



Systematics and Evolution of Inflorescence Structure in the Tradescantia Alliance (Commelinaceae)

Authors: Hertweck, Kate L., and Pires, J. Chris

Source: Systematic Botany, 39(1) : 105-116

Published By: The American Society of Plant Taxonomists

URL: <https://doi.org/10.1600/036364414X677991>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Systematics and Evolution of Inflorescence Structure in the *Tradescantia* Alliance (Commelinaceae)

Kate L. Hertweck^{1,2,3} and J. Chris Pires¹

¹Division of Biological Sciences, 1201 Rollins Street, Bond Life Science Center Room 311, University of Missouri, Columbia, Missouri 65211, U. S. A.

²National Evolutionary Synthesis Center, 2024 West Main Street, Suite A200, Durham, North Carolina 27705, U. S. A.

³Author for correspondence (k8hertweck@gmail.com)

Communicating Editor: Rachel Levin

Abstract—The *Tradescantia* alliance (subtribes Tradescantiinae and Thyrsantheminae of tribe Tradescantieae, family Commelinaceae) comprises a group of closely related New World genera exhibiting considerable variation in morphological, life history, and genomic traits. Despite ecological and cytogenetic significance of the *Tradescantia* alliance, phylogenetic relationships among genera and species remain uncertain. In particular, variation in inflorescence morphology has confounded classification and taxonomy. We inferred phylogenetic relationships using two plastid loci (*rpL16*, *trnL-trnF*) for 85 taxa in Commelinaceae, with sampling focused in the *Tradescantia* alliance. Constraint tests supported only subtribe Tradescantiinae, *Tripogandra* and *Tinantia* as monophyletic, with *Tripogandra* nested within *Callisia*. We estimated ancestral states for both breeding system and inflorescence condensation and tested for a correlation. Inflorescence morphology, an important character for generic identification, is more labile than previously expected, with condensed inflorescences evolving twice with three subsequent reversals. Breeding system evolution is more complex, with many more switches between self compatibility and self incompatibility and more uncertainty in ancestral state estimates. The presence of self compatible and incompatible species allowed us to test the hypothesis that self compatible species will have condensed inflorescences, as less allocation to floral display is necessary. While we did not find a correlation between self compatibility and inflorescence condensation, we propose additional floral and inflorescence characteristics that may have contributed to variation in breeding system.

Keywords—Breeding system, inflorescence condensation, monocots, *trnL-trnF*, *rpL16*, spiderworts

Taxa comprising subtribes Tradescantiinae and Thyrsantheminae of tribe Tradescantieae in the monocot family Commelinaceae (dayflower family, Faden and Hunt 1991) are known by a variety of amusing common names, including bridal veil, widow's tears, spiderwort, snotweed, grass violet, wandering Jew, and Moses-in-a-basket. Henceforth referred to as the *Tradescantia* alliance, these eleven New World genera (*Tradescantia*, *Gibasis*, *Callisia*, *Tripogandra*, *Elasis*, *Tinantia*, *Thyrsanthemum*, *Weldenia*, *Gibasoides*, *Matudanthus*, *Sauvallea*) maintain variable levels of genome change, including polyploidy, aneuploidy, hybridization, and genomic rearrangements (Jones and Jopling 1972, Jones and Kenton 1984), and exhibit considerable ecological diversity (Faden 1998). Of the 650 species in Commelinaceae, the *Tradescantia* alliance contains ca. 144; genera range from large (*Tradescantia*, ca. 70 species) to monotypic (*Elasis*, *Weldenia*, *Gibasoides*, *Matudanthus*, *Sauvallea*; Faden 1998).

Several factors contribute to a complicated history of classification in Commelinaceae, some of which are particularly problematic in the *Tradescantia* alliance. First, petals in Commelinaceae are short-lived and deliquescent; herbarium specimens rarely preserve floral characteristics relevant to some classification attempts (Fig. 1; Woodson 1942). Second, morphological characters in Commelinaceae are homoplasious (Evans et al. 2000a); both circumscription of the *Tradescantia* alliance and relationships among genera using a cladistic analysis of morphology were incongruent with previous classification schemes (Evans et al. 2000b). Collection of anatomical data confirmed the presence of convergent evolution for some diagnostic traits (Tomlinson 1966). Third, interspecific hybridization may have played a role in the evolution of the group. Historical hybridization in some *Tradescantia* species may have led to speciation by chromosomal differentiation (Jones 1990), and ongoing gene flow continues between closely related species, such as

the erect *Tradescantia* (Sect. *Tradescantia*, series *Virginianae*, Anderson 1936). While much progress has been made in circumscribing subtribes and genera, clarifying relationships between members of the *Tradescantia* alliance would allow for further explorations into the evolution of ecological and genomic traits.

The most recent Commelinaceae classification (Faden 1998) effectively resolves the shuffling of taxa between groups from several previous classification schemes (Faden and Hunt 1991). In the most recent treatment (Faden 1998), tribe Tradescantieae comprises 25 genera, 285 species, and is divided into seven subtribes: three from the Old World and four from the New World. This system places *Gibasis*, *Tradescantia*, *Callisia* and *Tripogandra* in subtribe Tradescantiinae; *Thyrsanthemum*, *Gibasoides*, *Tinantia*, *Elasis*, *Matudanthus*, and *Weldenia* into subtribe Thyrsantheminae. *Sauvallea* is an enigmatic monotypic genus from Cuba with uncertain placement in either of the two subfamilies (Faden and Hunt 1991).

Current generic circumscriptions for subtribes Tradescantiinae and Thyrsantheminae are the result of gradual dismemberment and then restructuring of groups. In his description of Mexican Commelinaceae, Hunt (1993) favored the inclusion of several minor genera into larger, broader genera of Tradescantiinae: *Tradescantia* (including *Campelia*, *Cymbispatha*, *Rhoeo*, *Separotheca*, *Setcreasea*, *Zebrina*), *Gibasis* (including *Aneilema* sensu Matuda, in part), *Callisia* (including *Aploleia*, *Cuthbertia*, *Hadrodemas*, *Leptorrhoeo*, *Phyodina*, *Spironema*) and *Tripogandra* (including *Neodonellia*). Hunt's (1980) treatment of *Tradescantia* initially identified eight sections, with four more subsequently added (Appendix 1, Hunt 1986a). *Gibasis* is classified into two sections (Heterobasis and Gibasis) using a suite of characters including chromosome morphology (Hunt 1985). Hunt (1986b) favored dividing *Callisia* into five sections rather than splitting into many genera of few species each.

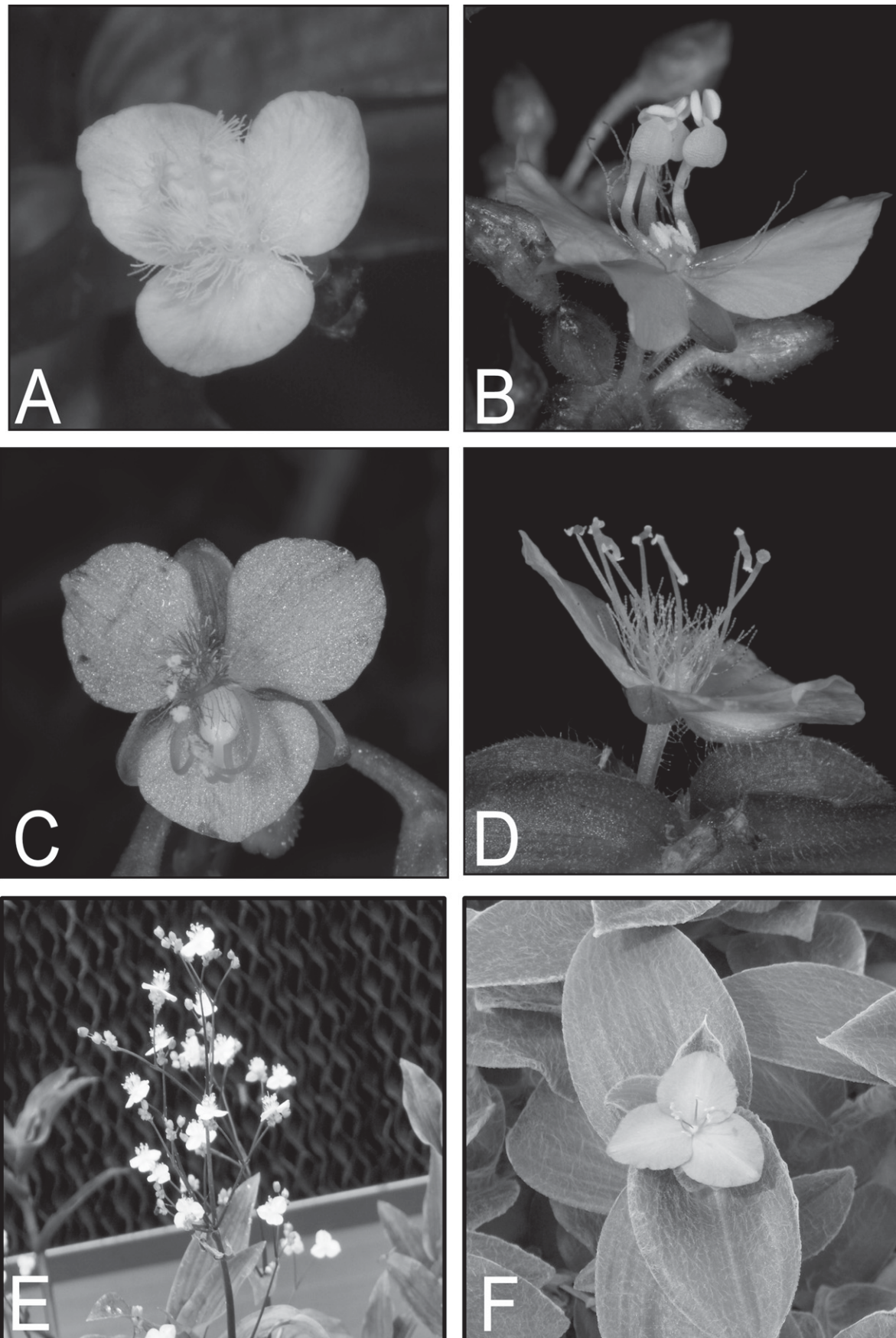


FIG. 1. Floral morphological diversity in the *Tradescantia* alliance. Selected exemplars represent characteristic features of each genus. Floral morphology: A. *Gibasis*. B. *Tripogandra*. C. *Tinantia*. D. *Tradescantia*. Inflorescence morphology: E. *Gibasis*. F. *Tradescantia*. Plates A–D taken by Travis Columbus.

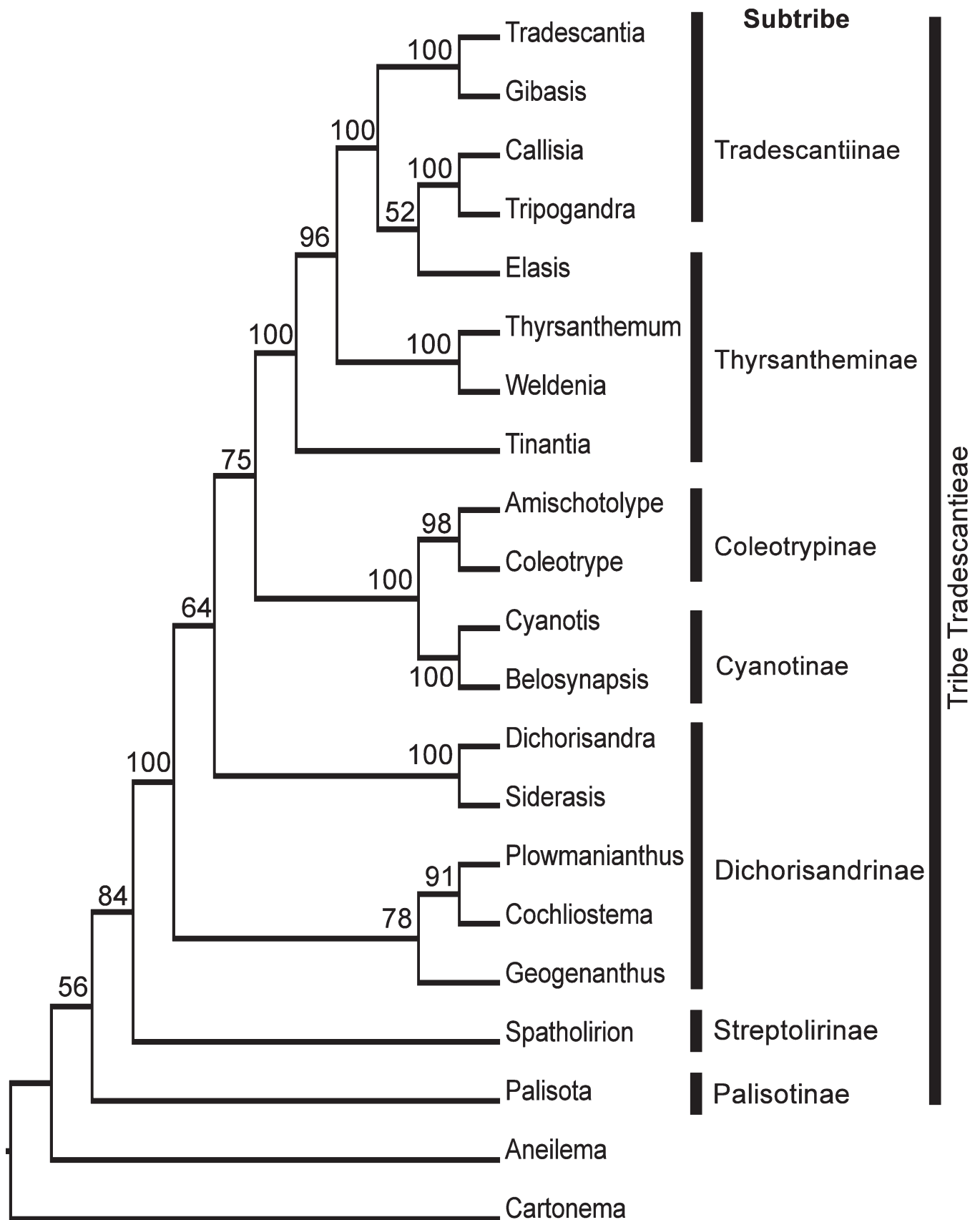


FIG. 2. Previous hypothesis for phylogenetic relationships in tribe Tradescantieae. Modified from Wade et al. (2006), inferred from one taxon per genus from morphological and molecular data. Numbers by nodes represent bootstrap support.

The first molecular phylogeny of the family suggested that tribe Tradescantieae is monophyletic with the exception of *Palisota* (Evans et al. 2003). As sampling was limited to one to few species per genus, however, further exploration of the relationships among genera is needed. A more recent phylogeny including comprehensive sampling of genera in tribe Tradescantieae used morphological and molecular data, and is the basis for sampling in the present study (Wade et al. 2006). It revealed a more derived New World clade composed of *Tradescantia*, *Gibasis*, *Callisia*, *Tripogandra*, *Elasis*, *Tinantia*, *Thyrsanthemum*, and *Weldenia* (Fig. 2). A combined analysis of a cpDNA locus (*trnL-trnF*) and a multiple copy nuclear locus (*5S NTS*) presents *Tradescantia* and *Gibasis* as both monophyletic, with *Callisia* as paraphyletic (Burns et al. 2011). Another phylogenetic study focused sampling on *Callisia*; two plastid loci nested *Tripogandra* inside *Callisia* with *Tradescantia* sister to that clade (Bergamo 2003).

Inflorescence structure is one of the most important characters for taxonomic classification in the *Tradescantia* alliance, especially to distinguish subtribes and genera (Table 1), although botanists historically disagreed on interpretation of relevant structures (Brenan 1966). The basic unit of inflorescence in Commelinaceae is a scorpioid cyme, or cincinnus. Inflorescences of taxa belonging to subtribe Tradescantiinae are characterized by a pair of such cymes fused back-to-back. The exception to this pattern is *Gibasis*, in which cymes are not fused but may be grouped in pairs or umbelliform clusters (Hunt 1985). Cymes from inflorescences representing subtribe Thyrsantheminae are never fused and appear thyrseform or as a single cincinni (Faden and Hunt 1991). The hypothesized trend in inflorescence evolution is towards reduced parts and axes (Brenan 1966). For example, *Gibasis* cyme bracts are reduced to the point of appearing absent

while *Tradescantia* possesses large, spatheaceous bracts (Faden 1998).

Variation in inflorescence structure in the *Tradescantia* alliance is matched by switches in breeding system between self compatible (SC) and self incompatible (SI). Owens (1981) comprehensively surveyed breeding system in Commelinaceae and noted that genera belonging to tribe Tradescantieae are predominantly SI, presumably to control outbreeding. The exception is *Tripogandra*, in which only one of six sampled species was SI. Four additional genera (*Callisia*, *Dichorisandra*, *Gibasis*, *Tradescantia*) contained both SI and SC species. A partial breakdown in SI appeared to be occurring in several species of *Tradescantia*, and additional intraspecific variation in breeding system in the alliance was attributed to different cytotypes (Owens 1981). Variation in both inflorescence structure and self incompatibility allows for examination of the relevance of these life history traits in the evolution of the *Tradescantia* alliance.

While it is clear which genera belong in the *Tradescantia* alliance, relationships among these genera remain confusing. The questions addressed by this research are twofold. First, are subtribes and genera monophyletic? The current classifications of family Commelinaceae (Faden 1998; Faden and Hunt 1991) and treatments for *Tradescantia* (Hunt 1980), *Gibasis* (Hunt 1985), *Tripogandra* (Handlos 1975) and *Callisia* (Hunt 1986b) serve as hypotheses of generic composition. Second, how does a molecular phylogeny inform evolution of inflorescence structures relevant to taxonomy in the *Tradescantia* alliance? We expect that selfing species will possess condensed inflorescences (Goodwillie et al. 2010). In this study, we examine these issues by inferring a molecular phylogeny from two plastid loci, *trnL-trnF* and *rpL16*, for 85 taxa and investigating trait evolution. Given the complicated nature of evolution and hypothesized

TABLE 1. Morphological characteristics of taxonomic groups in the *Tradescantia* alliance following Faden (1998). An asterisk (*) indicates genera not included in the current study, and a caret (^) indicates monotypic genera.

	Inflorescence structure	Stamens	Petals
Subtribe Tradescantiinae			
<i>Callisia</i>	Sessile cymes in pairs, often aggregated into larger units	Six or none to three, equal or subequal, filaments glabrous or bearded	Distinct, equal
<i>Gibasis</i>	Pairs or pseudo-umbels of stipitate cymes, axis angled at junction with peduncle	Six, equal, filaments bearded	Distinct, equal
<i>Tradescantia</i>	Sessile cymes in bifacially fused pairs subtended by spatheaceous bracts	Six, equal (slightly unequal), filaments bearded or glabrous	Distinct (connate basally), equal
<i>Tripogandra</i>	Pairs of sessile cymes	Six, dimorphic; external whorl shorter, internal whorl taller, filaments curved in front of the upper petal	Distinct, equal
Subtribe Thyrsantheminae			
<i>Elasis</i> [^]	Solitary cymes forming loose cluster	Six, subequal, filaments bearded	Distinct, equal
<i>Thyrsanthemum</i>	Thyrse or panicle of thyrses	Six, equal, free, filaments bearded	Distinct, equal
<i>Gibasoides</i> ^{*^}	Numerous elongate cymes, each with long peduncle not geniculate at apex; umbelliform	Six, subequal, free, filaments bearded	Distinct, equal
<i>Matudanthus</i> ^{*^}	Solitary sessile cymes	Six, subequal, filaments bearded	Equal
<i>Tinantia</i>	Cymes elongate, solitary, paired, or in paniculiform or umbelliform thyrses	Six, fertile, polymorphic, filaments fused basally. Posterior three stamens shorter with densely bearded filaments; anterior three with longer filaments, lateral bearded and medial glabrous	Distinct, unequal
<i>Sauvallea</i> ^{*^}	Solitary spathe inclosing single flower	Six, equal, filaments bearded	Subequal
<i>Weldenia</i> [^]	Sessile, congested thyrse in center of leaf rosette, numerous sessile cymes	Six, equal, epipetalous, filaments glabrous	Petals united at the base in an elongated tube, lobes free and equal

hybridization in the *Tradescantia* alliance, a phylogeny estimated from plastid loci can provide a simplified version of just matrilineal relationships.

MATERIALS AND METHODS

Taxon Selection—Sampling in our study includes 85 taxa obtained from field collections, botanical gardens, commercial sources, and research collections, as well as sequences previously published in GenBank (Appendix 1). When possible, living specimens were maintained in greenhouses at the University of Missouri for DNA extraction. Herbarium specimens have been deposited in the University of Missouri Dunn-Palmer Herbarium (UMO). The ingroup includes 70 taxa from eight genera, including 30 *Tradescantia* (ca. 70 species total in genus), nine *Gibasis* (11 species), 15 *Callisia* (ca. 20 spp.), five *Tripogandra* (ca. 22 spp.), one *Thyrsanthemum* (3 spp.), six *Tinantia* (14 spp.) and monotypic *Elasis* and *Weldenia*. Obtaining monotypic genera *Sauvallea*, *Gibasoides*, and *Matudanthus* was not possible for this study, and we also lack sampling for a handful of sections in *Tradescantia* and *Callisia*. The outgroup is represented by 17 species from other subtribes in tribe Tradescantieae as well as tribe Commelineae (Faden and Hunt 1991).

Molecular Methods—DNA extraction necessitated a 3 × 6 × CTAB method (Smith et al. 1991) from fresh or frozen leaf tissue. We amplified two plastid loci generally following PCR parameters in Shaw et al. (2005) with minor alterations in MgCl₂ concentrations for recalcitrant taxa. Conserved primers (F71, R1516, Shaw et al. 2005) amplified the *rpL16* intron and two additional internal primers assisted in sequencing (*rpL16F692* ATGGAGAAGCTGTGGGAACGA, *rpL16R690* CGTCCCA CAGCTTCTCCATTA). Conserved primers TabC and TabF amplified the *trnL* intron/*trnL-trnF* intergenic spacer with additional sequencing via internal primers TabD and TabE (Taberlet et al. 1991). The University of Missouri's DNA Core directly sequenced purified products.

Sequence Alignment and Phylogenetic Analysis—We edited resulting sequences using the Lasergene Core Suite (DNASTAR, Madison, Wisconsin) with manual curation and aligned each locus using MUSCLE (Edgar 2004a; Edgar 2004b). We constructed all phylogenetic inferences using RAxML v7.2.8 (Stamatakis 2006) implemented on-line in RAxML BlackBox (Stamatakis et al. 2008). We partitioned the analysis into two loci (*rpL16* and *trnL-trnF*) and implemented a GTR + GAMMA model of molecular evolution for each partition. We assigned members of tribe Commelineae (*Commelina*, *Pollia*, *Ancilema*, *Murdannia*) to the outgroup following Faden and Hunt's (1991) classification system. We used several methods to evaluate confidence intervals and explore alternative hypotheses in our resulting phylogeny. First, we obtained 100 bootstrap replicates in RAxML. Second, we conducted constraint tests to evaluate support for monophyly of subtribes (Tradescantiinae: *Tradescantia*, *Gibasis*, *Callisia*, *Tripogandra*; Thyrsantheminae: *Elasis*, *Thyrsanthemum*, *Tinantia*) and individual genera (*Tradescantia*, *Gibasis*, *Callisia*, *Tripogandra*, *Tinantia*). Constraint trees were inferred using the same parameters as the unconstrained trees. We compared constraint trees using several topology-based tests implemented in CONSEL (Shimodaira and Hasegawa 2001). Sequences were deposited in GenBank (accession numbers in Appendix 1), and alignments and trees were submitted to TreeBASE (study number 12595).

Trait Evolution—We assembled a dataset of two traits from literature and greenhouse observations (Appendix 1). Although sampling in the outgroup was sparse, exclusion of these taxa did not substantially alter results (data not shown). Assignment of species as self incompatible (SI) or compatible (SC) largely followed Owens (1981) and Burns Moriuchi (2006). When SI and SC were reported for the same taxon, we scored the species according to the most common occurrence, or in a few cases, as ambiguous/missing data. Assignment of inflorescence structure state was complicated by three issues. First, interpretation of inflorescence structures in the *Tradescantia* alliance varies widely among taxonomists (Brenan 1966). Second, terminology for inflorescence structure is inconsistent in historical literature (Endress 2010). Finally, we lacked developmental data for all taxa. As a result, we could only assign a general qualitative description for inflorescence condensation. Condensed inflorescences include single cymes, sessile inflorescences, and those subtended by spatheaceous bracts (which in the family are characteristically compressed). Uncondensed inflorescences included pairs or groups of expanded cymes (or cyme pairs) attached to a common rachis, which are thyrses, although sometimes called panicles in the literature.

We conducted trait analyses on inflorescence condensation and breeding system using Mesquite version 2.75 (www.mesquiteproject.org, Maddison and Maddison 2011). We calculated ancestral states for both traits using an Mk1 model (Xiang and Thomas 2008), and evaluated the relationship between inflorescence condensation and breeding system using Pagel's (1994) correlation test implemented in Mesquite's *correl* package (Midford and Maddison 2006). Because we were testing for relationships between two binary traits for the *Tradescantia* alliance, outgroup species and taxa for which compatibility data were missing or ambiguous (SI/SC, Appendix 1) were removed from the dataset prior to correlation analyses (59 total taxa included for correlation analysis). We ran the analysis for 10 iterations and 1,000 simulations.

RESULTS

Phylogenetic Inference—A description of each data partition and the combined two locus dataset is available in Table 2. The best-scoring ML tree is well supported along the backbone (Fig. 3); specific taxonomic groups are discussed below.

SUBTRIBE TRADESCANTIINAE—The phylogeny constraining subtribe Tradescantiinae as monophyletic possessed a higher, albeit not statistically significant, likelihood than the unconstrained tree (Table 3). Additionally, there was strong bootstrap support for the inclusion of *Elasis* in the Tradescantiinae (BS = 99), which suggests polyphyly of the subtribe as currently circumscribed (Fig. 3). Topology tests do not support *Tradescantia* as monophyletic (Table 3). *Tradescantia* species comprise a strongly supported clade with the inclusion of *Gibasis geniculata* and *G. linearis* (BS = 99), as well as the sister taxon *G. oaxacana* (BS = 98, Fig. 3). There is little reinforcement for taxonomic classification within *Tradescantia*, as only weak bootstrap support exists for most internal nodes in the clade. No currently named sections emerge as monophyletic (Fig. 3).

As two species of *Gibasis* are nested within *Tradescantia*, and a third species is sister to *Tradescantia*, there is no support for this genus as monophyletic (Fig. 3). Topology tests reinforce this interpretation, as the constraint tree with *Gibasis* monophyletic is significantly less likely than the unconstrained tree (Table 3). The exception is the SH test ($p = 0.79$), but this test is known to have a relatively high error rate in some cases (Goldman et al. 2000). With the exception of the three species mentioned in association with *Tradescantia*, *Gibasis* forms a strongly supported monophyletic clade (BS = 97) and is sister to the monotypic genus *Elasis* (BS = 91). This *Gibasis* + *Elasis* clade is sister to the *Tradescantia* clade. The *Gibasis* taxa grouping together are all from sect. *Gibasis*; the only member of this section not in the clade is *G. linearis*. The other two *Gibasis* species, *G. geniculata* and *G. oaxacana*, comprise sect. *Heterobasis*.

Tripogandra is a strongly supported clade with the inclusion of *Callisia gracilis* (BS = 99), although topology tests do not reject the monophyly of *Tripogandra* (Table 3). This clade is nested within a strongly supported *Tripogandra* + *Callisia* clade (BS = 98) that is sister to *Gibasis* + *Tradescantia*

TABLE 2. Characteristics of the two locus plastid dataset.

	<i>rpL16</i>	<i>trnL-trnF</i>	Combined
# included taxa	68	83	85
Total length (bp)	1,989	1,634	3,623
% variable	46	40	44
% missing/gaps	48	49	55

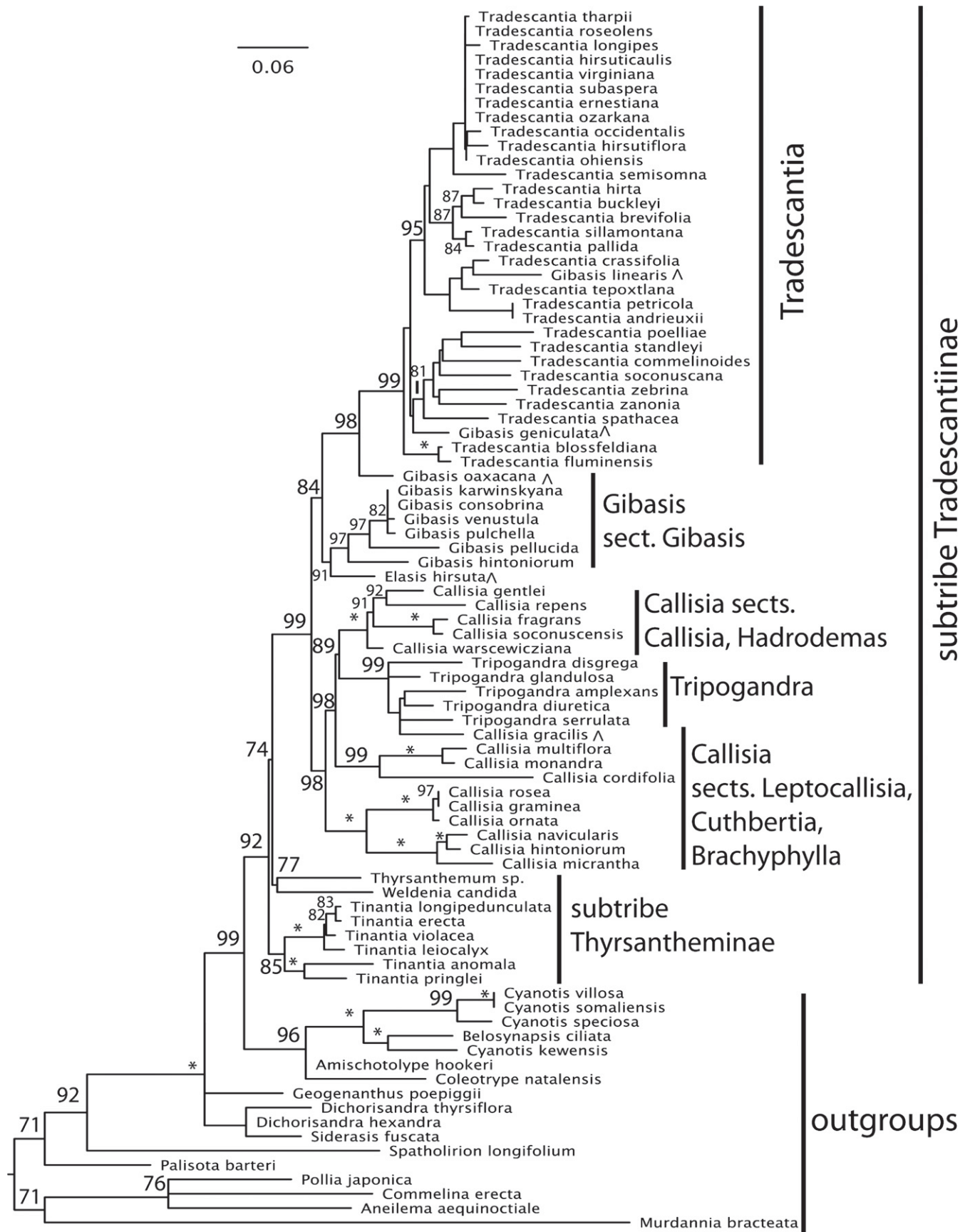


FIG. 3. cpDNA ML phylogram of the *Tradescantia* alliance from *trnL-trnF* and *rpL16*. Numbers by nodes represent bootstrap support (BS, 100 replicates). An asterisk (*) indicates BS = 100. Relevant taxonomic groups are labeled. Taxa labeled with a caret (^) are displaced from their current taxonomically assigned clade. *Tinantia* alone is confirmed as monophyletic; *Callisia*, *Gibasis* and *Tradescantia* are polyphyletic. *Tripogandra* is nested within *Callisia*.

TABLE 3. Constraint tests for monophyly of taxonomic groups. Asterisks (*) indicate constrained trees that were significantly different from the best (unconstrained) tree. Tree likelihoods and significance scores reported from CONSEL (Shimodaira and Hasegawa 2001). *p* values are indicated for each of the following topological hypothesis tests: AU = Approximately Unbiased (Shimodaira 2002), KH = Kishino-Hasegawa (Kishino and Hasegawa 1989), SH = Shimodaira-Hasegawa (Shimodaira and Hasegawa 1999), WKH = weighted KH, WSH = weighted SH.

Taxonomic group	Likelihood of best tree	AU	KH	SH	WKH	WSH
Unconstrained	-21,567.6300	0.679	0.559	0.963	0.559	0.971
<i>Tradescantia</i>	-21,612.0698	0.002*	0.007*	0.15	0.006*	0.019*
<i>Gibasis</i>	-21,755.5508	8.00E-042*	0.000*	0.000*	0.000*	0.000*
<i>Callisia</i>	-21,651.9326	1.00E-063*	0.000*	0.013*	0.000*	1.00E-004*
<i>Tripogandra</i>	-21,578.1923	0.6	0.61	0.766	0.47	0.524
Subtribe Tradescantiinae	-21,579.1913	0.275	0.264	0.683	0.264	0.617
<i>Tinantia</i>	-21,568.2425	0.657	0.441	0.974	0.441	0.966
Subtribe Thyrsantheminae	-21,639.0226	1.00E-005*	2.00E-004*	0.023*	3.00E-005*	0.001*

(Fig. 3). *Callisia* is not supported as monophyletic by topology tests (Table 3). There is substantial substructure within *Callisia*, including support for several taxonomic sections. Section *Cuthbertia* (BS = 100) and sect. *Brachyphylla* (BS = 100, including previously unplaced *C. hintoniorum*) are sister to each other (BS = 100) as the earliest diverging *Callisia* lineage. Three taxa of sect. *Leptocallisia* are monophyletic (BS = 99) and next to diverge (BS = 98); the other sampled member of the section is the previously mentioned *C. gracilis*. Remaining *Callisia* species are represented by two strongly supported clades: first, the aforementioned *Tripogandra* + *C. gracilis*, and second, *C. warszewicziana* (sect. *Hadrodemas*), sister to sect. *Callisia* (BS = 100). Hunt (1986b) described three informal but well-marked "groups" within section *Callisia* which our analysis supports collectively as monophyletic (BS = 91).

SUBTRIBE THYRSANTHEMINAE—Relationships among genera of subtribe Thyrsantheminae have moderate support along the tree's backbone (Fig. 3). With *Elasis* sister to *Gibasis* sect. *Gibasis* as previously mentioned, *Weldenia* + *Thyrsanthemum* are sister to subtribe Tradescantiinae. Constraint tests for the subtribe are consistent with paraphyly (Table 3). The largest genus in subtribe Thyrsantheminae, *Tinantia*, is supported as monophyletic (Fig. 3, BS = 85), and a constrained tree was not significantly different from the unconstrained tree (Table 3). *Tinantia* is strongly placed as the earliest diverging lineage of the *Tradescantia* alliance.

Trait Analysis—The trait matrix contained no missing data for inflorescence condensation; sampled taxa were about evenly split between condensed and incondensed states (Appendix 1, Dryad <http://dx.doi.org/10.5061/dryad.s2878>). For breeding system, 45% of sampled taxa were SI and 22% were SC. Remaining taxa were ambiguous/multistate (7%) or unknown (26%). ML ancestral state reconstructions indicate that both the *Tradescantia* alliance and subtribe Tradescantiinae evolved from ancestors possessing uncondensed inflorescences (Fig. 4, proportional likelihood 0.9906 and 0.9974, respectively). *Tinantia*, *Callisia* + *Tripogandra*, and *Gibasis* sect. *Gibasis* are also derived from ancestors with uncondensed inflorescences (proportional likelihoods 0.9984, 0.9887, 0.9995) while *Tradescantia* is the sole genus derived from an ancestor with condensed inflorescences (proportional likelihood 0.9904). There are more shifts between breeding systems than for inflorescence condensation and greater ambiguity of ancestral state assignment (Fig. 4). We found no correlations between inflorescence structure and breeding system ($p = 0.49$); various methods of assigning a

binary trait to taxa with missing and/or ambiguous compatibility data did not alter our results (data not shown).

DISCUSSION

A molecular phylogeny of the *Tradescantia* alliance from two plastid loci resolves relationships between notoriously difficult genera. Resulting implications for circumscription of genera provide insight into interpretation of morphological characters and their lability over evolutionary time.

Limitations of Data—We would be remiss if we did not mention inherent caveats in the methods we employ here to narrate the evolutionary history of this complex group. Both loci sampled for this study are from the plant plastomes; their relatively high rates of evolution often result in complex insertion/deletion polymorphisms (indels) that cause alignment difficulties (Golubchik et al. 2007). Despite the rapidly evolving nature of the two plastid loci utilized in this study, virtually no variation was found to differentiate the erect *Tradescantia*. As several members of the *Tradescantia* alliance are hypothesized to have arisen via hybridization (Anderson 1936), nuclear data will illuminate these issues. Increased taxon collection and data sampling from the nuclear genome may resolve some of the more difficult questions in the group, including the placement of additional uncertain and as yet unsampled taxa. Finally, coding of the traits analyzed here as binary characters simplifies the variation within both traits and species, so resulting conclusions should be interpreted accordingly.

Phylogenetic Classification—The phylogenetic reconstruction from two plastid loci recapitulates the evolutionary relationships between genera posited by previous studies with more limited taxon sampling (Fig. 2). Topological constraint tests provide information about the monophyly of genera and subtribes, which as a result inform understanding of morphological characters used to define taxonomic groups (see below, Evolution of inflorescence structure). The ingroup of the *Tradescantia* alliance is comprised of two closely related subtribes, Tradescantiinae and Thyrsantheminae, which while strongly supported as a single clade are both paraphyletic according to current classification. The polyphyly of subtribe Thyrsantheminae confirms previous findings from phylogenies constructed from both morphological and molecular loci (Faden and Hunt 1991; Evans et al. 2000b; Evans et al. 2003).

Previous phylogenetic research indicated substantial issues with poly- and paraphyly for several groups in the

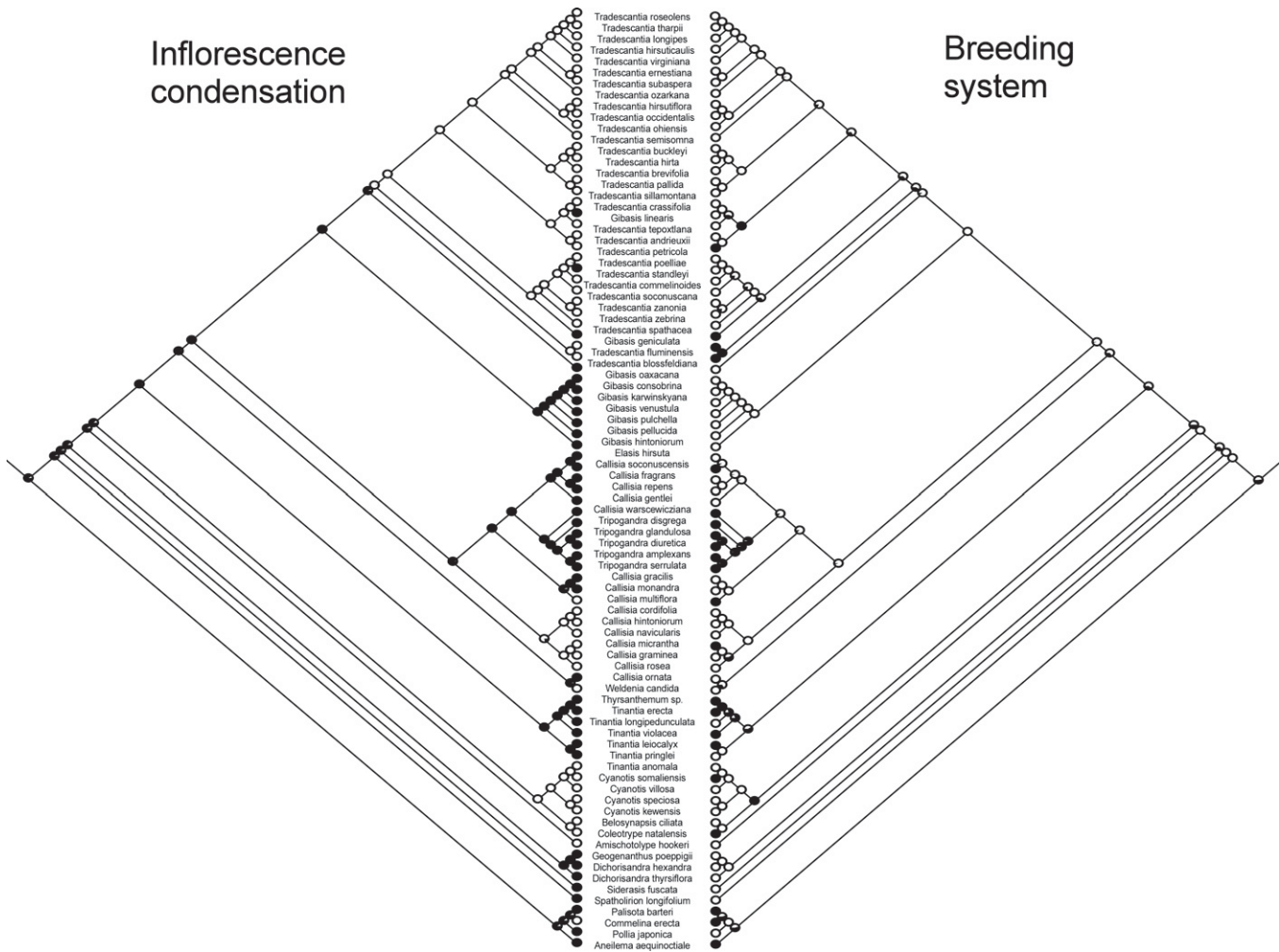


FIG. 4. Ancestral state reconstruction of inflorescence condensation and breeding system in the *Tradescantia* alliance. Phylogeny is the two-locus cpDNA ML analysis shown in Fig. 3. Traits were assigned according to Appendix 1. For inflorescence condensation, white and black circles indicate expanded (uncondensed) and condensed inflorescences, respectively. White and black circles represent self incompatible and self compatible breeding systems, respectively.

Tradescantia alliance (Bergamo 2003; Burns Moriuchi 2006); additional intrageneric sampling presented here increases these concerns. None of the currently circumscribed genera in subtribe Tradescantiinae are monophyletic; we identified two clades comprising *Callisia* + *Tripogandra* and *Tradescantia* + *Gibasis* (and *Elasis*). Classification of taxa in *Callisia* has been historically difficult, resulting in dissatisfying conclusions for both systematics (Hunt 1986b) and molecular phylogeneticists (Bergamo 2003). We confirmed monophyly of most sections in *Callisia* and resolved relationships among them. The exception is the placement of *Callisia gracilis* with *Tripogandra* instead of sect. *Leptocallisia*, which Bergamo (2003) also noted. *Tripogandra* is a relatively clearly marked genus characterized by slightly zygomorphic flowers and dimorphic stamens (Handlos 1975). While it is still nested within *Callisia*, the lack of resolution within the *Tripogandra* clade cannot preclude the genus as monophyletic. What accounts for the difficulty in circumscribing *Callisia* and *Tripogandra*? Our findings reaffirm the conclusions of Bergamo (2003); systematic problems in *Callisia* appear to be the result of rapid evolution, as shown by very short branch lengths throughout the clade but prolific insertion-deletion poly-

morphism (data not shown, but see TreeBASE study number 12595). Unlike many species in *Tradescantia* (Anderson 1936) and *Gibasis* (Kenton 1984), *Tripogandra* species lack the ability to hybridize (Handlos 1975), and there is little to no evidence of hybridization in *Callisia* (Bergamo 2003). Rapidly changing morphological characters coupled with emergence and reinforcement of prezygotic isolation mechanisms may account for the lack of consistency in these genera.

Burns Moriuchi (2006) found *Gibasis* to be strongly monophyletic; however, all three species included in that analysis were from section *Gibasis* (species from section *Heterobasis* were not included). Our results from molecular data suggest *Tradescantia* and *Gibasis* intergrade substantially with each other, and additional lines of evidence support this possibility (also see below, Evolution of inflorescence structure). First, chemotaxonomic studies in Commelinaceae indicate possible relationships between *Gibasis* sect. *Heterobasis* and some *Tradescantia* species (Del Pero Martinez and Swain, 1985). *Gibasis oaxacana* and *G. geniculata* share the presence of phenolic and sulfate derivatives, a trait also found in some *Tradescantia* and *Tripogandra*. Second, silica cells, which superficially seem to be a distinctive and uniting taxonomic

feature, occur in at least two different taxonomic groups in Commelinaceae (Tomlinson 1966). Finally, *G. linearis* and *G. geniculata* both possess *Tradescantia*-type pollen (tectum insulate, insulae forming cerebroid pattern; Poole and Hunt 1980), consistent with their placement in the *Tradescantia* clade. *Gibasis oaxacana*, which we place sister to *Tradescantia*, has an intermediate pollen type which suggests this species may serve as a link between *Tradescantia* and other genera (Poole and Hunt 1980). It is unlikely that these traits arose independently in the same family multiple times, but historical hybridization cannot be ruled out as a mechanism for traits to appear in seemingly disparate clades.

This is the first study to include substantial sampling from *Tinantia*. Floral zygomorphy and corresponding staminal characteristics make this a robustly delineated genus morphologically. *Tinantia anomala* was described as a monotypic genus, *Commelinantia*, because of morphological characters reminiscent of *Commelina* (Tharp 1922, 1956). Subsequent researchers, however, rejected this analysis and instead grouped it with *Tinantia* (e.g. Brenan 1966); our results confirm strong support for its inclusion in the genus. The remaining genera in subtribe Thyrsoideae are monotypic or only represented by one species. Of particular systematic interest are the still unsampled monotypic genera *Gibasoides*, *Matudanthus*, and *Sauvallea*; their inclusion in a molecular phylogeny could potentially solidify placement of the other genera and circumscription of subtribes. However, they possess distinct inflorescence variation, which could potentially complicate interpretation of evolution of such structural traits.

Evolution of Inflorescence Structure—Variation in inflorescence structure is an important driver of angiosperm evolution because of relationships with plant reproduction. Predictably, selfing species exhibit reduced allocation to flowers, since the need to attract pollinators is reduced (Goodwillie et al. 2010). Long-standing hypotheses indicate that angiosperm inflorescences evolved from highly branched displays, and suppression of various inflorescence structures results in condensation, like heads (Parkin 1914; Stebbins 1974; Wyatt 1982; Harris 1999). Pollination biology is traditionally floricentric, in which individual flowers are the focus of research (Harder et al. 2004). However, variation from pollinator movement and interactions with the entire inflorescence contribute to evolution of diverse structures (Harder et al. 2004). Moreover, inflorescence architecture can have widespread effects on pollinator interactions (Wyatt 1982). Empirical evidence suggests pollinators have little effect on inflorescence structure in *Cornus* (Feng et al. 2011), but inflorescence architecture is correlated with pollinator types in *Arecaceae* (Henderson 2002).

We did not find a correlation between breeding system and inflorescence structure in the *Tradescantia* alliance, but ancestral state reconstructions inform our knowledge of inflorescence evolution. The main distinction between subtribes Tradescantiinae and Thyrsoideae is the inflorescence structure. Our results indicate that this morphological feature is labile throughout the phylogeny. The inclusion of *Elasis* in subtribe Tradescantiinae is strongly supported in this analysis by at least two robust nodes in the backbone of the phylogeny. As a result, the single cyme of *Elasis* represents a reduced form of bifacially fused cyme pairs characteristic of subtribe Tradescantiinae, confirming the hypothesis of Evans et al. (2003). Further evidence of the

labiality of inflorescence characters over evolutionary time comes from the *Tradescantia* clade. Despite condensed inflorescences being a uniting character for most *Tradescantia* species, *T. standleyi* possesses diffuse, pedunculate umbels (Standley and Steyermark 1944). The strong support for two *Gibasis* species in two different *Tradescantia* clades also indicates that the diagnostic character of a paired, condensed inflorescence structure is perhaps reversible. We support the assertion of Wade et al. (2006) that developmental evidence is required to determine the mode of inflorescence evolution in this problematic clade.

The labiality in inflorescence morphology in the *Tradescantia* alliance may be related to variation in flowering phenology and pollination ecology among species. Evolution of condensed inflorescence structures may be an adaptation to early flowering or scarce pollinators (Feng et al. 2011); this ecological scenario is possible in the *Tradescantia* alliance given the deliquescent nature of most species' flowers. The only evidence for specialized pollinators in Commelinaceae comes from outgroup genera, and *Callisia repens* is the only known wind pollinated species in the *Tradescantia* alliance (Faden 1992). Some species, including erect *Tradescantia* (section *Tradescantia*, series *Virginianae*, Sinclair 1968) and *Tripogandra serrulata* (Schuster and Schuster 1971) utilize a wide variety of pollinating insects. However, despite having an expanded inflorescence and striking floral specializations, *Tinantia anomala* exhibits a paucity of insect pollinators and is self compatible (Simpson et al. 1986).

The failure of inflorescence condensation and pollinator syndromes to explain patterns of self compatibility in the *Tradescantia* alliance suggests that other floral characters may be contributing to this variation. Floral organogenesis in the *Tradescantia* alliance represents developmental variation found across the entire family, which may be coincident with floral morphological diversity (Hardy and Stevenson 2000). A dependence on insect pollinators and outcrossing may have influenced the arrangement of stamens and staminodes in *Tripogandra* (Moore 1960). Studies in *Commelina* reveal vertical orientation of bilateral flowers (Ushimaru and Hyodo 2005), and colored floral organs affect the frequency of pollinator visitation (Ushimaru et al. 2007). Such variation exists in the *Tradescantia* alliance as well. Faden (1992) notes several visual floral pollinator attractants for members of the alliance, including colored floral structures (axes, pedicels, calyces), anthers (and anther connectives), filament hairs and bearding on the androecium. Additional rewards like pollen and occasionally scent may also serve as attractants (Faden 1992).

A growing body of evidence indicates that a combination of factors, ranging from floral structures to spatial arrangement of entire inflorescences, best explains floral evolution in relation to pollinators. Floral display, a characteristic incorporating number and size of flowers, is a more accurate metric for measuring the attractant power of flowers compared to measures of individual flowers (Goodwillie et al. 2010). Even small changes in pedicel length can alter the three-dimensional arrangement of flowers, which alters pollinator behavior (Jordan and Harder 2006). Pedicel length in particular is a trait that varies among species in the erect *Tradescantia* group, where little to no molecular divergence exists. Seemingly uniform inflorescences can also vary in spatial and temporal arrangements of flowers; modular construction of the plant and flowering

sequence are more important to the mating system than inflorescence architecture (Reuther and Claßen-Bockhoff 2010). Modularity is particularly important to the alliance, in which many species can be propagated by cuttings and rely heavily on vegetative growth. A comparison of umbels, panicles, and racemes indicates differences in bee visitation and frequency of self pollination (Jordan and Harder 2006). The combined effects of many factors, including spatial arrangement of flowers, display size and plant density, can alter pollinator behavior (Ishii et al. 2008). The *Tradescantia* alliance would be an interesting group in which to model the combined effects of floral/inflorescence characteristics on breeding system given the variation among species in those traits, including clonal reproduction through vegetative growth.

Our two-locus plastid phylogeny of the *Tradescantia* alliance indicates a complex evolutionary history for this notoriously difficult group of plants. While inflorescence condensation is not correlated with the breeding system, our ancestral state reconstructions of inflorescence structure indicate lability in the character and the possible signature of historical hybridization. Further research would benefit from incorporating karyotype and other genomic data into analyses of life history traits, as chromosomal restructuring is hypothesized to reduce the importance of reproduction in speciation (Jones and Jopling 1972).

ACKNOWLEDGMENTS. KLH was funded by an MU Life Sciences Fellowship and graduate research grants from the Botanical Society of America, the Society for Systematic Biologists, and the MU Graduate School. The authors acknowledge the National Science Foundation (DEB 0829849 and DEB 1146603) for funding, T. Evans for DNA, R. Faden for plant materials, J. Burns for plant material and constructive feedback on the manuscript, T. Docktor for lab assistance, T. Columbus, H. Bell, D. McGoan, J. McGoan, and K. Klymus for field assistance, and one anonymous reviewer for feedback. I also acknowledge T. Columbus in particular for taking the photographs for plates A–D in Fig. 2.

LITERATURE CITED

- Anderson, E. 1936. Hybridization in American *Tradescantias*. *Annals of the Missouri Botanical Garden* 23: 511–525.
- Bergamo, S. 2003. *A phylogenetic evaluation of Callisia Loeft. (Commelinaceae) based on molecular data*. Ph. D. Dissertation. Athens, Georgia: University of Georgia.
- Brenan, J. P. M. 1966. The classification of Commelinaceae. *Journal of the Linnaean Society of London: Botany* 59: 349–370.
- Burns, J. H., R. B. Faden, and S. J. Steppan. 2011. Phylogenetic Studies in the Commelinaceae subfamily Commelinoideae inferred from nuclear ribosomal and chloroplast DNA sequences. *Systematic Botany* 36: 268–276.
- Burns Moriuchi, J. H. 2006. *A comparison of invasive and noninvasive Commelinaceae in a phylogenetic context*. Ph. D. Dissertation. Tallahassee, Florida: The Florida State University.
- Del Pero Martinez, M. A. and T. Swain. 1985. Flavonoids and chemotaxonomy of the Commelinaceae. *Biochemical Systematics and Ecology* 13: 391–402.
- Edgar, R. 2004a. MUSCLE: A multiple sequence alignment method with reduced time and space complexity. *BMC Bioinformatics* 5: 113.
- Edgar, R. C. 2004b. MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32: 1792–1797.
- Endress, P. K. 2010. Disentangling confusions in inflorescence morphology: Patterns and diversity of reproductive shoot ramification in angiosperms. *Journal of Systematics and Evolution* 48: 225–239.
- Evans, T. M., R. B. Faden, and K. J. Sytsma. 2000a. Homoplasmy in the Commelinaceae: a comparison of different classes of morphological characters, Pp. 109–128 in *Monocots: systematics and evolution*, eds. K. L. Wilson and D. A. Morrison. Melbourne: CSIRO Publishing.
- Evans, T. M., R. B. Faden, M. G. Simpson, and K. J. Sytsma. 2000b. Phylogenetic relationships in the Commelinaceae: I. A cladistic analysis of morphological data. *Systematic Botany* 25: 668–691.
- Evans, T. M., K. J. Sytsma, R. B. Faden, and T. J. Givnish. 2003. Phylogenetic relationships in the Commelinaceae: II. A cladistic analysis of *rbcl* sequences and morphology. *Systematic Botany* 28: 270.
- Faden, R. B. 1992. Floral attraction and floral hairs in the Commelinaceae. *Annals of the Missouri Botanical Garden* 79: 46–52.
- Faden, R. B. 1998. Commelinaceae. Pp. 109–128 in *The families and genera of vascular plants: volume 4. Flowering plants-monocotyledons*, ed. K. Kubitzki. Berlin: Springer-Verlag.
- Faden, R. B. and D. R. Hunt. 1991. The classification of the Commelinaceae. *Taxon* 40: 19–31.
- Feng, C.-M., Q.-Y. Xiang, and R. G. Franks. 2011. Phylogeny-based developmental analyses illuminate evolution of inflorescence architectures in dogwoods (*Cornus* s. l., Cornaceae). *The New Phytologist* 191: 850–869.
- Goldman, N., J. P. Anderson, and A. G. Rodrigo. 2000. Likelihood-based tests of topologies in phylogenetics. *Systematic Biology* 49: 652–670.
- Golubchik, T., M. J. Wise, S. Eastal, and L. S. Jermin. 2007. Mind the gaps: Evidence of bias in estimates of multiple sequence alignments. *Molecular Biology and Evolution* 24: 2433–2442.
- Goodwillie, C., R. D. Sargent, C. G. Eckert, E. Elle, M. A. Geber, M. O. Johnston, S. Kalisz, D. A. Moeller, R. H. Ree, M. Vallejio-Marin, and A. A. Winn. 2010. Correlated evolution of mating system and floral display traits in flowering plants and its implications for the distribution of mating system variation. *The New Phytologist* 185: 311–321.
- Handlos, W. L. 1975. The taxonomy of *Tripogandra* (Commelinaceae). *Rhodora* 77: 213–319.
- Harder, L. D., C. Y. Jordan, W. E. Gross, and M. B. Routley. 2004. Beyond floriculture: The pollination function of inflorescences. *Plant Species Biology* 19: 137–148.
- Hardy, C. R. and D. W. Stevenson. 2000. Floral organogenesis in some species of *Tradescantia* and *Callisia* (Commelinaceae). *International Journal of Plant Sciences* 161: 551–562.
- Harris, E. M. 1999. Capitula in the Asteridae: A widespread and varied phenomenon. *Botanical Review* 65: 348–369.
- Henderson, A. 2002. *Evolution and ecology of palms*. New York: New York Botanical Garden Press.
- Hunt, D. R. 1980. Sections and series in *Tradescantia*: American Commelinaceae IX. *Kew Bulletin* 35: 437–442.
- Hunt, D. R. 1985. A revision of *Gibasis* Rafin. *Kew Bulletin* 4: 107–129.
- Hunt, D. R. 1986a. *Campelia*, *Rhoeo*, and *Zebrina* united with *Tradescantia*: American Commelinaceae XIII. *Kew Bulletin* 41: 401–405.
- Hunt, D. R. 1986b. Amplification of *Callisia* Loeft.: American Commelinaceae XV. *Kew Bulletin* 41: 407–412.
- Hunt, D. R. 1993. The Commelinaceae of Mexico. Pp. 421–437 in *Biological diversity of Mexico: Origins and distribution*. eds. T. P. Ramamoorthy, R. Bye, A. Lot, and J. Fa. New York: Oxford University Press.
- Ishii, H., Y. Hirabayashi, and G. Kudo. 2008. Combined effects of inflorescence architecture, display size, plant density and empty flowers on bumble bee behaviour: experimental study with artificial inflorescences. *Oecologia* 156: 341–350.
- Jones, K. 1990. Robertsonian change in allies of *Zebrina* (Commelinaceae). *Plant Systematics and Evolution* 172: 263.
- Jones, K. and C. Jopling. 1972. Chromosomes and the classification of the Commelinaceae. *Botanical Journal of the Linnean Society* 65: 129–162.
- Jones, K. and A. Kenton. 1984. Mechanisms of chromosome change in the evolution of the tribe Tradescantieae (Commelinaceae). Pp. 143–168 in *Chromosomes in Evolution of Eukaryotic Groups* vol. 2, eds. A. K. Sharma and A. Sharma, Boca Raton, Florida: CRC Press.
- Jordan, C. Y. and L. D. Harder. 2006. Manipulation of bee behavior by inflorescence architecture and its consequences for plant mating. *American Naturalist* 167: 496–509.
- Kenton, A. 1984. Chromosome evolution in the *Gibasis linearis* group (Commelinaceae) 3. DNA variation, chromosome evolution and speciation in *Gibasis venustula* and *Gibasis heterophylla*. *Chromosoma (Berlin)* 90: 303–310.
- Kishino, H. and M. Hasegawa. 1989. Evaluation of the maximum-likelihood estimate of the evolutionary tree topologies from DNA sequence data, and the branching order in Hominoidea. *Journal of Molecular Evolution* 29: 170–179.
- Maddison, W. and D. R. Maddison. 2011. Mesquite, version 2.75. website: <http://mesquiteproject.org>.
- Midford, P. E. and W. Maddison. 2006. Corel package for Mesquite, version 0.1. website: <http://mesquiteproject.org>.
- Moore, H. E. 1960. *Tripogandra grandiflora*. *Baileya* 8: 77–83.
- Owens, S. J. 1981. Self-incompatibility in the Commelinaceae. *Annals of Botany* 47: 567–581.

- Pagel, M. 1994. Detecting correlated evolution on phylogenies: A general method for the comparative analysis of discrete characters. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 255: 37–45.
- Parkin, J. 1914. The evolution of the inflorescence. *Journal of the Linnean Society of London. Botany* 42: 511–563.
- Poole, M. M. and D. R. Hunt. 1980. Pollen morphology and the taxonomy of the Commelinaceae: An exploratory survey: American Commelinaceae 8. *Kew Bulletin* 34: 639–660.
- Reuther, K. and R. Claßen-Bockhoff. 2010. Diversity behind uniformity inflorescence architecture and flowering sequence in Apiaceae-Apioideae. *Plant Diversity and Evolution* 128: 181–220.
- Schuster, L. and J. Schuster. 1971. Interacciones diurnas entre insectos y las flores de *Tripogandra cumananensis* (Commelinaceae). *Anales 1er. Congreso Latinoamericano de Entomología* 14: 253–258.
- Shaw, J., E. B. Lickey, J. T. Beck, S. B. Farmer, W. Liu, J. Miller, K. C. Siripun, C. T. Winder, E. E. Schilling, and R. L. Small. 2005. The tortoise and the hare II: relative utility of 21 noncoding chloroplast DNA sequences for phylogenetic analysis. *American Journal of Botany* 92: 142–166.
- Shimodaira, H. 2002. An approximately unbiased test of phylogenetic tree selection. *Systematic Biology* 51: 492–508.
- Shimodaira, H. and M. Hasegawa. 1999. Multiple comparisons of log-likelihoods with applications to phylogenetic inference. *Molecular Biology and Evolution* 16: 1114–1116.
- Shimodaira, H. and M. Hasegawa. 2001. CONSEL: for assessing the confidence of phylogenetic tree selection. *Bioinformatics* 17: 1246–1247.
- Simpson, B. B., J. L. Neff, and G. Dieringer. 1986. Reproductive Biology of *Tinantia anomala* (Commelinaceae). *Bulletin of the Torrey Botanical Club* 113: 149–158.
- Sinclair, C. B. 1968. Pollination, hybridization, and isolation factors in the erect *Tradescantias*. *Bulletin of the Torrey Botanical Club* 95: 232–240.
- Smith, J. F., K. J. Sytsma, J. S. Shoemaker, and R. L. Smith. 1991. A qualitative comparison of total cellular DNA extraction protocols. *Phytochemical Bulletin* 23: 2–9.
- Stamatakis, A. 2006. RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688–2690.
- Stamatakis, A., P. Hoover, and J. Rougemont. 2008. A rapid bootstrap algorithm for the RAxML web servers. *Systematic Biology* 57: 758–771.
- Standley, P. C. and J. A. Steyermark. 1944. Studies of Central American Plants-IV. *Field Museum of Natural History Botanical Series* 23: 32–38.
- Stebbins, G. L. 1974. *Flowering plants: Evolution above the species level*. Cambridge Massachusetts: Belknap Press.
- Taberlet, P., L. Geilly, G. Pautou, and J. Bouvet. 1991. Universal primers for amplification of three non-coding regions of chloroplast DNA. *Plant Molecular Biology* 17: 1105–1109.
- Tharp, B. C. 1922. *Commelinantia*, a new genus of the Commelinaceae. *Bulletin of the Torrey Botanical Club* 49: 269–275.
- Tharp, B. C. 1956. *Commelinantia* (Commelinaceae): An evaluation of its generic status. *Bulletin of the Torrey Botanical Club* 83: 107–112.
- Tomlinson, P. B. 1966. Anatomical data in the classification of the Commelinaceae. *Journal of the Linnean Society of London: Botany* 59: 371–395.
- Ushimaru, A. and F. Hyodo. 2005. Why do bilaterally symmetrical flowers orient vertically? Flower orientation influences pollinator landing behaviour. *Evolutionary Ecology Research* 7: 151–160.
- Ushimaru, A., T. Watanabe, and K. Nakata. 2007. Colored floral organs influence pollinator behavior and pollen transfer in *Commelina communis* (Commelinaceae). *American Journal of Botany* 94: 249–258.
- Wade, D. J., T. M. Evans, and R. B. Faden. 2006. Subtribal relationships in tribe Tradescantieae (Commelinaceae) based on molecular and morphological data. *Aliso* 22: 520–526.
- Woodson, R. E. Jr. 1942. Commentary on the North American Genera of Commelinaceae. *Annals of the Missouri Botanical Garden* 29: 141–154.
- Wyatt, R. 1982. Inflorescence architecture: How flower number, arrangement, and phenology affect pollination and fruit-set. *American Journal of Botany* 69: 585–594.
- Xiang, Q. Y. and D. T. Thomas. 2008. Tracking character evolution and biogeographic history through time in Cornaceae-Does choice of methods matter? *Journal of Systematics and Evolution* 46: 349–374.
- An asterisk (*) indicates a sequence obtained for this study. A caret (^) represents a sequence too short to be accepted to GenBank, but see TreeBASE accession number 12595. NA indicates sequence data missing from the analysis. Assignations of SI/SC (self compatible and incompatible) follow Owens (1981) and Burns Moriuchi (2006); inflorescence condensation is derived from the species description for the taxon. “NA” and “SI/SC” represent taxa for which breeding system is unknown or for taxa in which both states occur, respectively. Data matrix available from Dryad (<http://dx.doi.org/10.5061/dryad.s2878>). Herbaria include MO (Missouri Botanical Garden Herbarium), NY (New York Botanical Garden William and Lynda Steere Herbarium), FSU (Florida State University R. K. Godfrey Herbarium), UMO (University of Missouri Dunn-Palmer Herbarium), GA (University of Georgia), US (Smithsonian Institution United States National Herbarium), and K (Royal Botanic Gardens Herbarium). Order of data: taxon, collection source, source, collection, voucher location, *rpl16* Genbank accession, *trnL-trnF* Genbank accession, SI/SC, Inflorescence condensation.

TRIBE TRADESCANTIEAE MEISNER

Subtribe *Tradescantiinae* Rohweder

Tradescantia L.; Section *Austrotradescantia* D. R. Hunt; *Tradescantia fluminensis* Vellozo. cultivation, K. L. Hertweck, *Hertweck* 0676, UMO, KC512007*, KC512086*, SC, condensed. Section *Campelia* (L. C. Rich.) D. R. Hunt; *Tradescantia zanonia* (L.) Sw. cultivation, K. L. Hertweck, *Hertweck* 0686, UMO, KC512028*, KC512109*, SI, condensed. Section *Corrina* D. R. Hunt; *Tradescantia soconuscana* Matuda, MEXICO. Smithsonian Institution 1980-365, *Faden* 76/98, US, KC512026*, KC512106*, SI, condensed. Section *Cymbispatha* (Pichon) D. R. Hunt; *Tradescantia commelinoidea* Schultes & Schultes f., MEXICO. K. L. Hertweck, *Hertweck* 07161, UMO, KC512006*, KC512085*, SI/SC, condensed. *Tradescantia poelliae* D. R. Hunt, COSTA RICA. Smithsonian Institution 1992-049, *Grant* 92-1863, US, KC512019*, KC512098*, SI, condensed. *Tradescantia standleyi* Steyermark. unknown, Kew Gardens, *Kew* 18847, K, NA, EF092899, NA, uncondensed. Section *Mandonia* D. R. Hunt; *Tradescantia petricola* J. R. Grant. COSTA RICA. Smithsonian Institution 1995-317, *Grant* 95-2347, US, KC512018*, KC512097*, SC, condensed. *Tradescantia crassifolia* Cav. MEXICO. Smithsonian Institution 2003-010, *Peterson et al.* 16911, US, KC511986*, KC512063*, SI, condensed. *Tradescantia tepoxtlana* Matuda, MEXICO. K. L. Hertweck, *Hertweck* 07175, UMO, KC512001*, KC512079*, SI, condensed. Section *Parasetcreasea* D. R. Hunt; *Tradescantia andrieuxii* C.B.Clark. MEXICO. K. L. Hertweck, *Hertweck* 08079, UMO, NA, KC512081*, SI, condensed. Section *Rhoeo* (Hance) D. R. Hunt; *Tradescantia spathacea* Sw. cultivation, K. L. Hertweck, *Hertweck* 0678, UMO, KC512027*, KC512107*, SI/SC, condensed. Section *Setcreasea* (K. Schum. & Sydow) D. R. Hunt; *Tradescantia brevifolia* (Torrey) Rose. cultivation, J. H. Burns, *Burns* 283, FSU, KC512004*, KC512083*, SI, condensed. *Tradescantia buckleyi* (I. M. Johnston) D. R. Hunt. U. S. A. Texas: Smithsonian Institution 1980-363, *Lewis* 287, US, KC512005*, KC512084*, SI, condensed. *Tradescantia hirta* D. R. Hunt. MEXICO. K. L. Hertweck, *Hertweck* 07196, UMO, KC512008*, KC512087*, SI, condensed. *Tradescantia pallida* (Rose) D. R. Hunt. cultivation, K. L. Hertweck, *Hertweck* 0502, UMO, KC512017*, KC512096*, SI, condensed. Section *Tradescantia*; *Tradescantia semisonna* Standl. MEXICO. K. L. Hertweck, *Hertweck* 07133, UMO, KC512000*, KC512078*, NA, condensed. Series *Sillamontanae* D. R. Hunt; *Tradescantia sillamontana* Matuda. cultivation, K. L. Hertweck, *Hertweck* 0682, UMO, KC512025*, KC512105*, SI, condensed. Series *Virginianae* D. R. Hunt (erect Tradescantia). *Tradescantia ernestiana* Anderson & Woodson. U. S. A. Arkansas: K. L. Hertweck, *Hertweck* 0617, UMO, KC511994*, KC512072*, SI, condensed. *Tradescantia hirsuticaulis* Small, U. S. A. Arkansas: K. L. Hertweck, *Hertweck* 0735, UMO, KC512002*, KC512080*, SI, condensed. *Tradescantia hirsutiflora* Bush, U. S. A. Florida: J. H. Burns, *Burns* 279, FSU, KC512009*, *, SI, condensed. *Tradescantia longipes* Anderson & Woodson. U. S. A. Missouri: K. L. Hertweck, *Hertweck* 07123, UMO, KC511998*, KC512076*, SI, condensed. *Tradescantia occidentalis* (Britton) Smyth. cultivation, J. H. Burns, *Burns* 286, FSU, KC512016*, KC512095*, SI, condensed. *Tradescantia ohioensis* Raf. U. S. A. Missouri: K. L. Hertweck, *Hertweck* 0637, UMO, KC511996*, KC512074*, SI, condensed. *Tradescantia ozarkana* Anderson & Woodson. U. S. A. Missouri: K. L. Hertweck, *Hertweck* 0610, UMO, KC511993*, KC512071*, SI, condensed. *Tradescantia roseolens* Small. U. S. A. Florida: University of Georgia, *Bergamo* 99-186, GA, NA, EF092909, SI, condensed. *Tradescantia subaspera* Ker Gawler, U. S. A. Missouri: K. L. Hertweck, *Hertweck* 0646, UMO, KC511997*, KC512075*, SI, condensed. *Tradescantia tharpii* Anderson & Woodson. U. S. A. Missouri: K. L. Hertweck, *Hertweck* 07203, UMO, KC511999*, KC512077*, SI, condensed. *Tradescantia virginiana* L. U. S. A. Indiana: K. L. Hertweck, *Hertweck* 0631, UMO,

APPENDIX 1. Taxa in the *Tradescantia* alliance phylogeny. Taxa without previous affiliation with generic sections are placed according to the ML phylogeny. Accession information includes collector, collection number, location where taxon was collected, and voucher location; commercial indicates it was obtained from a horticultural source.

KC511995*, KC512073*, SI, condensed. Section *Zebrina* (Schnizlein) D. R. Hunt; *Tradescantia blossfeldiana* Mildbr. cultivation, J. H. Burns, *Smithsonian Institution* 80-362, US, KC512003*, KC512082*, SC, condensed. *Tradescantia zebrina* Heynh. ex. Bosse. cultivation, K. L. Hertweck, *Hertweck* 0501, UMO, KC512029*, KC512110*, SI, condensed.

Gibasis Raf.; Section *Gibasis*; *Gibasis consobrina* D. R. Hunt. MEXICO. Kew 18843, *Kew* 18843, K, NA, EF092892, SI, uncondensed. *Gibasis karwinskyana* (Roem. & Schult.) Rohweder. unknown, Kew 18844, *Kew* 18844, K, NA, EF092893, SI, uncondensed. *Gibasis hintoniiorum* Turner. MEXICO. K. L. Hertweck, *Hertweck* 07191, UMO, KC511982*, KC512057*, NA, uncondensed. *Gibasis linearis* (Benth) Rohweder. MEXICO. K. L. Hertweck, *Hertweck* 07126, UMO, KC511985*, KC512062*, SI, uncondensed. *Gibasis pellucida* (M.Martens & Galeotti) D. R. Hunt. U. S. A. Florida: J. H. Burns, *Burns* 248, FSU, KC511988*, KC512065*, SI/SC, uncondensed. *Gibasis pulchella* Raf. MEXICO. K. L. Hertweck, *Hertweck* 07192, UMO, KC511983*, KC512058*, SI/SC, uncondensed. *Gibasis venustula* (Kunth) D. R. Hunt. MEXICO. Smithsonian Institution 2003-081, J. Bogner s. n., US, KC511989*, KC512066*, SI, uncondensed. Section *Heterobasis* D. R. Hunt; *Gibasis geniculata* (Jacq) Rohweder. cultivation, K. L. Hertweck, *Hertweck* 0681, UMO, KC511984*, KC512060*, SC, uncondensed. *Gibasis oaxacana* D. R. Hunt. cultivation (Munich), Smithsonian Institution 2003-078, J. Bogner s. n., US, KC511987*, KC512064*, SI, uncondensed.

Callisia Loeffl.; Section *Brachyphylla* D. R. Hunt; *Callisia hintoniiorum* Turner. MEXICO. K. L. Hertweck, *Hertweck* 07197, UMO, KC511968*, KC512036*, NA, condensed. *Callisia micrantha* (Torrey) D. R. Hunt. U. S. A. Texas: J. H. Burns, *Bergamo* 00-268 T. F. Patterson s. n., GA, KC511969*, KC512038*, SI, condensed. *Callisia navicularis* (Ortgies) D. R. Hunt. cultivation, K. L. Hertweck, *Hertweck* 0697, UMO, KC511971*, KC512041*, SI/SC, condensed. Section *Callisia*; Group "*gentlei*"; *Callisia gentlei* Matuda. cultivation, K. L. Hertweck, *Hertweck* 0689, UMO, KC511966*, KC512034*, SI, uncondensed. Group "*fragrans*"; *Callisia fragrans* (Lindley) Woodson. cultivation, K. L. Hertweck, *Hertweck* 0674, UMO, KC511965*, KC512033*, SI, uncondensed. *Callisia soconuscensis* Matuda. ECUADOR. University of Georgia, *Bergamo* 86-203 *Munich Botanical Garden* 84/3362, GA, KC511975*, KC512045*, SI, uncondensed. Group "*repens*"; *Callisia repens* (Jacq.) L. MEXICO. K. L. Hertweck, *Hertweck* 07201, UMO, KC511973*, KC512043*, SI/SC, uncondensed. Section *Cuthbertia* (Small) D. R. Hunt; *Callisia graminea* (Small) G.C. Tucker. unknown, University of Georgia, *Bergamo* 99-189 *Giles* 93L-1, GA, NA, EF092887, SI, condensed. *Callisia ornata* (Small) G. C. Tucker, U. S. A. Florida: K. L. Hertweck, *Bergamo* 02-256, GA, KC511972*, KC512042*, NA, condensed. *Callisia rosea* (Ventenat) D. R. Hunt. unknown, University of Georgia, *Bergamo* 99-198, GA, KC511974*, KC512044*, NA, condensed. Section *Hadrodemas* (H.E.Moore) D. R. Hunt; *Callisia warszewicziana* (Kunth & Bouché) D. R. Hunt. unknown, University of Georgia, *Bergamo* 97-068 *Giles* s. n., GA, KC511976*, KC512046*, SI, uncondensed. Section *Leptocallisia*; *Callisia cordifolia* (Swartz) Anderson & Woodson. U. S. A. Florida: Smithsonian Institution 83-197, *Faden* 83/37, US, KC511964*, KC512032*, SC, uncondensed. *Callisia gracilis* (Kunth) D. R. Hunt. ECUADOR. Smithsonian Institution, *Faden* 01-075 *Grant* 3984, US, KC511967*, KC512035*, NA, uncondensed. *Callisia monandra* (Sw.) Schult. et Schult. f. cultivation, Smithsonian Institution 1993-092, J. Bogner s. n. *Munich Botanical Garden*, US, NA, KC512039*, SI, uncondensed. *Callisia multiflora* (M.Martens & Galeotti) Standl. cultivation, University of Georgia, *Bergamo* 80-395 J. Bogner s. n. *Munich Botanical Garden*, GA, KC511970*, KC512040*, SI, uncondensed.

Tripogandra Raf.; *Tripogandra amplexans* Handlos. MEXICO. K. L. Hertweck, *Hertweck* 07172, UMO, KC512021*, KC512101*, SC, uncondensed. *Tripogandra disgrega* (Kunth) Woodson. MEXICO. K. L. Hertweck, *Hertweck* 07159, UMO, KC512020*, KC512100*, SC, uncondensed. *Tripogandra diuretica* (Mart.) Handlos. BRAZIL. Smithsonian Institution 1980-368, *Ploverman* 10171, US, KC512023*, KC512103*, SC, uncondensed. *Tripogandra glandulosa* (Seub.) Rohweder. Uruguay, Smithsonian Institution 2003-082, J. Bogner s. n. *Munich Botanical Garden*, US, KC512024*, KC512104*, SC, uncondensed. *Tripogandra*

serrulata (Vahl) Handlos. cultivation, K. L. Hertweck, *Hertweck* 0679, UMO, KC512022*, KC512102*, SC, uncondensed.

Subtribe *Thyrsantheminae* Faden & D. R. Hunt

Elasis hirsuta (Kunth) D. R. Hunt. unknown, T. Evans, *MacDougal and Lalumondier* 4953, K, KC511981*, KC512055*, NA, uncondensed.

Thyrsanthemum sp., unknown, unknown, M. Chase 606, K, KC512010, AJ387745, NA, uncondensed.

Weldenia candida Schult. f. unknown, unknown, M. Chase 592, K, NA, AJ387746, SI, uncondensed.

Tinantia Scheidw.; *Tinantia anomala* (Torrey) C. B. Clarke. U. S. A. Texas: K. L. Hertweck, *Hertweck* 07094, UMO, KC512013*, KC512091*, SC, uncondensed. *Tinantia erecta* (Jacq.) Fenzl. MEXICO. K. L. Hertweck, *Hertweck* 07186, UMO, KC512012*, KC512090*, SC, uncondensed. *Tinantia leiocalyx* C. B. Clarke ex J. D. Sm. MEXICO. K. L. Hertweck, *Hertweck* 08077, UMO, KC512015*, KC512093*, NA, uncondensed. *Tinantia longipedunculata* Standl. & Steyerl. MEXICO. K. L. Hertweck, *Hertweck* 08075, UMO, KC512014*, KC512092*, NA, uncondensed. *Tinantia pringlei* (S.Wats.) Rohweder. unknown, R. B. Faden, *Burns* 267, FSU, NA, EF092881, SC, uncondensed. *Tinantia violacea* Rohw. MEXICO. K. L. Hertweck, *Hertweck* 07162, UMO, KC512011*, KC512089*, NA, uncondensed.

Subtribe *Coleotrypinae* Faden & D. R. Hunt

Amisotolype hookeri (Hassk.) H. Hara. THAILAND. Smithsonian Institution 1990-023, *Hahn* 6041, US, NA, KC512030*, NA, condensed.

Coleotrype natalensis C. B. Clarke. SOUTH AFRICA. Smithsonian Institution 1983-399, *Faden* 74/206, US, KC511977*, KC512047*, SC, condensed.

Subtribe *Cyanotinae* (Pichon) Faden & D. R. Hunt

Belosynapsis ciliata (Blume) R. S. Rao. NEW GUINEA. Smithsonian Institution 1982-232, *Winters Higgins & Higgins* 186, US, KC511963*, KC512031*, NA, uncondensed.

Cyanotis kewensis C. B. Clarke. cultivation, K. L. Hertweck, *Hertweck* 06105, UMO, KC511978*, KC512049*, NA, condensed. *Cyanotis somaliensis* C. B. Clarke. cultivation, Missouri Botanical Garden, *MOBOT* 1972-1486, MO, KC511979*, KC512050*, SC, condensed. *Cyanotis speciosa* (L. f.) Hassk. cultivation, J. H. Burns, *Burns* ?, FSU, NA, EF092879, NA, condensed. *Cyanotis villosa* (Spreng.) Schult. f. unknown, University of Georgia, *Faden* 76/555, GA, NA, EF092877, NA, condensed.

Subtribe *Dichorisandrinae* (Pichon) Faden & D. R. Hunt

Dichorisandra hexandra (Aubl.) Standl. FRENCH GUIANA. Smithsonian Institution 89-070, *DeGraville et al.* s. n., US, NA, EF092883, NA, uncondensed. *Dichorisandra thyrsiflora* Mikn. cultivation, Missouri Botanical Garden, *MOBOT* 1980-1258, MO, KC511980*, KC512054*, SI, uncondensed.

Geogenanthus poeppigii (Miq.) Faden. cultivation, Missouri Botanical Garden, *MOBOT* 1998-1414, MO, NA, KC512056*, NA, condensed.

Siderasis fuscata (Lodd.) H. E. Moore. cultivation, K. L. Hertweck, *Hertweck* 0699, UMO, KC511992*, KC512069*, NA, uncondensed.

Subtribe *Palisotinae* Faden & D. R. Hunt

Palisota barberi Hook. cultivation, New York Botanical Garden, NYBG 507/45A, NY, NA, KC512067*, NA, uncondensed.

TRIBE COMMELINEAE BRUCKNER

Aneilema aequinoctiale (P. Beauv.) G. Don. MOZAMBIQUE. Smithsonian Institution 2002-202, *Bolnick* s. n., US, KC511962*, NA, SC, uncondensed.

Commelina erecta L. U. S. A. Florida: J. H. Burns, *Burns* 250, FSU, NA, EF092858, SC, condensed.

Murdannia bracteata (C. B. Clarke) D. Y. Hong. cultivation, Missouri Botanical Garden, *MOBOT* 1995-1919, MO, KC511990*, NA, SC, uncondensed.

Pollia japonica Thunb. cultivation, Missouri Botanical Garden, *MOBOT* 1978-0933, MO, KC511991*, KC512068*, SC, uncondensed.

Spatholirion longifolium (Gagnep.) Dunn. unknown, unknown (GenBank), unknown, unknown, NA, AJ387744, NA, uncondensed.