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SUBTRIBAL RELATIONSHIPS IN TRIBE TRADESCANTIEAE (COMMELINACEAE) BASED ON MOLECULAR AND MORPHOLOGICAL DATA

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ABSTRACT

Tribe Tradescantieae (Commelinaceae) consists of seven subtribes and 25 genera. Previous attempts to evaluate phylogenetic relationships within the group using morphology or the chloroplast-encoded *rbcL* have either been highly homoplasious (morphology) or provided only weak support for subtribal relationships due to insufficient variability (*rbcL*). In this study, phylogenetic analysis of nucleotide sequence data from the chloroplast-encoded *ndhF* and *rbcL* genes, as well as 47 morphological and anatomical characters, were used to evaluate relationships within and among the subtribes of Tradescantieae. The addition of *ndhF* resulted in a more highly resolved phylogeny and greater bootstrap and decay values than were obtained by *rbcL* alone or *rbcL* and morphology. The analyses suggest the following: (1) subtribes Coleotrypinae, Cyanotinae, and Tradescantiinae (with the addition of *Elasis*) are monophyletic; (2) subtribe Thyrsantheminae is polyphyletic; and (3) subtribe Dichorisandrinae is polyphyletic. Members of Dichorisandrinae are united into two clades (*Dichorisandra* and *Siderasis*; *Cochliostema*, *Geogenanthus*, and *Plowmanianthus*) whose relationships are more clearly resolved. The position of Old World subtribes Cyanotinae and Coleotrypinae, nested within New World taxa suggested by *rbcL* studies, are supported by the addition of *ndhF* data.

Key words: Commelinaceae, molecular phylogeny, *ndhF*, *rbcL*, Tradescantieae.

INTRODUCTION

Tribe Tradescantieae (Meisn.) Faden & D. R. Hunt is the most diverse group within subfamily Commelinoideae (Faden and Hunt 1991). Meisner (1842) defined the tribe based on the presence of six fertile stamens. Clarke (1881) used both staminal characters and fruit type to separate Tradescantieae from tribes Commelineae and Polllieae. Woodson (1942) and Rohweder (1956) each emphasized inflorescence characters. Brenan (1966) used several characters to divide the whole family into 15 informal groups and this classification was followed until Faden and Hunt (1991). Faden and Hunt (1991) and Faden (1998) employed a broad array of morphological and anatomical characters to divide the tribe into seven subtribes, containing 26 genera and approximately 285 species.

Circumscription of tribe Tradescantieae has varied greatly due to high amounts of homoplasy in morphological characters (Evans et al. 2000b). The tribe is naturally split into Old World and New World components, with Cyanotinae, Coleotrypinae, Palisotinae, and Streptoliriinae restricted to the Old World, and Dichorisandrinae, Thyrsantheminae, and Tradescantiinae to the New World (Faden and Hunt 1991; Evans et al. 2000a, 2003).

Evans (1995) and Evans et al. (2000a) conducted a cladistic analysis of morphological characters in Commelinaceae, and the results were largely incongruent with Faden and Hunt's classification, presumably due to a high degree of homoplasy in the data. Evans et al. (2003) provided a

phylogenetic analysis using the chloroplast-encoded gene *rbcL* as well as a combined molecular/morphological data set. Both molecular and combined analyses produced phylogenies that were largely congruent with Faden and Hunt's classification and incongruent with the morphological phylogeny. The phylogenies are in disagreement with Faden and Hunt's classification in that: (1) *Palisota* Rchb. ex Endl. is basal to both Tradescantieae and Commelineae (making Tradescantieae paraphyletic); (2) Thyrsantheminae are polyphyletic; and (3) the monophyly of Dichorisandrinae is in question, as it is weakly supported by the combined *rbcL*/morphology analysis, but not supported by the *rbcL* data alone. Hardy (2001), with a more detailed study of morphological and molecular characters in Dichorisandrinae provided support for a monophyletic subtribe. Finally, the DNA data exhibited less homoplasy than the morphological data.

Relationships among subtribes of Tradescantieae were only weakly supported in the molecular analysis of Evans et al. (2003) as evidenced by low bootstrap and decay values. Thus, there was a need to perform an analysis using another gene to aid in providing a well-supported phylogeny for members of Tradescantieae. Givnish and Sytsma (1997) demonstrated that including a higher number of variable or informative characters in an analysis increased the chances of obtaining the correct phylogeny. The chloroplast-encoded gene *ndhF* was chosen for this study because: (1) *ndhF* is 1.5 times longer than *rbcL* (Olmstead and Palmer 1994; Kim and Jansen 1995); (2) *ndhF* has a relatively high substitution rate (approximately twice that of *rbcL*) (Olmstead and Palmer 1994; Kim and Jansen 1995); and (3) *ndhF* has been known to provide informative characters in several families

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Table 1. Taxa included for analysis of *rbcL* and *ndhF* in Commelinaceae. *Indicates sequence obtained for this study.

Taxa	Source	GenBank accession number (<i>rbcL</i>)	GenBank accession number (<i>ndhF</i>)
<i>Amischotolype monosperma</i> (C. B. Clarke) I. M. Turner	<i>Bogner 1811</i>	AF312239	AY198178
<i>Belosynapsis kewensis</i> Hassk.	Horticulture—University of Chicago greenhouse	AF312257	*AY624111
<i>Callisia</i> Loeffl.			
<i>C. repens</i> (Jacq.) L.	<i>Graf s. n.</i>	AF312247	*AY624109
<i>Cochliostema</i> Lem.			
<i>C. odoratissimum</i> Lem.	ex Marie Selby Botanical Garden s. n.	AF312244	*AY624114
<i>Coleotrype natalensis</i> C. B. Clarke	<i>Goldblatt 6587</i>	AF312243	*AY624115
<i>Cyanotis repens</i> Faden & D. M. Cameron subsp. <i>repens</i> ined.	<i>Faden 8/82</i>	AF312241	*AY624116
<i>Dichorisandra</i> J. C. Mikan			
<i>D. thyrsoflora</i> Mikan	Horticulture—Missouri Botanical Garden s. n.	AF312242	*AY624117
<i>Elasis</i> D. R. Hunt			
<i>E. hirsuta</i> (Kunth) D. R. Hunt	<i>MacDougal & Lalumondier 4953</i>	AF312251	*AY624118
<i>Geogenanthus</i> Ule			
<i>G. poeppigii</i> (Miq.) Faden	Des Moines Botanical Center	AF312261	*AY624119
<i>Gibasis geniculata</i> (Jacq.) Rohweder	Horticulture—Missouri Botanical Garden s. n.	AF312250	*AY624127
<i>Palisota</i> Rchb.			
<i>P. ambigua</i> (P. Beauv.) C. B. Clarke	<i>Faden 86/55</i>	AF312240	*AY624120
<i>Plowmanianthus</i> Faden & C. R. Hardy			
<i>P. sp.</i>	<i>Encarnación et al. 93–542</i>	AF312258	*AY624121
<i>Siderasis</i> Raf.			
<i>S. fuscata</i> (Lodd.) H. E. Moore	Horticulture—Missouri Botanical Garden s. n.	AF312254	*AY624128
<i>Spatholirion</i> Ridl.			
<i>S. longifolium</i> Dunn	<i>Chase 593</i>	AF036887	AY198179
<i>Tradescantia soconuscana</i> Matuda	<i>Faden 76/98</i>	AF312238	*AY624124
<i>Thyrsanthemum</i> Pichon			
<i>T. sp.</i>	<i>Chase 606</i>	AF312246	*AY624122
<i>Tinantia</i> Scheidw.			
<i>T. leiocalyx</i> C. B. Clarke	<i>Illis 3065</i>	AF312260	*AY624123
<i>Tripogandra</i> Raf.			
<i>T. diuretica</i> (Martius) Handlos	<i>Plowman 10102</i>	AF312249	AY624125
<i>Weldenia</i> Schult. f.			
<i>W. candida</i> Schult. f.	<i>Chase 592</i>	AF312245	*AY624126
OUTGROUPS:			
<i>Aneilema</i> R. Br.			
<i>A. calceolus</i> Brenan	<i>Faden & Faden 77/565</i>	AF036889	AY198180
<i>Cartonema</i> R. Br.			
<i>C. phylloides</i> F. Muell.	Horticulture—Munich Botanical Garden	AF036890	AY198181

(e.g., Olmstead and Palmer 1994; Kim and Jansen 1995; Terry et al. 1997; Backlund et al. 2000; Givnish et al. 2000).

The objectives of this study were to determine phylogenetic relationships among members of tribe Tradescantieae using *ndhF* and *rbcL* sequence data and to use the resulting phylogenies to evaluate systematic and biogeographical trends within tribe Tradescantieae.

MATERIALS AND METHODS

The gene *ndhF* was sequenced from a single plant of 19 species, representing 19 genera from Tradescantieae (Table 1). Additionally, a single plant from one species each of *Cartonema* and *Aneilema* were included for outgroup comparison, based upon results of Evans et al. (2003). All sam-

ples used in this study were from the same DNA samples used in Evans et al. (2003).

Total DNA for all species was extracted from frozen leaf tissue following the CTAB procedure of Doyle and Doyle (1987) as modified by Smith et al. (1991). The *ndhF* gene was amplified in two fragments on a Hybaid thermocycler (Thermo Electron Corporation, Marietta, Ohio, USA), using deoxynucleotides from United States Biochemical (Cleveland, Ohio, USA), and Taq polymerase from Promega (Madison, Wisconsin, USA). Primers for the 5'-region annealed near positions 32 (forward) and 1318 (reverse) of *ndhF* (Terry et al. 1997). For amplification of the 3'-region, primers that annealed near position 972 (forward) and 2110 (reverse) were used (Olmstead and Sweere 1994). Sequencing reactions were performed using BigDye[®] Terminator Reaction

Mix (Applied Biosystems, Inc., Foster City, California, USA) or the DYEnamic ET terminator cycle sequencing kit (Amersham Biosciences Corporation, Piscataway, New Jersey, USA). Cycle sequencing fragments were purified using Centri-Sep columns (Princeton Separations, Inc., Adelphia, New Jersey, USA) and sequenced on an ABI 310 automated sequencer before being assembled using Autoassembler vers. 2.0 (ABI Prism®). All sequences were manually aligned before phylogenetic analysis. The resulting *ndhF* data set was combined with *rbcL* data from Evans et al. (2003) and 47 morphological characters from Evans et al. (2000a).

Phylogenetic Analyses

All phylogenetic analyses were performed using PAUP* vers. 4.0b4a (Swofford 2003). A multiple-islands approach was used to find the most parsimonious trees (Maddison 1991). A heuristic search was conducted using a random addition sequence with 1000 replicates, tree-bisection-reconnection (TBR) branch swapping, steepest descent on, and 100 trees saved for each replicate. Bootstrap and decay values were determined to evaluate support for each node. For the bootstrap analysis, one hundred replicate searches were performed using TBR with random addition of 100 replicates and 100 trees saved from each replicate. Decay values were determined using AutoDecay vers. 2.9.9 (Eriksson 1997) to produce a constraint command file. This file was executed in PAUP* using a heuristic search, TBR branch swapping, and 10 replications of the random addition sequence. The "Converse Enforce" command in PAUP* was employed to save only those trees lacking the clade being examined.

Character State Mapping

To examine biogeographical trends within the tribe, geographic distributions were overlaid onto the total data phylogeny using MacClade vers. 4.0 (Maddison and Maddison 2000) assuming accelerated transformation (ACCTRANS).

RESULTS

One most parsimonious tree of 1392 steps was produced from the combined *ndhF/rbcL* data set; consistency index (CI) = 0.69, retention index (RI) = 0.61 without autapomorphies (Fig. 1). The phylogeny was largely congruent with the *rbcL* phylogeny (see Evans et al. 2003), though the support for the deeper clades was notably higher in the combined analysis (Fig. 1). The shallow branches were well supported, with the exception of the clade containing *Callisia*, *Tripogandra*, and *Elasis* (62% bootstrap). The deeper branches were also relatively well supported, though two of the deeper branches were supported by bootstrap values of less than 70% (Fig. 1).

When morphological data were added to the *rbcL/ndhF* data, two most-parsimonious trees of 1540 steps were found; CI = 0.66, RI = 0.58 without autapomorphies (Fig. 2). One tree was identical to the *rbcL/ndhF* phylogeny and the other differed in the position of *Elasis*.

Of the seven subtribes within Tradescantieae, Coleotrypiniae, and Cyanotinae were monophyletic, Tradescantiinae were paraphyletic (due to the inclusion of *Elasis*, a member

of Thyrsantheminae, in the clade), and Thyrsantheminae and Dichorisandrinae were polyphyletic. Members of Dichorisandrinae were placed into two clades: a *Dichorisandra* and a *Siderasis* clade, and a *Cochliostema/Plowmanianthus/Geogenanthus* clade. Subtribe Palisotinae is comprised of a single genus, *Palisota*, and subtribe Streptoliriinae (three genera) was represented by a single genus, *Spatholirion*.

DISCUSSION

The *rbcL* and combined *rbcL/morphology* data sets placed *Palisota* as sister to all genera of Commelinaceae except *Cartonema*, making tribe Tradescantieae paraphyletic (Evans et al. 2003). Deep branches in the *rbcL* and *rbcL/morphology* phylogenies were only weakly supported, however, as determined by bootstrap and decay values, and basal relationships within the tribe could not be inferred with confidence.

Addition of *ndhF* produced a monophyletic Tradescantieae (both the *ndhF/rbcL* and *ndhF/rbcL/morphology* data sets), with *Palisota* sister to the rest of the tribe (Fig. 1, 2). While support for most clades in the total data phylogeny was high, the branch uniting *Palisota* with the remainder of Tradescantieae is supported by a decay value of only 1 (or 2 when morphology is included), and a bootstrap value of 56% (less than 50% when morphology is included) (Fig. 1, 2). Additionally, only a single representative of tribe Commelineae, *Aneilema*, was included in this study. Until additional representatives of Commelineae are examined, as well as sequences from additional rapidly evolving regions, the exact placement of *Palisota*, and thus the monophyly of tribe Tradescantieae, will remain unclear.

Members of subtribe Dichorisandrinae are found in two separate clades (Fig. 1, 2). Analysis of morphological data produced a highly polyphyletic Dichorisandrinae, but a high degree of homoplasy among specific morphological characters makes those relationships suspect (Evans et al. 2000a). The combined *rbcL/morphology* data yielded a monophyletic Dichorisandrinae, albeit with low bootstrap and decay support (Evans et al. 2003). Hardy (2001) examined morphological and molecular data to evaluate relationships within Dichorisandrinae and found support for a monophyletic subtribe. That study, while providing a thorough sampling within Dichorisandrinae, did not include many representatives from other subtribes of Tradescantieae. Additionally, the jackknife value (Farris 1997) was relatively low for the branch supporting the monophyly of the subtribe.

Nearly every analysis to date (except for morphology alone) places the five genera of Dichorisandrinae into two well-supported clades with *Dichorisandra* and *Siderasis* in one and *Cochliostema*, *Plowmanianthus* (represented as "undescribed genus" in Evans et al. [2000a, b, 2003]), and *Geogenanthus* in the other. While this analysis places these clades separate from each other, a tree of only one additional step is required to obtain a monophyletic subtribe. All members of the subtribe share a similar karyotype of 19 large chromosomes (Jones and Jopling 1972; Faden and Hunt 1991; Faden 1998), but no unique morphological characters are known that unambiguously unite these five genera. Inclusion of sequences from additional rapidly evolving regions of the genome, as well as more thorough sampling of

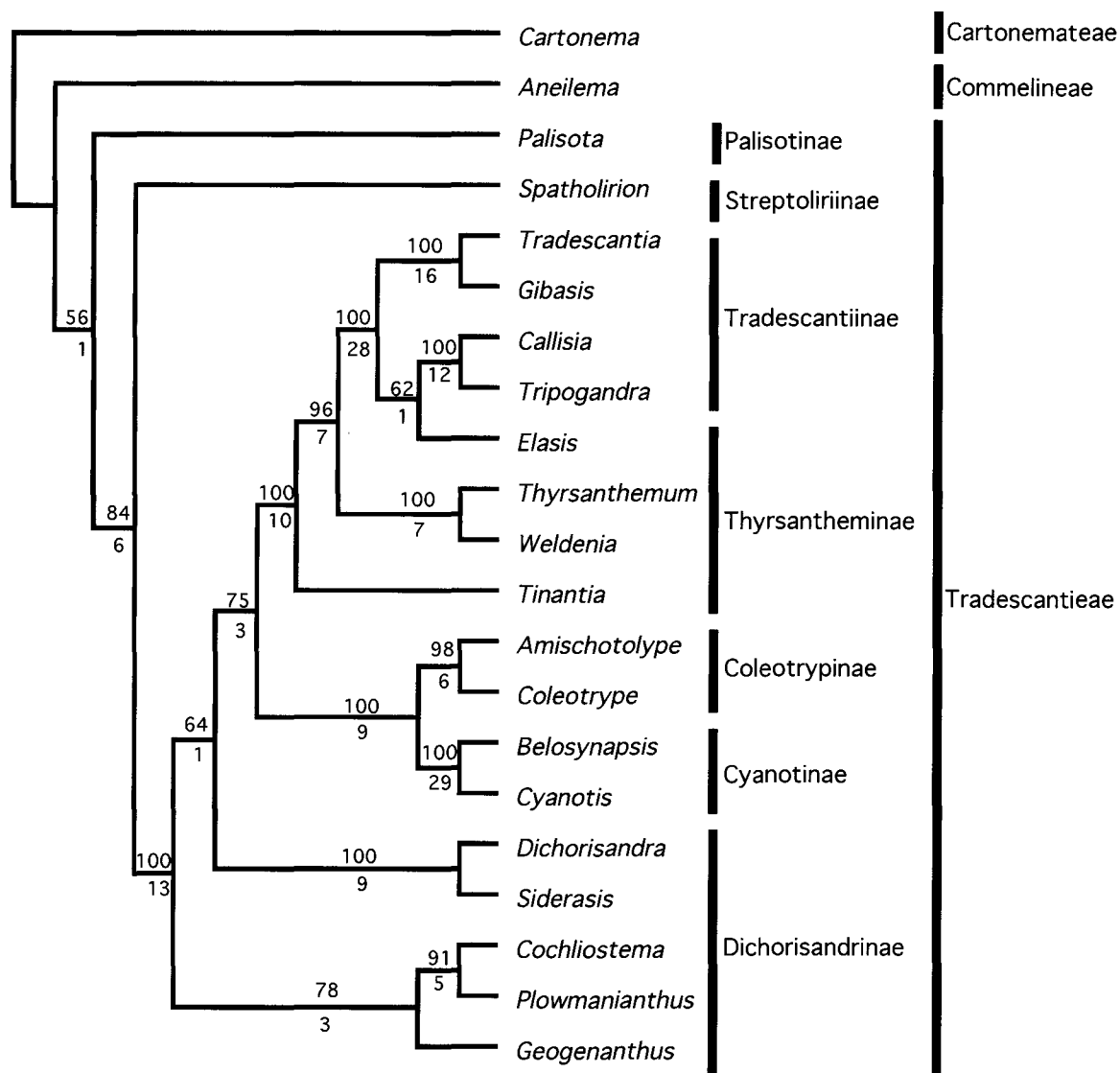


Fig. 1.—Single most-parsimonious tree produced by cladistic analysis of *rbcL* and *ndhF* sequences in Commelinaceae, tribe Tradescantieae (length = 1392 steps, CI = 0.69, RI = 0.61). Numbers above each branch indicate bootstrap support; numbers below each branch indicate the number of additional steps required before that branch collapses (decay value). Subtribal and tribal affinities are indicated with the bars to the right of the cladogram.

taxa within Dichorisandrinae will likely be needed to confidently determine the monophyly of the subtribe.

Subtribe Thyrsantheminae is polyphyletic, with representatives appearing in three different clades (Fig. 1, 2). The *rbcL*/morphology data united *Weldenia* and *Thyrsanthemum*, placed *Elasis* in a clade with members of subtribe Tradescantiinae, but failed to resolve the position of *Tinantia* (Evans et al. 2003). Addition of *ndhF* has yielded the same set of relationships, but with stronger support for each clade. Additionally, the placement of *Tinantia* has been resolved as sister to a clade containing the remainder of Thyrsantheminae and tribe Tradescantieae, again with strong support (Fig. 1, 2).

There is clearly a relationship between *Elasis* (subtribe Thyrsantheminae) and members of subtribe Tradescantiinae. Molecular data alone (*rbcL*/*ndhF*) place *Elasis* well within the Tradescantiinae clade (Fig. 1). With the addition of mor-

phological data, the position of *Elasis* with respect to Tradescantiinae becomes unresolved, with *Elasis* being placed either within or sister to the subtribe (Fig. 2). All members of subtribe Tradescantiinae share a common inflorescence type, in which two cincinni are fused back-to-back or in which two-to-several stipitate cincinni form a pseudoumbel (Faden and Hunt 1991). Evans et al. (2003) hypothesized that *Elasis*, which lacks this inflorescence type, may represent a reduced form in which one of the two cincinni has been lost. Alternatively, if *Elasis* is resolved as sister to Tradescantiinae, then fused cincinni within the subtribe may represent the derived condition with respect to *Elasis*. As there are currently no morphological characters known that clearly unite *Elasis* with members of Tradescantiinae, examination of inflorescence structure and development might shed light upon this unresolved node of the phylogeny.

The Old World subtribes Coleotrypinae and Cyanotinae

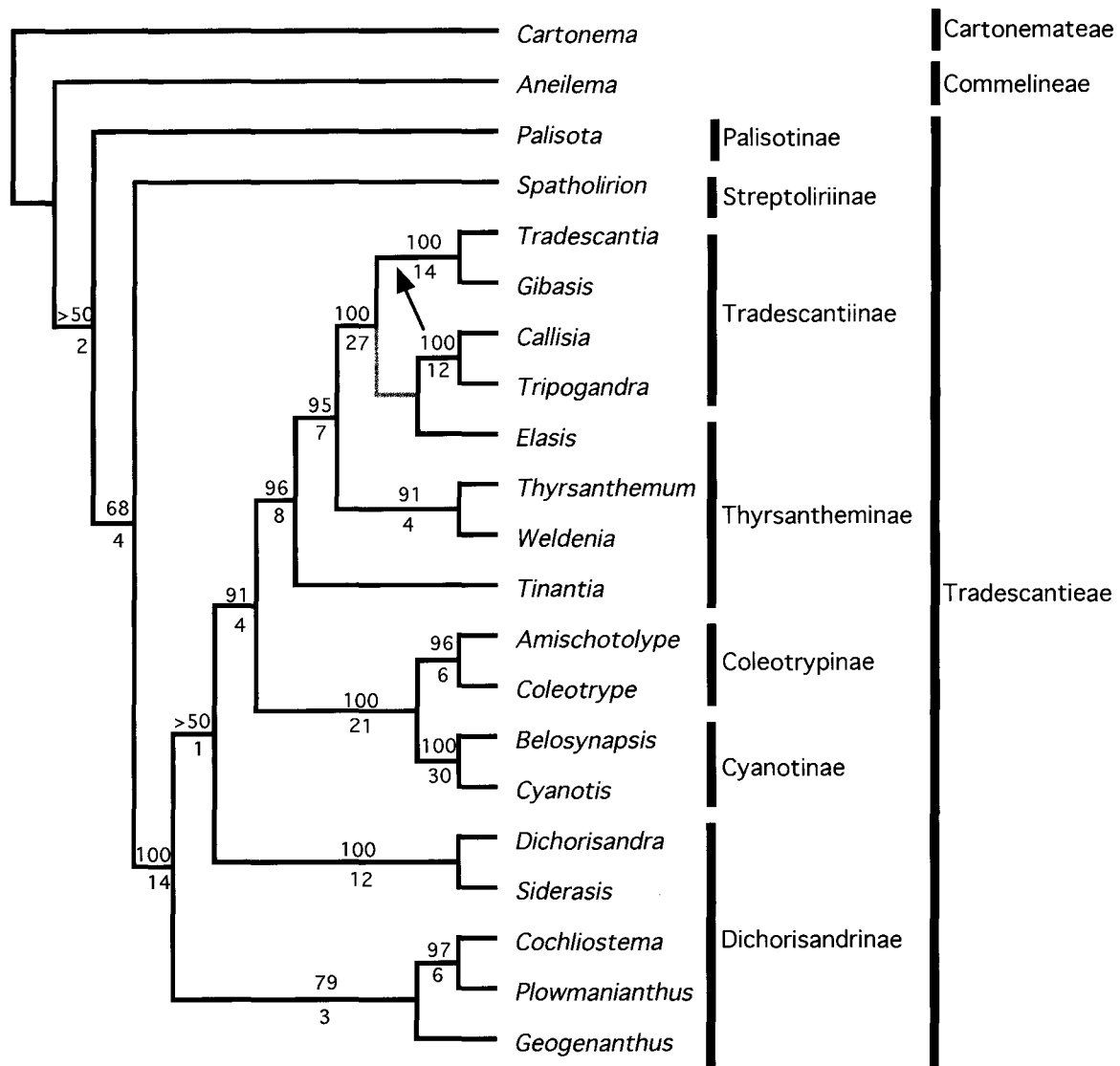


Fig. 2.—One of two most-parsimonious trees produced by cladistic analysis of combined morphology/*rbcL*/*ndhF* in Commelinaceae tribe Tradescantieae (length = 1540 steps, CI = 0.66, RI = 0.58). Numbers above each branch indicate bootstrap support; numbers below each branch indicate the number of additional steps required before that branch collapses (decay value). Gray line represents branch that collapses in strict consensus of the two most-parsimonious trees. Arrow indicates the position of branches in the second most-parsimonious tree. Subtribal and tribal affinities are indicated with the bars to the right of the cladogram.

are each monophyletic and together form a monophyletic Old World clade (Fig. 1, 2). The monophyly of each of these two subtribes is strongly supported by both molecular and morphological data. The inflorescence of members of Coleotrypinae consists of axillary, highly congested cincinni and perforates the leaf sheath. The Cyanotinae are united by the seeds with a terminal embryotega. As noted in Evans et al. (2003), biogeography provides some evidence of relationship between these two subtribes, but no morphological characters are known that unambiguously unite them.

The addition of *ndhF* data has helped to clarify the biogeographical relationships of Cyanotinae and Coleotrypinae to other Tradescantieae subtribes. Of the seven subtribes within Tradescantieae, three (Dichorisandrinae, Thyrsantheminae, and Tradescantiinae) are found exclusively in the New World and four (Coleotrypinae, Cyanotinae, Palisotinae, and Streptoliriinae) are found exclusively in the Old

World (Faden and Hunt 1991; Hunt 1993, 1994; Faden 1998) (Fig. 3). The placement of Coleotrypinae and Cyanotinae within, but not sister to, the New World clade was noted by Evans et al. (2003) in their *rbcL*/morphology analysis. Three possible scenarios were proposed to explain the distribution: (1) a single shift from the Old World to the New World, either through vicariance or dispersal, followed by a single dispersal back to the Old World (ACCTRANS optimization); (2) two independent introductions to the New World (DELTRANS optimization); or (3) the Boreotropical Flora Hypothesis (Wolfe 1975), in which the current distribution reflects a relictual distribution of a formerly widespread northern temperate group. The third scenario was determined to be unlikely due to the relatively early divergence of Dichorisandrinae and the relatively derived position of Tradescantiinae. The first two scenarios, however, were equally likely as a result of the ambiguous optimization of

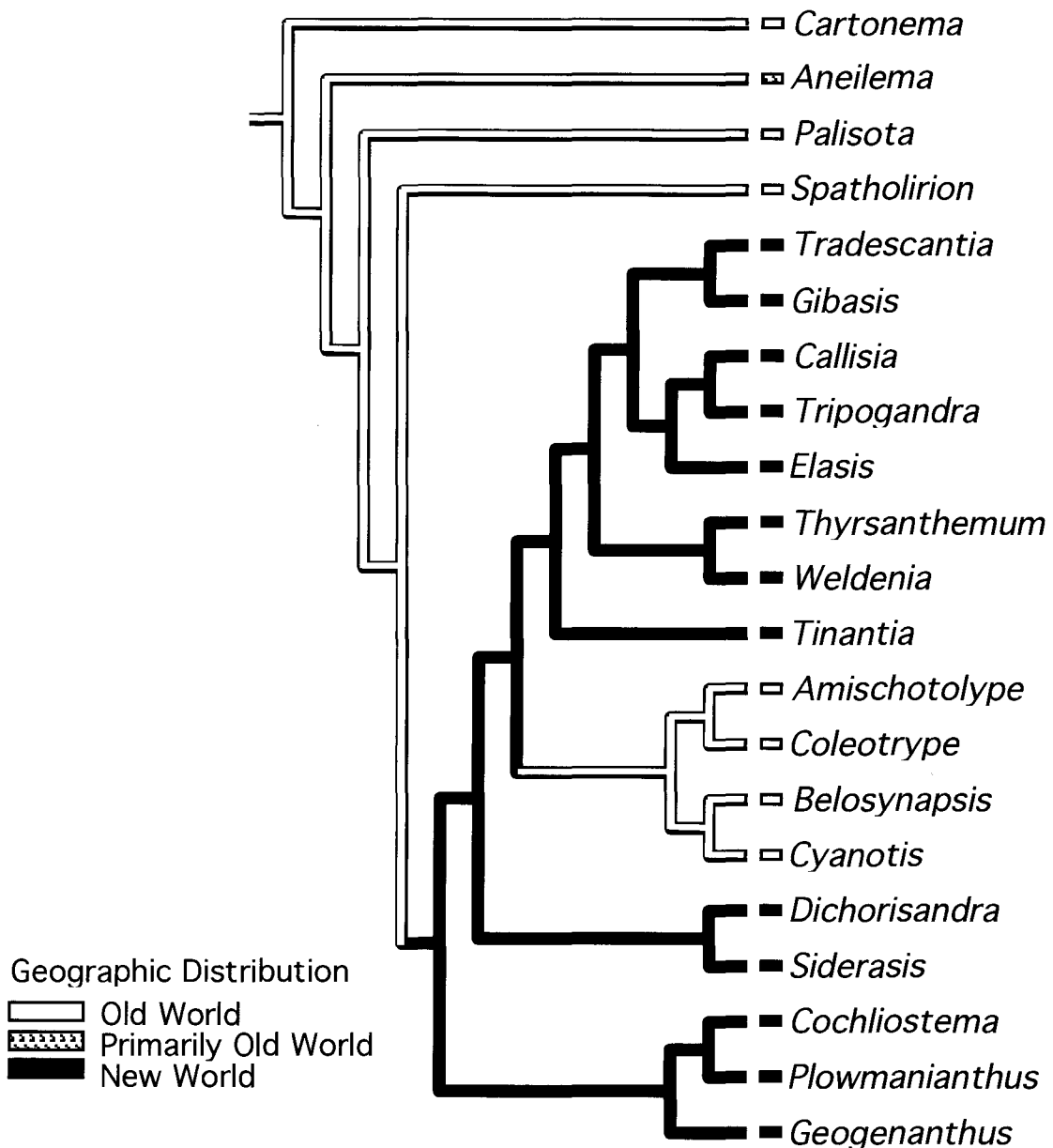


Fig. 3.—Geographic distributions mapped onto single most-parsimonious tree produced by analysis of *rbcL/ndhF* sequences. A single shift from the Old World to the New World, followed by a dispersal back to the Old World is supported, due to the position of Old World subtribes Coleotrypinae and Cyanotinae nested well within a New World clade.

biogeography onto the *rbcL*/morphology phylogeny (Fig. 6 of Evans et al. 2003). The addition of *ndhF* to the analysis clarifies the issue by placing the Old World subtribes Coleotrypinae and Cyanotinae well within the New World clade, thus removing ambiguity to the optimization of biogeography and favoring the first hypothesis (one shift from the Old World to the New World followed by dispersal back to the Old World; Fig 3).

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