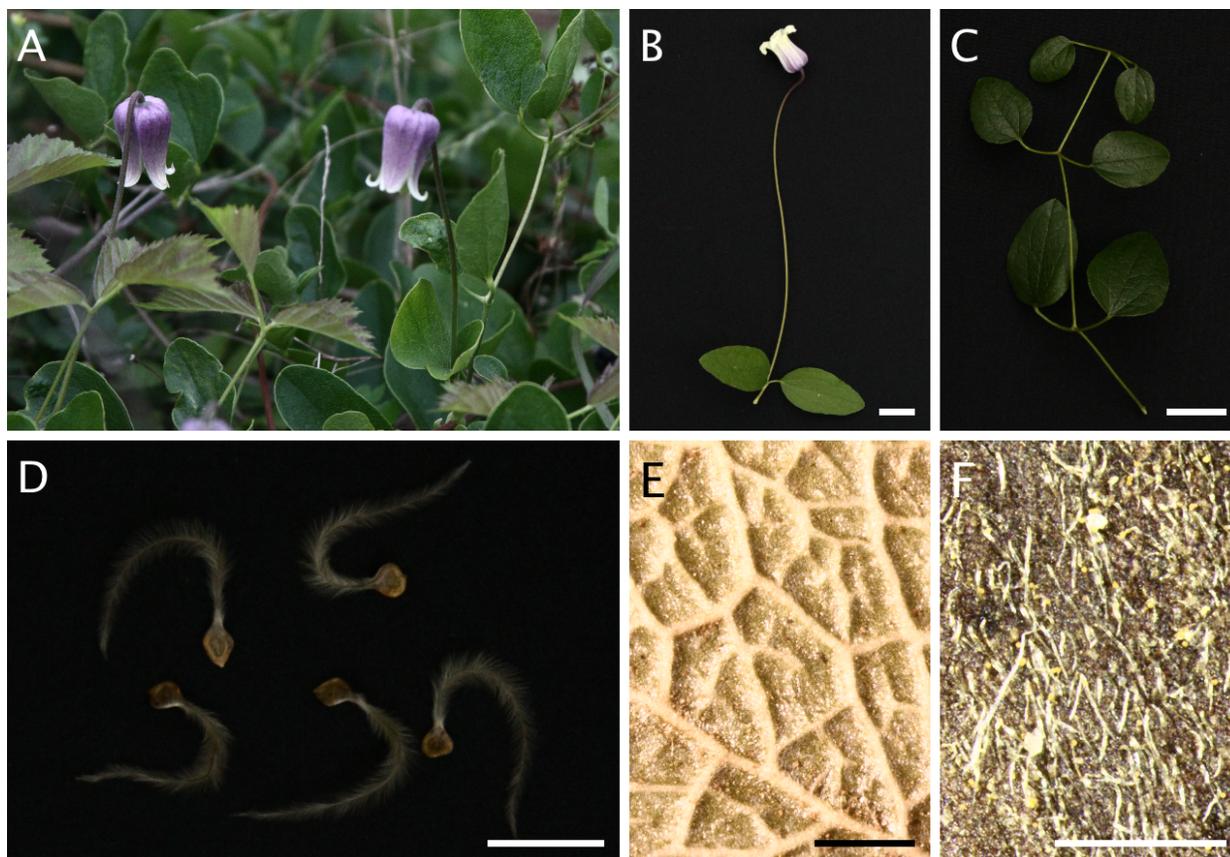
The following species descriptions should not be considered effective publication. For all descriptions, ranges of quantitative characters indicate 99% bootstrapped (to account for heteroscedasticity) confidence intervals. Any values indicated in parentheses before and after the range indicate maximum and minimum outliers, respectively. For “specimens examined”

sections, TBD indicates duplicate collections made by one of the authors that are to be distributed to other herbaria from APSC. In species protologues and “Specimens examined” sections, superscripts of “M” indicate specimens used for both multivariate and univariate analyses while superscripts of “U” indicate specimens used only for univariate analyses. If one collection is represented by multiple collection numbers (sequential), then the collection number underlined indicates the specimen measured. Note that sepal trichome characters may be better found on sepals on either side of sepal directly pressed, as trichomes may be rubbed off during the pressing and drying process. As with any taxonomic group deemed as technically difficult, we advise that the morphological characters be examined across multiple morphological structures (leaflets, flowers, etc.) and nodes, when possible.

**1. CLEMATIS ARENICOLA** T.Murphy & D.Estes, sp. nov. TYPE: USA. Texas: Smith Co., Tyler State Park, northwest of Dogwood Ridge, on south side of Tyler State Park Lake, located at end of Park Rd 16 within immediate vicinity of Group Picnic Area #2, 21 May 2019, *Thomas H. Murphy 247 with Mason Brock* (Holotype: APSC<sup>M</sup>; Isotype: TEX)

**Diagnosis**— *Clematis arenicola* differs from *C. ouachitensis* sp. nov. in its erect (vs. pendulous) and relatively longer pedicels, longer anther connective extensions, broader leaflet apices, wider leaflet primary veins, thicker leaflets, and smaller closed leaflet areole area; from *C. cumberlandensis* sp. nov. in its broader leaflet apices, lighter achene tail hairs, wider leaflet primary veins, thicker leaflets, smaller closed leaflet areole area, and longer trichomes on leaf and sepal abaxial surfaces; from *C. reticulata* s.s. in its longer anther connective extensions, longer trichomes on leaf and sepal abaxial surfaces, and basal or near-basal (vs. elevated) bract placement (lesser peduncle to combined peduncle and pedicel ratio); from *C. subreticulata*

comb. nov. in its broader leaflet apices, wider leaflet primary veins, smaller closed leaflet areole area, and basal or near-basal (vs. elevated) bract placement (lesser peduncle to combined peduncle and pedicel ratio); from *C. terminalis* sp. nov. in its climbing habit when in flower (vs. erect-herbaceous), mostly axillary cymose inflorescences, and longer petioulules.

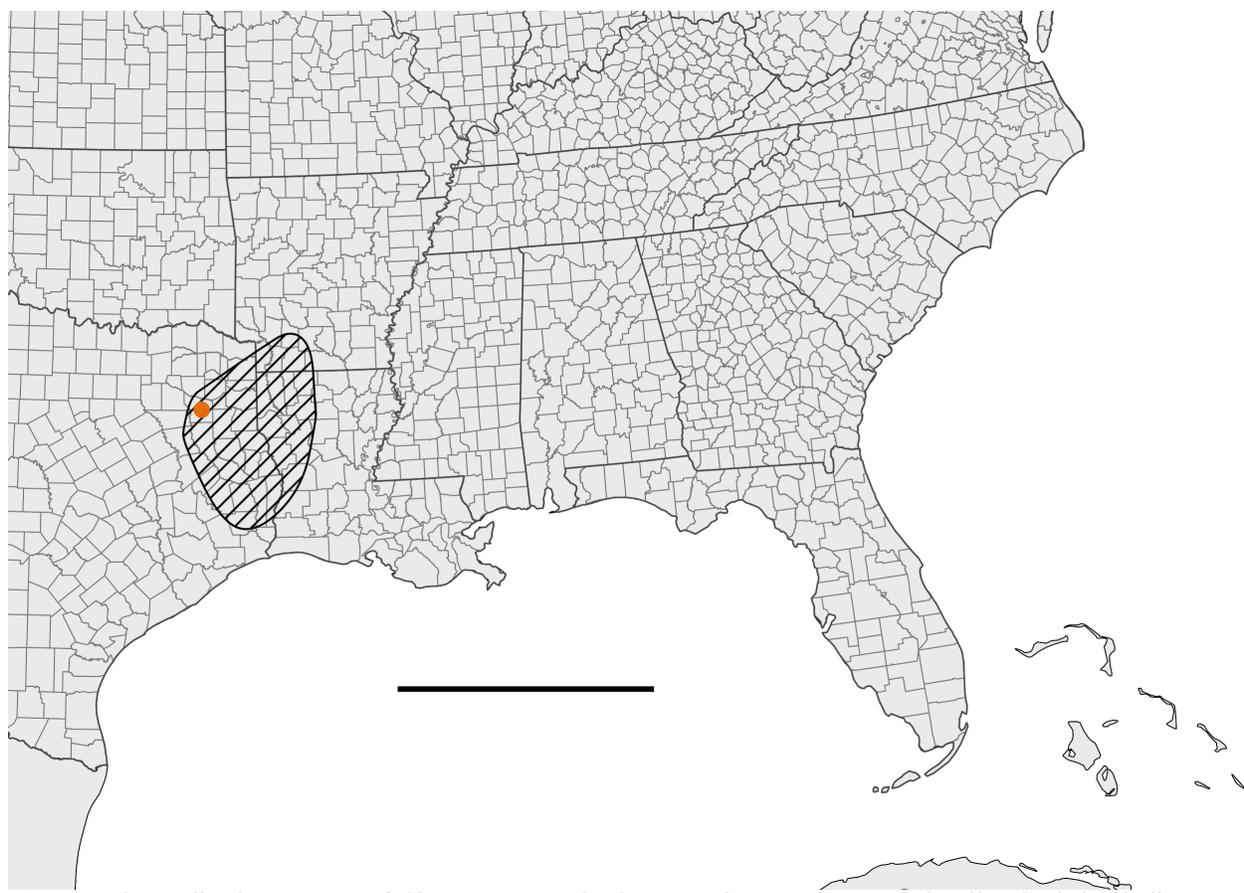


**Figure 6.** Diagnostic characters of *Clematis arenicola*. A) Erect habit of pedicels, B) inflorescence with basal or near-basal bract placement and relatively long pedicel (scale bar= 20 mm), C) leaflet with rounded apices (scale bar= 20 mm), D) achenes with yellowish-white tail hairs and long tails (scale bar= 20 mm), E) leaflet adaxial venation with small closed areoles and wide veins (scale bar= 1 mm), and F) sepal abaxial with relatively long trichomes (scale bar= 1 mm).

**Description**— Perennial climbing or scandent **vine** to ca. 3 m tall, one to multiple stems from a woody caudex bearing smooth coarse roots. **Stems** six angled, six ribbed, reddish-brown, usually densely covered in spreading-pilose to appressed trichomes, trichome density increasing distally. **Leaves** oppositely decussate, spreading, proximal most leaves simple and entire or deeply lobed, becoming imparipinnately compound, longest at mid-stem, longer than wide;

petioles (2.1) 3.4–4.9 (6.3) cm, increasingly shorter from proximal to distal leaves, sparsely to moderately puberulent, opposing petioles conjoined at node, distal-most leaflet modified into tendril-like structure or greatly reduced leaflet; leaflets distinctly coriaceous, (2.9) 4.6–5.8 (7.6) cm long, (2.3) 2.7–4.3 (6.9) cm wide at widest point, usually rotund, elliptic-oblong, or ovate, symmetrical or asymmetrical, usually with broad and rounded to broadly acute apices, rarely narrowly acute, leaflets of mid-stem leaves typically simple, rarely lobed, conspicuously raised-reticulate, most noticeable in dried material, primary veins (0.07) 0.10–0.13 (0.21) mm wide, lowest order of closed areoles (0.19) 0.35–0.51 (1.22) mm<sup>2</sup>, adaxial surface typically sparsely to moderately puberulent, abaxial surface glabrate to densely puberulent with longest trichomes (0.48) 0.58–0.64 (0.76) mm long, pubescence confined to mid-veins or both mid-veins and lower order veins; petiolules (9.4) 15.5–21.7 (49.0) mm long, margins ciliate, entire or sometimes appearing irregularly and broadly undulate. **Inflorescences** most often axillary cymes or solitary, rarely producing terminal flowers, nodding on decidedly erect pedicels, mostly ovoid in shape, rarely urceolate; when axillary, peduncles (1.7) 5.2–10.9 (19.6) mm long, primary pedicels (55.0) 85.3–131.3 (178.9) mm long, ratio of peduncle to combined peduncle and pedicel length (0.03) 0.07–0.09 (0.20) with foliose bracts appearing basal or near-basal on combined peduncle and pedicel; foliose bracts (9.8) 17.5–29.0 (38.3) mm long. **Sepals** erect, connivent, oblong-ovate to oblong-lanceolate, reflexed and spreading at apex, (17.0) 17.6–23.3 (24.8) mm long, (5.6) 7.4–10.0 (10.7) mm wide at widest point, coriaceous, abaxially usually faded lilac or lavender at base, rarely vibrant pink to purple, concolorous or becoming cream distally, abaxially concolorous or cream; margins narrowly crispate, white-tomentulose, abaxial surface moderately puberulent, rarely glabrate, with longest trichomes (0.48) 0.58–0.63 (0.69) mm long. **Stamens** linear, (1.3) 1.6–1.8 (2.1) cm long, filaments flattened, spreading-pilose from middle to apex,

connective extended (0.62) 0.89–1.26 (1.57) mm beyond anthers. **Fruit** tightly clustered in spherical heads, light brown, body rhomboidal-ovate to rotund, (5.2) 5.7–7.0 (7.4) mm long, (3.5) 4.2–5.6 (6.1) mm wide, acuminate or rounded on proximal end and acuminate on distal end, marginally thickened, sericeous; thickened achene rims (0.60) 0.70–0.85 (1.02) mm wide at mid-point; style curvate, (3.5) 4.2–4.9 (5.1) cm long, with a light yellowish plumose tail hairs, spreading to ascending, (3.1) 3.8–4.3 (4.7) mm long at mid-point, becoming shorter proximally and distally. Chromosome number unknown.



**Figure 7.** Generalized range map of *Clematis arenicola*. Orange point represents type locality. Scale bar indicates 500 km.

***Distribution and Habitat***—The distribution of *C. arenicola* is confined to the West Gulf Coastal Plain of Arkansas, Louisiana, and Texas (Fig. 7). This distribution conforms to a previously recognized phytogeographic area of endemism (Sorrie and Weakley 2001). *Clematis*

*arenicola* is typically found in sandy soils of sandhill prairies, pine-oak savannas and woodlands, and shrublands. Populations can also be found in anthropogenically-influenced habitats that mimic *C. arenicola*'s natural habitat, including roadside banks, powerline rights-of-ways, and margins of forested areas. While many populations of *C. arenicola* were found to occur in xeric environments, there were several populations observed in low-lying sandy soils that would be considered mesic.

**Phenology**—*Clematis arenicola* primarily flowers from the last week of April to mid-June with sparse flowering occurring into the fall. Fruit matures from mid-July through late fall.

**Etymology**—The epithet “arenicola” refers to the deep sandy soils to which this species appears to be confined.

**Conservation**—Based on the number of herbarium specimens, ease of locating during fieldwork, and observations of this species inhabiting both conservative and degraded habitat, *C. arenicola* should not be afforded federal protection at this time. State protection in Arkansas may be warranted because this is the northern edge of *C. arenicola*'s range, where it is found in few protected areas in the state. Evidence of roadside herbicide application and subsequent extirpation seems to be the primary reason for inability to locate several populations based on recently collected herbarium specimens (pers. obs.). Efforts to conserve this species should be focused on the conservation of savanna and sandhill prairie habitat.

**Specimens examined (paratypes)**—USA—ARKANSAS: Miller Co., 33°11.749' N, 94°01.807' W, 30 May 2017, Zach Irick 791 with Jesse Harris (APSC); west of AR Hwy 237, south of private drive, 33.195546, -94.030683, 19 July 2018, Thomas H. Murphy 137 with Mason Brock (APSC, TBD); Ouachita Co., Chidester, 8 July 1967, G. E. Tucker 5730 (NCU<sup>U</sup>); Red Hill Township. North and south sides of County Rd 387, 19 June 2018, Thomas H. Murphy 103 with

*Joseph Aroh* (APSC, TBD); **LOUISIANA:** Bienville Parish, beside La. 4, just east of Saline Bayou and east of Lucky, Sec. 27 and 34 T15N R6W, 20 May 1975, *R. Dale Thomas 43721 with David Moreland* (UARK<sup>M</sup>); along Saline Bayou, 1.25 miles east of Lucky, Secs. 27 and 34, T15N, R6W, 21 May 1976, *R. Dale Thomas 49206/ David Moreland 01576* (FLAS, NCU<sup>M</sup>); along east side of branch of Saline Bayou at La. 4 bridge east of Lucky, Sec. 34 T15N R5W, 25 July 1987, *R. Dale Thomas 101065 with Dennis Bell and Dendrology Class* (USCH<sup>U</sup>); Caddo Parish, along US 71, ca. 1.3 miles north of Mira, 5 June 1979, *Charles M. Allen 8999/ Karl Vincent 2263* (NCU<sup>M</sup>); just off Hwy 71, 2.8 miles south of Ida, nw-nw-26-23n-15w, 22 June 1976, *D. T. MacRoberts 1801* (NO<sup>U</sup>); Ida, along Hwy 71, 6 July 1979, *Dr. L. D. Newsom s.n.* (LSU); Road No. 2 at Texas State Line south of La. 168, west of Rodessa, 11 June 1982, *R. Dale Thomas 81408* (MO, NCU<sup>U</sup>); along Kendrick Road, 2 miles north of Vivian and west of La. 1, Sec. 11 T12N R16W, 16 August 1990, *R. Dale Thomas 120633 with Barbara G. Thomas* (USCH<sup>U</sup>); south side of Bowen Road at intersection with private drive, 545 road meters west of intersection with Boyter Lane, 32.818794, -94.023446, June 2018, *Thomas H. Murphy 84 with Joseph Aroh* (APSC<sup>U</sup>, TBD); DeSoto Parish, unmarked road to DeSoto Lookout Tower, ca. 9.8 miles southeast of Mansfield, Sec. 10 T11N R12W, 23 June 1979, *Charles M. Allen 9065/ Karl Vincent 2333 with Larry Erbe* (USF); Mansfield, south of Par Road 122, 2.2 air kilometers from intersection with La-175, 850 air meters from intersection with Desoto Fire Tower Road, 19 June 2018, *Thomas H. Murphy 104 with Joseph Aroh* (APSC<sup>M</sup>, TBD); Natchitoches Parish, eastern slope of Sang-pour-sang, near Cloutville, 21 June 1939, *Claire A. Brown 7936* (LSU); near LA Hwy 118, ca. 16.5 miles west of intersection with LA Hwy 8, 6 May 1992, *Neyland 64* (LSU); Vernon Parish, 7 miles northeast of junction of Haddens Ferry road, 30 April 1955, *Cooley 4048 with Brass* (USF<sup>M</sup>); 1.1 miles north of junction with route 10 at Pickering, 4 June 1956, *David P.*

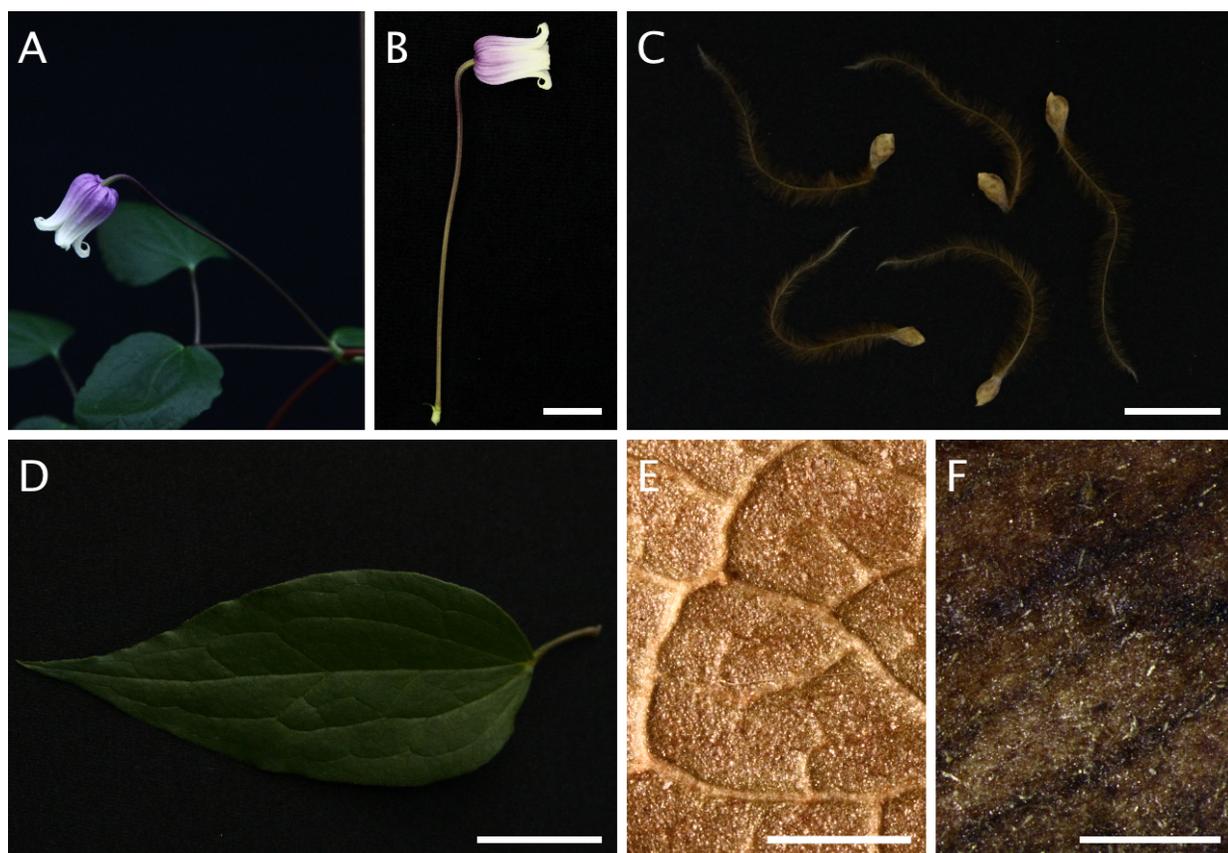
*Gregory 20 with George Eiten (GH, MO<sup>M</sup>); Red Dirt Game Management Area, Kisatchie National Forest, Montrose Road at entrance gate, 27 July 1991, W. C. Holmes 5320 (NO<sup>U</sup>); TEXAS: Anderson Co., bridge over Neches River, ca. 9 miles northeast of Slocum, 14 August 2002, W. C. Holmes 12419 with R. S. Baldrige (TEX<sup>U</sup>); Cass Co., Atlanta, 11 May 1925, E. J. Palmer 27156 (AA<sup>M</sup>); 10 ½ miles NE. of Hughes Springs, 19 May 1937, V. L. Cory 22824 (AA); Cherokee Co., east of Hwy 320 and north of Neches River at bridge crossing, 32.023258, -95.426131, 18 June 2018, Thomas H. Murphy 101 with Joseph Aroh (APSC<sup>M</sup>, TBD<sup>U</sup>); Hardin Co., near Village Creek, 3 miles south of Silsbee off Old Beaumont Road, 15 August 1964, Geraldine Watson H-4 (LL<sup>U</sup>); Big Thicket National Preserve, Turkey Creek Unit, ca. 7.5 miles by road northeast of Visitor Center, 30°31'N 94°15'W, 16 May 2002, G. L. Webster 33666 with B. Westlund and John Young (TEX<sup>M</sup>); north of McNeely Road just southwest of Big Thicket National Preserve, ca. 300 meters northeast of Jordan Road and McNeely Road, 19 June 2018, Thomas H. Murphy 105 with Joseph Aroh (APSC<sup>U</sup>, TBD); Harrison Co., west side of N Liberty Road, directly across from unnamed cemetery and Hope Springs Lake, 21 May 2019 Thomas H. Murphy 235 with Mason Brock (APSC<sup>U</sup>, TBD); Jasper Co., Jasper, 18 May 1937, V. L. Cory 22658 (AA<sup>M</sup>); Morris Co., Daingerfield State Park, 12 June 1957, D. S. Correll 16749 with H. B. Correll (LL); Nacogdoches Co., Woodland Hills Golf Club, south of Woodland Hills Drive, ca. 155 meters east of enter-exit split at road entrance from US-59, 18 June 2018, Thomas H. Murphy 102 with Joseph Aroh (APSC<sup>U</sup>, TBD); Newton Co., along west side of Little Cow Creek, east of Old Hemphill Road, ca. 15 miles northwest of Burkeville, 16 May 1964, D. S. Correll 29634 with Lance Rosier, Oza Hall, and C. Earle Smith, Jr. (LL<sup>M</sup>); south side of US 190, 8.8 miles east of Texas 63 intersection near Jasper and 4.3 miles west of Newton, 7 September 1987, R. Dale Thomas 101809 with Charles M. Allen (MO<sup>U</sup>, USCH<sup>U</sup>); Polk Co., 14*

May 1942, *B. C. Tharp s.n.* (GH<sup>M</sup>); along Highway 1276 14 miles southeast of Livingston, 10 May 1975, *Stephan L. Hatch 1418* (UTC<sup>M</sup>); Longleaf Pine Woodlands Trail (Champion International), ca. 100-500 feet south of St. Rt. 62 from a point ca. 0.5-0.6 miles west of its junction with US Rt. 287 northwest of Chester, Camden Quadrangle, 20 May 1997, *W. R. Carr 16451* (TEX<sup>M</sup>); Smith Co., 8 miles northeast of Tyler, 21 May 1994, *H. E. Moore, Jr. 813* (GH<sup>M</sup>); Tyler Co., 4 miles north of Doucette, route #69, 25 May 1959, *D. S. Correll 22331 with I. M. Johnston and G. Edwin* (LL<sup>M</sup>); Upshur Co., along Cypress Creek, 5 miles north of Ore City, 13 July 1946, *D. S. Correll 13152* (LL); bottoms of Big Sandy River, 0.3 miles north of Big Sandy, 11 June 2000, *R. Kral 89879* (GH<sup>U</sup>).

**2. CLEMATIS CUMBERLANDENSIS** D.Rogers, T.Murphy, & D.Estes, sp. nov. TYPE: USA. Tennessee: Cumberland Co., 11 miles northeast of Crossville, east of Fairfield Glade, south side of Hwy 101, Daddy's Creek, 9 June 2004, *Dwayne Estes 6235* (Holotype: APSC; Isotype: NCU, TENN<sup>M</sup>)

**Diagnosis**— *Clematis cumberlandensis* differs from *C. ouachitensis* sp. nov. in its erect (vs. pendulous) and relatively longer pedicels, longer achene tails, and shorter trichomes on leaflet and sepal abaxial surfaces; from *C. arenicola* sp. nov. in its larger closed leaflet areole area, narrower leaflet primary veins, shorter trichomes on leaflet and sepal abaxial surfaces, thinner leaflets, and narrower leaflet apices; from *C. reticulata* s.s. in its larger closed areole area, basal (vs. elevated) bract placement (lesser peduncle to combined peduncle and pedicel ratio), relatively shorter primary pedicel length, lesser sepal length to width ratio, narrower leaflet primary veins, and narrower leaflet apices; from *C. subreticulata* comb. nov. in its basal (vs. elevated) bract placement (lesser peduncle to combined peduncle and pedicel ratio), lesser

sepal length to width ratio, and shorter trichomes on leaflet and sepal abaxial surfaces; from *C. terminalis* sp. nov. in its climbing habit (vs. erect-herbaceous) when in flower, mostly axillary cymose inflorescences, lesser sepal length to width ratio, shorter trichomes on leaflet and sepal abaxial surfaces, and longer petiolules.



**Figure 8.** Diagnostic characters of *Clematis cumberlandensis*. A) Erect habit of pedicel, B) inflorescence with basal bract (note bracts are greatly reduced to scales) placement (scale bar= 20 mm), C) achenes with yellowish-brown tail hairs and longer tails (scale bar= 20 mm), D) leaflet with acuminate apex (scale bar= 20 mm), E) leaflet adaxial with larger areoles and narrower veins (scale bar= 1 mm), and F) sepal abaxial with short trichomes (scale bar= 1 mm).

**Description**— Perennial climbing or scandent **vine** to ca. 3 m tall, one to multiple stems from a woody caudex bearing smooth coarse, fleshy roots. Stems six angled, six ribbed, reddish-brown, usually sparsely to moderately covered in spreading-pilose to appressed trichomes, trichome density increasing distally. **Leaves** oppositely decussate, spreading, proximal most leaves simple and entire or deeply lobed, becoming imparipinnately compound, longest at mid-stem, longer than wide; petioles (2.4) 4.3–5.0 (7.5) cm, increasingly shorter from proximal to

distal leaves, sparsely to moderately pilose, opposing petioles conjoined at node, distal-most leaflet modified into tendril-like structure or greatly reduced leaflet; leaflets membranaceous to subcoriaceous, (4.2) 5.5–7.8 (11.3) cm long, (2.3) 3.1–4.5 (7.2) cm wide at widest point, symmetrical or asymmetrical, ovate or ovate-lanceolate, acute to acuminate apices, leaflets of mid-stem leaves usually simple, rarely 2 or 3 lobed, inconspicuously raised-reticulate on adaxial and abaxial surface, most noticeable in dried material, primary veins (0.03) 0.06–0.08 (0.12) mm wide, lowest order of closed areoles (0.59) 0.96–1.27 (1.92) mm<sup>2</sup>, adaxial and abaxial surfaces glabrate to sparsely puberulent, with longest trichomes (0.30) 0.40–0.49 (0.73) mm long, pubescence confined to mid-veins or both mid-veins and lower order veins; petiolules (7.2) 16.0–22.0 (50.0) mm long, margins ciliate, entire. **Inflorescences** most often axillary cymes or solitary, rarely producing terminal flowers, nodding on decidedly erect pedicels, with flowers borne above leaflets of corresponding node, ovoid in shape; when axillary, peduncles (1.5) 3.5–10.4 (36.0) mm long, primary pedicels (38.0) 63.1–104.8 (180.3) mm long, ratio of peduncle to combined peduncle and pedicel length (0.02) 0.06–0.11 (0.20) with foliose bracts appearing basal or near-basal on combined peduncle and pedicel; foliose bracts (6.2) 17.2–28.5 (42.9) mm long. **Sepals** erect, connivent, oblong-ovate to ovate, reflexed and spreading at apex, (11.4) 14.9–22.1 (25.6) mm long, (4.4) 6.6–9.7 (11.2) mm wide at widest point, coriaceous, abaxially faded pink to vibrant purple, becoming white or cream distally, adaxially cream, rarely purple; margins narrowly crispate, white-tomentulose, abaxial surface glabrate to sparsely puberulent, with longest trichomes (0.25) 0.29–0.42 (0.47) mm long. **Stamens** linear, (9.8) 13.4–15.9 (19.9) mm long, filaments flattened, spreading-pilose from middle to apex, connective extended (0.57) 0.79–0.97 (1.30) mm beyond anthers. **Fruit** tightly clustered in spherical heads, light brown, body rhomboidal-ovate to rotund, (4.5) 5.1–7.5 (7.7) mm long, 4.0–5.2 mm wide, acuminate or

rounded on proximal end and acuminate on distal end, marginally thickened, sericeous; thickened achene rims (0.46) 0.53–0.72 (0.76) mm wide at mid-point; style curvate, (3.9) 4.0–5.7 cm long, with a yellowish-brown to coppery brown tail hairs, hairs spreading to ascending, 2.6–4.1(4.4) mm long at mid-point, becoming shorter proximally and distally. Chromosome number unknown.

***Distribution and Habitat***— *Clematis cumberlandensis* is currently known only from Tennessee where it is restricted to the Cumberland Plateau and Eastern Highland Rim ecoregions with a few populations extending into the neighboring Ridge and Valley and eastern Outer Nashville Basin (Fig. 9). A single, likely aberrant, specimen was collected from the Southeastern Plains and Hills Ecoregion of Tennessee in Carroll County, Tennessee (*Anonymous s.n.*, HTTU). In the Cumberland Plateau of Tennessee, where *C. cumberlandensis* is most prevalent, populations are found in riparian riverscours grasslands, shrublands, and woodlands over sandstone. It should, however, be noted that *C. cumberlandensis* exhibits a high degree of ecological amplitude in the other ecoregions listed; populations persist on limestone bluffs, in acidic wetlands, and in calcareous mesic coves. Because many populations in riparian riverscours communities are located in remote areas, more populations of *C. cumberlandensis* may be discovered by exploring undocumented portions of this habitat on the Cumberland Plateau. Given that the Cumberland Plateau, Eastern Highland, and Ridge and Valley Rim extend into Kentucky and Alabama, it is possible that *C. cumberlandensis* could be found in these states where it is currently not known, although many attempts have been made to search suitable habitats in these states with no success.



**Figure 9.** Generalized range map of *Clematis cumberlandensis*. Orange point represents type locality. Scale bar indicates 500 km.

**Phenology**— Flowering specimens of *C. cumberlandensis* have been noted to flower from the last week of April to mid-August, with plants fruiting into late November.

**Etymology**— The epithet “cumberlandensis” is a reference to the Cumberland Plateau, from which a majority of the known populations of *C. cumberlandensis* are known.

**Conservation**— *Clematis cumberlandensis* should be afforded protection at the state level in Tennessee due to its restricted range and tendency to occupy conservative habitat. Alteration in hydrology through damming and subsequent inundation has likely led to the extirpation of undocumented populations along the Caney Fork River and Tennessee River (in the Tennessee River Gorge). The location of a small population on the banks of the Tennessee River, that was revisited based on a previous collection, (*Roger McCoy s.n.*, TENN) could

suggest a relictual presence when flood-maintained riparian grasslands and shrublands were more extensive.

*Specimens examined (paratypes)*—USA—TENNESSEE: Coffee Co., 7.22 km north on Hwy 53/ Woodbury Hwy from intersection with Hwy 41, just south of intersection with Park Creek Rd., 24 June 2019, *Thomas H. Murphy 337 with Kate Love* (APSC<sup>M</sup>, TBD<sup>M</sup>); [same locality as last], 6 September 2019, *Thomas H. Murphy 520 with Annie Lindsey and Claire Ciafre* (APSC<sup>M</sup>, TBD<sup>M</sup>); Cumberland Co., rocky islands in Daddy's Creek above Peavine Road, north of Fairfield Glade, 20 June 1977, *R. Kral 60485* (TENN, VDB<sup>M</sup>); west bank of major bend in Daddy's Creek, ca. 0.25 miles downstream from Antioch Bridge, Ozone Quad., 35° 59' 57" N, 84° 49' 10" W, 12 July 1980, *Thomas S. Patrick 1291 with Bretta E. Perkins* (TENN<sup>M</sup>); Daddy's Creek, 22 kilometers east of Crossville, 900 meters downstream of Yellow Creek's confluence with Daddy's Creek, 36.03736, -84.81232, 16 August 2014, *Devin Rodgers 424 with Chris Mausert-Mooney & Taylor Hay* (APSC<sup>M</sup>, TBD); Daddy's Creek, 22 kilometers northeast of Crossville, off Peavine Road's (Rd. 101) crossing of Daddy's Creek at Antioch Bridge, 600 meters upstream of bridge, 35.997450, -84.831100, 15 August 2014, *Devin Rodgers 385 with Chris Mausert-Mooney & Taylor Hay* (APSC<sup>M</sup>, TBD); Daddy's Creek, 22 kilometers northeast of Crossville off Peavine Road's (Rd. 101) crossing of Daddy's Creek at Antioch Bridge, 600 meters upstream of bridge, 35.997554, -84.831434, 15 September 2013, *Devin Rodgers 84 with Mason Brock* (APSC<sup>M</sup>, TBD); DeKalb Co., Tech Aqua, 25 June 1976, *Kathman s.n. with Burgess, Lane, & McDougal* (HTTU<sup>U</sup>); Jackson Co., stream bank, 25 June 1965, *Michele Stern s.n.* (HTTU); Hilham, 3871 Roaring River Road, Roaring River Watershed, 36.3461690 N, 85.5386660 W, 17 June 1999, *Meredith Moore MM-333, 334, 335*, (HTTU<sup>M</sup>); [same locality as last], 28 June 1999, *Meredith Moore MM-374* (HTTU); [same locality as last], 7 July 1999,

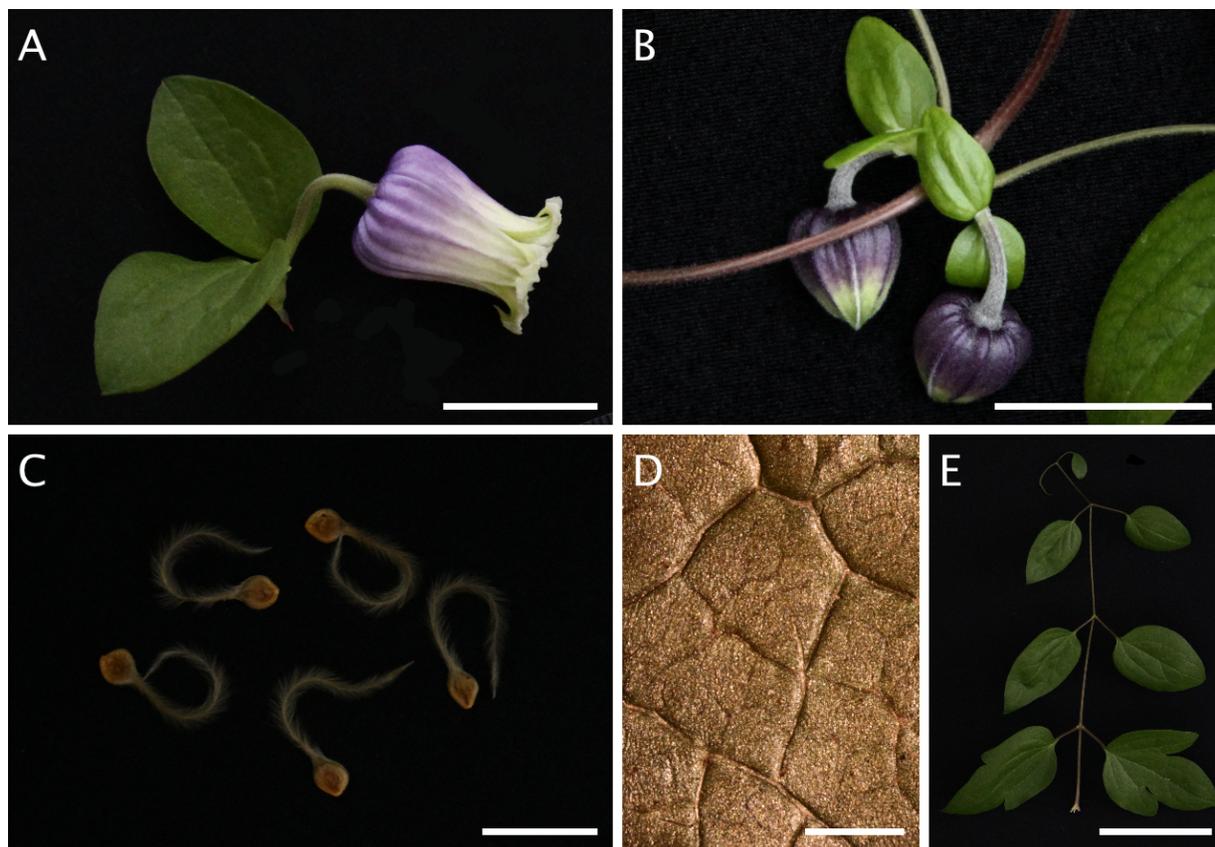
*Meredith Moore MM-421* (HTTU<sup>M</sup>); Gainesboro, Roaring River Road, Dead Dog Cove, 4 July 1999, *Felix Coe 12353<sup>U</sup>, 12354<sup>M</sup>, 12355* (HTTU); [same locality as last], 7 July 1999, *Felix Coe 12506* (HTTU); Dead Dog Cove, 17 May 2000, *Felix Coe 13959* (HTTU<sup>M</sup>); roadside along Roaring River, 500 meters west of Dead Dog Cove, 7 June 2000, *Felix Coe 14183, 14184, 14185* (HTTU<sup>U</sup>); Morgan Co., Obed Wild and Scenic River, north side of Obed River, downstream from Ramsey Creek, near Obed Junction, Hebbertsburg Quad., 1 July 1981, *Paul A. Schmalzer 1108* (TENN<sup>M</sup>); north side of Obed River ca. 0.2 mile upstream from Obed-Clear Creek junction, Lancing Quad, *Paul A. Schmalzer 674 with Thomas S. Patrick* (TENN<sup>M</sup>); Lancing Quadrangle, near Morgan Co. Road 158 at Lily Bridge, 3.5 miles west-southwest of Lancing, 19 June 1990, *Dan Dyrick 356 with Vern McNeilus & Jenny Small* (TENN<sup>U</sup>); Obed [National] Wild and Scenic River, northwest side of Lily Bridge, 15 July 2003, UTM East 705481, UTM North 3997545, *C. Bailey s.n. & R. McCoy* (NCU); Obed National Wild and Scenic River, upstream of Lily Bridge, northeast bank, Lat. 360613, Long. 844306, 15 July 2003, *Claude Bailey s.n. & Roger McCoy* (APSC<sup>M</sup>, TENN<sup>M</sup>); Overton Co., Waterloo, 29 June 1965, *V. K. Jones s.n.* (HTTU<sup>U</sup>); Putnam Co., Cookeville, 19 May 1965, *P. Weaver s.n.* (HTTU<sup>U</sup>); I-40 E Burgess Falls Road Exit to Burgess Falls, 25 June 1979, *Annell S. Shaffer 122* (HTTU<sup>M</sup>); Window Cliffs, 27 June 1985, *Richard Clements 4416 with H. R. DeSelm* (APSC<sup>M</sup>); Approximately 50 meters west of intersection of Poplar Grove Road and Isaacs Pass, 8 June 2019, *Thomas H. Murphy 278* (APSC<sup>M</sup>, TBD); Rhea Co., 22.9 km SE of Dogwood and 4 km W of Glen Alice, 7 June 2019, *Thomas H. Murphy 371 with Kate Love and Steve Scarborough* (APSC<sup>M</sup>, TBD<sup>M</sup>); Roane Co., 3 June 1981, *Thomas S. Patrick 3469* (BRIT<sup>M</sup>); Smith Co., above Caney Fork River, 8.1 miles west of Smithville exit off Interstate 40, 8 July 1972, *R. Kral 47445* (VDB); Van Buren Co., banks of Cane Creek by county road, ca. 4.3 miles east of Cummingsville, 9 July 1972, *R. Kral*

47502 (MO, VDB<sup>M</sup>); Fall Creek Falls State Park, ca. 3 kilometers north of junction of Hwy 285 and 30, ca. 1 kilometer east of old Cane Creek Church, Bald Knob Quad., 23 May 2002, *Chris A. Fleming FCF-2079 with D. K. Smith & Keith Bowman* (VDB<sup>M</sup>); Warren Co., Rock Island, near power house, 7 June 1968, *Joe Wooden 112* (HTTU); White Co., Carr Farm, 25 June 1965, *Mary Jane Cassetty s.n.* (HTTU<sup>M</sup>); County not determined, Roaring River, 25 June 1961, *Bowling 43* (HTTU); between Sparta and Cookeville, 1 July 1961, *Anonymous s.n.* (HTTU<sup>M</sup>).

**3. CLEMATIS OUACHITENSIS** T.Murphy & D.Estes, sp. nov. TYPE: USA. Arkansas: Howard Co., Hwy 278 bridge crossing over Baker Creek, south of creek, southeast of bridge, 34.297117, -94.1602414, 20 May 2019. *Thomas H. Murphy 519 with Mason Brock* (Holotype: APSC<sup>M</sup>; Isotype: ANHS<sup>M</sup>)

**Diagnosis**— *Clematis ouachitensis* differs from *C. cumberlandensis* sp. nov. with its pendulous (vs. erect) and relatively shorter pedicels, longer trichomes on sepal and leaflet abaxial surfaces, and shorter achene tails; from *C. arenicola* sp. nov. with its pendulous (vs. erect) and relatively shorter pedicels, shorter extensions of anther connectives, thinner leaflets, narrower leaflet primary veins, smaller closed leaflet areole area, and narrower leaflet apices; from *C. terminalis* sp. nov. with vining (vs. erect) habit when in flower, axillary (vs. terminally) borne inflorescences, and longer petiolules; from *C. reticulata* s.s. in its basal (vs. elevated) bract placement (lesser peduncle to combined peduncle and pedicel ratio), greater achene length to width ratio, shorter achene tails, smaller closed leaflet areoles, thinner leaflets, relatively shorter (vs. erect) and pendulous pedicels, longer trichomes on leaflet and sepal abaxial surfaces, narrower adaxial leaflet veins, and narrower leaflet apices; from *C. subreticulata* in its basal (vs.

elevated) bract placement (lesser peduncle to combined peduncle and pedicel ratio), relatively shorter and pendulous (vs. erect) pedicels, and lesser achene length to width ratio

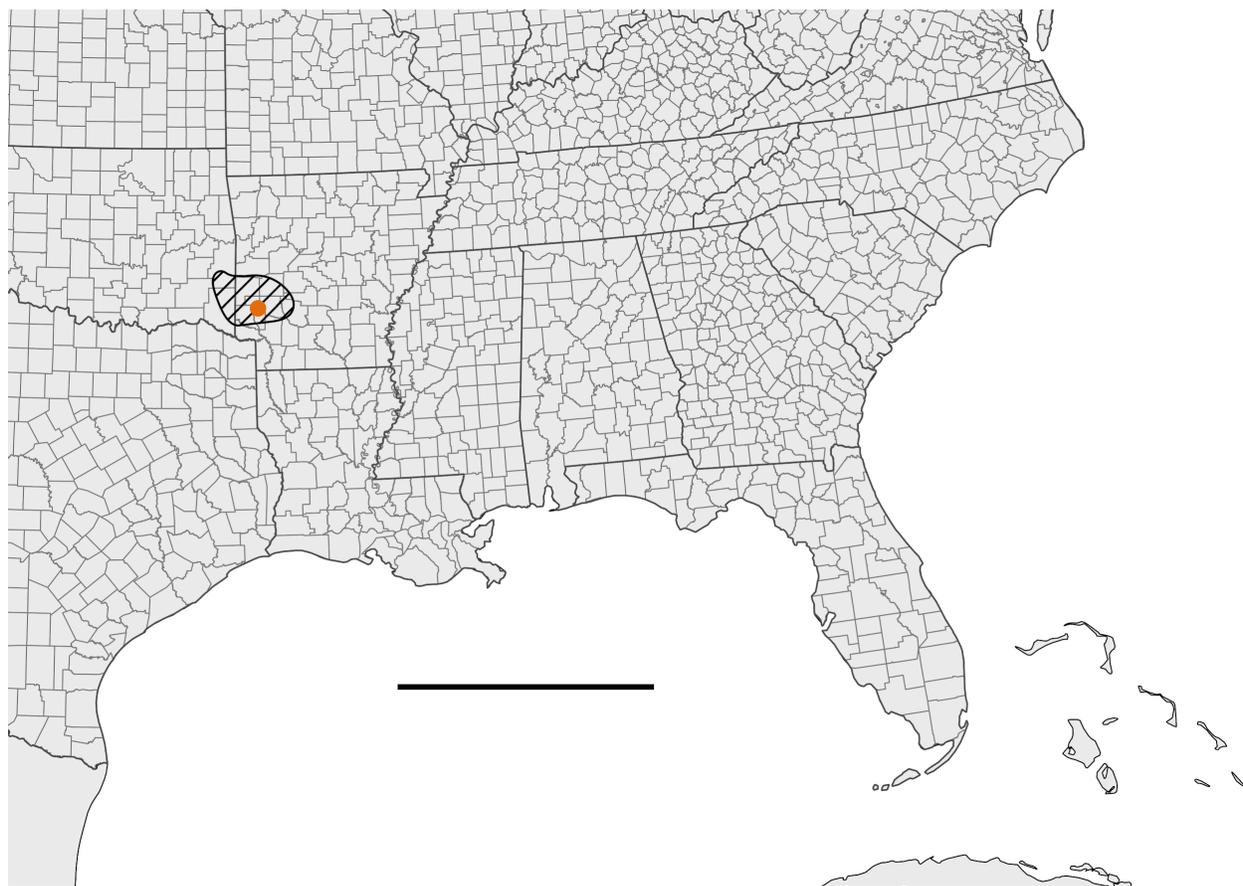


**Figure 10.** Diagnostic characters of *Clematis ouachitensis*. A) Inflorescence with basal bract placement and relatively short pedicels (scale bar= 20 mm), B) pendulous habit of pedicels, C) achenes with relatively short tails (scale bar= 20 mm), D) leaflet adaxial with larger closed areoles and narrower veins (scale bar= 1 mm), and E) leaf with acute leaflet apices (scale bar= 50 mm).

**Description**— Perennial climbing or scandent **vine** to ca. 3 m tall, one to multiple stems from a woody caudex bearing smooth coarse, fleshy roots. **Stems** six angled, six ribbed, reddish-brown, usually densely covered in pilose to appressed trichomes, trichome density increasing distally. **Leaves** oppositely decussate, spreading, proximal most leaves simple and entire or deeply lobed, becoming imparipinnately compound, longest at mid-stem, longer than wide; petioles (3.1) 3.9–4.7 (5.2) cm, increasingly shorter from proximal to distal leaves, sparsely to moderately pilose, opposing petioles conjoined at node, distal-most leaflet modified into tendril-like structure or greatly reduced leaflet; leaflets membranaceous to subcoriaceous, (3.5) 4.4–7.0

(9.1) cm long, (2.1) 2.7–4.6 (6.9) cm wide, ovate, apices acute to acuminate, leaflets of mid-stem entire or 2-3 lobed, inconspicuously raised-reticulate on adaxial and abaxial surface, most noticeable in dried material, primary veins (0.04) 0.06–0.09 (0.10) mm wide, lowest order of closed areoles (0.62) 0.75–1.21(2.39) mm<sup>2</sup>, adaxial and abaxial surfaces glabrate to sparsely puberulent, with longest trichomes (0.51) 0.55–0.68 (0.90) mm long, pubescence confined to mid-veins or both mid-veins and lower order veins; petiolules (10.7) 15.7–29.5 (31.7) mm long, margins ciliate, entire. **Inflorescences** most often axillary cymes or solitary, rarely producing terminal flowers, nodding on decidedly pendulous pedicels in flower, erect in fruit, with flowers borne below leaflets of corresponding node, ovoid in shape; when axillary, peduncles (1.3) 2.5–5.3 (11.1) mm long, primary pedicels (16.2) 23.1–38.9 (69.2) cm long, ratio of peduncle to combined peduncle and pedicel length (0.03) 0.08–0.14 (0.19) with foliose bracts appearing basal or near-basal on combined peduncle and pedicel; foliose bracts (8.5) 9.2–30.7 (32.8) mm long. **Sepals** erect, connivent, oblong-ovate to oblong-lanceolate, reflexed and spreading at apex, 12.1–26.2 mm long, 4.9–9.6 mm wide at widest point, coriaceous, abaxially lilac to dark violet, becoming white or cream distally, adaxially cream; margins narrowly crispate, white-tomentulose, abaxial surface glabrate to sparsely puberulent, with longest trichomes (0.52) 0.51–0.66 (0.69) mm long. **Stamens** linear, 11.6–17.8 mm long, filaments flattened, spreading-pilose from middle to apex, connective extended 0.61–0.85 mm beyond anthers. **Fruit** tightly clustered in spherical heads, light brown, body rhomboidal-ovate to rotund, (5.0) 5.5–6.5 (6.6) mm long, (4.6) 4.9–5.6 (5.9) mm wide, acuminate or rounded on proximal end and acuminate on distal end, marginally thickened, sericeous; thickened achene rims (0.72) 0.73–0.89 (0.95) mm wide at mid-point; style curvate, (2.7) 3.3–4.2 (5.1) cm long, with a light yellowish plumose tail hairs, spreading to ascending, (3.4) 3.7–4.4 (5.1) mm long at mid-point, becoming shorter proximally

and distally. Chromosome number unknown.



**Figure 11.** Generalized range map of *Clematis ouachitensis*. Orange point represents type locality. Scale bar indicates 500 km.

***Distribution and Habitat***— The distribution of *C. ouachitensis* is confined to the southern portion of the Ouachita Mountains of Arkansas and Oklahoma (Fig. 11). The habitat would broadly be described under the Ozark-Ouachita Riparian ecological system as described by NatureServe (2020). More specifically, *C. ouachitensis* grows in zones of riverscours habitat, often near the upper limit of the flood zone where it climbs and scrambles in infrequently inundated, shrublands or woodlands over sandstone or shale bedrock. Associated species include *Acer floridanum* (Chapm.) Pax, *Amorpha fruticosa* L. s.l, *A. ouachitensis* Wilbur, *Asplenium platyneuron* (L.) Britton, Sterns & Poggenb., *Chasmanthium latifolium* (Michx.) H.O.Yates, *Chionanthus virginicus* L., *Dichantheium lanuginosum* (Elliott) Gould, *Elymus villosus* Muhl.

ex Willd., *Galactia regularis* (L.) Britton, Sterns & Poggenb., *Helianthus hirsutus* Raf., *Hypericum prolificum* L., *Ilex longipes* Chapm. ex Trel., *Liatris hirsuta* Rydb., *Myriopteris tomentosa* Fée, *Parthenium integrifolium* L., *Quercus margerettae* (Ashe) Small, *Q. stellata* Wangenh., *Solidago arguta* Aiton, *Spigelia marilandica* (L.) L., and *Vaccinium arboreum* Marshall.

**Phenology**— *Clematis ouachitensis* flower from the last week of April to the last week of June, with plants fruiting into late November.

**Etymology**— The epithet refers to the Ouachita Mountains, the region to which *C. ouachitensis* is apparently endemic.

**Conservation**— Because *C. ouachitensis* seems to be confined to riparian riverscours and woodland habitat, conservation efforts should focus on protective measures for this ecosystem. The authors have only seen a total of four extant populations of *C. ouachitensis*, so state protection in Arkansas and Oklahoma should be afforded for this endemic and presumably rare species. Due to the remoteness of and danger in accessing suitable habitat (due to fast-moving currents, rocky channels, and rapids), there are likely more populations that are currently unknown. Further field surveys and research is needed to determine whether *C. ouachitensis* should be afforded federal protection.

**Specimens examined (paratypes)**—USA—ARKANSAS: Clark Co., near Lat. 34-04-55.87, Long. 93-09-40.34, 23 June 2008, *Roy Bledsoe RF-08-47* (ANHC<sup>M</sup>); Howard Co., Hwy 278 bridge crossing over Baker Creek, 5 October 2019, *D. Estes s.n.* (APSC<sup>U</sup>, TBD); Cossatot River at Hwy 4, 23 April 1988, *Sundell 8140 with McDougald* (VDB<sup>M</sup>); Montgomery Co., NW of Mt. Ida at crossing of Ouachita River, 27 June 2013, *D. Estes 12833* (APSC<sup>M</sup>, TBD); Sevier Co., 24 July 1974, *Clye Brimbley 268* (TEX<sup>M</sup>); along Rolling Fork Creek, UTM 15S/ 370376/

3782753, T7S R32W S9 NE1/4, 27 May 2004, *Matt Nutt 862 with Robert McElderry* (UARK<sup>M</sup>); north of Cedar Bluff Road and south of Rolling Fork, 34.182535, -94.402268, 18 July 2018, *Thomas H. Murphy 132 with Mason Brock* (APSC<sup>M</sup>, TBD<sup>M</sup>); **OKLAHOMA:** Le Flore Co., Ca. 9 miles due east and 1 mile south of Talihina, T3N, R23E, Sec. 16., 6 June 2006, *Bruce Hoagland CTH-023* (OKL<sup>M</sup>); northeast of Octavia at the Nature Conservancy's Cucumber Creek Preserve, 9 August 2005, *Bruce Hoagland CC332 with Amy Buthod* (BRIT<sup>M</sup>); northeast of Octavia at the Nature Conservancy's Cucumber Creek Preserve, T1N, R25E, Sec. 12, 15S 349309, 3825649, 14 June 2005, *Bruce Hoagland CC214 with Amy Buthod* (OKL<sup>U</sup>); McCurtain Co., north of Wey Co. 28000 and east of Mountain Fork, 34.399141, -94.685039, 17 July 2018, *Thomas H. Murphy 124 with Mason Brock* (APSC<sup>M</sup>, TBD); along Beech Creek ca. 7 miles northeast of Smithville, 21 October 1976, *John Taylor 23930* (BRIT<sup>M</sup>); 9 kilometers south-southwest of Smithville off US-259 S, 200 meters upstream of Wey Co. 28000 on east bank of Mountain Fork of Little River, n.d., *Devin Rodgers 203.5 with Dwayne Estes, Mason Brock, Kelly Anderson, and Chris Mausert-Mooney* (APSC<sup>U</sup>); along east side of Forked Lake about 7 miles southeast of Eagletown, 5 June 1976, *John & Connie Taylor 21642* (VDB<sup>M</sup>).

**4. CLEMATIS RETICULATA** Walter, Fl. Carol., 156. 1788.—*Viorna reticulata* (Walter) Small, Man. S.E. Fl., 527. 1933.—*Clematis viorna* subsp. *reticulata* (Walter) Kuntze, Verh. Bot. Vereins Prov. Brandenburg 26: 133. 1885.—*Coriflora reticulata* (Walter) W.A.Weber, Phytologic 79: 67. 1996. NEOTYPE: USA, South Carolina, Lexington Co., from 4 mi. S of Brookland, 7 July 1936, *Wherry s.n.* (GH!<sup>M</sup>)

**Diagnosis**— *Clematis reticulata* s.s. differs from *C. subreticulata* comb. nov. in its relatively thinner achene rims, smaller closed leaflet areole area, shorter trichomes on leaflet and

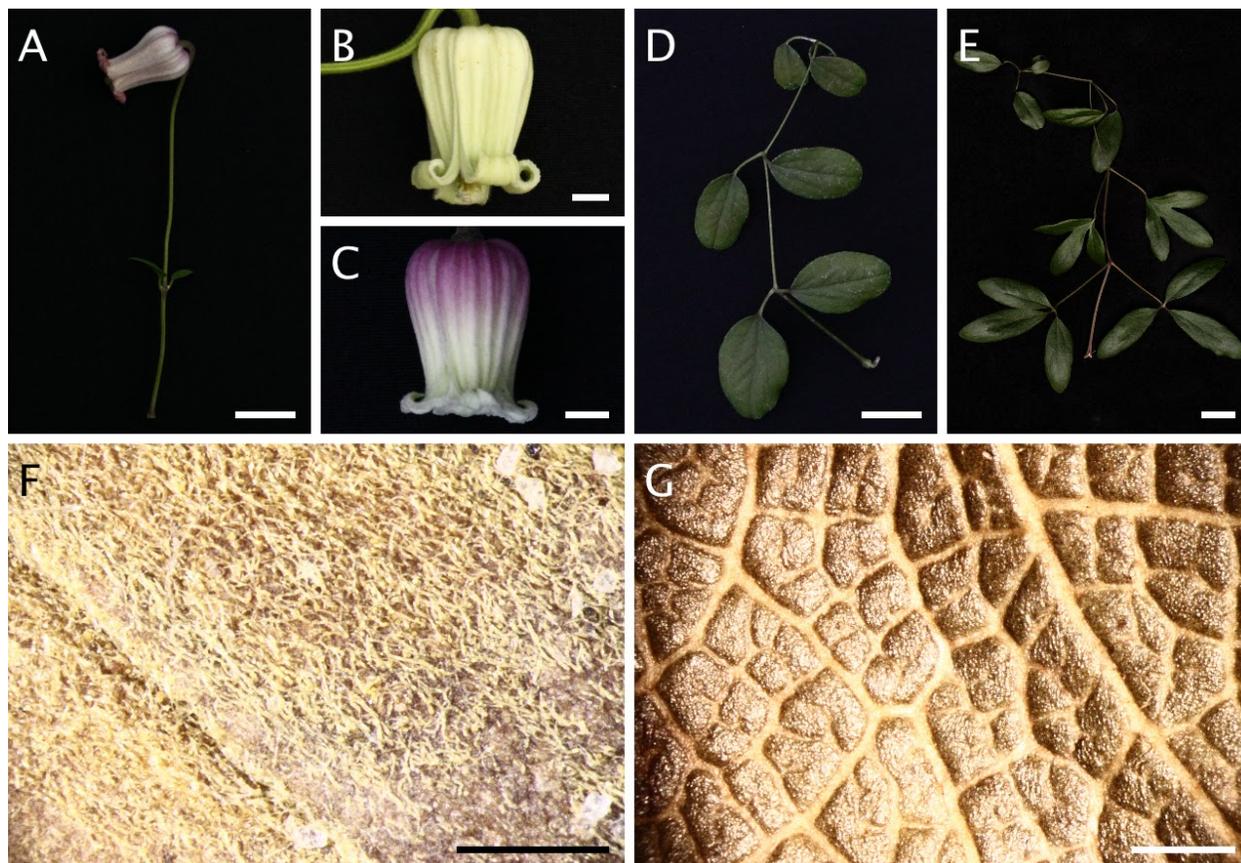
sepal abaxial surfaces, thicker leaflets, wider leaflet primary veins, and typically broader leaflet apices; from *C. terminalis* sp. nov. in its vining (vs. erect-herbaceous) habit when in flower, axillary (vs. terminal) inflorescences, smaller closed leaflet areole area, longer petiolules, shorter trichomes on leaflet and sepal abaxial surfaces, and narrower leaflet primary veins; from *C. arenicola* sp. nov. in its elevated (vs. basal) bract placement (greater peduncle to combined peduncle and pedicel ratio), shorter extensions of anther connective, shorter trichomes on leaflet abaxial and sepal abaxial surfaces, and wider leaflet veins; from *C. cumberlandensis* sp. nov. in its elevated (vs. basal) bract placement (greater peduncle to combined peduncle and pedicel ratio), smaller closed leaflet areole area, greater sepal length to width ratio, wider leaflet primary veins, thicker leaflets, and broader leaflet apices; from *C. ouachitensis* sp. nov. in its elevated (vs. basal) bract placement (greater peduncle to combined peduncle and pedicel ratio), greater achene length to width ratio, longer achene tails, smaller closed leaflet areole area, thicker leaflets, erect (vs. pendulous) and relatively longer pedicels, shorter trichomes on leaflet and sepal abaxial surfaces, wider leaflet primary veins, and broader leaflet apices.

**Description**— Perennial climbing or scandent **vine** to ca. 3 m tall, one to multiple stems from a woody caudex bearing smooth coarse, fleshy roots. Stems six angled, six ribbed, reddish-brown, usually sparsely to densely covered in pilose to appressed trichomes, trichome density increasing distally. **Leaves** oppositely decussate, spreading, proximal most leaves simple and entire or deeply lobed, becoming imparipinnately compound, longest at mid-stem or node directly below inflorescence, longer than wide; petioles (2.5) 3.8–4.7 (8.8) cm, increasingly shorter from proximal to distal leaves, sparsely to moderately pilose, opposing petioles conjoined at node, distal-most leaflet modified into tendril-like structure or greatly reduced leaflet; leaflets subcoriaceous to coriaceous, (2.5) 4.1–5.0 (7.2) cm long, (1.3) 2.2–2.8 (5.2) cm wide, oblong,

rotund, or ovate-elliptic, rounded to broadly acute apices with mucro, leaflets of mid-stem leaves simple, 2 or 3 lobed, or ternate, conspicuously raised-reticulate on adaxial and abaxial surface, most noticeable in dried material, primary veins (0.09) 0.13–0.15 (0.28) mm wide, lowest order of closed areoles (0.19) 0.38–0.45 (0.84) mm<sup>2</sup>, adaxial surface typically sparsely, abaxial surface glabrate to sparsely pilose, with longest trichomes (0.23) 0.37–0.42 (0.85) mm long, pubescence confined to mid-veins or both mid-veins and lower order veins; petiolules (8.0) 15.3–22.7 (40.6) mm long, margins ciliate, entire or sometimes appearing irregularly and broadly undulate.

**Inflorescences** prevailing axillary cymes or solitary, rarely producing terminal solitary flowers, nodding on decidedly erect pedicels, with flowers borne above leaflets of corresponding node, ovoid in shape; peduncles, when axillary, (13.2) 33.4–54.2 (161.8) mm long, primary pedicels (26.5) 72.1–85.4 (151.7) mm long, ratio of peduncle to combined peduncle and pedicel length (0.20) 0.33–0.39 (0.63) with foliose bracts appearing elevated on combined peduncle and pedicel; foliose bracts (4.2) 24.7–32.8 (47.6) mm long. **Sepals** erect, connivent, oblong-ovate to ovate, reflexed and spreading at apex, 19.8–22.1 mm long, (4.6) 6.7–7.6 (9.2) mm wide at widest point, coriaceous, abaxially variable in color, faded to vibrant pink, purple, or reddish-purple, sometimes becoming white or cream distally, adaxially cream or similar to abaxial color; margins narrowly crispate, white-tomentulose, abaxial surface usually white-canescens to short yellow-pubescent, occasionally glabrate, with longest trichomes (0.27) 0.32–0.40 (0.47) mm long. **Stamens** linear, (14.2) 15.5–17.1 (21.5) mm long, filaments flattened, spreading-pilose from middle to apex, connective extended (0.43) 0.67–0.90 (1.54) mm beyond anthers. Fruit tightly clustered in spherical heads, light brown, body rhomboidal-ovate to rotund, (4.1) 5.0–6.0 (7.9) mm long, (3.3) 3.6–4.5 (5.5) mm wide, acuminate or rounded on proximal end and acuminate on distal end, marginally thickened, sericeous; thickened achene rims (0.41) 0.55–

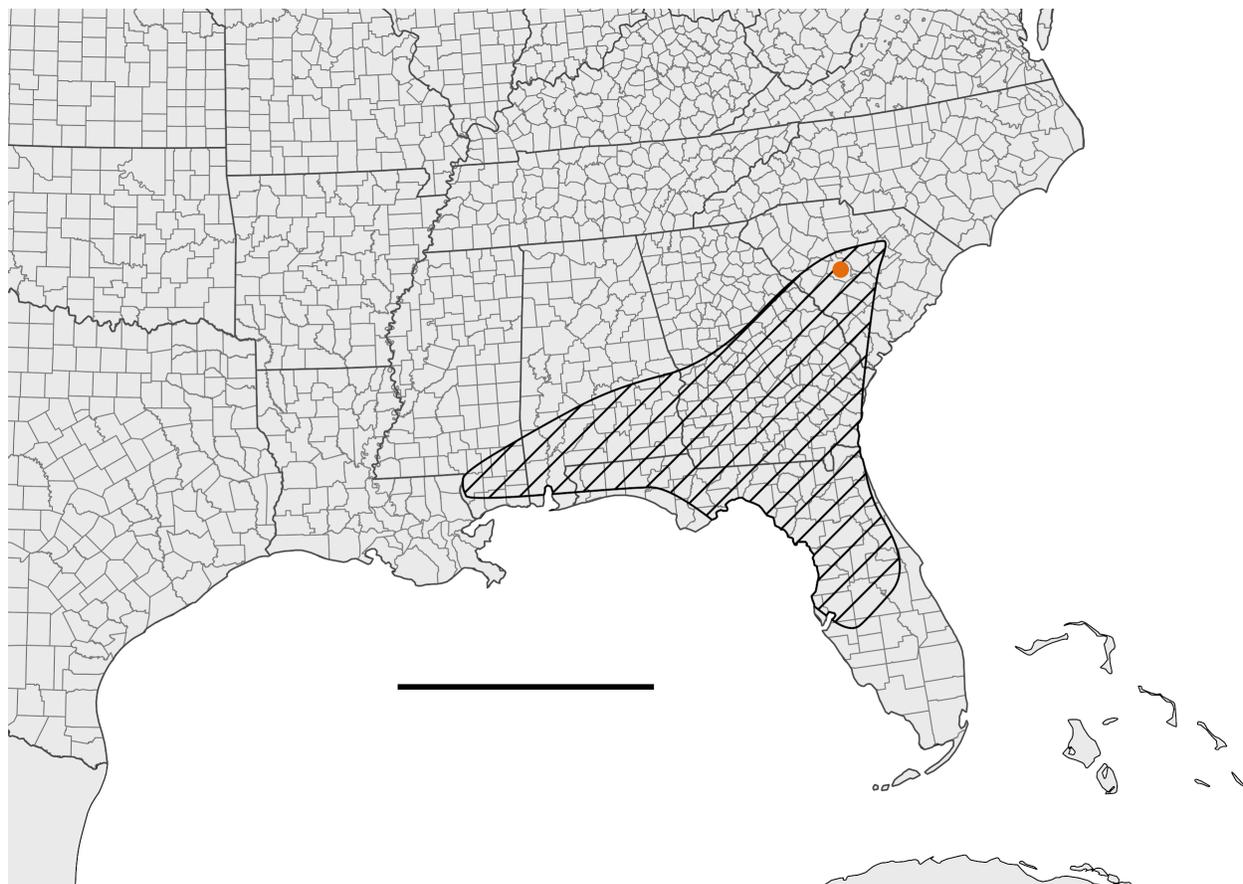
0.64 (0.88) mm wide at mid-point; style curvate, (3.2) 4.5–5.5 (8.0) cm long, with a light yellowish plumose tail hairs, spreading to ascending, (1.5) 2.1–4.6 (5.3) mm long at mid-point, becoming shorter proximally and distally. Chromosome number unknown.



**Figure 12.** Diagnostic characters of *Clematis reticulata* s.s. A) Typical inflorescence with elevated bract placement (scale bar= 20 mm), B) and C) variation in flower color (scale bar= 5 mm), D) and E) variation in leaflet shape with rounded apices (scale bar= 20 mm), F) sepal abaxial surface with relatively short trichomes (scale bar= 1 mm), and G) leaflet adaxial venation with small closed areoles and relatively thick veins (scale bar= 1 mm).

**Distribution and Habitat**— *Clematis reticulata* s.s. is widespread throughout the lower Atlantic and East Gulf Coastal Plains in the southern half of Alabama and Georgia, extreme southern Mississippi, and the Sandhill region of South Carolina, south to central Peninsular Florida (Fig. 13). Habitats where *C. reticulata* s.s. can be found include sandy soils of longleaf pine savannas and woodlands and shrubby thickets and sandhill scrub. Several populations visited had evidently been burned recently with plants thriving, indicating *C. reticulata* s.s. is tolerant, and perhaps benefits, from fire. Multiple populations, seen by the first author, persisted

in heavily disturbed thickets and forest margins, oftentimes found on roadsides. These roadside habitats may be mimicking open woodlands and savannas, serving as a refuge for *C. reticulata* s.s.



**Figure 13.** Generalized range map of *Clematis reticulata* s.s. Orange point represents type locality. Scale bar indicates 500 km.

**Phenology**— *Clematis reticulata* s.s. flowers from the last week of April to mid-July with few plants flowering in August and September. Plants fruit into October and November.

**Conservation**— *Clematis reticulata* s.s. appears to be quite common throughout its range, which is evident from the frequency and number of collections in herbaria. In Mississippi, it is known from few populations and should be afforded state protection.

**Notes**— A neotype designation for *C. reticulata* (*Harry E. Ahles* 25350, GA) was made by Dennis (1976) but was not effectively published per Article 30.9 of Turland et al. (2018) and

therefore does not hold priority per Article 7.10. Ward (2007) validly published and designated the neotype (*Wherry s.n.*, GH), therefore holding priority type designation.

***Specimens examined (paratypes)***—USA—ALABAMA: Barbour Co., ca. 8 miles south of Eufala, roadside of county Hwy. 57 at ¼ mile east of junction with Hwy. 431, 10 May 1997, *John R. MacDonald 10442* (MO); near N31.78348 W85.63888, south side of County Road 9, 31 May 2017, *T. Wayne Barger SP#3127* (ALNHS); Bullock Co., near N32.16832 W85.60177, south side of County Road 40, 1 June 2017, *T. Wayne Barger SP#3202* (ALNHS); Clarke Co., Suggsville, 1852, *Dr. Denny s.n.* (UNA); Coffee Co., on margin of oxbow lake on Pea River, 2.6 mi ENE of Kinston, 31.234562, -86.133439, 4 July 1967, *Ross C. Clark 15609* (NCU); Conecuh Co., Evergreen, 2 June 1897, *F. S. Earle s.n.* (MO, UNAM); Covington Co., above Lightwood Knot Creek, north of Opp on US 331, 11 June 1971, *R. Kral 43236* (MO); sandy Conecuh River bottoms 4.5 mi. W of Andalusia, 29 June 1989, *R. Kral 76733* (APSC); Crenshaw Co., North of Petrey and South of Lapine, growing along Lapine Hwy (Hwy 59) at bridge over Dry Creek, 31.889883, -86.22615, 14 June 2019, *Thomas H. Murphy 304 with Zach Irick* (APSC, TBD); Dale Co., along Pea River, 14 May 1925, *E. J. Palmer 27234* (MO); along Bear Creek, Dillard community, 27 July 1966, *Ross C. Clark 6023* (NCU); Elmore Co., roadside, Union Springs, 15 May 1964, *Gene A. Bozarth s.n.* (JSU); Geneva Co., north side of the Geneva State Forest Lake, 31°08'45"N, 86°10'57"W, 20 May 2007, *A. R. Diamond 17621 with R. Kral* (UNAM); S shores of Geneva State Forest Lake, 8 May 2000, *R. Kral 89598* (CLEMSM); banks of Pea River ca. 4 miles west of Samson by Ala. 52, 4 June 1972, *R. Kral 47174* (MO); by Ala. 52, just w. of Samson, 25 June 1974, *R. Kral 53477* (JSU); along Pea River near Beck's Mill, 16 May 1925, *John K. Small 12593 with Edgar T. Wherry* (NCU); Henry Co., 2.3 miles south Abbeville by US 431, 12 August 1973, *R. Kral 51196* (MO); Houston Co., Dothan Trail Park Forever Wild Tract,

N31.21549 W85.45831, south of Beaver Creek, 20 May 2016, *T. Wayne Barger DTP-253* (ALNHS); Marengo Co., North of Putnam and South of Nanafalia on west side of US Hwy 69. ca. 175 m South of Sweetwater Creek, 32.09108, -88.00277, 13 June 2019, *Thomas H. Murphy 301 with Zach Irick, Brian Keener, Kaleigh Young, and Joan Rundles* (APSC, TBD); Montgomery Co., on Catoma Creek, 19 August 1884, *John Donnell Smith s.n.* (GH<sup>U</sup>); Monroe Co., near N31.77039 W87.35787, 3 May 2012, *T. Wayne Barger SP#459 with Brian D. Holt* (ALNHS); Pike Co., Big Pocosin, ca. 5 miles east of Troy, 11 May 1977, *R. Kral 59996* (JSU<sup>M</sup>, MO); Big Pocosin, ca. 5 miles southeast of Troy, 12 August 1973, *R. Kral 51214* (MO); by US 281, 21 miles northwest of Ozark, just south of Brundidge, 23 June 1974, *R. Kral 53322* (MO); 4.5 mi. e. Brundidge on Ala 10, 20 May 1968, *R. Kral 30839 with Delzie Demaree* (NCU<sup>U</sup>);

**FLORIDA:** Alachua Co., just NW of jct. of NW 71st St. and FL232, NW of Gainesville, S16, T9S, R19E, July 1979, *Troy Auffmanberg s.n.* (FLAS<sup>U</sup>); Gainesville, University of Florida campus, northwest corner of the Natural Area Teaching Lab West, west of Upland Pine Nature Trail, Lat. 29°38'4"N, Long. 82°22'11"W, 27 August 2008, *Kei Andrews 2008-5 with J. Richard Abbott* (FLAS<sup>U</sup>); SW of main campus near junction of Florida State Highway 24 & SW 34<sup>th</sup> St., Univ. of Florida, 28 April 1965, *Ira L. Wiggins 19839* (FLAS<sup>M</sup>); San Velasco Hammock, northwest of Gainesville on Fla. 232, 4 June 1966, *G. T. Crosby 283 with W. G. D'Arcy* (USF); west of University of Gainesville, 19 May 1940, *W. A. Murrill s.n.* (MO); June- July 1898, *A. S. Hitchcock s.n.* (MO); Devil's Millhopper, Gainesville, 21 June 1931, *Lillian E. Arnold s.n.* (FLAS); Devils Millhopper, Gainesville, 22 May 1932, *Lillian Arnold s.n.* (FLAS); N29°38.636', W82°25.262', Gainesville, Cedar Ridge area at Tower Rd & SW 8th Ave. under large radio towers, 13 August 2001, *Derek Tilley 2173* (FLAS); Gainesville, on S.W. 34th St. just east of Doyle-Conner building, 19 October 1991, *Monica Morris 129 with M. W. Morris*

(FLAS); at SW 8th Ave and Tower Rd. (SW 75th St), 1 September 2001, *Christince Notis 125* (FLAS); Tower Rd., 0.5 mi. north of S.W. 24th Ave., 1 June 2001, *Cathleen Kabat A300 with Steven Kabat*, (FLAS); Baker Co., along C-127, 0.8 mi. S of C-120, ca. 5 mi. S of Baxter, T1S, R21E, Sec. 5, NW of NE, 11 July 1984, *Bruce Hansen 10075 with George Robinson* (USF<sup>U</sup>); east side of Glen St. Mary, 2 July 1977, *R. Kral 60579* (FLAS, MO); Bradford Co., near Jct. Fla. 21A along Fla. 100, S11, T8S, R22E, 1 August 1961, *R. R. Smith 555 with T. Myint and B Moore* (FLAS); Brevard Co., 2 mi. north of Cocoa, 25 September 1936, *A. S. Rhoads, s.n.* (FLAS<sup>M</sup>); Calhoun Co., Clarksville, 6.5 m. W. of Hi[gh]way 73 on SR 20, R & G Wood Prop., N30.43310, W85.29169, 4 June 2009, *Travis MacClendon 928* (USF<sup>M</sup>); Citrus Co., ca. three miles sw. of Homosassa, 11 August 1961, *James D. Ray, Jr. 11041 with Olga Lakela* (GH<sup>U</sup>, USF<sup>U</sup>); Fort Cooper State Park, road to fort site, T19S R20E Sect. 28 NW1/4 of SE1/4, 22 June 1983, *N. L. Mawhinney 214* (JSU, USF); Clay Co., in Green Cove Springs, 27 June 1947, *C. E. Wood, Jr. 7155 with I. D. Clement* (GH<sup>M</sup>); ca. 3.5 mi. ENE of the jct. of FL 100 and FL 21, ca. ¼ mi. SSE of Silver Sands Lake (Ten Mile Pond), N side of Overlook Terrace, E of Silver Sands Lake Dr., T8S R23E, Sec. 14, SW1/4, 17 May 2004, *John M. Kunzer 540* (FLAS<sup>M</sup>); 2 miles west of Penny Farms by Fla. 16, 9 July 1976, *R. Kral 58548* (FLAS<sup>M</sup>, MO); 1 mile south of Fort Gaines, 9 May 1947, *M. Z. Thorne 3789* (GH); ca. 1 air mi S of Duval Co line and ca. 0.7 air mi W od Yellow Water Creek, ca. 8.1 air mi NW of Middleburg, Jennings Forest, Black Creek WMA, 30°10'20" N, 81°55'59" W, 9 July 1992, *Steve L. Orzell 20117 and Edwin L. Bridges* (FLAS<sup>M</sup>); Columbia Co., along U.S. 2, Lake City Junction, 2 miles northwest of Ft. White, 2 May 1965, *J. Beckner 680* (FLAS, USF); 1.6 miles south of Ft. White on S/R 47, 26 June 1976, *A. Gholson, Jr. 5766* (FLAS); near the south parking lot of Ichetucknee Springs State Park, 18 September 1988, *Gerald F. Guala II 1004* (FLAS); 1 mile west of Lake City, 1 August 1927, *K. M. Wiegand 1204*

with *W. E. Manning* (GH); O'Leno State Park, path leading south from main drive, opposite entrance to limestone trail, 13 October 1989, *Bian Tan 232* (FLAS<sup>U</sup>); Dixie Co., river bank (Suwannee), 8 June 1975, *A. Gholson, Jr, 4266* (FLAS); near Rock Bluff ferry landing, S8, T8S, R14E, 18 September 1960, *D. B. Ward 2211 with A. A. Will* (FLAS); Duval Co., near Jacksonville, Fl[ower]s 16 May, Fr[uit] 6 July 1894, *A. H. Curtis 4836* (NCU<sup>U</sup>); St. Nicholas, 12 May 1997, *Rev. L. H. Lighthipe 195* (MO, NCU<sup>M</sup>); 12 May 1902, *A. Fredholm 5190* (GH<sup>M</sup>, MO); St. Nicholas, south Jacksonville, 20 April 1897, *J. R. Churchill s.n.* (GH<sup>M</sup>, MO); Girvin Road, Arlington, 24 May 1963, *D. B. Creager III* (FLAS); 1 mile north of Tisonia, 26 July 1927, *K. M. Wiegand 1202 with W. E. Manning* (GH); Franklin Co., East Bay boat landing, 2.9 miles south of Rte. 65, ca. 4 air miles northwest of town of Eastpoint, 8 July 1987, *Loran C. Anderson 10725* (MO); Gilchrist Co., east of unnumbered sand road, ca. 1.7 miles north of County Road 232 at a point 2.9 miles east of FL 47, ca. 10 air miles east of Bell, SWQ, NEQ, Sec. 34 T8S R16, Waters Lake 7.5' Quad., 29°44'44"N 82°41'54"W, 2 August 1990, *Steve L. Orzell 14505 with Edwin L. Bridges* (FLAS, USF); Wayside Park on Suwannee River, S/R 340, 10 June 1975, *A. Gholson, Jr, 4321* (FLAS); along the Suwannee River east of Old Town, 14 July 1924, *John K. Small 11468 with John W. Small and John DeWinkler* (GH<sup>U</sup>); Hernando Co., old highway #50 southwest of Brooksville, 31 August 1962, *O. Lakela 25303* (USF); ca. 4 mi. northeast of Brooksville at Chinsegut Hill, 30 April 1961, *George R. Cooley 8104 with Jason Swallen et al.* (GH<sup>U</sup>); one mile south of County line north of Chinsegut Hill, 24 April 1959, *George R. Cooley 6665 with Richard J. Eaton* (GH<sup>M</sup>); south side of Chinsegut Hill, about 6 miles north of Brooksville, 23 July 1961, *O. Lakela 24441* (LL); four miles n. of Brooksville, base of Chinsegut Hill, 9 August 1960, *James D. Ray, Jr, 9886 with Olga Lakela and Jackie Patman* (GH); Highlands Co., Josephine Creek, 20 June 1945, *L. J. Brass 15316* (GH);

Hillsborough Co., Northwest of Mango, at junction of Hwy 92 and Moores Lake Rd, 25 September 1987, *Fred Essig 870925-1* (USF); along Rte. 579, just south of 301, 2 October 1986, *F. B. Essig 851002-1* (USF); Holmes Co., about Choctawatchee River bridge on Highway #2, 21 July 1954, *E. S. Ford 3486* (FLAS<sup>U</sup>); Jackson Co., Apalachee WMA, about 5 miles north of Sneads, west of Hwy 271 on Rocky Pond Road, 13 October 2000, *Susan C. Carr 2331* (FLAS<sup>U</sup>); west side of S/R 27, 9.1 miles North jct. with US 90, 14 May 1983, *A. Gholson, Jr. 10440* (FLAS<sup>M</sup>); 0.8 miles south of U.S. route 90 on Florida route 71, 24 May 1973, *D. E. Boufford 9265 with H. E. Ahles* (AA<sup>M</sup>); near Jacksonville, Fl[ower] 16 May, fr[uit] 6 July, 1894, *A. H. Curtiss 4813* (GH<sup>M</sup>); along route 71, S of Marianna, 1.2 mi S of I-10, 18 May 1979, *Loran C. Anderson 4863* (NCU); 3.2 mi. S of US 90 on Fla. 71, 0.4 mi. S of Oakdale, T4N, R10W, Sec. 36, SW of NE, 5 July 1979, *Bruce Hansen 5941 with Don Richardson* (USF); on S/R 71, ca. 1.2 miles south of I-10, S/E of Marianna, 18 May 1979, *A. Gholson, Jr. 7745 with Dr. Loran Anderson* (FLAS); S/R 71, east of Marianna, ca. ½ mile south of I-10, 2 May 1982, *A. Gholson, Jr. 9648 with Randy Cameron* (FLAS<sup>M</sup>); Lafayette Co., by the bridge over the Suwannee River along C-250, just across the river from Dowling Park, T3S, R11E, Sec. 7, NE 1/4, 12 June 2008, *Bruce Hansen 13199 with JoAnn Hansen* (USF); Lake Co., vicinity of Eustis, 1- 15 May 1894, *Geo V. Nash 611* (AA, GH<sup>U</sup>, MO); in vicinity of Eustis, 16-31 July 1894, *Geo V. Nash 1466* (AA); Lane Park, Tavares, 22 June 1941, *W. A. Murrill s.n.* (FLAS); E. of Lake Yale, 22 July 1975, *R & J. Daubenmire s.n.* (USF<sup>U</sup>); Leon Co., near Lake Bradford, 23 July 1957, *R. K. Godfrey 55674* (FLAS, GH, UNA, USF<sup>U</sup>); Liberty Co., 1.2 miles north of Fla. 12 on Fla. S-271, north of Bristol, 20 May 1976, *J. Solomon 2151* (MO); Madison Co., along Hwy 53, 3.5 mi. N of Madison, 1.6 mi. N of junction with FL 146, T1N, R9E, Sec. 4, NE1/4, 1 September 1987, *F. B. Essig 870901-1* (USF); east side of Hwy Fla-145, 3 miles south of Ga-Fla state line, 18 May

1975, *Greg Johnston s.n.* (NCU); Suwannee River State Park, E1/2 of NE1/4 of sec24, T1S, R11E, 21 October 1976, *David L. Martin 939 & S. T. Cooper* (FLAS); Manatee Co., Wingate Creek State Park, adjacent to burn zone 7, NE1/4 SE1/4 SE1/4 S7 T35S R22E, 10 June 2005, *C. Becker WC0630 with A. Bishop and C. Olson* (USF); Marion Co., T14S, R24E, Sec. 26, along roadside to Lake Eaton landing, E of S314A, 17 July 1975, *D.L. Martin 716 with S.T. Cooper* (FLAS); near Salt Springs, T13S R26E, northeast corner of Marion County, 3 June 1959, *D. B. Ward 1411 with E. West and S. S. Ward* (FLAS); Silver Springs, Silver Springs State Park, Lat. 29°12.713'N, Long. 082°03.011'W, 18 June 2006, *Jeffery Hubbard 550* (FLAS); 0.6 mi. E of junction of FLA. 329 on FLA 320, T12S, R20E, Sect. 10, SW 1/4, 18 July 1985, *R. P. Wunderlin 9969 with B. F. Hansen & M. Van Etten* (USF); 2 mi. N.W. of Reddick, 15 May 1956, *Curtis Jackson s.n.* (FLAS); Okaloosa Co., Eglin Air Force Base (W of Rte 85), T1N, R23W, NW1/4, of SE1/4 Sec. 20, 9 June 1994, *Loran C. Anderson 14953* (USCH<sup>U</sup>); along Little Rocky Creek, near Fla. 285, ca. 9 mi. n. of Niceville, S3, T1N, R22W, 11 May 1967, *D. B. Ward 6456 with C. Chapman & R. R. Smith* (FLAS<sup>M</sup>); Yellow River at Highway 2, 28 July 1978, *Royal D. Suttkus 78-31-46* (NO<sup>U</sup>); near Pearl Creek, ca. 1 mile east Junction Fla. 85, along No. 211, ca. 6 miles south of Crestview, S9 T2N R23W, 22 June 1967, *R. R. Smith 1594* (LSU, FLAS); near Little Rocky Creek, along Fla. 285, ca. 7 mi n.e. of Niceville, S3, T1N, R22W, 8 May 1967, *C. Chapman 0604 & C. Chapman* (FLAS); Orange Co., Oak Ridge near the Suwanee, May 1928, *John K. Small s.n.* (GH<sup>M</sup>); Winter Park, n.d., *N. Barron s.n.* (NCU<sup>M</sup>); NW corner of US 17/ US 93 and Magnolia Road, adjacent to Enzian Theatre, Maitland, 11 June 2014, *William F. Grey s.n.* (USF<sup>U</sup>); Pasco Co., Fivay, 4 July 1929, *Hugh O'Neill s.n.* (FLAS); Bear Creek off E side of Plaza Dr. ca. 3/4 mi. S of SR 52, 18 July 1976, *Kathryn Zeiler 45* (USF); Polk Co., Tiger Creek Preserve, northwest side of preserve, Lat. 27.83606N, Long. 81.49231W, 29 July 2007, *Paul*

*Corogin TC542* (FLAS); 6 mi. E. of Haines City via Fla. 544S, near Lake Marion, 10 August 1963, *H. S. Conard s.n.* (FLAS); just east of Homeland, across Peace River, 11 July 1972, *T. Perkins s.n., W. Webb, S. Todd, and J. Wassmer* (USF); Putnam Co., Palatka, 24 June 1910, *S.C. Hood 22008* (FLAS<sup>U</sup>); Ordway-Swisher Biological Station, management unit H-1, between Goose Lake and Smith Lake, Lat. 29.69819 N., Long. 81.96728 W, 8 May 2014, *Lucas C. Majure 5093 with Kurt Neubig, Mark Whitten, and Walter Judd* (FLAS<sup>M</sup>); in the Palatka Ravine Gardens, 10 August 1936, *D. S. Correll 6402* (AA<sup>M</sup>); Seminole Co., Altamonte Springs, 1 May 1950, *Paul O. Schallert 18305* (NCU); Sanford, 1 June 1904, *A. A. Eaton 1043* (AA, GH<sup>U</sup>); St. Johns Co., ca. 1 miles southeast of US 1 along road to Faver-Dykes State Park, T10S R30E Sec. 37, 29 September 1983, *Bruce and JoAnn Hansen 9869* (USF); Sumter Co., 3 miles southeast of Wildwood, 6 July 1968, *L. Baltzell 548* (FLAS); Suwannee Co., T6S, R15E, S14, six miles NW of Fort White off of CR 238 in Ichetucknee Springs State Park, ca. 3.2 miles SW of North Entrance in W portion of section 2F, N of power lines and S of planted pines, 23 May 1992, *Brenda Herring 761 with Don Herring* (FLAS<sup>M</sup>); T6S, R15E, S23, five miles NW of Fort White off of US 27 in Ichetucknee Springs State Park, ca. 0.7 mi. W of Old South Entrance at southwestern most gate, 0.7 mi. NE of gate by fencerow bordering section 3A, 19 May 1991, *Brenda Herring 238 with Don Herring* (FLAS); Taylor Co., near Perry, 17 May 1925, *John K. Small 1260 with Edgar T. Wherry* (GH); S side of FL 51, N bank of Steinhatchee River, Steinhatchee, 27 September 2014, *Alan R. Frank 3592* (USF); Walton Co., ca. 3 mi. s. of Mossy Head Jct. US 90, along Fla. 285, S31-32, T3N, R21W, 19 July 1966, *C. Chapman 1063 with G. Crosby and R. R. Smith* (FLAS<sup>U</sup>); 16 mi. N of Niceville, 22 September 1952, *William H. Duncan 14154* (NCU); Rocky Run, 9 May 1929, *W. W. Ashe s.n.* (NCU<sup>U</sup>); Eglin Air Force Base, east of Rte. 285, 23 July 1992, *Loran C. Anderson 13729* (USCH<sup>U</sup>, MO); Defuniak, 15 May 1906, *S. M. Tracy 9450*

(MO); 4 mi. n.e. of Okaloosa County line, along Fla. 285, 3 mi. s. of Mossy Head, 29 June 1966, *J. Beckner 1351 with C. Chapman and R. R. Smith* (FLAS); NE of Niceville, 10 May 1929, *T. G. Harbison s.n.* (NCU<sup>M</sup>); County not determined, near Jacksonville, June/August, *A. H. Curtiss s.n.* (GH); **GEORGIA**: Bacon Co., 0.7 mi. NE of Big Hurricane Creek, & 1.4 mi. W/NW of Ga. 32 off road S1303, 12 June 1967, *J. R. Bozeman 9487* (NCU<sup>U</sup>); northeast side of Little Hurricane Creek, 5 miles south of Alma on Ga. 64, 20 June 1966, *John R. Bozeman 4507* (NCU<sup>M</sup>); Brooks Co., at Elam Church, 6.0 mi WSW of Quitman, 13 July 1966, *Wayne R. Faircloth 3455* (MO, NCU<sup>U</sup>); Quitman, Hickory Head Baptist Church, north of cemetery, 30.713466, -83.610912, 29 May 2018, *Thomas H. Murphy 79* (APSC, TBD); oak-hickory woods adjacent to church yard and cemetery at Hickory Head Church, 6.7 miles SSE of Quitman, 25 June 1965, *Wayne R. Faircloth 1887* (NCU); Burke Co., S. of Ga. 80 on Allens Chapel Rd., 1.3 mi. N. of Clair Branch Creek, 1 August 1966, *John R. Bozeman 6901* (NCU); Camden Co., off Rte. 17, 2 miles south of Kingsland, 5 June 1976, *Clyde F. Reed 99563* (MO); Covington Co., right-of-way and ecotone to Pigeon Creek swamp, 6 miles northwest of Red Level, 20 June 1967, *Ross C. Clark 14388* (NCU); Echols Co., Alapaha River, 6 miles south of Stockton, US-129, 31 October 1963, *Juanita Norsworthy s.n.* (MO); Grady Co., About 10 miles north of Whigham, 8 July 1948, *Arthur Cronquist 5466* (GH<sup>U</sup>, MO); Hancock Co., w. of Ga. 15 at Washington Co. line, 8 August 1966, *John R. Bozeman 7318* (NCU<sup>U</sup>); Jefferson Co., 0.2 mile northeast of Ogeechee River on U.S. Hwy 1, 26 July 1967, *John R. Bozeman 10774 with John F. Logue* (NCU); Lowndes Co., west of North Valdosta Exit, I-75, Valdosta, 13 May 1971, *Carol Robinson s.n.* (MO); 5.8 miles north of Valdosta, 20 April 1970, *Scott Chase 9* (MO); 0.3 miles west of Hornes Motor Lodge, 13 May 1971, *Carolyn Herin s.n.* (MO); N shore of Grassy Pond, 10.3 miles S of Valdosta, 28 June 1965, *Wayne R. Faircloth 1898* (NCU); Marion Co., west of Buena Vista, 9 July 1902,

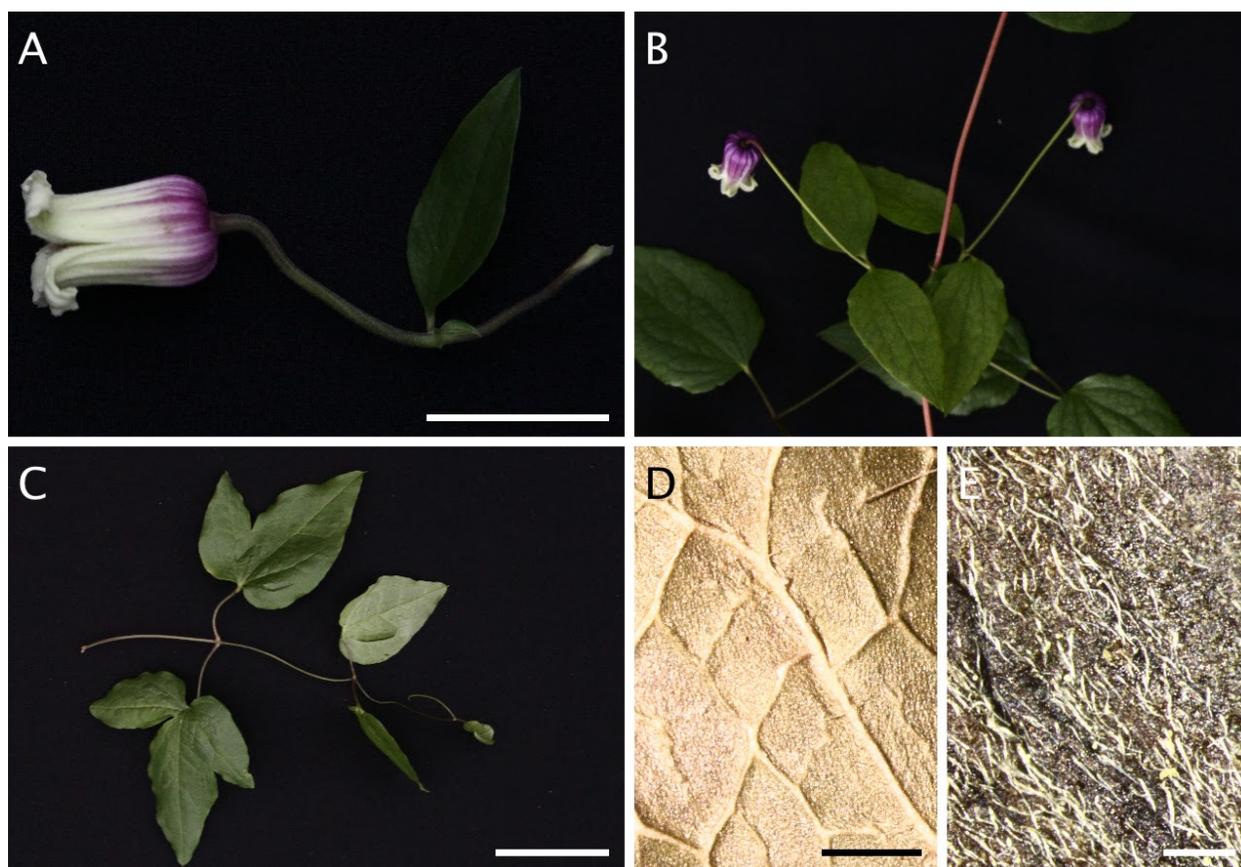
*Roland M. Harper 1408*; Town of Buena Vista, east and west sides of Eddie Edge Road, 32.354444, -84.598889, 28 May 2018, *Thomas H. Murphy 75* (APSC<sup>M</sup>, TBD<sup>M</sup>); west of Buena Vista, 9 July 1902, *Roland M. Harper 1408* (GH); Mitchell Co., town of Pelham, east side of Mill Pond Road, 31.160391, -84.138044, 29 May 2018, *Thomas H. Murphy 80* (APSC, TBD); 1.3 mi west of Pelham, 15 July 1966, *Wayne R. Faircloth 3513* (NCU); Murray Co., above Apalachicola River, Ft. Gaines, 7 June 1976, *R. Kral 58180* (MO); Richmond Co., along Horseshoe Rd., 1.5 mi. east of Ga. 56, 4 August 1966, *John R. Bozeman 6945* (NCU); Sumter Co., Americus, 20 August 1897, *S. M. Tracy s.n.* (MO); Taylor Co., alongside Hwy Ga-96, 3.0 miles west of Butler, 16 May 1974, *Wayne R. Faircloth 7522* (NCU); Washington Co., slope and bottomland of Ogeechee River along Ga. 88, N.E. sect. of co., 5 August 1966, *John R. Bozeman 7133* (NCU); Wayne Co., top of bluff on Altamaha River, 3.5 miles n. of Ogden community, approx. 10 miles n. of Odum, 6 June 1966, *John R. Bozeman 3688* (NCU); County not determined, 1875, *A. H. Curtis s.n.* (AA); **MISSISSIPPI:** Marion Co., Clear Creek Road ca. 5 miles east of Hwy 43, 7 June 1996, *S. Rosso 96409 with S. Leonard and J. D. Allen* (USMS); Pearl River Co., Picayune, 20 May 1964, *Delzie Demaree 50046* (NCSC); Henleyfield, Birds Chapel, 10 May 1960, *F. H. Sargent 7744* (MO); north of Crossroads Hwy 43, 19 July 1966, *S. B. Jones 8660* (NCU<sup>U</sup>); Perry Co., Janice Recreation Area, 1 miles south of Janice at Black Creek, 7 June 1967, *S. B. Jones 13119 with Carlee Jones* (MISS); **SOUTH CAROLINA:** Aiken Co., near S.C. 126, Belvedere, 23 July 1967, *A. E. Radford 45423* (FLAS<sup>U</sup>); 9 mi. N.E. of Aiken, highway 215, 11 July 1964, *Sara Anderson 18* (USCH<sup>U</sup>); near Aiken, 24 June 1901, *A. Cuthbert s.n.* (FLAS); along SC 126, 1.6 miles east jct. of US 25, 23 August 1971, *S. W. Leonard 4952 with J. R. Massey and A. E. Radford* (USCH<sup>U</sup>); Calhoun Co., above Lyons Creek, Whetstone property on Stiffmire Road, approx. one-half mile from intersection with Hwy. 6, approx. 4

miles south of St. Matthews, 19 September 2004, *Amanda C. McNulty 33 with E. C. Z. Wimberly* (USCH<sup>U</sup>); Halfway Swamp Creek on SC. 267 (east northeast of Cameron), 19 May 1957, *Harry E. Ahles 25517 with John G. Haesloop* (NCU); Darlington Co., between Darlington County and Chesterfield County about 8 miles north of Hartsville, 10 June 1941, *B. E. Smith 619* (NCU<sup>U</sup>); Kershaw Co., adj. to Ratcliffe Pond along S-631, east of Sandy Grove, Cassett Quad., 9 October 1987, *D. A. Rayner 2760* (USCH), Lee Co., 0.8 mile northeast of Lucknow, 26 July 1957, *A. E. Radford 27341* (USF); Lexington Co., 10 miles on Orangeburg Road, 3 October 1941, *Dorothy Derrick s.n.* (USCH<sup>U</sup>); south of junction of S-32-266 and S-32-740 in city of Cayce, 4 October 1995, *K. A. Boyle 95100406* (USCH<sup>U</sup>); 25 May 1925, *Anonymous s.n.* (USCH<sup>M</sup>); Orangeburg Road, 17 May 1940, *O. G. Philson s.n.* (USCH); Lexington, 18 May 1936, *O. G. Philson s.n.* (MO); State Record Recreation Center Lake, 1.4 air miles due east of jct. of U.S. 321 and S-32-719, north of Gaston, 5 November 1982, *Margaret La Caruba 18* (USCH); Newberry Co., near Chappels, 19 May 1969, *W. T. Batson s.n.* (USCH<sup>U</sup>); Orangeburg Co., Orangeburg Co. 73, 2.1 mi. S of US 178, ca. 12 mi. WNW Orangeburg, 20 May 1987, *Charles N. Horn 1729* (UNA<sup>M</sup>); County not determined, 1875, *Curtis s.n.* (USF<sup>M</sup>).

**5. CLEMATIS SUBRETICULATA** (Harbison ex Small) Harbison ex T. Murphy & D. Estes, comb. nov. Type: USA. Alabama: Cullman Co., rocky banks of creek at Garden City, 23 May 1902, *Biltmore Herbarium 15011* (Holotype: NY!<sup>M</sup>; Isotype: US)

**Diagnosis**— *Clematis subreticulata* differs from *C. reticulata* s.s. in its narrower leaflet primary veins, smaller closed leaflet areoles, thinner leaflets, longer trichomes on leaflet and sepal abaxial surfaces, narrower leaflet apices, and relatively thicker achene rims; from *C. terminalis* sp. nov. in its longer petiolules, axillary (vs. terminal) inflorescences, and vining (vs.

erect-herbaceous) habit when in flower; from *C. cumberlandensis* sp. nov. in its elevated (vs. basal) bract placement (greater peduncle to combined peduncle and pedicel ratio), greater sepal length to width ratio, and shorter trichomes on leaflet and sepal abaxial surfaces; from *C. arenicola* sp. nov. in its elevated (vs. basal) bract placement (greater peduncle to combined peduncle and pedicel ratio), narrower leaflet adaxial veins, larger closed leaflet areoles, thinner leaflets, and narrower leaflet apices; from *C. ouachitensis* sp. nov. in its elevated (vs. basal) bract placement (greater peduncle to combined peduncle and pedicel ratio), erect (vs. pendulous) and relatively longer pedicels, and greater achene length to width ratio.



**Figure 14.** Diagnostic characters of *Clematis subreticulata*. A) Inflorescence with elevated bract position (scale bar= 20 mm), B) general erect habit of pedicels, C) leaf possessing leaflets with ovate shape and acute apices (scale bar= 50 mm), D) leaflet adaxial with relatively larger closed areoles and narrower veins (scale bar= 1 mm), and E) sepal abaxial with relatively long trichomes (scale bar= 0.5 mm).

**Description**— Perennial climbing or scandent **vine** to ca. 3 m tall, one to multiple stems from a woody caudex bearing smooth coarse, fleshy roots. Stems six angled, six ribbed, reddish-

brown, sparsely to densely covered with pilose to appressed trichomes, trichome density increasing distally. **Leaves** oppositely decussate, spreading, proximal most leaves simple and entire or deeply lobed, becoming imparipinnately compound, longest at mid-stem or node directly below inflorescence, longer than wide; petioles (2.5) 3.5–4.7 (7.1) cm, increasingly shorter from proximal to distal leaves, sparsely to moderately pilose, opposing petioles conjoined at node, distal-most leaflet modified into tendril-like structure or greatly reduced leaflet; leaflets membranaceous to subcoriaceous, (3.9) 5.8–7.6 (11.4) cm long, (1.7) 3.1–5.7 (9.6) cm wide, ovate, apices acute to acuminate, rarely rounded, leaflets of mid-stem leaves usually simple, 2 or 3 lobed, or ternate, inconspicuously raised-reticulate on adaxial and abaxial surface, most noticeable in dried material, primary veins (0.04) 0.07–0.09 (0.14) mm wide, lowest order of closed areoles (0.36) 0.61–0.95 (2.69) mm<sup>2</sup>, adaxial surface typically sparsely pubescent, abaxial surface glabrate, sparsely to moderately pilose with longest trichomes (0.37) 0.55–0.64 (0.82) mm long, pubescence confined to mid-veins or both mid-veins and lower order veins; petiolules (5.5) 13.6–30.9 (45.5) mm long, margins ciliate, entire or irregularly and broadly wavy.

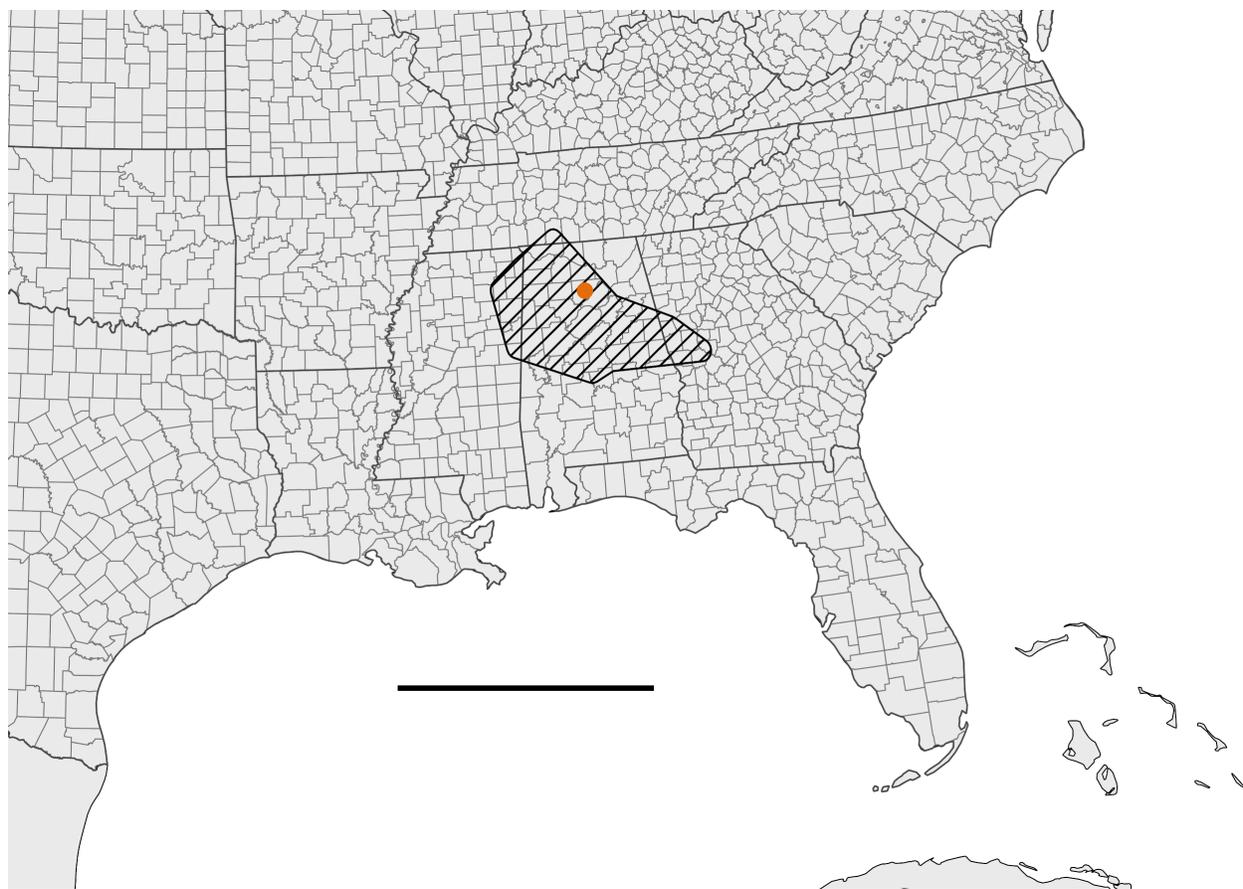
**Inflorescences** most often axillary cymes or solitary, rarely producing terminal flowers, nodding on decidedly erect pedicels, with flowers borne above leaflets of corresponding node, ovoid to cylindrical in shape; peduncles, when axillary, (11.7) 34.1–51.0 (101.9) mm long, primary pedicels (25.8) 45.1–75.2 (118.6) mm long, ratio of peduncle to combined peduncle and pedicel length (0.23) 0.36–0.48 (0.70) with foliose bracts appearing elevated on combined peduncle and pedicel; foliose bracts (7.9) 32.0–45.0 (91.1) mm long. **Sepals** erect, connivent, oblong-lanceolate, reflexed and spreading at apex, (18.0) 18.8–26.6 (30.0) mm long, (5.2) 6.4–8.1 (8.7) mm wide at widest point, coriaceous, abaxially faded pink to vibrant purple, becoming white or cream distally, adaxially cream or faded pink to vibrant purple; margins narrowly crispate,

white-tomentulose, abaxial surface sparsely to densely pilose, occasionally glabrate, with longest trichomes (0.45) 0.52–0.66 (0.84) mm long. **Stamens** linear, (12.3) 15.2–17.6 (22.4) mm long, filaments flattened, spreading-pilose from middle to apex, connective extended (0.51) 0.67–1.09 (1.60) mm beyond anthers. **Fruit** tightly clustered in spherical heads, light brown, body rhomboidal-ovate to rotund, (5.3) 5.5–6.7 (6.9) mm long, (3.7) 3.9–4.8 (5.2) mm wide, acuminate or rounded on proximal end and acuminate on distal end, marginally thickened, sericeous; thickened achene rims (0.67) 0.74–0.96 (1.12) mm wide at mid-point; style curvate, (3.9) 4.3–5.5 (6.6) cm long, with a light yellowish plumose tail hairs, spreading to ascending, (3.5) 3.7–5.1 (5.5) mm long at mid-point, becoming shorter proximally and distally. Chromosome number unknown.

***Distribution and Habitat***— *Clematis subreticulata* is distributed in various regions of northern and central Alabama, western Georgia, northeastern Mississippi, and extreme south-central Tennessee (Fig. 15). Within these states, it occurs primarily in the upper East Gulf Coastal Plain, specifically the Fall Line Hills and Transition Hills ecoregions and extends barely into southern sections of adjacent Western Highland Rim, southern Ridge and Valley, southern Southwestern Appalachians (Cumberland Plateau), and western Piedmont ecoregions. Habitats consist of rocky pine-oak woodlands, montane longleaf pine savanna, sandstone riverscour shrublands, xeric sandstone outcrop and glades, sandy bluffs and river banks.

***Phenology***— *Clematis subreticulata* flowers from the last week of April to mid-June. Plants fruit into October and November.

***Conservation***— State protection for Georgia, Mississippi, and Tennessee is recommended for *C. subreticulata*, as it is known from few populations in these states and represents the edge of *C. subreticulata*'s range.



**Figure 15.** Generalized range map of *Clematis subreticulata*. Orange point represents type locality. Scale bar indicates 500 km.

**Notes**— Evidence of introgression between *C. glaucophylla* and *C. subreticulata*, based on morphology, has been observed in Bibb County, Alabama. Populations in Bibb County are sympatric with no observation of syntopy. Additional investigation is needed to determine whether hybrids are forming populations and reproductively isolated from parental species.

The holotype of *Viorna subreticulata* Harbison ex Small (*Biltmore herb.* 15011, NY) was designated by Small (1933). Dennis (1976) designated an isotype from the same locality with the same collection number (*ex Biltmore herb.* 15011, US), but the date differs by exactly one year. Because all text, except for the year, is identical, it is likely this is due to a transcription error. Therefore, the US specimen should continue to be regarded with isotype status.

*Specimens examined (paratypes)*—USA—ALABAMA: Bibb Co., north bank Six Mile Creek at end of McKinney Road, northwest of Six Mile, 21 May 1973, *R. Kral 50264* (VDB); Six Mile Creek, Cahaba Refuge, 28 June 1974, *R. Kral 53586* (GH<sup>M</sup>, MO); Six Mile Creek, ca. 4 miles west of Six Mile, 16 April, 1973, *R. Kral 49665* (MO); West Blocton, Cahaba National Wildlife Refuge, west of River Trace Road, 33.08330, -87.064891, 21 April 2018, *Thomas H. Murphy 47* (APSC<sup>M</sup>, TBD); Blount Co., Sandy woods growing in partial shade. North bank of the Locust fork river east of swan bridge growing on shrubbery, 28 April 2017, *Zach Irick 763* (APSC<sup>M</sup>); Hwy 8, trail leading to Skirum Creek and Bluff, east of bridge 2.3 miles west of Cleveland Community, 24 July 1969, *Jerry A. Clonts s.n.* (JSU); Locust Fork of Black Warrior River near Shoal Creek Church on County Road 13 (just off Highway 231), 17 August 1997, *J. M. Ballard 7380 with T. L. Ballard* (JSU); 2.5 air miles west of Cleveland, south side of Locust Fork where the river bends just north of AL 160, T12S R1W S14, 33°59'52"N 86°34'52"W, 6 June 1998, *Brian R. Keener 891* (UNA); northwest of Cleveland 1.39 air miles at Locust Fork, northeast (upstream) of Swan Covered Bridge to 0.3 miles, northwest side of river, N33.998 W86.599, 21 May 2013, *Kelly Anderson 169* [I and II] *with Dwayne Estes and Devin Rodgers* (APSC<sup>M</sup>); northwest of Cleveland 1.34 airmiles at Locust Fork, northeast (upstream) of Swan Covered Bridge 0.22 miles, northwest side of river, 28 July 2013, *Kelly Anderson 384 with Brittney Georgic and Devin Rodgers* (APSC<sup>M</sup>); southwest of Cleveland 2.33 airmiles at Locust Fork, southeast (downstream) of AL-60 bridge crossing 0.07 miles, northeast side of river, 19 May 2015, *Kelly Anderson 854 with Chris Mausert-Mooney and Mason Brock* (APSC); Calhoun Co., top of Chimney Peak, 16 July 1966, *Ross. C. Clark 5215 with Ken Landers and L. G. Sandford* (NCU<sup>M</sup>); Clay Co., Ca. 9.6 km Southeast of Munford, upstream of FS Road 637E bridge over Cheaha Creek, 33.453216, -85.902609, 15 June 2019, *Thomas H. Murphy 550*

(APSC<sup>M</sup>); ca. 7 miles south-southeast of Oxford, Cheaha Mountain around northcentral T18S R8E section 9, Odum Trail and service road from towers, 23 September 1982, *Melanie G. Bussey 443 with K. E. Landers, R. D. Whetstone, and Plant Ecology Class* (JSU<sup>M</sup>, NCU); [same locality as last], 15 June 1983, *Melanie G. Bussey 715 with R. D. Whetstone and M. S. McCarthy* (JSU<sup>M</sup>); along Chinabee Creek above Lake Chinabee, T18S R7E sect. 14, 9 May 1983, *C. F. Nixon 118 with R. D. Whetstone and C. M. DeFiori* (JSU); along Cheaha Creek above water flow bridge on FS 637, T18S R7E S14&15, 19 July 1992, *J. M. Ballard 383 with T. L. Dobson* (JSU<sup>M</sup>); Chilton Co., south shore of Lake Pearl, T19N R12E NW1/4 Sec. 2, 31 May 1980, *Russell A. Meigs 693* (UNA<sup>M</sup>); Cleburne Co., near road to Chimney Peak, Jacksonville, 1 May 1954, *Lewis Leath s.n.* (JSU<sup>M</sup>); near lodge of Cheaha State Park, 13 May 1955, *Bob Dyar s.n.* (JSU<sup>U</sup>); tower, Cheaha Park, 6 May 1967, *J. Reynolds s.n.* (JSU<sup>M</sup>); below swimming pool area in Cheaha State Park, 24 May 1992, *J. M. Ballard 157 with T. L. Dobson* (JSU<sup>M</sup>); Talladega National Forest, near N33.45301 W85.90278, southwest side of bridge over Cheaha Creek, 3 June 2017, *T. Wayne Barger SP#3193[A-C] with Priscilla Barger* (ALNHS<sup>U</sup>); summit of Cheaha mountain directly behind the state park observation center, 22 July 2017, *Zach Irick 834* (APSC<sup>U</sup>); Coosa Co., Rockford, along County Road 121, ca. 10 feet north of road, 32.836894, -86.435982, 21 April 2018, *Thomas H. Murphy 48* (APSC<sup>M</sup>); Franklin Co., Ca. 4.1 km northeast of Atwood, ca. 8.8 km east of Vina. Along County Road 27, above Bear Creek Reservoir, before road meets Horseshoe Bend Campground, 12 June 2019, *Thomas H. Murphy 296 with Zach Irick and Kevin England* (APSC<sup>M</sup>); along Little Bear Creek, near junction of CR-81 north of CR-71 between Phil Campbell and Trapptown, 34°20'47"N 87°39'21"W, 9 May 2004, *Daniel D. Spaulding 12093* (UNA<sup>M</sup>); Jefferson Co., along Camp Nod Road off of Camp Piers Road from junction with County Road 61 (Alliance Road), 28 May 1984, *J. P. Barber 259 with R. D.*

*Whetstone and M. G. Bussey* (JSU); Lamar Co., upper slopes of the Buttahatchee River 0.2 miles east of the intersection of HWY 17 and River Road, collected on the west side of the road, 27 July 2017, *Zach Irick 853* (APSC<sup>M</sup>); 2 miles north of Sulligent, T13 R15W S17, above Buttahatchie River, near AL-35, 18 May 1988, *Sidney McDaniel 29799* (FLAS, MO<sup>M</sup>); Sulligent, 15 June 2013, *D. Estes 12797* (APSC, TBD); Montgomery Co., Ca. 9.6 km Northeast of Ramar, along Stephens Road, ca. 730 m southwest of intersection with Hwy 39, 32.09165, -86.130167, 14 June 2019, *Thomas H. Murphy 324 with Zach Irick* (APSC, TBD); Shelby Co., upper slopes of Oak Mountain, Oak Mountain State Park, 29 May 1974, *R. Kral 53136* (MO); north bank of Six Mile Creek at end of McKinney Road, northwest of Six Mile, 21 May 1973, *R. Kral 50264* (MO); off of highway 280 in area known as “the Narrows”, 20 July 1993, *J. M. Ballard 3006 with R. D. Whetstone* (JSU<sup>M</sup>); St. Clair Co., Margin of sandstone rock outcrop in partial shade on the West side of Heart of Dixieland Highway Hwy 231, 28 April 2017, *Zach Irick 799* (APSC<sup>M</sup>); mountain range 20 miles northeast of Birmingham, 29 May 1962, *Rebecca Deramus 186* (GH, UNA); 3.5 air miles north of Wattsville, west of side US Hwy 23 about 2 miles south of junction with County Road 22, 33°43’42”N 86°17’11”W, 5 July 2006, *Brian R. Keener 2983* (UNA); Talladega Co., west slopes of Mt. Cheaha, in state park, 28 May 1974, *R. Kral 53096* (MO); **GEORGIA:** Upson Co., along Flint River, 9 miles (airline) WSW of Thomaston at Sprewell Bluffs, 19 May 1973, *Samuel B. Jones 22467* (GA); **MISSISSIPPI:** Lee Co., 1 mile east of Pontoc-Lee County line, off Hwy 6 east, 10 June 1996, *M. B. Huneycutt s.n.* (MISS); Noxubee Co., 1 miles south of Bigbee Valley, 31 August 1968, *Susan Bridges 6821* (UARK<sup>M</sup>); 1 miles south of Cliftonville, 23 September 1965, *Arthur G. Marler s.n.* (MISS); Tishomingo Co. ca. 6.7 km northeast of Dennis, ca. 6.1 km southeast of Tishomingo. South side of State Park Road, close to where road meets swimming pool, 34.604254, -88.178578, 11 June

2019, *Thomas H. Murphy 287 with Zach Irick* (APSC<sup>U</sup>, TBD); above Bear Creek, Tishomingo State Park, 15 June 1956, *James D. Ray, Jr. 6374* (FLAS, NCU<sup>M</sup>); along Rock Quarry Branch, Tishomingo State Park, 6 August 1956, *James D. Ray, Jr. 7396* (USF); Tishomingo State Park, 10 August 1966, *Louis C. Temple 3902* (NCU<sup>M</sup>). **TENNESSEE:** Lawrence Co., Bluewater Creek, TN 227, southeast side of Loretto, 19 May 1995, *R. Kral 84745* (APSC); Loretto, 16 June 2013, *D. Estes 12799* (APSC<sup>M</sup>).

**6. CLEMATIS TERMINALIS** T.Murphy, A.Floden, & D.Estes, sp. nov. TYPE: USA.

Georgia: Harris County: Pine Mountain Ridges, 8.7 miles west of Manchester, 4.6 miles southeast of White Sulphur Springs, just south of Ga. 190 [coordinates redacted due to rarity], 14 April 2018. *Dwayne Estes 12663* (Holotype: APSC<sup>M</sup>; Isotypes: AUA<sup>M</sup>, BRIT<sup>M</sup>, FLAS<sup>M</sup>, MO, NCU, NY, UWAL).

**Diagnosis**— *Clematis terminalis* differs from *C. arenicola* sp. nov., *C. cumberlandensis* sp. nov., *C. ouachitensis* sp. nov., *C. reticulata* s.s., and *C. subreticulata* comb. nov. with its erect (vs. vining) herbaceous habit when in flower, stems with terminal (vs. axillary) inflorescences, shorter petiolules, and early spring flowering period (vs. mid-spring to early summer).

**Description**— Perennial **herb** 20-77 cm tall, erect in flower, becoming scandent in the late season, one stem, rarely multiple, from a woody caudex bearing smooth coarse roots. **Stems** six angled, six ribbed, reddish-brown, glabrous to glabrate proximally, becoming increasingly pilose distally. **Leaves** oppositely decussate, spreading, proximal most leaves simple and entire or deeply lobed, becoming imparipinnately compound, longest at mid-stem or node directly below inflorescence, longer than wide; petioles (1.4) 2.4–3.0 (3.1) cm, increasingly shorter from

proximal to distal leaves, sparsely to moderately pilose, opposing petioles conjoined at node, distal-most leaflet modified into tendril-like structure or greatly reduced leaflet; leaflets subcoriaceous, (4.1) 4.2–6.1 (6.5) cm long, (2.4) 2.5–3.9 (4.3) cm wide, lanceolate to ovate, with acute apices, rarely rounded, leaflets of mid-stem leaves typically entire, rarely lobed, inconspicuously reticulate with raised venation, most noticeable in dried material, primary veins (0.05) 0.06–0.11 (0.12) mm wide, lowest order of closed areoles (0.52) 0.54–1.19 (2.4) mm<sup>2</sup>, adaxial and abaxial surfaces glabrate to moderately puberulent with longest trichomes (0.48) 0.53–0.75 (0.82) mm long, pubescence confined to mid-veins or on both mid-veins and secondary veins; petiolules sometimes absent, when present 3.1–10.3 (14.9) mm long, margins ciliate, irregularly and broadly undulate. **Inflorescences** solitary on short terminal pedicels, rarely producing axillary flowers in late season, nodding, mostly cylindrical in shape, rarely urceolate; when terminal, pedicels erect, recurved at apex in flower, (18.2) 23.5–70.5 (79.5) mm long, ebracteate; when axillary, pedicels 49.6–60.8 mm long, peduncles 28.1–29.0 mm long; foliose bracts 40.7 mm long. **Sepals** erect, connivent, lanceolate, reflexed at apex, (19.7) 21.0–28.3 (28.8) mm long, (5.3) 6.0–9.4 (12.7) mm wide at widest point, coriaceous, abaxially pink to purple at base, becoming cream distally, adaxially purple to maroon; margins narrowly crispate, white-tomentulose, abaxial surface mildly puberulent with longest trichomes 0.46–0.76 mm long. **Stamens** linear, (12.0) 12.1–15.3 (15.8) mm long, filaments flattened, spreading-pilose from middle to apex, connective extended 0.40–0.85 mm beyond anthers. **Fruit** tightly clustered, light brown, body rhomboidal-ovate, 5.0–5.8 mm long, 3.2–3.6 mm wide, acuminate at both ends, marginally thickened, sericeous; thickened achene rims 0.73–0.77 mm wide at mid-point; style curvate, 50–53 mm long, with a light yellowish plumose tail hairs, spreading to ascending, 3.2–5.0 mm long at mid-point, shorter proximally and distally. Chromosome number unknown.



**Figure 16.** Diagnostic characters of *Clematis terminalis*. A) Terminal, ebracteate inflorescence, B) plant becoming scandent in fruit, C) leaf with short-petiolulate to sessile leaflets (scale bar= 20 mm), and D) sepal abaxial with relatively long trichomes (scale bar= 1 mm).

***Distribution and Habitat***— *Clematis terminalis* is endemic to the Pine Mountain Ridges ecoregion of the Georgia Piedmont; Pine Mountain is known for its unique assemblage of plant species and communities from both the Southern Appalachians and Coastal Plain (Jones 1974; Carter and Floyd 2013). The only known extant population in Harris County grows along the ridge of Pine Mountain in gravelly sandy loam soils developed over Hollis-Quartzite of a dry oak-hickory-pine woodland. Associates at the type locality include a canopy of *Carya pallida* (Ashe) Engl. & Graebn., *Pinus palustris* Mill., *P. taeda* L., and *Quercus montana* Willd., shrub layer of *Prunus alabamensis* C.Mohr, *Prunus umbellata* Elliott, *Quercus georgiana* M.A.Curtis, and *Vaccinium arboreum* Marshall, and herbaceous layer of *Baptisia bracteata* Muhl. ex Elliott, *Houstonia longifolia* Gaertn., *Hypoxis hirsuta* Coville, and *Scutellaria elliptica* Muhl. var.

*hirsuta* (Short & R.Peter) Fernald. Historically, the ridge tops of Pine Mountain were dominated by fire adapted, open montane longleaf pine (*Pinus palustris*) and *Quercus* spp. woodland communities (Klaus 2019). One collection notes a population growing in exposed full sun at the time of collection (e.g. *Samuel B. Jones 20708*, NCU). The only known extant population persists under a dense, fire-suppressed, hardwood-dominated canopy with deep leaf litter. *Clematis terminalis* was likely more abundant on Pine Mountain prior to widespread fire suppression on the mountain (see Conservation). The deeply branched roots of many *Clematis* species are likely to be well adapted to fire (pers. obs.; Floden 2013). Efforts to locate the Meriwether County population were not successful. Multiple collections from Harris County, Georgia by S. B. Jones (*21764*, US; *20708*, NCU) were made, shown by different collection numbers, but locality data are too ambiguous to infer whether they represent different populations.

**Phenology**— *Clematis terminalis* exhibits a distinctly early season phenology. Collections indicate it flowers from mid to late April. The flowering period likely extends into early May. A single collection of fruiting material (*Thomas H. Murphy 315*, APSC, MO) has nearly mature fruit present in mid-June.

**Etymology**— The epithet “terminalis” describes a diagnostic character of the terminal inflorescence this taxon possesses, which is unique as a member of the *C. reticulata* species complex.

**Conservation**— Because *C. terminalis* has only been relocated at a single extant site, we recommend the highest level of protection at the state and federal levels. Still, additional surveys are needed to determine if there are additional extant populations. The only known population has few reproductive individuals, most likely due to the dense canopy, resulting from decades of

fire suppression. On the eastern edge of the Pine Mountain escarpment, a dendrochronological study found mean fire intervals of 1.2 and 2.6 years for pre-1840 and 1840 to 1915, respectively (Klaus 2019). The period of 1915 to present was found to have a dramatically altered mean fire interval of 11.4 years. This also corresponded to change in canopy composition with decreased fire tolerance in the longleaf pine systems of Pine Mountain. This suggests that frequent fire events are needed to maintain a sparser canopy for the persistence of herbaceous species. Efforts to locate new populations should be focused within similar geologic formations along the ridges of Pine Mountain and Oak Mountain of Georgia, as well as extensions of this formation into eastern Alabama (Adams 1930). Asexual propagation by cuttings have been successfully rooted by the first author in a 5:1, perlite: peat mix after being dipped in indolebutyric acid concentration of 2,000 ppm (pers. obs.) and could serve as a method to safeguard plants.

***Specimens examined (paratypes)***—USA—**Georgia**: Harris Co., along Hwy 190 at E end of FDR State Park on Pine Mt., 13 April 1972, *Samuel B. Jones 21764 with Vince Coffey* (GA<sup>U</sup>); roadside along top of Pine Mountain, 1 April 1971, *Samuel B. Jones 20610* (GA); roadside along top of Pine Mountain, Roosevelt State Park, 25 April 1971, *Samuel B. Jones 20708 with Gerald and Glenda Miller* (BRIT<sup>U</sup>, FLAS<sup>M</sup>, GH<sup>U</sup>, NCU<sup>U</sup>, TENN, USF);. Georgia Route 190 along the ridge of Pine Mountain, ca. 7 mi. from the junction with U.S. Route 27, 27 April 1959, *C.E. Woods, Jr. 9023 with K.A. Wilson* (GH<sup>U</sup>);. Pine Mountain Ridges, 4.6 miles southeast of White Sulphur Springs [abbreviated due to rarity], 14 June 2019, *Thomas H. Murphy 315 with Zach Irick* (APSC<sup>U</sup>, MO<sup>U</sup>); Meriwether Co., 2.6 mi via air ESE of Warm Springs on road along Cooler Branch, Pine Mountain, 16 May 1972, *Samuel B. Jones 21827 with Caywood Chapman* (GA).

### Key to the *Clematis reticulata* Species Complex

- A.** Plants erect-herbaceous in flower, becoming scandent in late season. Initial inflorescences always terminal, solitary, ebracteate (occasional axillary and bracteate in late season). Proximal-most leaflets of mid-stem leaves sessile or short-petiolulate, petiolules 3.1–9.4 (10.3) mm. Endemic to the Pine Mountain Ridges of west-central Georgia.....**6. *Clematis terminalis***
- AA.** Plants vining in habit when in flower. Primary inflorescences axillary. Proximal-most leaflets of mid-stem leaves usually long-petiolulate, petiolules (5.5) 16.9–22.7 (49.0) mm.....**B**
- B.** Ratio of peduncle to combined peduncle and pedicel (0.20) 0.35–0.41 (0.70), foliaceous bracts appearing elevated on inflorescence. Ratio of sepal length to sepal width (2.1) 2.8–3.2 (4.6)....**C**
- C.** Leaflets distinctly coriaceous with dense network of raised reticulate venation, average areole area (0.19) 0.37–0.44 (0.84) mm<sup>2</sup>. Widest adaxial leaflet veins (not including mid-vein) (0.09) 0.13–0.15 (0.28) mm. Leaflet apices usually rounded to broadly acute. Sepal trichomes short-pubescent with longest trichomes (0.27) 0.32–0.39 (0.47) mm. Achene rim (sum of both ends) to achene width ratio (0.22) 0.26–0.32 (0.38). Native to lower coastal plain of Alabama, Florida, Georgia, Mississippi, and South Carolina.....**4. *Clematis reticulata* s.s.**
- CC.** Leaflets distinctly membranaceous to subcoriaceous, average areole area (0.36) 0.61–0.94 (2.69) mm<sup>2</sup>. Raised reticulate venation forming a sparsely concentrated network. Widest adaxial leaflet veins (not including mid-vein) (0.04) 0.07–0.09 (0.14) mm. Leaflet apices acute to acuminate, rarely rounded. Sepal trichomes puberulent with longest trichomes (0.45) 0.52–0.66 (0.84) mm. Achene rim (sum of both ends) to achene width ratio (0.30) 0.32–0.46 (0.50). Native to northern and central (mostly north of Alabama River), west-central Georgia, northeastern Mississippi, and extreme south-central Tennessee.....**5. *Clematis subreticulata***

**BB.** Ratio of peduncle to combined peduncle and pedicel (0.02) 0.07–0.10 (0.20), appearing basal or near-basal on inflorescence. Ratio of sepal length to sepal width (1.8) 2.2–2.6 (3.6).....**D**

**D.** Leaflet abaxial usually densely puberulent, occasionally glabrous or sparsely puberulent.

Leaflet shape elliptic-oblong to rotund, occasionally ovate, with generally rounded apices.

Leaflets coriaceous. Raised reticulate venation forming a densely concentrated network, average closed areole area (0.19) 0.33–0.46 (1.22) mm<sup>2</sup>. Widest adaxial leaflet veins (not including mid-vein) (0.07) 0.11–0.14 (0.21) mm. Endemic to the West Gulf Coastal Plain of Arkansas,

Louisiana, and Texas..... **1. *Clematis arenicola***

**DD.** Leaflet abaxial glabrate to moderately pubescent. Leaflet shape lanceolate to ovate, never rotund or elliptic-oblong, generally with distinctly acute or acuminate apices, rarely rounded.

Leaflets membranaceous to subcoriaceous. Raised reticulate venation forming a sparsely concentrated network, average closed areole area (0.59) 0.98–1.21 (2.4) mm<sup>2</sup>. Widest adaxial leaflet veins (not including mid-vein) (0.03) 0.06–0.08 (0.12) mm.....**E**

**E.** Primary pedicels short, (16.2) 13.5–38.0 (69.19) mm long and pendulous, hanging below leaflets of corresponding node when in flower (erect in fruit). Longest sepal trichomes 0.51–0.66 (0.69) mm long. Sepal base color dark purple to faded lilac. Achene length to width ratio 1.0–1.2. Achene tail hairs white to yellow. Endemic to the southern Ouachita Mountains of southwestern Arkansas and southeastern Oklahoma.....**3. *Clematis ouachitensis***

**EE.** Primary pedicels long, (38) 58.5–104.0 (180.3) mm, held erect above leaflets of corresponding node when in flower and fruit. Longest sepal trichomes (0.25) 0.28–0.40 (0.47) mm long. Sepal base color light vibrant pink to purple. Achene length to width ratio 1.1–1.5 (1.9). Achene tail hairs dark yellowish brown to coppery brown. Endemic to east-central Tennessee.....**2. *Clematis cumberlandensis***

### Literature Cited

- Adams, G. I. 1930. The significance of the quartzites of Pine Mountain in the crystallines of West Central Georgia. *The Journal of Geology*, 38(3): 271–279.
- Aquino, D., Cervante, R. C., Gernandt, D. S., and S. Arias. 2019. Species delimitation and phylogeny of *Epithelantha* (Cactaceae). *Systematic Botany* 44(3): 600–615.
- Correll, D. S. and M. C. Johnston. 1979. *Manual of the Vascular Plants of Texas* (2nd printing). The University of Texas at Dallas, Richardson.
- Carter, R. and R. Floyd. 2013. Landscape scale ecosystems of the Pine Mountain Range, Georgia. *Castanea* 78(4): 231–255. <https://doi.org/10.2179/13-012>.
- Dennis, W. M. 1976. A Biosystematic Study of *Clematis* Section *Viorna* Subsection *Viornae*. University of Tennessee, Knoxville.
- De Queiroz, K. 2007. Species concepts and species delimitation. *Systematic Biology* 56:879–886.
- Erickson, R. O. 1943. Taxonomy of *Clematis* section *Viorna*. *Annals of the Missouri Botanical Garden* 30:1–62.
- Estes, D. 2006. A new narrowly endemic species of *Clematis* (Ranunculaceae: subgenus *Viorna*) from northeastern Texas. *SIDA* 22:65–77.
- Estill, J. C. and M. B. Cruzan. 2001. Phylogeography of rare plant species endemic to the southeastern United States. *Castanea* 66:3–23.
- Fleming, G. P., J. B. Nelson, and J. F. Townsend. 2011. A new hedge-nettle (*Stachys*: Lamiaceae) from the Mid-Atlantic Piedmont and Coastal Plain of the United States. *Journal of the Botanical Research Institute of Texas* 5 (1): 9–18.
- Floden, A. 2013. A new leatherflower (*Clematis*: Ranunculaceae) from the Southern Appalachians. *Journal of Botanical Research Institute of Texas* 7:1–7.
- Floden, A. 2016. A new endemic hedgenettle (*Stachys*: Lamiaceae) from Tennessee. *Phytoneuron* 2016-53: 1–6.
- Johnson M. 2001. The genus *Clematis*. Södertälje: Magnus Johnsons Plantskola AB.
- Jones, S. B. 1974. The flora and phytogeography of the Pine Mountain region of Georgia. *Castanea* 39:113–149.

- Kartesz, J.T., The Biota of North America Program (BONAP). 2015. North American Plant Atlas. (<http://bonap.net/napa>). Chapel Hill, N.C. [maps generated from Kartesz, J.T. 2015. Floristic Synthesis of North America, Version 1.0. Biota of North America Program (BONAP). (in press)].
- Keener, B. R. and L. J. Davenport. 2016. Two new hedge-nettles (*Stachys*: Lamiaceae) from the Blue Ridge outliers of East Central Alabama, U.S.A. *Journal of Botanical Research Institute of Texas* 10 (2): 315–323.
- Keener, C. S. 1967. A biosystematic study of *Clematis* subsection *Integrifoliae* (Ranunculaceae). *Journal of the Elisha Mitchell Scientific Society* 83:1–41.
- Keener, C. S. 1975. Studies in the Ranunculaceae of the southeastern United States. III *Clematis* L. *SIDA* 6(1): 33–47.
- Keener, C. S. and M. W. Dennis. 1982. The subgeneric classification of *Clematis* (Ranunculaceae) in temperate North America north of Mexico. *Taxon* 31:37–44.
- Klaus, N. 2019. Fire history of a Georgia montane longleaf pine (*Pinus palustris*) community. *Georgia Journal of Science* 77 (2): Article 5.
- Kral, R. 1982. A new *Clematis* species from northeastern Alabama. *Rhodora* 84:285–291.
- Kral, R. 1987. A new “Viorna” *Clematis* from Northern Alabama. *Annals of the Missouri Botanical Garden* 74:665–669.
- Le, S., Josse, J., and F. Husson. 2008. FactoMineR: An R Package for Multivariate Analysis. *Journal of Statistical Software* 25(1): 1–18.
- Lehtonen, S., M. J. M. Christenhusz, and D. Falck. 2016. Sensitive phylogenetics of *Clematis* and its position in Ranunculaceae. *Botanical Journal of the Linnean Society* 182: 825–867.
- MacRoberts, M. H., B. A. Sorrie, B. R. MacRoberts, and R. Evans. 2002. Endemism in the West Gulf Coastal Plain: Importance of xeric habitats. *SIDA, Contributions to Botany* 20:767–780.
- Majure, L. C., W. S. Judd, P. A. Soltis, and D. E. Soltis. 2017. Taxonomic revision of the *Opuntia humifusa* complex (Opuntieae: Cactaceae) of the eastern United States. *Phytotaxa* 290 (1): 1–101.
- Mohr, C. 1892. Variation in the leaves of *Clematis reticulata* and other notes. *Bulletin of the Torrey Botanical Club* 19:308–309.
- NatureServe. 2020. NatureServe Explorer [web application]. NatureServe, Arlington, Virginia. Available <https://explorer.natureserve.org/>. Accessed May 04, 2020.

- Naczi, R. F. C. 1997. *Carex pigra*, a new species of *Carex* section *Griseae* (Cyperaceae) from the Southeastern United States of America. *Novon* 7(1): 67–71. doi:10.2307/3392075.
- Naczi, R. F. C., A. A. Reznicek, and B. A. Ford. 1998. Morphological, geographical, and ecological differentiation in the *Carex Willdenowii* complex (Cyperaceae). *American Journal of Botany* 85 (3): 434–447.
- Naczi, R., R. Kral, , and C. Bryson. 2001. *Carex cumberlandensis*, a new species of section *Careyane* (Cyperaceae) from the Eastern United States of America. *SIDA, Contributions to Botany* 19(4): 993–1014.
- Naczi, R. F. C. and B. A. Ford. 2001. Systematics of the *Carex jamesii* complex (Cyperaceae: sect. *Phyllostachyae*). *SIDA, Contributions to Botany* 19 (4): 853–884.
- Naczi, R. F. C., C. T. Bryson, and T. S. Cocharane. 2002. Seven new species and one new combination in *Carex* (Cyperaceae) from North America. *Novon* 12 (4): 508–532. doi: 10.2307/3393132.
- Nelson, J. B. 2008. A new hedge-nettle (*Stachys*: Lamiaceae) from the Interior Highlands of the United States, and keys to the southeastern species. *Journal of the Botanical Research Institute of Texas* 2 (2): 761–769.
- Nelson, J. B. and D. B. Rayner. 2014. A new hedge-nettle (*Stachys*: Lamiaceae) from South Carolina, U.S.A. *Journal of the Botanical Research Institute of Texas* 8 (2): 431–440.
- Nery, K. E. and P. Fiaschi. 2019. Geometric morphometrics dismiss the polymorphic *Hydrocotyle quinqueloba* (Araliaceae) from the Neotropics. *Systematic Botany* 44 (2): 451–469.
- Noss, R. F., W. J. Platt, B. A. Sorrie, A. S. Weakley, D. B. Means, J. Costanza, and R. K. Peet. 2015. How global biodiversity hotspots may go unrecognized: lessons from the North American Coastal Plain. *Diversity and Distributions* 21: 236–244.
- Pohlert, T. 2020. PMCMRplus: Calculate Pairwise Multiple Comparisons of Mean Rank Sums Extended. R package version 1.4.4. <https://CRAN.R-project.org/package=PMCMRplus>.
- Poindexter, D. B. and J. B. Nelson. 2011. A new hedge-nettle (*Stachys*: Lamiaceae) from the Southern Appalachian Mountains. *Journal of the Botanical Research Institute of Texas* 5 (2): 405–414.
- Prebble, J. M., H. M. Meudt, J. A. Tate, and V. V. Symonds. 2018. Bolstering species delimitation in difficult species complexes by analyzing herbarium and common garden morphological data: a case study using the New Zealand native *Myosotis pygmaea* species group (Boraginaceae). *Systematic Botany* 43:266–289.

- Pringle, J. S. 1997. *Clematis*. In: Flora of North America Editorial Committee, eds. 1993+. Flora of North America North of Mexico. 19+ vols. New York and Oxford. Vol. 3.
- R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Rohart, F., B. Gautier, A. Singh, and K.-A. Le Cao. 2017. mixOmics: An R package for 'omics feature selection and multiple data integration. *PLoS computational biology* 13(11):e1005752.
- Schilling, E. E., A. Floden, and S. B. Farmer. 2013. A new sessile-flowered *Trillium* species from Tennessee. *Castanea* 78 (2): 140–147.
- Schilling, E. E., A. Floden, J. Lampley, T. S. Patrick, and S. B. Farmer. 2017. A new species of *Trillium* subgen. *Delostylium* (Melanthiaceae, Parideae). *Phytotaxa* 296 (3): 287–291.
- Schilling, E. E., A. Floden, J. Lampley, T. S. Patrick, and S. B. Farmer. 2019. A new species of *Trillium* (Melanthiaceae) from Central Georgia and its phylogenetic position in subgenus *Sessilium*. *Systematic Botany* 44 (1): 107–114.
- Small, J. K. 1933. Ranunculaceae. *Manual of the Southeastern Flora*. University of North Carolina Press, Chapel Hill, NC. Pages 525–528.
- Sorrie, B. A. and A. S. Weakley. 2001. Coastal plain vascular plant endemics: phytogeographic patterns. *Castanea* 66:50–82.
- The Tennessee Flora Committee. 2015. *Guide to the Vascular Plants of Tennessee*. C. Bailey, E. W. Chester, D. Estes, C. Fleming, A. Floden, D. Horn, J. Shaw, D. H. Webb, and B. E. Wofford, Eds. The University of Tennessee Press, Knoxville.
- Thiers, B. 2016. Index Herbariorum: A Global Directory of Public Herbaria and Associated Staff. New York Botanical Garden's Virtual Herbarium. <http://sweetgum.nybg.org/science/ih/>.
- Turland, N. J., J. H. Wiersema, F. R. Barrie, W. Greuter, D. L. Hawksworth, P. S. Herendeen, S. Knapp, W.-H. Kusber, D.-Z. Li, K. Marhold, T. W. May, J. McNeill, A. M. Monro, J. Prado, M. J. Price, and G. F. Smith (eds.) 2018: International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. *Regnum Vegetabile* 159. Glashütten: Koeltz Botanical Books. doi: <https://doi.org/10.12705/Code.2018>.
- Wang, W. T. and L.-Q. Li. 2005. A new system of classification of the genus *Clematis* (Ranunculaceae). *Acta Phytotaxonomica Sinica* 43:431–488.

- Ward, D. B. 2007. Thomas Walter typification project, IV: neotypes and epitypes for 43 Walter names, of genera A through C. *Journal of the Botanical Research Institute of Texas* 1 (2): 1091–1100.
- Weakley, A. S. 2015. Flora of the Southern and Mid-Atlantic States, Working Draft of 29 May, 2015, University of North Carolina Herbarium, Chapel Hill, [http://www.herbarium.unc.edu/FloraArchives/WeakleyFlora\\_2015-05-29.pdf](http://www.herbarium.unc.edu/FloraArchives/WeakleyFlora_2015-05-29.pdf).
- Wencai, W. and B. Bartholomew. 1997. *Clematis*. In: Wu, Z. Y., P. H. Raven and D. Y. Hong, eds. 2001. *Flora of China*. Vol. 6 (Caryophyllaceae through Lardizabalaceae). Science Press, Beijing, and Missouri Botanical Garden Press, St. Louis.
- Xie, L., J. Wen, and L.Q. Li. 2011. Phylogenetic analyses of *Clematis* (Ranunculaceae) based on sequences of nuclear ribosomal ITS and three plastid regions. *Systematic Botany* 36:907–921.
- Yang, T. Y. A. and D. M. Moore. 1999. A revision of the *Viorna* group of species (section *Viorna sensu* Prantl) in the genus *Clematis* (Ranunculaceae). *Systematics and Geography of Plants* 38:281–303.
- Yang, W. J., L. Q. Li, and L. Xie. 2009. A revision of *Clematis* section *Atragene* (Ranunculaceae). *Journal of Systematics and Evolution* 47 (6): 552–580.
- Zollner, D., B. R. MacRoberts, M. H. MacRoberts, and D. Ladd. 2005. Endemic vascular plants of the Interior Highlands, U.S.A. *SIDA, Contributions to Botany* 21:1781–1791.

## Appendices

**Appendix A.** Character collection methods, guidelines, and calculations.

Character	Data type	Method of data collection	Measuring guideline	Method of calculation
ACLW	ratio	Digital calipers	As many available, up to three, from corresponding node.	Average up to 3
ACRTW	ratio	Digital calipers for achene body width, ocular micrometer for achene rim thickness	As many available, up to three	Average up to 3, when possible
ACTL	mm	Measuring tape	As many available, up to three	Average up to 3, when possible
ANCOL	mm	Digital calipers	From three available anthers of flower with longest available sepal	Average up to 3, when possible
AREAR	mm <sup>2</sup>	Image from dissecting scope	From longest, proximal-most available leaflet of node measured	Average of as many were present within a fixed rectangle (6.40 mm x4.27 mm)
BRPL	ratio	Digital calipers or measuring tape	Pedicle/ peduncle selected based on corresponding node measured	Average up to 2, when possible
INFHAB	nominal	Visual	Assessed across entire plant	NA
INFPOS	nominal	Visual	Assessed across entire plant/ specimen	NA
LFTH	ordinal	Visual	Assessed across entire plant/ specimen	NA
PTULL	mm	Digital calipers	From longest, proximal-most leaflets of each leaf	Average up to 2, when possible
PDLST	ratio	Digital calipers	Pedicle/ peduncle selected based on corresponding node measured, stem width taken immediately below enlarged stem leading up to node	Average up to 2, when possible
SPLW	ratio	Digital calipers	From longest sepals on each flower measured of node	Average up to 2, when possible
TLLF	mm	Ocular micrometer	From longest, proximal-most available leaflet of node measured	Average up to 3, when possible
TLSP	mm	Ocular micrometer	From longest available sepal of node being measured	Average up to 3, when possible
VNWD	mm	Image from dissecting scope	From longest, proximal-most available leaflet of node measured	Average of 3 widest vein segments in fixed rectangle (6.40 mm x4.27 mm)
W90LL	ratio	Digital calipers	From longest, proximal-most available leaflet of node measured	Single measurement

**Appendix B.** Sample size summary of specimens measured for multivariate and univariate analyses of herbarium specimens and common garden datasets, subset by flowering and fruiting individuals. Note that all specimens used for multivariate analyses were included in univariate analyses, which is shown in sample sizes listed here. Fruiting specimens are not indicated for common garden dataset because it only included flowering individuals. Multivariate and univariate analyses are indicated together in the common garden dataset because all hypothesized taxa had the same sample size for both sets of analyses. More detailed information on the number of specimens that had a single character available for univariate analyses, see sample sizes listed in Table 5. Values with ‘\*’ are corrected for the two specimens that contained flowering and fruiting material and were therefore included more than once in subsets.

<b>Herbarium specimens</b>							<b>Common Garden</b>
Multivariate Analyses			Univariate Analyses			Multivariate and Univariate Analyses	
	Flowering	Fruiting	Total	Flowering	Fruiting	Total	Flowering
AGCP	33	23	<b>56</b>	42	35	<b>77</b>	24
CPTN	22	9	<b>31</b>	26	10	<b>36</b>	3
NOAL	11	7	<b>18</b>	12	7	<b>19</b>	14
OUMT	7	7	<b>14</b>	8	9	<b>17</b>	6
TMAL	4	4	<b>8</b>	6	5	<b>11</b>	3
PMGA	5	0	<b>5</b>	10	2	<b>12</b>	1
WGCP	17	13	<b>30</b>	18	16	<b>34</b>	20
<b>Total</b>	<b>99</b>	<b>63</b>	<b>160*</b>	<b>122</b>	<b>84</b>	<b>204*</b>	<b>71</b>

**Appendix C.** Pairwise comparisons of hypothesized taxa of herbarium specimens dataset.

Each comparison lists characters that are significantly different with Games-Howell test for quantitative characters and Dwass-Steel test for the ordinal character, LFTH, at  $p < 0.05$ . Nominal character differences were inferred when both hypothesized taxa possessed different states of a given character. Nominal characters are indicated in bold.

BRPL indicates bract placement.

	AGCP	CPTN	NOAL+TMAL	OUMT	PMGA	WGCP
AGCP	–	AREAR, BRPL, LFTH, PDLST, SPLW, VNWD, W90LL	ACRW, AREAR, LFTH, PDLST, TLLF, TLSP, VNWD, W90LL	ACLW, AREAR, BRPL, LFTH, PDLST, TLLF, TLSP, VNWD, W90LL	<b>INFPOS</b> , LFTH, PTLU, TLLF, TLSP, VNWD	ANCOL, BRPL, TLLF, TLSP, VNWD
CPTN	–	–	ACRW, BRPL, LFTH, SPLW, TLLF, TLSP, VNWD	ACTL, PDLST, TLLF, TLSP	ANCOL, <b>INFPOS</b> , LFTH, PTLU, SPLW, TLLF, TLSP, W90LL	AREAR, LFTH, TLLF, TLSP, VNWD, W90LL
NOAL+TMAL	–	–	–	ACLW, ACRW, ACTL, BRPL, PDLST	ANCOL, <b>INFPOS</b> , PTLU	AREAR, BRPL, LFTH, SPLW, VNWD, W90LL
OUMT	–	–	–	–	BRPL, <b>INFPOS</b> , LFTH, PTLU	ANCOL, AREAR, LFTH, PDLST, VNWD, W90LL
PMGA	–	–	–	–	–	ANCOL, BRPL, <b>INFPOS</b> , LFTH, PTLU, VNWD
WGCP	–	–	–	–	–	–

**Appendix D.** Pairwise comparisons of hypothesized taxa of common garden dataset. Each comparison lists characters that are significantly different with Games-Howell test for quantitative characters and Dwass-Steel test for the ordinal character, LFTH, at  $p < 0.05$ . Nominal character differences were inferred when both hypothesized taxa possessed different states of a given character. Nominal characters are indicated in bold. BRPL indicates bract placement. Hypothesized species groups with a '\*' indicates too small of a sample size to test for statistical significance. In this case, characters listed maintained directional differences with herbarium specimens dataset listed in Appendix B.

	AGCP	CPTN*	NOAL+TMAL	OUMT	PMGA*	WGCP
AGCP	–	AREAR, BRPL, LFTH, PDLST, SPLW, VNWD, W90LL	AREAR, LFTH, SPLW, TLLF, TLSP, VNWD, W90LL	AREAR, BRPL, <b>INFHAB</b> , LFTH, PDLST, TLLF, TLSP, VNWD, W90LL	<b>INFPOS</b> , LFTH, PTLU, TLLF, TLSP, VNWD	ANCOL, BRPL, TLLF, TLSP, VNWD
CPTN*	–	–	BRPL, LFTH, SPLW, TLLF, TLSP, VNWD	<b>INFHAB</b> , PDLST, TLLF, TLSP	ANCOL, <b>INFPOS</b> , LFTH, PTLU, SPLW, TLLF, TLSP, W90LL	AREAR, LFTH, TLLF, TLSP, VNWD, W90LL
NOAL+ TMAL	–	–	–	ANCOL, BRPL, <b>INFHAB</b> , PDLST, SPLW	ANCOL, <b>INFPOS</b> , PTLU	ANCOL, AREAR, BRPL, LFTH, SPLW, VNWD, W90LL
OUMT	–	–	–	–	BRPL, <b>INFHAB</b> , <b>INFPOS</b> , LFTH, PTLU	ANCOL, AREAR, <b>INFHAB</b> , LFTH, PDLST, TLLF, VNWD, W90LL
PMGA*	–	–	–	–	–	ANCOL, BRPL, <b>INFPOS</b> , LFTH, PTLU, VNWD
WGCP	–	–	–	–	–	–