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Toward an understanding of the global phylogeny of the Trilliaceae

Susan Baker Farmer

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To the Graduate Council:

I am submitting herewith a thesis written by Susan Baker Farmer entitled "Toward an understanding of the global phylogeny of the Trilliaceae." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Botany.

Edward E. Schilling, Major Professor

We have read this thesis and recommend its acceptance:

B. E. Wofford, J. L. Gittleman

Accepted for the Council:

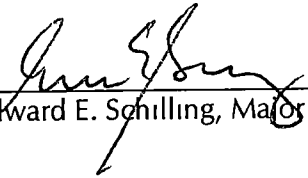
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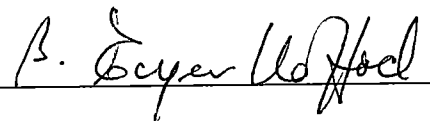

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To the Graduate Council

I am submitting herewith a thesis written by Susan B Farmer entitled "Toward an understanding of the global phylogeny of the Trilliaceae." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a Major in Botany


Edward E. Schilling, Major Professor

We have read this thesis
and recommend its acceptance

Accepted for the Council


Associate Vice Chancellor and
Dean of The Graduate School

**Toward an Understanding
of the
Global Phylogeny
of the
Trilliaceae**

A Thesis
Presented for the
Master of Science
Degree
The University of Tennessee, Knoxville

Susan Baker Farmer
May 2000

DEDICATION

To my Wildflower Gardeners and their spouses who have so graciously poured their knowledge into my brain over the years: Jean and Clarence Freshour, Eddie Franklin and his late wife Glenna, Mearl and Jim Macres, Dixie and Bob Vineyard, the late Hedy Wood, and especially to Don and Sue Williams who started my feet down this path.

To the members of the Trillium-L mailing list who have provided support, questions, and even answers. Especially Jim McClements and Carl Denton

To the Memory of J.D Freeman who inspired us all

Most importantly to my family: my parents and in-laws, my husband John and my son Tom – without your help, tolerance, and patience, I never could have done this at all.

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The members of the faculty of the Botany Department for their encouragement.

The staff of Interlibrary Loan at the University of Tennessee library – without them, this work would have been much less complete.

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Dr. Carl Denton, Dr. Soichi Kawano, Jim McClements, Dr. Gene Wofford, Mrs. Ken Thurmond, the USDA NRCS, and Konrad Lauber and the Akademischer Verein der Pharmaziestudierenden for permission to use their photographs.

And to God, who provided the plants.

ABSTRACT

The purpose of this study was to make a comprehensive analysis of the systematic relationships within Trilliaceae, a family of flowering herbaceous plants found in north temperate mixed forests. As currently circumscribed it includes *Trillium* L., *Paris* L., *Kinugasa* Tatew. and Sutô, and *Daiswa* Raf. Results of previous *rbcl* studies showed that the members of Trilliaceae segregate out into a distinct, cohesive unit separate from other liliaceous genera, and reinforced the concept that Trilliaceae are not a part of the Liliaceae and should in fact be an independent family. The present study focused on the relationships within *Paris* s.l.; (i.e., *Paris*, *Daiswa*, and *Kinugasa*); between *Paris*, s.l. and *Trillium*, and within *Trillium* itself. A total of 86 taxa, including all of those currently recognized, was selected for morphological, cladistic analysis and scored for 110 morphological characters. It was also possible to obtain *matK* and ITS molecular characters for a subset of taxa used in the morphological analysis. Several genera outside the family were considered for outgroup selection, but none of those taxa proved satisfactory. Based on preliminary analyses, *Trillium rivale* was shown to be distinctive and was used as the outgroup. The data sets were analyzed with the PAUP* program using maximum parsimony as well as maximum likelihood. Character congruence analysis gave contradictory results with the Mickevich and Farris measures showing less than 5% variation between data set, and the Paup* Homogeneity of Partitions test indicating incongruence between the morphological and molecular data sets. Taxonomic congruence gave results showing that most clades were supported across all analyses, and rival trees were less than 5% longer than the constraint tree for a given data set. Analysis of the combined ITS and *matK* sequence data produced 6 shortest trees, the morphological data for the same set of taxa for which molecular data were available produced 13 shortest trees,

the combined morphological and molecular data sets produced 3 trees, and the full data set of 86 taxa produced 1,296 shortest trees with an average CI (consistency index) of 0.74. *Trillium rivale* is distinct from both *Paris* and *Trillium* and should be placed in its own genus. *Trillium* and *Paris* are clearly distinct based on molecular as well as morphological evidence. *Trillidium govanianum* is more similar to *Paris* than it is to *Trillium*, but should be recognized as a distinct monotypic genus. *Trillium undulatum* is clearly a *Trillium* based on morphology and biogeography. The cladistic analyses provided support for the separation of *Paris s.l.* into *Daiswa*, *Kinugasa*, and *Paris*. The monophyly of *Trillium* was supported in all analyses.

PREFACE

I am Spock, a dealer in *Kevas* and *Trillium*

- Gene L. Coon, *Errand of Mercy*

Consider the Lilies of the field how they grow, they toil not, neither do they spin: And yet I say unto you, That even Solomon in all his glory was not arrayed like one of these

- Matthew 6 28b-29

This genus is a very interesting one. Under great simplicity and conformity of habit, 3 leaves at the summit of a stem, supporting one solitary terminal flower, it contains and conceals many species."

- Stephen Elliott, *A Sketch of the Botany of South Carolina and Georgia* p.430

But all I wanted to do was identify my photographs!

- Susan Farmer

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1.0 INTRODUCTION

Despite its distinctiveness and a long history of study, confusion exists about the systematics of Trilliaceae, a family of flowering herbaceous plants which occur in north temperate mixed forests. These plants are morphologically distinct and quite similar: a stem topped by a single whorl of reticulate-veined leaves with a single flower.

One major question regards the generic delineation in Trilliaceae: are the traditional generic groupings correct, or would these species be better considered a single genus? The taxa from Trilliaceae included in a recent study using DNA sequences from the ribulose-1,5-bisphosphate carboxylase/oxygenase (*rbcl*) gene show far less differentiation than for other genera included in the study (Chase, 1993, personal communication) leading to the possible conclusion that there is only one genus. If the circumscription of the traditional genera is correct, what are the relationships within Trilliaceae: are *Paris* L. *sensu lato* and *Trillium* L. sister genera, is one derived from the other, or should *Paris s.l.* be split into *Paris*, *Kinugasa* Tatew & Sutô, and *Daiswa* Raf? For the purposes of this study, the taxa included in Trilliaceae are those recognized by Tamura (1998): *Trillium*, *Paris*, *Daiswa*, and *Kinugasa*.

With this lack of differentiation between genera in the molecular data, it was felt that an examination of the morphology should be undertaken to determine if the traditional separation of *Paris s.l.* and *Trillium* was valid.

1.1 Taxonomic History

The core genera in Trilliaceae, *Trillium* and *Paris*, s l , were both recognized by Linnaeus in *Species Plantarum* (1753). He also named four of the species included in this family *Trillium sessile*, *T. cernuum*, *T. erectum*, and *Paris quadrifolia* (Figure 1). He separated *Paris* and *Trillium* based on numbers of carpels and anthers, placing *Trillium* in his "hexandria trigynia" and *Paris* in "octandria tetragynia." Several genera have been proposed since the work of Linnaeus for plants referable to Trilliaceae, most of which are now considered to be synonyms. A summary of the genera with the rationale for their creation is given in Table 1. The name *Alopicarpous* Neck. was proposed as a substitute for *Paris* because Necker (1790) felt that *Paris* was too significant as the "voice of France" ("*Paris, vox gallica*") and thus should be rejected as a genus name. Hoffmann (1808) recognized *Demidovia* as different because it is apetalous. *Delostylis*, *Phyllantherum*, and *Daiswa* were named by Rafinesque for species that possess a common style, lack a pedicel, or are 5-merous, respectively (Rafinesque, 1819, 1820, 1836). Kunth (1836) saw *Trillidium* as halfway between *Paris* and *Trillium* because in this species the whole perianth is colored and the anther dehiscence is extrorse, *Paris* generally has greenish-yellow petals and latrorse anther dehiscence, and *Trillium* has colored petals and green sepals with (most commonly) introrse anther dehiscence. *Cartalinia* Szov. is a *nomen nudum* that was listed by Kunth (1836) in synonymy without comment or reference for *Paris incompleta* M. Bieb. *Esdra* and *Euthrya* were separated out by Salisbury (1866) for species that have all aerial organs strictly sessile or have a capsular fruit with a common style, respectively. Tatewaki and Sutô (1935) define *Kinugasa* to be distinct from *Paris* because it has petaloid sepals and a caespitose habit; different from *Trillium* by the shape of the leaves and the number of

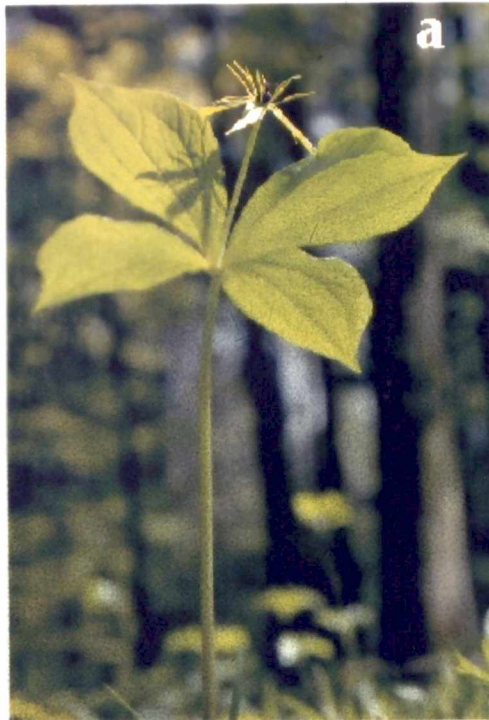


Figure 1 Linnaean taxa included in Trilliaceae. a. *Paris quadrifolia* (used by permission of the Akademischer Verein der Pharmaziestudierenden) b. *Trillium erectum* c. *T. sessile* d. *T. cernuum* (used by permission of Dr. Carl Denton).

Table 1. Generic types and synonymy from Trilliaceae following Tamura (1998).

genus name	type	reason	synonymy
<i>Trillium</i> L.	<i>T. cernuum</i> L.	<i>hexandria tryginia</i>	<i>Delostylis</i> Raf, <i>Phyllantherum</i> Raf, <i>Trillidium</i> Kunth, <i>Esdra</i> Salisbury,
<i>Paris</i> L.	<i>P. quadrifolia</i> L.	<i>octandria tetragyna</i>	<i>Alopicarpus</i> Neck, <i>Euthrya</i> Salisb, <i>Daiswa</i> Raf, <i>Demidovia</i> Hoffm, <i>Trillidium</i> Kunth, <i>Cartalina</i> Szov ex Kunth, <i>Kinugasa</i> Tatew & Sutô
<i>Alopicarpus</i> Neck	<i>Alopicarpus quadrifolia</i> here designated the type	because "Paris, vox gallica," was too significant and should be rejected as a genus name	
<i>Demidovia</i> Hoffm	<i>D. polyphylla</i> Hoffm (= <i>Paris incompleta</i>)	species that are apetalous	
<i>Delostylis</i> Raf	<i>D. cernuum</i> Raf (= <i>T. stylosum</i>)	species that possess a common style	
<i>Phyllantherum</i> Raf	<i>P. sessile</i> Raf	species that lack a pedicel	
<i>Cartalina</i> Szov in Kunth	<i>nom nudum</i> without species	in synonymy for <i>Paris incompleta</i> M Bieb	
<i>Daiswa</i> Raf	<i>D. polyphylla</i> (Smith) Raf <i>P. polyphylla</i> Smith in Rees	because it was 5-merous	
<i>Trillidium</i> Kunth	<i>T. govanianum</i> Kunth	between <i>Paris</i> and <i>Trillium</i> because the whole perianth is colored, extrorse anther dehiscence, subulate stigma, and hexamerous perianth	
<i>Esdra</i> Salisb	<i>E. sessilis</i> Salisb (= <i>T. sessile</i> L.)	species that have all its aerial organs strictly sessile	
<i>Euthrya</i> Salisb	<i>E. polyphylla</i> Salisb	species that have a capsular fruit with a common style	
<i>Kinugasa</i> Tatew & Sutô	<i>K. japonica</i> (Franch & Sav.) Tatew & Sutô <i>Trillidium japonicum</i> Franch & Sav	distinct from <i>Paris</i> because it has petaloid sepals and caespitose habit, different from <i>Trillium</i> by the shape of the leaves and the number of floral parts, different from <i>Trillidium</i> by rhizome characters, merosity, and shape of pistil and leaves	

floral parts, and different from *Trillidium* by rhizome characters, merosity, and shape of pistil and leaves. Current taxonomists frequently split *Paris* into *Paris*, *Kinugasa*, and *Daiswa* (Takhtajan, 1987, 1997; Tamura, 1998, Dahlgren, Clifford, and Yeo, 1985). Other authors, notably Hara, Stearn, and Williams (1978) split *Trillium* by recognizing both *Trillium* and *Trillidium*.

There have been a number of other genera associated with *Paris* and *Trillium*, whether Trilliaceae is placed in a sub-familial group within Liliaceae *s.l.* or as an independent family (**Table 2**). *Medeola* L. and *Scoliopus* Torr. are the most frequently included in a suprageneric taxon with *Paris* and *Trillium*: sometimes both *Medeola* and *Scoliopus* are included as in Dalla Torre and Harms (1908) and Watson and Dallwitz (1991b), other taxonomists include only *Medeola* (Engler, 1888; Melchior, 1964); still others include only *Scoliopus* (Dahlgren et al., 1985; Brummit and Powell, 1992b). *Clintonia* Raf. was included by Bentham and Hooker (1880). The additional taxa that are sometimes included in the family are shown in **Figure 2**.

The Trilliaceae have led a vagabond existence since their initial recognition by Lindley in 1846 (note that although Lindley has long been credited with naming the family, Reveal (1998) has recently discovered that the family was named first by Chevallier in 1827). It has been afforded tribal status within various families, reincorporated back into the Liliaceae, or elevated to familial status within different orders of the monocots. Takhtajan, alone, placed the family in four different orders (1969, 1980, 1987, 1997). Even though Dahlgren was not the first to segregate Trilliaceae, or the only taxonomist to perform a rigorous morphological analysis (q.v. Huber, 1969, 1977); it seems that he is credited as being influential in leading most taxonomists to segregate the family.

Table 2. Historical placement and composition of genera associated with Trilliaceae.

Reference	date	included genera						other	family	order
		<i>Trillium</i>	<i>Paris</i>	<i>Medeola</i>	<i>Scolopopus</i>					
de Jussieu	1789							Liliaceae		
Dumortier	1829	X	X	6				Parideae	Paridales	
Endlicher	1836-40	X	X	X			2	Smilacaceae (Parideae)		
Lindley	1846	X	X	1				Trillaceae	Dioscorales	
Kunth	1850	5	X					Smilacineae		
Watson	1879	5	X	X	X			Liliaceae (Trillaceae)		
Bentham & Hooker	1883	X	X	X	X		3	Liliaceae (Medeoleae)		
Engler	1888	X	X	X				Liliaceae (Parideae)		
Bessey	1915							Liliaceae		
Dalla Torre & Harms	1908	X	X	X	X			Liliaceae (Parideae)		
Hutchinson	1926	X	X	X	X			Trillaceae	Liliales	
Rendle	1930	X	X					Liliaceae		
Lawrence	1951	X						Liliaceae		
Cronquist	1968							Liliaceae		
Takhtajan	1959							Liliaceae		
Melchior	1964	X	X	X				Trillaceae	Dioscorales	
Thorne	1968							Liliaceae (Parideae)		
Huber	1969							Liliaceae		
Takhtajan	1969							Trillaceae	Stemonales	
Willis	1973	X	X	X	X			Liliaceae		
Dahlgren	1975							Trillaceae		
Huber	1977							Trillaceae	Stemonales	
Takhtajan	1980	X	X					Trillaceae	Roxburghiales	
Dahlgren	1985	X	X		X			Trillaceae	Smilicales	
Takhtajan	1987	X	4		X			Trillaceae	Dioscorales	
Watson & Dallwitz	1991b	X	X	X	X			Trillaceae	Dioscorales	
Brummitt	1992b	X	4	X	X			Trillaceae	Dioscorales	
Thorne	1992	X	X		X			Trillaceae		
Nolle	1994	5	X					Trillaceae	Liliales	
Stevenson & Loconte	1995							Trillaceae		
Watson & Dallwitz	1996	X	4					Trillaceae	Stemonales	
Takhtajan	1997							Trillaceae	Dioscorales	
								Trillaceae	Trilliales	

1 Listed in synonymy for *Trillium*, but mentioned in text

2 Demidovia Hoffm

3 Clintonia Raf

4 *Paris sensu stricto*, *Kinugasa*, and *Daiswa*

5 *Trillium* and *Trillichium*

6 *Medeola* as *Gyroonia*

- excluded

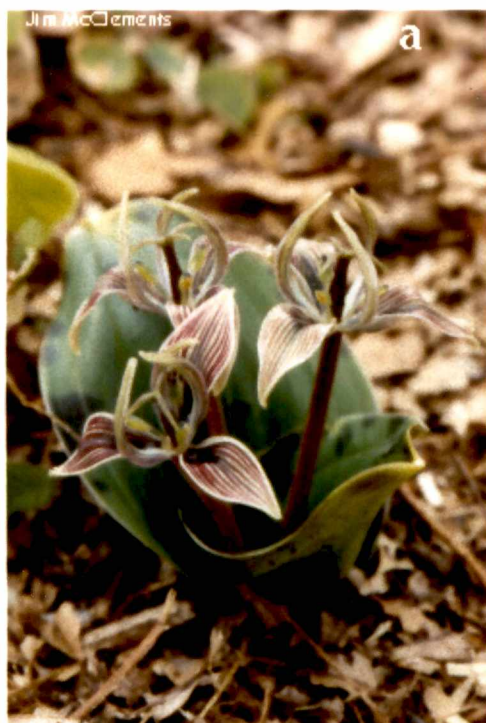


Figure 2. Genera sometimes included in Trilliaceae. a. *Scoliopus bigelovii* (used by permission of Jim McClements) b. *Clintonia umbellata* (used by permission of Ken Thurmond) c. *Medeola virginiana* (used by permission of Mrs. Ken Thurmond)

Recent studies such as those using the *rbcl* gene (Chase, personal communication, Chase et al , 1993, 1995a; Kato et al , 1995b), chloroplast DNA (cpDNA) restriction-site analysis (Davis, personal communication, 1995, Kato et al., 1995a), and combined morphological-restriction site analyses (Stevenson and Loconte, 1995, Chase et al , 1995b) are reinforcing the concept that Trilliaceae is not a part of Liliaceae and should in fact be an independent family. When Trilliaceae is recognized as a family, it is not the only family removed from Liliaceae s.l which is a heterogeneous assemblage of genera united only by the fact that they possess modified underground storage stems, 6 perianth segments, usually 6 stamens, and a 3-carpellate ovary (Cronquist, 1981). Within the Liliaceae s.l there is extensive variation for many features. For example, leaves vary from simple, undifferentiated, and strap-like to having a distinct petiole and lamina, leaves are alternate, opposite, or whorled, leaves have parallel or palmate venation, the inflorescence is a raceme or solitary, flowers are bisexual or unisexual, floral symmetry is actinomorphic or zygomorphic, the perianth is composed of tepals or distinct sepals and petals, and anthers are basifixed or dorsifixed. It is when the Liliaceae is narrowly defined as a more homogeneous family that Trilliaceae, as well as many other more narrowly circumscribed families such as Agavaceae, Amaryllidaceae, Asparagaceae, Melanthiaceae, and Smilacaceae are separated out (Judd et al , 1998). The molecular evidence indicates that a narrow definition of Liliaceae is most consistent with phylogeny (Chase et al., 1995a, Chase et al , 1995b, Davis, 1995; Davis et al , 1998, Stevenson and Loconte, 1995).

1.2 Relationships within Trilliaceae

The simplest and traditional view of Trilliaceae is to separate the species into two genera based on floral merosity. *Trillium* is trimerous, whereas *Paris* s.l. is 4- to 11-merous (Figure 3). However, 4- and 5-merous *Trillium* monstrosities exist, as do trimerous *Paris*. In fact there is no clear and absolute set of morphological characters that separates any of the groups within the family. When *Paris fargesii* var. *brevipetalata* was transferred from *Daiswa* to *Paris*, *Trillium taiwanense* was listed by Huang, Huang, and Yang (1989) as a new synonym. Other than *Kinugasa japonica*, which is distinctive enough to have been placed in every genus except *Daiswa*, this is the only occurrence of cross-generic synonymy between *Trillium* and *Paris*.

Because *Trillidium* and *Kinugasa* each share characters with both *Trillium* and *Paris*, they underscore the difficulty that sometimes occurs in separating *Paris* and *Trillium*. *Trillidium* was based on one species, *T. govanianum*, and was seen as halfway between *Trillium* and *Paris* (Kunth, 1836). *Trillidium govanianum* possesses characters normally restricted to *Paris* such as filiform petals and ellipsoid, monosulcate pollen (Zomlefer, 1996), but it shares having trimerous flowers with *Trillium*. *Trillidium japonicum*, which is now *Kinugasa japonica*, was added to the genus in 1877 by Franchet & Savatier and appears to possess chromosome types from both *Trillium* and *Paris* (Tatewaki and Sutô, 1935, Haga, 1937b). Characters that it shares with *Trillium* include having a large showy inflorescence and caespitose habit even though it has the filiform petals characteristic of *Paris*, as well as merosity and narrow leaves. *Trillidium* is now considered by some botanists to be a valid monotypic genus containing only *T. govanianum* (Hara et al., 1978;



Figure 3. Morphologically distinct taxa included in Trilliaceae. a. *Paris fargesii* b. *P. polyphylla* var. *chinensis* c. *Trillium grandiflorum* d. *T. stamineum*. (a and b used by permission of Dr. Victor G. Soukup)

Noltie, 1974), *Kinugasa* is accepted by Takhtajan (1983, 1987), Dahlgren et al. (1985), Zomlefer (1996) and Tamura (1998).

Even though the different subgroups within *Paris s.l.* are relatively consistently defined, views of their taxonomic rank have varied (Table 3). Takhtajan (1983) recognizes separate genera, but Li (1984b, 1986, 1998) and Hara (1969) prefer to retain the single genus *Paris*. Each of these taxonomists uses a slightly different character set to delineate the taxonomic groups. Takhtajan separates *Paris* from *Kinugasa* and *Daiswa* on the basis of a slender, creeping rhizome, round ovary, and fruit being an indehiscent, black berry. *Daiswa* is characterized by a thick rhizome, an ovary with a transverse rim, a fleshy loculicidal capsule, and seeds with a scarlet sarcotesta. *Kinugasa* shares several features with *Paris* such as slender stigmatic branches, indehiscent berry, and seeds without a sarcotesta; it also shares features with *Daiswa* such as a thick rhizome, and angular ovary. Li (1984b, 1986, 1998) and Hara (1969) separate Takhtajan's genera into subgenera and sections on the basis of placentation and number of locules, presence/absence of an aril, fruit type, rhizome morphology, and basal merosity (e.g., parts 2x-6x the base number). There appear to be some problems with this characterization (Li and Noltie, 1997)

- *P. fargesii* - has the thick rhizome of *Daiswa* (where it is placed by Takhtajan), but the indehiscent fruit of *Paris sensu stricto* (where it is placed by Li).
- *P. tibetica* - has the rhizome and capsule of *Daiswa*, but the seeds are *Paris*-like.

Despite its distinctive morphology, *Kinugasa* has been recognized only by those who also separate *Daiswa* from *Paris s.s.*

For *Trillium* the focus has been on infrageneric groups; *Trillium* is divided into two subgenera based on the presence or absence of a pedicel (Freeman, 1969a). Subgenus *Trillium* consists of pedicellate plants, whereas subg. *Phyllantherum* includes sessile-

Table 3. Three views on *Paris sensu lato*: a comparison of the taxonomy of Hara, Li, and Takhtajan.

		H Hara 1969	H Li 1984, 1986	A Takatajan 1983
<i>Paris</i>	taxonomy	genus <i>Paris</i>	genus <i>Paris</i> , subgenus <i>Paris</i>	genus <i>Paris</i>
	rhizome	slender, creeping	short and thick (<i>Axiparis</i>) *or* long and slender (<i>Paris</i>)	slender, creeping
	ovary	roundish, 4-5 locules, few ovules	4-10 locules with axillary placentation	roundish, without an apical transverse rim
	stigma	slender		slender
	fruit	indehiscent berry	indehiscent berry	indehiscent berry, poison, blue-black
	seeds		with or without imperfect aril	without sarcotesta (aril)
<i>Kinugasa</i>	taxonomy	genus <i>Paris</i> , subgenus <i>Kinugasa</i>	genus <i>Paris</i> , subgenus <i>Paris</i> , section <i>Kinugasa</i>	genus <i>Kinugasa</i>
	rhizome	very thick	short and very thick	
	ovary	roundish with disk at the top, 6-10 locules, many ovules	4-10 locules with axillary placentation	angular, truncate and depressed apically
	stigma	slender		slender
	fruit	indehiscent berry	indehiscent berry	indehiscent berry, edible, dark purple
	seed		without aril	without sarcotesta (aril)
<i>Daiswa</i>	taxonomy	genus <i>Paris</i> , subgenus <i>Daiswa</i>	genus <i>Paris</i> , subgenus <i>Daiswa</i>	genus <i>Daiswa</i>
	rhizome	thick	thick	thick or very thick
	ovary	angular, numerous ovules	unilocular with > 4 parietal placentas	angular, truncate with apical transverse rim
	stigma	short, thick		thick
	fruit	dehiscent capsule	dehiscent capsule	fleshy loculicidal capsule
	seeds	enclosed by a scarlet juicy coat	enclosed by juicy red aril	scarlet and juicy sarcotesta

flowered plants. In addition to the lack of a pedicel, most sessile-flowered *Trillium* have spotted leaves, but the trait occurs sparingly in pedicellate *Trillium* as well as in *Paris* s.l

Relationships among the sessile-flowered *Trillium* were studied in the only thorough treatment of the subgenus by Freeman (1969a, 1975), previously they had been surveyed by Small (1897) Freeman separated *T. subg. Phyllantherum* into informal groupings based on morphology which were formalized by Murray (1983, 1984) The "*Trillium recurvatum* group," sect *Recurvata*, possesses basally recurved sepals, incurved anthers, and slender elongated rhizomes. The "*Trillium sessile* group," sect. *Sessilia*, possesses prolonged anther connectives, introrse or extrorse (but not lateral) dehiscence, angled ovaries, linear stigmas, and thick compact rhizomes The "*Trillium maculatum* group," sect *Maculata*, is characterized by lateral anther dehiscence, no anther prolongation, and subulate stigmas

Formal subgroups have not been proposed for *Trillium subg. Trillium*, but two subgroups are often mentioned: the "*erectum* group" and the "*grandiflorum* group" (Patrick, 1984, Gleason, 1906, Barksdale, 1938; Ihara and Ihara, 1978, 1982). Even though these two groups have been typically defined by the texture and aging characteristics of the petals (Patrick, 1984), the studies that make such taxonomic judgements have used other characters (**Table 4**). Barksdale (1938) defines 3 groups on the basis of leaf and ovary characters an "*erectum* group" with rhombic leaves and globose, 6-angled ovaries, a "*grandiflorum* group" with elliptic to ovate leaves and green, 6-angled ovaries, and an "*undulatum* group" with petiolate leaves and 3-angled ovary. Gleason (1906) also defined his groups also on the basis of pistil characters: an "*erectum* group" with a sharply 6-angled ovary and recurved, subulate stigmas, a "*grandiflorum* group" with a less deeply angled 3-lobed ovary and slender, cylindrical stigmas, and a "*catesbaei* group" with a slender and

Table 4. Taxa and their placement within the pedicellate *Trillium*.

author	Barksdale	Gleason	Ihara and Ihara
erectum group	<i>T cernuum</i>	<i>T cernuum</i>	<i>T cernuum</i>
	<i>T erectum</i>	<i>T erectum</i>	<i>T erectum</i> (with var <i>simile</i> , <i>sulcatum</i> , <i>vaseyi</i>)
	<i>T gleasoni</i> (= <i>T flexipes</i>)	<i>T declinatum</i> (= <i>T flexipes</i>) <i>T kamtschaticum</i> (= <i>T camtschatcense</i>)	<i>T flexipes</i>
	<i>T rugelii</i>	<i>T rugelii</i> <i>T simile</i> <i>T smallii</i> <i>T tschonoskii</i>	<i>T rugelii</i>
	<i>T vaseyi</i>	<i>T vaseyi</i>	
			<i>T affine</i> (=unknown) <i>T latifolium</i> (=unknown)
grandiflorum group	<i>T.catesbaei</i>		
	<i>T.grandiflorum</i>	<i>T govanianum</i> <i>T.grandiflorum</i> <i>T nivale</i> <i>T ovatum</i>	<i>T grandiflorum</i> <i>T nivale</i> <i>T ovatum</i>
	<i>T pusillum</i>	<i>T rivale</i> <i>T undulatum</i>	<i>T rivale</i> <i>T undulatum</i>
		<i>T.scouleri</i> (= <i>T ovatum</i> ?)	
other	<i>undulatum</i> group	<i>catesbaei</i> group	<i>pusillum</i> group
	<i>T undulatum</i>	<i>T catesbaei</i> <i>T pusillum</i>	<i>T catesbaei</i> <i>T persistens</i> <i>T pusillum</i>
		<i>T affine</i> (=unknown)	

cylindrical stigma and style. Ihara and Ihara (1978, 1982) also use pistil morphology to define three groups: an “*erectum* group” which they define by karyotype and microsporogenesis as well as the variability in pistil characters – even though that variability helps categorize this group. “Their gynoecium forms are variable in the ovary shape as well as in the stigmatic portion, though the variability *per se* characterizes the present assemblage”; a heterogenous “*grandiflorum* group” which may be an artificial group on the basis of slender stigmas, and a “*pusillum* group” having a pale green ovary with a style

1.3 Biogeography

Trilliaceae are plants of North Temperate forests with a holarctic distribution (Figure 4), and have been proposed to be Arcto-Tertiary in origin (Tamura, 1998). However, at the genus level, distribution patterns become evident. In North America only *Trillium* are found, with subg *Phyllantherum* endemic; in Europe, only *Paris* occurs; but in Asia, representatives of all the genera occur. The center of diversity of *Trillium* is in the southeastern United States; the center of diversity for *Paris* and *Daiswa* is in China. *Kinugasa* is endemic to Japan.

Genetically, another distribution pattern develops: polyploidy is restricted to the Old World. All North American *Trillium* are diploid; although there are scattered reports of triploid specimens (Haga, 1942, Sparrow and Pond, 1950; Kozuka, Channell, and Fukuda, 1964). Of the eleven *Trillium* in Asia, only one is diploid, the rest are triploid, tetraploid, or hexaploid. Within *Paris*, the primary European taxon, *Paris quadrifolia*, is tetraploid.

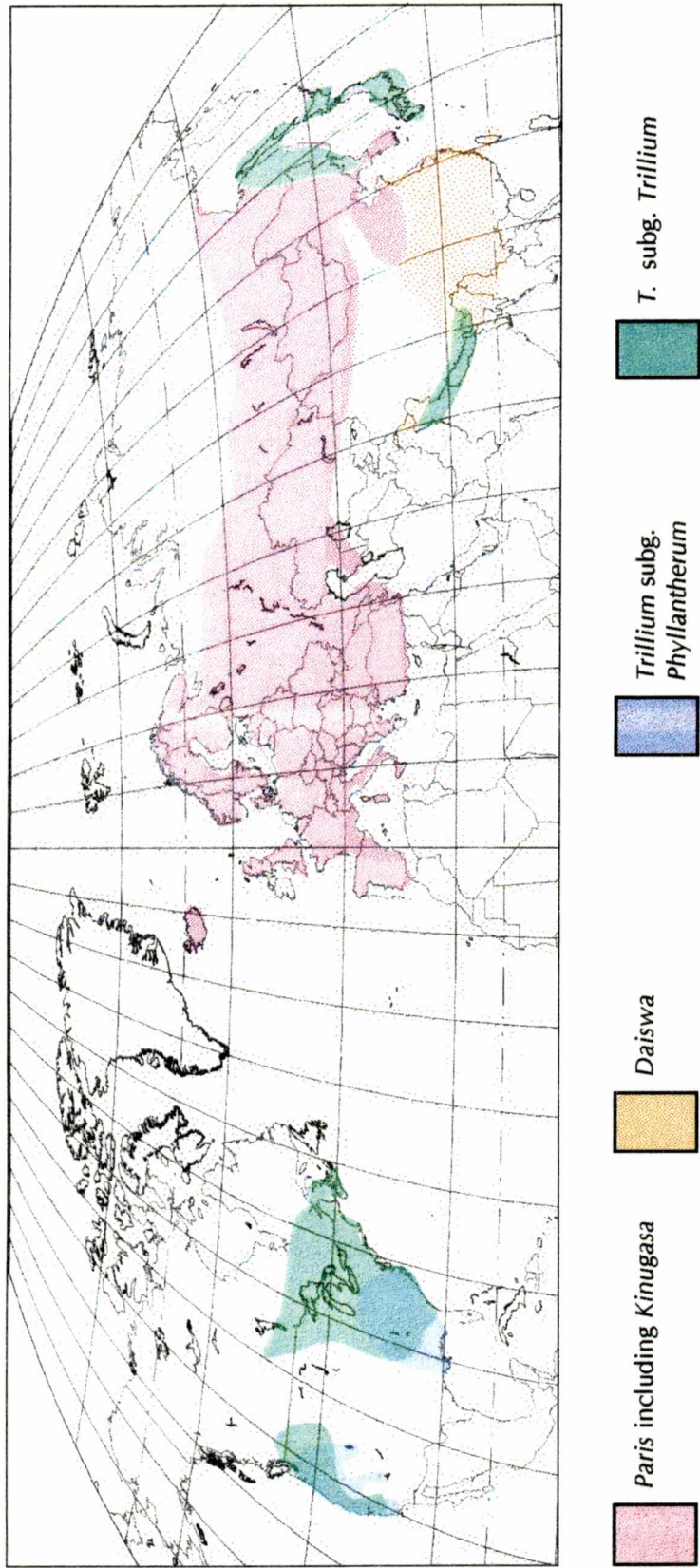


Figure 4. Distribution map for Trilliaceae. (After Samejima and Samejima, 1987; Li, 1998)

Paris incompleta from the Caucasus Mountains is diploid as are most of the other Asian taxa including all members of *Daiswa* (Li, 1998). *Kinugasa japonica* is octoploid (Tatewaki and Sutô, 1935)

1.4 Relationships with Higher Taxa

Because of its simple and distinctive morphology (a single flower subtended by a single whorl of leaves on an otherwise naked aerial stem), the family Trilliaceae has been easy to circumscribe, but because of its unusual morphology, it has been difficult to place (q v **Table 2**) both from a familial as well as an ordinal standpoint. The plants comprising this family have been placed in a variety of families: the Smilacaceae (Endlicher, 1836-40), Smilacineae (Kunth, 1836), as well as the customary Liliaceae (Bentham and Hooker, 1880; Engler, 1892; Cronquist, 1981). As a separate family, Trilliaceae have been placed in Liliales (Hutchinson, 1926), Dioscorales (Takhtajan, 1959, Dahlgren et al., 1985), and Stemonales (Dahlgren, 1975, Huber, 1969), the most recent work by Takhtajan (1997) and also by Reveal (1997) places Trilliaceae in Trilliales.

Even though Trilliaceae and Liliaceae s.s. share a few characters (**Table E1**), Trilliaceae are responsible for significant variation in Liliaceae s.l. When not segregated as a separate family, the taxa in Trilliaceae are usually placed within Liliaceae s.l. because the Liliaceae s.l. is composed of perennial herbs with modified underground storage stems, 6 perianth segments, usually 6 stamens, and a 3-carpellate ovary. Current research, however, shows that Liliaceae s.l. should be split into smaller families (Chase et al., 1995a). Liliaceae s.s. typically has a tepaloid inflorescence with showy and often spotted tepals as

well as parallel-veined, sheathing, cauline or basal leaves. Liliaceae and Trilliaceae are both autotrophic, perennial herbs with successive microsporogenesis, dry stigmatic surfaces, leaves without stipules, and lacking xylem vessels. In Trilliaceae the flower exhibits differentiated sepals and petals, and the fruit is either a berry or a fleshy capsule.

Molecular studies suggest that Melanthiaceae are the most closely related to Trilliaceae (Chase, personal communication; Chase et al., 1995a; Kato et al., 1995b; Davis, personal communication, 1995). Even though there is strong molecular support for this relationship, these are not families or genera that would normally be associated with each other based on morphology (Table E2). Trilliaceae are different from Melanthiaceae in that Melanthiaceae usually have a racemose or spicate inflorescence, and flowers with a perianth of inconspicuous tepals, whereas in Trilliaceae the inflorescence is solitary and showy and the flowers have a perianth composed of sepals and petals. The fruit is also usually a capsule or aggregate fruit with winged seeds in Melanthiaceae. Characters that Trilliaceae and Melanthiaceae share, which include basifixed anthers, dry stigmas, lack of xylem vessels, and the presence of steroid saponins, seem to be more plesiomorphic in nature rather than synapomorphic as they are not restricted to the two families.

1.5 Recent Molecular and Morphological Studies

Recent studies show that the Trilliaceae *s.s.* (i.e., including only *Paris s.l.* and *Trillium*) are a cohesive group. These studies have included general analyses of the monocotyledons as well as studies specifically on some part of Trilliaceae, and have used sequences from the *rbcL* gene (Chase, personal communication, Chase et al., 1995a; Kato

et al., 1995b), cpDNA restriction site data (Davis, 1995; Kato et al., 1995a), the *matK* gene (Kazempour Osaloo et al., 1999), *rbcL*, ITS, and *matK* (Kazempour Osaloo and Kawano, 1999) as well as morphological characters (Goldblatt, 1995; Kawano and Kato, 1995, Stevenson and Loconte, 1995). Unfortunately, some of these studies have been unsatisfactory as far as the family is concerned, either because of incomplete sampling (e.g., only *Trillium*), outgroup selection, or contradictory results between studies. However, one of the most recent studies (Kazempour Osaloo and Kawano, 1999) involving *matK*, ITS, and *rbcL* sequences with 18 *Trillium*, 8 *Paris s l* and *Veratrum mackii* showed the monophyly of *Trillium* subg. *Phyllantherum*, the monophyly of an "erectum group," the monophyly of *Paris s l*; but *Trillium rivale* is basal to the rest of the members of the family in both *matK* and ITS analyses.

Results of *rbcL* studies show that the members of Trilliaceae *s s.* segregate out into a distinct, cohesive unit (**Figure 5b**) obviously separate from other liliaceous genera examined. Members of Trilliaceae, however, not only do not separate out into genera, they do not separate out into recognizable morphological groups. The earliest study (Chase, personal communication, q.v., 1993, 1995a) used several taxa within the Trilliaceae *s l* (*Trillium kamtschaticum*, *T. sessile*, *T. erectum*, *Paris polyphylla*, *P. tetraphylla*, *Kinugasa*, *Medeola*, and *Scoliopus*) as part of a study of the monocotyledons. Mark Chase, who performed the molecular analysis, said, "*Medeola* is some distance from *Trillium* and is closer to *Lilium*, ... From our molecular work, it seems pretty clear that there is only one genus in the family. The segregates from *Trillium* all have relationships to one or another *Trillium* species or group, so you should not accept generic concepts without proof from character analyses. It is possible that with our limited sampling that we are not getting the 'right' tree, but it is worth taking a broad view to determine if the genera are good," (Chase,

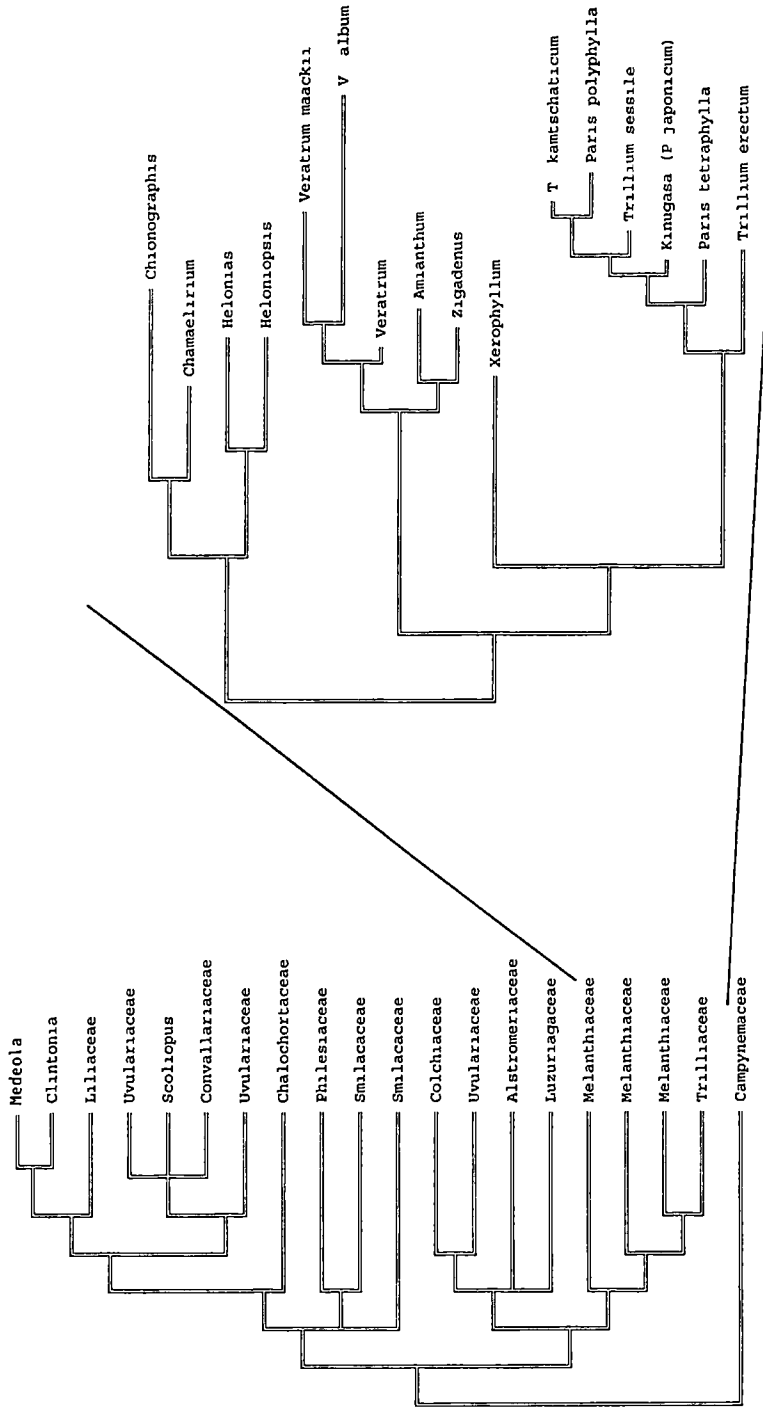


Figure 5. Cladograms based on molecular analysis by M.Chase. a (left) Condensed Liliales clade showing position of Trilliaceae taxa. b. (right) A single *rbcL* tree for the Trilliaceae taxa included plus near outgroups

personal communication) **Figure 5** shows excerpts from cladograms that were produced in Chase's study. The Kato study (Kato et al., 1995b) used a subset of the taxa used in the Chase study (monocots versus Trilliaceae), except that *T. erectum* was omitted. Not surprisingly, the results of the Kato study corroborate those produced by Chase. A more recent study by Kazempour Osaloo and Kawano (1999) using 20 *Trillium* and *Paris s l* taxa produced a polytomy with only three clades defined: *erectum-rugelii*, *govanianum-undulatum*, and *Daiswa*.

Several studies have been performed which are illustrative of putative placement of the family within a larger clade containing the Melanthiaceae. The earliest restriction-site analysis (Davis, 1995) used only *Trillium grandiflorum* from Trilliaceae and indicated that *Veratrum* L. and *Amianthium* A. Gray are the nearest neighbors to *Trillium* as was indicated in the *rbcL* study. As an interesting footnote to the analysis, Davis found that removal of *Trillium* destabilizes the tree causing the taxa from Liliales to be no longer monophyletic. Stevenson and Loconte (1995) performed a morphological analysis of the monocots that included Trilliaceae only as a family rather than as one or more distinct species. In this analysis, Trilliaceae was basal to the rest of the monocots and was sister to the Stemonales rather than the Melanthiales. The cladograms resulting from a combined morphological-molecular analysis performed by Chase et al. (1995b) were more representative of those produced by the all-molecular analysis (Chase et al., 1995a) in that *Trillium* was placed as sister to the Melanthiaceae rather than the Stemonaceae. Even though current studies using the *matK* gene (Fuse and Tamura, 1999), *ndhF* genes (Zomlefer and Perkins, 1999), and *atpA* gene (Davis et al., 1998) show that Trilliaceae is nested within the Melanthiaceae, it is Tamura's opinion (personal communication) that the families should remain separate.

To further complicate the picture, another recent morphologically-based study (Goldblatt, 1995) examining Dahlgren's orders of Liliales and Melanthiales concludes that the Trilliaceae is basal to Smilacaceae, Melanthiaceae, Uvulariaceae, and Liliaceae *s.s*. Trilliaceae and Smilacaceae were included in this study because of Dahlgren's controversial treatments. In this study, however, because the selection of families used in the analysis was limited, Goldblatt recommends against inferring "too much" from the analysis. *Trillium* shared with its ingroups septal nectaries, perigonal nectaries, and stomata without subsidiary cells and differed in that the inflorescence was not bracteate, and the perianth was differentiated.

Studies that focus on *Trillium* taxa fail to support the monophyly of both subgenera: the monophyly of the sessile-flowered subgenus of *Trillium* is evident, but the pedicellate *Trillium* are not monophyletic. Kato et al. (1995a) performed a restriction site analysis, using 24 species of *Trillium*, with *Paris tetraphylla* as the outgroup. Even though this may not adequately demonstrate the relationships between *Trillium* and *Paris*, conclusions can be drawn about the affinities within *Trillium*. In fact, the monophyly of the sessile-flowered *Trillium* is supported as is the monophyly of the *T. erectum* complex. In a morphological study, Kawano and Kato (1995) showed that *T.* subg. *Phyllantherum* is monophyletic. The pedicellate-flowered *Trillium* are polyphyletic with two species groups showing up in their analysis: a monophyletic group consisting of a basal "grandiflorum-ovatum group" with a monophyletic "erectum group," and the rest of the pedicellate *Trillium* in a paraphyletic grade. A *matK* analysis by Kazempour Osaloo et al. (1999) had similar results. *T.* subg. *Phyllantherum* is monophyletic, an "erectum group" is monophyletic, a "grandiflorum group" is monophyletic, but pedicellate *Trillium* are paraphyletic.

1.6 Previous Studies

Virtually all of the studies of groups of taxa in the family have been generic or subgeneric in nature. Only the most recent study by Kazempour Osaloo and Kawano (1999) using sequences from the *rbcl* gene, the ITS region, and the *matK* gene for 8 species of *Paris* s l and 18 species of *Trillium* could be considered a broad survey of the family. Although there have been numerous studies of various aspects of the pedicellate-flowered *Trillium*, and several of these studies draw some preliminary phylogenetic conclusions, there has not been a single unifying study comparable to the ones that Li has performed on *Paris* and Freeman has done with the sessile-flowered *Trillium*. Many of the studies of taxa included in the Trilliaceae have been individual in nature rather than taxonomic and have included such topics as morphological abnormalities (Hall, 1961, Andrews, 1927; Gibson, 1978), in vitro propagation (Pence and Soukup, 1986, 1993), mycoplasmal infection (Hooper, Case, and Myers, 1971), apomixis (Jeffrey and Haertl, 1939) and ecology (Anderson, 1994, Gunther and Lanza, 1989).

The phytochemistry of the family related to steroid saponins and anthocyanin pigments has also been studied. Because of folk medicine claims for both *Trillium* and *Paris*, the chemical constituency has been studied (Fukuda et al., 1981; Nohara, Miyahara and Kawasanti, 1975a; Nohara et al., 1975b; Hufford, Liu and Clark, 1988). Variability of petal color in sessile-flowered trilliums has led to the study of anthocyanins (Asbury, 1973; Les et al., 1989; Murrell, 1969) as well as other chemical compounds (Grove, 1933).

Trillium has 5 large chromosomes which have been referred to as the *Drosophila* of the plant world (Warmke, 1937), and have been the subject of extensive studies of structure. Many of these studies were simply DNA or chromosomal studies rather than

studies of *Trillium* chromosomes *Paris s l*, even though similar chromosomally, has not been as extensively studied until recently (Miyamoto and Kurita, 1990, Miyamoto, Gu, and Li, 1992) When treated with cold and stained, the heterochromatin forms specific banding patterns that have been found to be of taxonomic significance. identification of the putative parents of the Japanese hybrid species of *Trillium* (Haga, Watanabe, and Kanazawa, 1974a), separation of four Pacific Coast trilliums (Warmke, 1937), and separation of *Trillium rugelii* from other species in Rutherford Co, North Carolina (Serota, 1969) Various aspects of chromosome morphology and banding patterns have been studied by Bailey (1951, 1954a, 1954b, 1958), Haga (1934), Haga and Watanabe (1966) and Kurabayashi (1952, 1957) including the differences between the H-segments of Japanese and American species (Darlington and Shaw, 1959). In addition, the cytogeography of *Paris* has been studied (Li, Gu, and Na, 1988; and Li, Gu, and Yang, 1998)

Other aspects of morphology as well as the life-cycle of *Trillium* have also been studied, even though this information is important biologically, it appears to convey little or no information of phylogenetic importance perhaps due in part to inadequate sampling of species. Berg studied the embryology of *Scoliopus*, *Paris s l*, *Trillium*, and *Medeola* (1962a) and seed dispersal and morphology of *Trillium* (1958) He concluded that *Medeola* and *Scoliopus* were not near relatives of *Trillium* The use of pollen morphology as taxonomically significant has been extensively studied by Patrick (1982), Takahashi (1982, 1983, 1984, and 1989), and Wei (1995), it has been shown that *Paris s l* has ellipsoidal, monosulcate pollen whereas *Trillium* has spherical, omniaperturate pollen The life-cycle studies have included such aspects of the life of the plant as growth stages, pollination and breeding systems, fruit and seed dispersal, and life span (Ihara, 1973;

Ohara and Kawano 1986a, 1986b; Kawano, Ohara, and Utech, 1986, 1992; Ohara and Utech 1986, 1988; Ohara, 1989)

1.7 This Study

Because there was a lack of differentiation between genera of Trilliaceae reported from the original molecular data, an examination of the genera was undertaken to determine if the traditional genera (e.g., *Paris s l* and *Trillium*) are valid and elucidate what the relationships are. This study focused on the following relationships

- within *Paris*; (i.e., *Paris*, *Daiswa*, and *Kinugasa*);
- within *Trillium* itself; and
- between *Paris s l* and *Trillium*.

These relationships were examined using a cladistic analysis of a comprehensive morphological data set plus molecular data sets from the nucleus as well as the chloroplast.

2.0 METHODS

2.1 Taxa Selection

A total of 86 taxa, including all of those currently recognized as valid, were selected for the morphological analysis (Table 5). Other varietal taxa were included either because of the unique nature of the plant (*T pusillum* var. *virginianum*: a sessile-flowered variety of a pedicellate plant); or because of cross-generic synonymy (*P. fargesii* var *brevipetalata*). Samejima and Samejima (1987), Li (1984b), and Takhtajan (1983) served as primary source material for taxa as well as character states, taxa that were first recognized after these publications were also included. *Trillium komarovii*, *T channellii*, *T taiwanense*, *T parviflorum*, *Paris wenxianensis*, *P dulongensis*, *P rugosa*, *P undulatis*, *P polyandra*, and *P daliensis*. Because of non-congruence between the treatments as published by Li (1984b) and Takhtajan (1983), all of the taxa recognized by both authors were included.

2.2 Character Selection

One hundred and ten morphological characters were scored (Table 6). These characters were selected because they were easily identifiable field morphological characters (leaf shape, petal color, anther dehiscence), were important taxonomically to their particular genus or sub-generic group (placentation, seed arils), or conveyed diagnostic

Table 5. Taxa of Trilliaceae included in the analysis.

TAXON	JUSTIFICATION or SOURCE
<i>Trillium albidum</i>	Samejima & Samejima, 1987
<i>Trillium angustipetalum</i>	Samejima & Samejima, 1987 – key only
<i>Trillium apetalon</i>	Samejima & Samejima, 1987
<i>Trillium camtschaticense</i>	Samejima & Samejima, 1987 as <i>T kamtschaticum</i>
<i>Trillium catesbaei</i>	Samejima & Samejima, 1987
<i>Trillium cernuum</i>	Samejima & Samejima, 1987
<i>Trillium x channellii</i>	published after Samejima & Samejima, 1987
<i>Trillium chloropetalum</i>	Samejima & Samejima, 1987 – key only
<i>Trillium cuneatum</i>	Samejima & Samejima, 1987
<i>Trillium decipiens</i>	Samejima & Samejima, 1987
<i>Trillium decumbens</i>	Samejima & Samejima, 1987
<i>Trillium discolor</i>	Samejima & Samejima, 1987
<i>Trillium erectum</i>	Samejima & Samejima, 1987
<i>Trillium flexipes</i>	Samejima & Samejima, 1987
<i>Trillium foetidissimum</i>	Samejima & Samejima, 1987
<i>Trillium govanianum</i>	Samejima & Samejima, 1987
<i>Trillium gracile</i>	Samejima & Samejima, 1987
<i>Trillium grandiflorum</i>	Samejima & Samejima, 1987
<i>Trillium hageae</i>	Samejima & Samejima, 1987
<i>Trillium x hageae</i>	Samejima & Samejima, 1987
<i>Trillium x komarovii</i>	published after Samejima & Samejima, 1987
<i>Trillium kurabayashi</i>	Samejima & Samejima, 1987 – key only
<i>Trillium lancifolium</i>	Samejima & Samejima, 1987
<i>Trillium ludovicianum</i>	Samejima & Samejima, 1987
<i>Trillium luteum</i>	Samejima & Samejima, 1987
<i>Trillium maculatum</i>	Samejima & Samejima, 1987
<i>Trillium x miyabeianum</i>	Samejima & Samejima, 1987
<i>Trillium nivale</i>	Samejima & Samejima, 1987
<i>Trillium ovatum</i>	Samejima & Samejima, 1987
<i>Trillium parviflorum</i>	published after Samejima & Samejima, 1987
<i>Trillium persistens</i>	Samejima & Samejima, 1987
<i>Trillium petiolatum</i>	Samejima & Samejima, 1987
<i>Trillium pusillum</i>	Samejima & Samejima, 1987
<i>Trillium pusillum</i> var. <i>texanum</i>	controversy over position – variety or species
<i>Trillium pusillum</i> var. <i>virginianum</i>	sessile-flowered variety of pedicellate species
<i>Trillium recurvatum</i>	Samejima & Samejima, 1987
<i>Trillium reliquum</i>	Samejima & Samejima, 1987 – key only
<i>Trillium rivale</i>	Samejima & Samejima, 1987
<i>Trillium rugelii</i>	Samejima & Samejima, 1987
<i>Trillium sessile</i>	Samejima & Samejima, 1987
<i>Trillium simile</i>	listed in Kartesz,
<i>Trillium smallii</i>	Samejima & Samejima, 1987
<i>Trillium stamineum</i>	Samejima & Samejima, 1987
<i>Trillium sulcatum</i>	Samejima & Samejima, 1987

Table 5. (continued).

TAXON	JUSTIFICATION or SOURCE
<i>Trillium taiwanense</i>	published after Samejima & Samejima, 1987
<i>Trillium tschonoskii</i>	Samejima & Samejima, 1987
<i>Trillium underwoodii</i>	Samejima & Samejima, 1987
<i>Trillium undulatum</i>	Samejima & Samejima, 1987
<i>Trillium vaseyi</i>	Samejima & Samejima, 1987
<i>Trillium viride</i>	Samejima & Samejima, 1987
<i>Trillium viridescens</i>	Samejima & Samejima, 1987
<i>Trillium</i> x <i>yezoense</i>	Samejima & Samejima, 1987
<i>Daiswa birmanica</i>	accepted by Takhtajan
<i>Daiswa bockiana</i>	accepted by Takhtajan
<i>Daiswa chinensis</i>	accepted by Takhtajan
<i>Daiswa cronquistii</i>	accepted by both Li and Takhtajan
<i>Daiswa daliensis</i>	accepted by Li
<i>Daiswa delavayi</i>	accepted by both Li and Takhtajan
<i>Daiswa dunniana</i>	accepted by both Li and Takhtajan
<i>Daiswa fargesii</i>	accepted by both Li and Takhtajan
<i>Daiswa fargesii</i> var <i>brevipetalata</i>	cross generic synonymy with <i>T taiwanense</i>
<i>Daiswa forrestii</i>	accepted by both Li and Takhtajan
<i>Daiswa hainanensis</i>	accepted by Takhtajan
<i>Daiswa lancifolia</i>	accepted by Takhtajan
<i>Daiswa luquanensis</i>	accepted by Li
<i>Daiswa mairei</i>	accepted by Li
<i>Daiswa marmorata</i>	accepted by Li
<i>Daiswa polyandra</i>	published 1985, not synonymized by Li
<i>Daiswa polyphylla</i>	accepted by both Li and Takhtajan
<i>Daiswa pubescens</i>	accepted by Takhtajan
<i>Daiswa thibetica</i>	accepted by both Li and Takhtajan
<i>Daiswa undulatis</i>	accepted by Li
<i>Daiswa vietnamensis</i>	accepted by Li
<i>Daiswa violacea</i>	accepted by Takhtajan
<i>Daiswa wenxianensis</i>	published in 1986; not synonymized by Li or Takhtajan
<i>Daiswa yunnanensis</i>	accepted by Takhtajan
<i>Kinugasa japonica</i>	accepted by Li and Takhtajan
<i>Paris axialis</i>	accepted by Li
<i>Paris bashanensis</i>	accepted by Li
<i>Paris dulongensis</i>	accepted by Li
<i>Paris incompleta</i>	accepted by Li
<i>Paris quadrifolia</i>	accepted by Li
<i>Paris rugosa</i>	accepted by Li
<i>Paris tetraphylla</i>	accepted by Li
<i>Paris vanioti</i>	accepted by Li
<i>Paris verticillata</i>	accepted by Li

Table 6. Characters with mostly assumed states and those assumed states.

no	character	assumed state	justification
1	hybrid status	no	
2	flowering time		
3	chromosome number	2n = 10	
4	geographical area		
5	genus		
6	subgenus		
7	section		
8	Rafinesque		
9	PLANT type	herb	family description
10	foliaceousness	scapose	family description
11	plant sexuality	monoclinous	family description
12	inflorescence type	solitary	family description
13	number flowers	1	family description
14	composition	sepals + petals	family description
15	PEDICEL vertical posture	erect to above the leaves	
		none	subgenus <i>Phyllantherum</i>
16	ROOT type	rhizome	family description
17	rhizome size		
18	STEM habit	glabrous	
19	vestiture	green	
20	stem color	throughout	
21	stem color distribution		
22	LEAF number	3	<i>Trillium</i> only
23	leaf location	terminal	family description
24	leaf arrangement	whorled	family description
25	leaf # whorls	1	family description
26	leaf attachment		
27	leaf shape widest point		
28	leaf shape width (LxW)		
29	leaf shape sides		
30	leaf margin	entire	
31	leaf color distribution	throughout	
32	leaf color	green	
33	leaf lower surface	glabrous	
34	leaf apex type	entire	
35	leaf apices		
36	leaf base type	entire	
37	leaf bases		
38	leaf texture	herbaceous	
39	leaf # main nerves		
40	BRACTS	absent	family description
41	SEPAL form	normal	
42	sepal fusion	separate	family description
43	sepal number	3	<i>Trillium</i> only
44	sepal shape widest point		
45	sepal shape width (LxW)		

Table 6. (continued).

no	character	assumed state	justification
46	sepal shape sides		
47	sepal duration	persistent	
48	sepal texture	herbaceous	
49	sepal color	green	
50	sepal color distribution	throughout	
51	sepal apices		
52	sepal apex type	entire	
53	PETAL form	normal	
54	petal presence	present	
55	petal number	3	<i>Trillium</i> only
56	petal fusion	separate	family description
57	petal shape widest point		
58	petal shape width (LxW)		
59	petal shape sides		
60	petal duration	persistent	
61	petal color		
62	petal color distribution	throughout	
63	petals pigmented		
64	petal transverse posture		
65	petal vertical orientation	straight	
66	petal longitudinal posture		
67	petal apices		
68	petal apex type	entire	
69	STAMEN form	normal	
70	stamen number	3	<i>Trillium</i> only
71	stamen fusion	free	family description
72	stamen transverse posture		
73	stamen vertical posture		
74	ANTHERS dehiscence		
75	POLLEN shape	spherical elliptic	<i>Trillium</i> <i>Paris</i>
76	pollen aperture	omniaperturate monosulcate	<i>Trillium</i> <i>Paris</i>
77	pollen ornamentation		
78	CONNECTIVE prolongation		
79	FILAMENT color		
80	pollen color		
81	connective color		
82	stamen color distribution	throughout	
83	PISTIL form	normal	
84	OVARY position	superior	family description
85	ovary # locules		
86	ovary placentation		
87	ovary plane shape		
88	ovary X-section shape		

Table 6. (continued).

no	character	assumed state	justification
89	ovary # ribs		
90	ovary apex		
91	STYLE presence	absent	
92	STIGMA number	3	<i>Trillium</i> only
93	stigma shape		
94	stigma vertical posture		
95	stigma transverse posture		
96	stigma duration	persistent	
97	stigma size		
98	ovary color		
99	ovary color distribution	throughout	
100	stigma color		
101	stigma color distribution	throughout	
102	pistil color distribution	throughout	
103	FRUIT type		
104	fruit dehiscence		
105	fruit plane shape		
106	fruit color		
107	fruit color distribution	throughout	
108	SEED arils	incomplete	<i>Trillium</i>
109	endosperm development	helobial	<i>Trillium</i>
		nuclear	<i>Paris</i>
110	cotyledon shape	strap-like	<i>Trillium</i>
		cordate	<i>Paris</i>

information (pollen data or endosperm type). For details about all of these characters and their states, see **Appendix C**, an account of the source for each character state has been deposited at TENN or is available from the author

Character states were scored or measured based on a combination of literature reports and observations of herbarium specimens and live plants. To supplement and verify published information, living and pressed material was examined for as many of the characters as possible. Other printed sources that were used for character states included nomenclatural papers (Freeman, 1969a, 1975, Soukup, 1980, Ying, 1989; Fukuda, Freeman, and Itou, 1996; Case and Case, 1997; Peng and Zhao, 1986; and Franchet, 1888) or various national or regional floras (Ohwi, 1965, Steward, 1958, Hara et al , 1978; Tutin et al., 1980) Original protocols were also consulted where necessary.

A search of the literature was undertaken to see if other characters had been recorded widely enough across the family to add them to the list of characters in the study. Characters of this type included pollen exine ornamentation, karyotype analysis, reproductive biology, life history, and chemotaxonomic characters. The only characters either scored broadly enough across the family or consistently enough to be assumed to be constant across certain taxonomic groupings were gross pollen morphology and endosperm type (q v , Zomlefer, 1996)

Certain characters have "assumed states" associated with them which were used only in the absence of other data. These assumed states are based on prevalent states (e.g., glabrous leaf surface), family states (e.g , solitary inflorescence), or generally recognized states (e.g., green stems).

It was possible to obtain molecular characters for a subset of taxa used in the morphological analysis. The two molecular data sets included the ITS (Internal Transcribed

Spacer) region (ITS1, 5.8s, ITS2 sequences) of ribosomal RNA, and the chloroplast DNA sequences for the maturase (*matK*) gene. DNA sequences were obtained from gene repositories and were aligned visually; all gaps were treated as missing data. The ITS sequences, which were obtained from GenBank, were deposited by Kazempour Osaloo and Kawano (1999) and consisted of 648 base pairs of which 199 were variable; there were 27 indels (**Table D1**) which were not used as characters in the analysis. The *matK* sequences, deposited by Kazempour Osaloo et al. (1999), were obtained from the Japanese GenBank (DDBJ) and consisted of 1578 base pairs, 84 of which were variable; there were 7 indels (**Table D2**).

2.3 Outgroup Selection

The outgroup method is the customary method used in performing phylogenetic analyses, the outgroup provides the “basis for making strong inferences” about ancestral states for the characters under consideration (Throckmorton, 1968). The presence of synapomorphies thus defines the groups and relationships within the ingroup (Nixon and Carpenter, 1993)

Genera under consideration for outgroup selection were *Dioscorea*, *Amianthium*, *Veratrum*, *Xerophyllum*, *Medeola* and *Scoliopus*. *Medeola* and *Scoliopus* were shown in **Figure 2** (page 7); the rest of the putative outgroups are shown in **Figure 6**. *Dioscorea* (**Table E3**) was considered because Dahlgren et al. (1985) placed the Trilliaceae and the Dioscoreaceae together in the Dioscorales; it was not used because the molecular data do not support the contention that these two groups of taxa are closely related. *Scoliopus* and



Figure 6. Outgroups under consideration for use in the analysis with Trilliaceae.
a. *Amianthium muscaetoxicum* b. *Xerophyllum asphodeloides* c. *Veratrum viride*
d. *Dioscorea quaternata*. All images copyright USDA, NRCS and used by permission.

Medeola (Table E4) were also considered because they have both been placed in Trilliaceae, but neither is particularly close to Trilliaceae on a molecular or morphological level. *Amianthium*, *Veratrum*, and *Xerophyllum* (Table E5) were considered because results of recent molecular studies have placed them close to Trilliaceae. *Amianthium* was used initially in the morphological analysis because of the results of the molecular studies (Chase et al., 1993, Angiosperm Phylogeny Group, 1998; Fuse and Tamura, 1999) even though its morphology was quite different from Trilliaceae. However, the morphology was so dissimilar that many characters and character states had to be added just to accommodate the taxa within the Melanthiaceae. *Veratrum maackii* was initially used as the outgroup for the molecular studies, but the ITS sequence in particular was so dissimilar that ITSf sequences could not be reliably aligned with taxa of Trilliaceae.

None of the taxa outside of Trilliaceae proved satisfactory as an outgroup in all of the studies. Based on both preliminary morphological analyses (Appendix F) and independent molecular analyses (Kazempour Osaloo and Kawano, 1999; Kazempour Osaloo et al., 1999; Kawano, personal communication), *Trillium rivale* was basal within Trilliaceae and was thus chosen as the outgroup for the final analysis rather than either *Amianthium muscaetoxicum* or *Veratrum maackii*. This basal position was clearly shown in the *matK* analysis, and was corroborated in the other analyses as well. Changing the outgroup to *T. rivale* in the morphological analysis resulted in a much more coherent tree; in all cases, fewer, better resolved trees resulted from any analysis with *T. rivale* as outgroup. (When the outgroup was changed from *Amianthium* to *T. rivale* in the full morphological analysis, the numbers of trees found dropped from over 100,000 to less than 1,300 with much more resolution and a higher consistency index.)

2.4 Congruency Analysis

When multiple data sets from different sources are under consideration, decisions must be made on how the data sets are to be treated.

- separate analyses followed by combination of trees (taxonomic congruence),
- combined analyses (character congruence), or
- conditional combined analyses – combination if the data sets are congruent.

The primary argument for taxonomic congruence is that characters with different underlying evolutionary assumptions or unequal rates of evolution should not be combined (Bull et al. 1993). However, even in a single sequence, it is known that the third codon position evolves at a more rapid rate than the other codon positions. Conditional combined analyses are favored by those who believe that any amount of incongruence will cause an incorrect phylogeny to be generated. The primary advantage of character congruence is that characters from different data sets can strengthen weak phylogenetic signal to the point that it can overcome noise (Sullivan, 1996).

Measures of taxonomic congruence and character congruence were both employed even though the data sets were combined believing that the total evidence method (Huelsenbeck, Bull, and Cunningham, 1996; Kluge, 1989; Soltis et al., 1998, 1999) was more applicable in this case. Measures of taxonomic congruence examined included assessment of support for major clades and support for rival trees. The assessment for major clades was performed by comparing bootstrap values for each of the clades from each of the analyses (Mason-Gamer and Kellogg, 1996, Davis et al., 1998). For the other measure of taxonomic congruence, a tree was constructed which was the putative correct

tree to use in addition to the strict consensus trees generated from each of the analyses. These trees were then used as constraint trees on which the fit of rival data sets were assessed (Davis et al., 1998; related to the Miyamoto incongruence index q v. Swofford, 1991b, Kluge, 1989)

Measures of character congruence examined were the Mickevich and Farris original measures computing percent variation due to data, percent variation between characters, and percent variation between data sets (Mickevich and Farris, 1981); and the Farris measure of incongruence as implemented in Paup* via the Homogeneity of Partitions test (Farris et al., 1995a, 1995b, Swofford, 1998).

2.5 Phylogenetic Analysis

The data sets were analyzed with the PAUP* program (Swofford, 1998) using maximum parsimony as well as maximum likelihood. The searches for most parsimonious trees used heuristic search methods with TBR and MULPARS with a simple addition sequence. Random addition with steepest descent was used to check for islands of trees (Maddison, 1991); maximum likelihood was used with the simple addition sequence to check for long-branch attraction in the molecular analyses (Kennedy et al., 1999; Swofford et al., 1996). Once a minimal tree length was found, branch and bound analysis was used to insure finding of all shortest trees. Bootstrap support (Felsenstein, 1985) was estimated based on 1,000 replicates with the same search strategy (simple addition) as simple

parsimony. In addition, as noted above, an examination of congruency of data sets and characters was undertaken before performing the combined analysis.

The morphological data set consisted of 86 taxa and 109 characters; the ITS data included 26 of the above taxa, the *matK* 48. Four separate data sets (ITS, *matK*, small morphological, and full morphological) were analyzed either separately or in combination, 7 of which used the same subset of taxa:

- ITS data,
- *matK* data,
- morphological data,
- ITS + morphology,
- *matK* + morphology,
- ITS + *matK*,
- ITS + morphology + *matK*, and
- 86 taxon morphological data set.

The major statistics for each of these data sets is given in **Table 7**; the statistics for the trees are given in **Table 8**. Of these 8 analyses, only 4 (ITS- *matK*, small morphology, ITS-*matK*-morphology, and full morphology) are presented here; the remainder are shown in **Appendix G**.

Table 7. Statistics for the data sets.

data set	# characters used	# constant	# uninformative	# informative
ITS	641	444	92	105
<i>matK</i>	1578	1494	44	40
morphology	97	21	13	63
ITS- <i>matK</i>	2219	1936	138	145
ITS-morphology	738	463	107	168
<i>matK</i> -morphology	1675	1515	57	103
all data	2316	1957	151	208
full morphology	97	17	9	71

Table 8. Statistics for the most parsimonious trees.

tree	# trees	length	min	CI	HI	RI	RC
ITS	6	331	231	.70	.30	.72	.50
<i>matK</i>	6	107	92	.86	.14	.90	.77
morphology (dna taxa)	13	646	498	.77	.61	.58	.45
ITS- <i>matK</i>	6	455	334	.73	.28	.76	.56
ITS-morphology	6	1005	740	.74	.51	.63	.46
<i>matK</i> - morphology	54	768	590	.77	.55	.67	.50
all data	3	1120	832	.74	.48	.65	.49
full morphology	1,296	1785	1410	.70	.63	.44	.82

3.0 RESULTS

3.1 Congruency Analysis

Because three separate data sets containing the same taxa were used (morphology, nuclear genome, and chloroplast genome), two measures of character congruence (congruence between data sets) were examined as well as two measures of taxonomic congruence (congruence between trees). Homogeneity of partitions analyses using 100 random re-partitions as provided in Paup* were performed on each of the combined data sets. The results indicated that there was congruency between the molecular data sets, but incongruency between the molecular and morphological data sets. The original Mickevich-Farris measures of percent variation indicated that there was little variation between data sets. The character congruency measures are summarized in **Table 9**. The bootstrap support values for the major clades are presented in **Table 10**; conflicts between analyses included position of clades, the relationships among pedicellate *Trillium*, and the placement of *Kinugasa*. The rival tree analyses values are presented in **Table 11** by indicating the number of extra steps required to map a particular set of data onto a particular tree, in several cases, a putative tree was actually the shortest tree for a given data set.

Table 9. Summary of character congruence measures for the combined data sets.

	ITS- <i>matK</i>	ITS- morphology	<i>matK</i> - morphology	all data
Homogeneity of Partitions test	P = 0.20	P = 0.01	P = 0.01	P = 0.01
variation within data	70.99%	72.54%	76.82%	73.3%
variation between characters	25.27%	24.68%	21.22%	23.48%
variation between data sets	3.74%	2.69%	1.95%	3.21%

Table 10. Bootstrap support for major clades in each of the analyses.

	ITS	matK	morphology	ITS-matK	ITS-morphology	matK-morphology	all data
Phyllanthum clade (9 taxa)	99%	76%	60%	100%	99%	93%	100%
Grandiflorum clade (3)	polytomy	98% ¹	62% ¹	51% ¹	polytomy	99% ¹	86% ¹
Erectum clade (3)	98%	67%	polytomy	99%	94%	polytomy	97%
Daiswa clade (4 + Kinugasa)	57% ²	85% ²	polytomy	80% ²	63% ²	51% ³	75% ²
Paris clade (3)	96%	55%	52%	95%	97%	63%	97%
govanianum + undulatum	72%	polytomy	separate	73%	separate	separate	polytomy

- Note 1 excludes *T pusillum*
 2 100% if *K japonica* is excluded
 3 70% excluding *K japonica*

Table 11. A comparison of lengths of constraint consensus trees optimized against rival data sets.

data set	ITS	<i>matk</i>	morphology	ITS- <i>matk</i>	ITS-morphology	<i>matk</i> - morphology	ITS- <i>matk</i> - morphology
ITS	349	+9	+23	+8	+24	+26	+30
<i>matk</i>	+32	110	+19	+31	+52	+13	+49
morphology	+50	+32	660	+81	+51	+26	+80
ITS- <i>matk</i>	-1**	+2	+18	460	+18	+14	+17
ITS-morphology	0*	+11	-1**	+10	1008	+4	+8
<i>matk</i> - morphology	+14	+5	+1	+18	+16	776	+18
ITS- <i>matk</i> - morphology	-1**	0*	+3	-2**	+3	-3**	1121
TEST tree	0*	+11	-4**	+10	-3**	+1	+5

Note numbers in **bold** pertain to a tree tested against its own data set
 * indicates trees that are the same length as the tree tested against its own data
 ** indicates trees that are shorter than the tree tested against its own data

3.2 Molecular Data

Analysis of the ITS and *matK* sequence data produced 6 shortest trees of length 455 with a CI (consistency index) of 0.73. This data set included a total of 2219 base pair positions of which 283 were variable and 145 informative (q.v. Table 7), there were also 34 indels

A basal dichotomy separated *Paris s l* and *Trillium* as sister clades with bootstrap support of 65% and 81%, respectively, as shown in the strict consensus tree (Figure 7). Within the "Paris clade," *Paris* and *Daiswa* were placed as sister clades with bootstrap support of 95% and 100%, respectively. *Kinugasa* was basal to *Daiswa* and the latter clade had a bootstrap value of 80%. In the "Trillium clade," a basal split separated *T. govanianum* and *T. undulatum* with bootstrap support of 73% from the remaining *Trillium* (bootstrap support of 81%) *Trillium* subg. *Phyllantherum* was placed in a well-defined, monophyletic clade with 99% bootstrap support. The pedicellate *Trillium* were placed in a grade, within that grade, there was a subclade consisting of the members of the "Erectum clade" with 99% support. The "Grandiflorum clade," which received marginal support in the bootstrap (51%), formed a polytomy at the base of *T. subg. Phyllantherum*. The bootstrap tree is shown in Figure G11.

3.3 Small Morphological Data Set

Parsimony analysis of the morphological data (q.v. Table 6) for the same set of taxa for which molecular data were available produced 13 shortest trees in two islands of length 646 with a CI of 0.77. This data set included 97 characters, 76 of which were variable, and

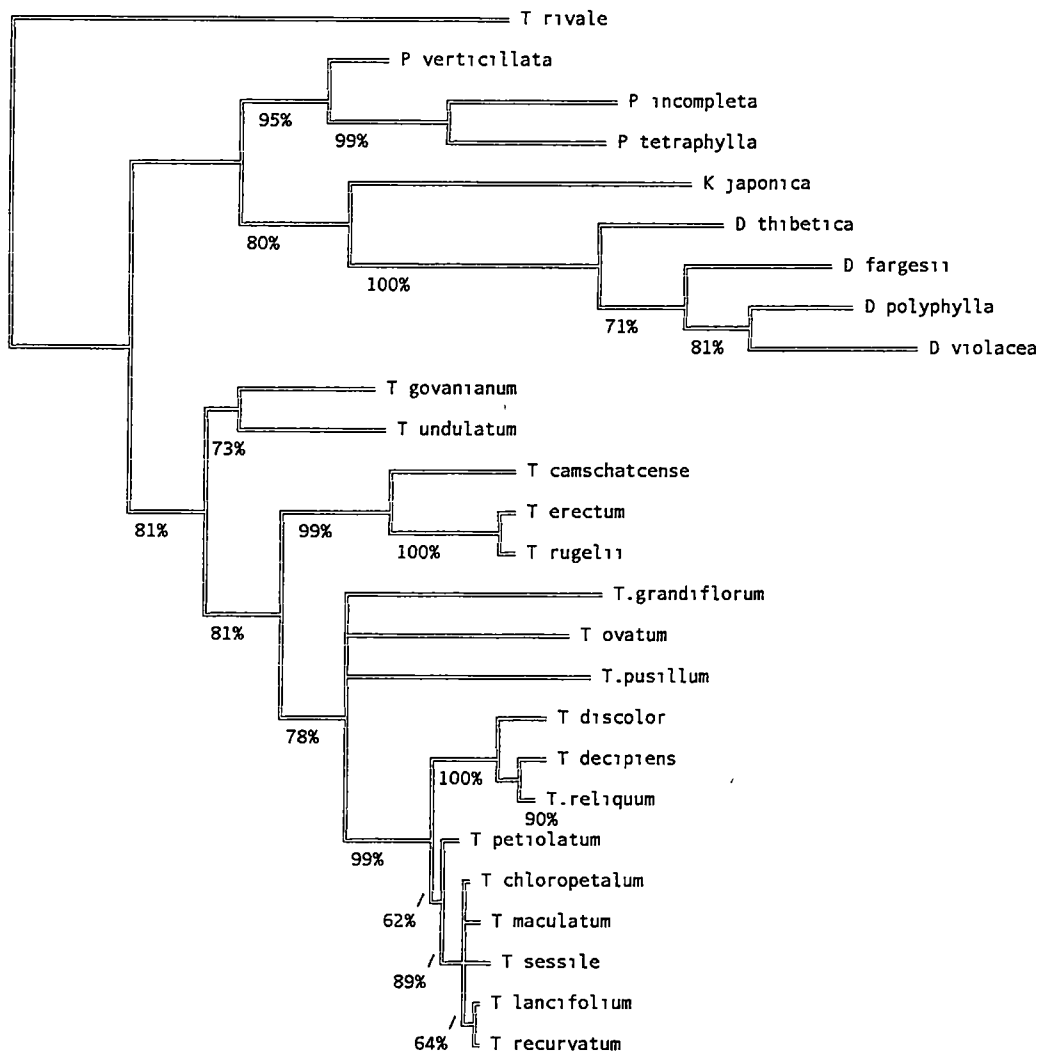


Figure 7. Strict consensus of 6 trees from the ITS-matK analysis of Trilliaceae.

63 informative (q.v. **Table 7**) Eight additional characters that were non-morphological were included in the data set to plot their distribution on the final trees, the 5 merosity characters were excluded to test whether other morphological characters separated *Trillium* and *Paris s l*

A basal split in the tree separated *Paris s l* + *T govanianum* (74%) from *Trillium* (**Figure 8**) In the bootstrap, *Trillium* subg. *Trillium* were part of a polytomy, but *T* subgen *Phyllantherum* had 60% support. The “Paris clade” was the most strongly supported clade in the bootstrap analysis (69%), *Trillium* subg. *Phyllantherum* was supported at a 53% level. *Trillium govanianum* was basal to *Paris s.l* ; within the “Paris clade,” *Kinugasa japonica* was basal to sister clades containing *Paris* and *Daiswa* The bootstrap tree is shown in **Figure G8**

3.4 Combined Analysis

The combination of morphological and both molecular data sets produced 3 trees, the strict consensus of which was almost fully resolved (**Figure 9**) The 3 trees, which differed only for the relative placement of members of *Trillium* subg. *Phyllantherum*, were 1120 steps long with a CI of 0.74. This data set included 2219 base pairs, and 97 morphological characters; 359 were variable and 208 were informative (q.v. **Table 9**); there were also 34 indels and the same 13 excluded morphological characters (q.v. Section 3.3) .

A basal split separated *Paris s l* (91%) from *Trillium* (56%). Within the “Paris clade,” *Paris* and *Daiswa* + *Kinugasa* were placed in sister clades (97% and 75%) *Kinugasa* was separated as the sister taxon to *Daiswa*, with the latter having a 100% support level

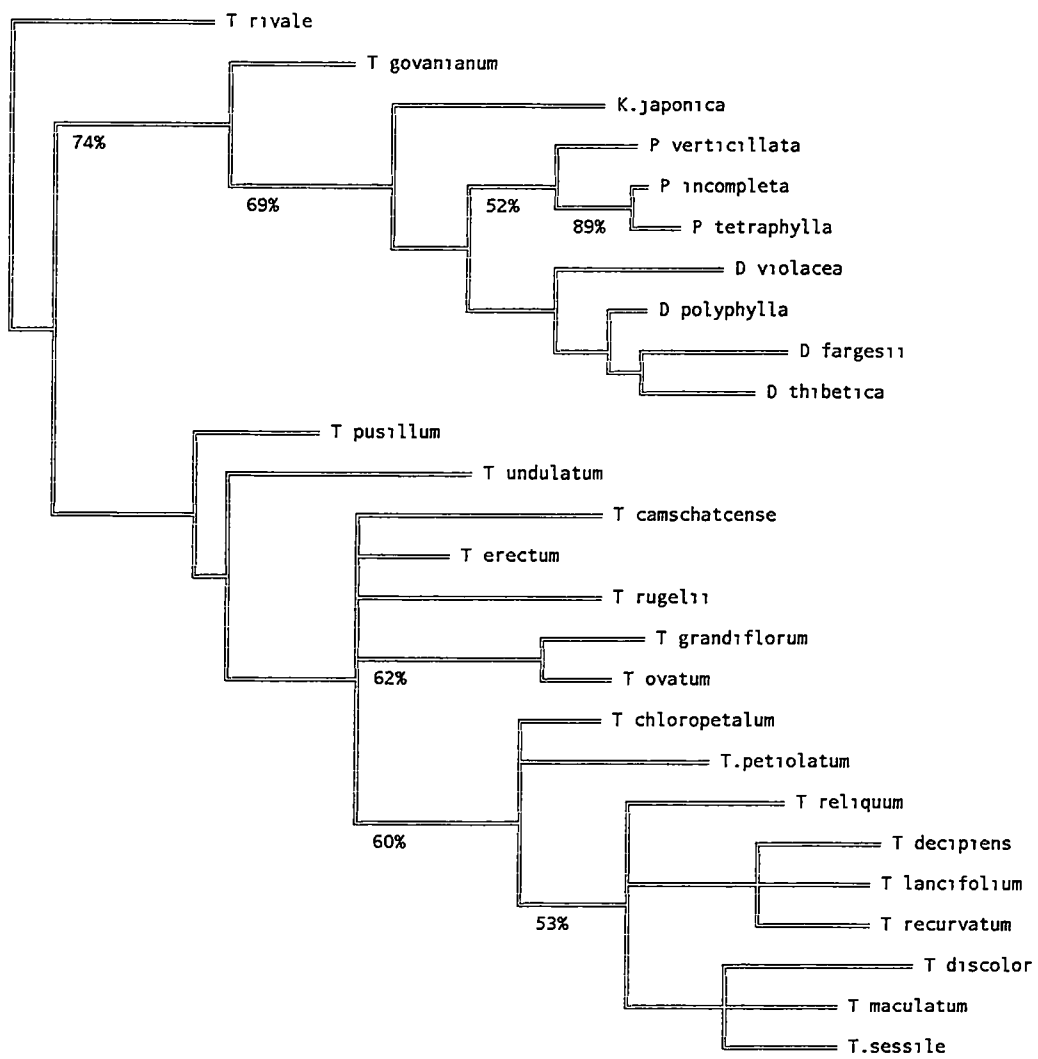


Figure 8. Strict consensus of 13 trees from the small morphological analysis of Trilliaceae.

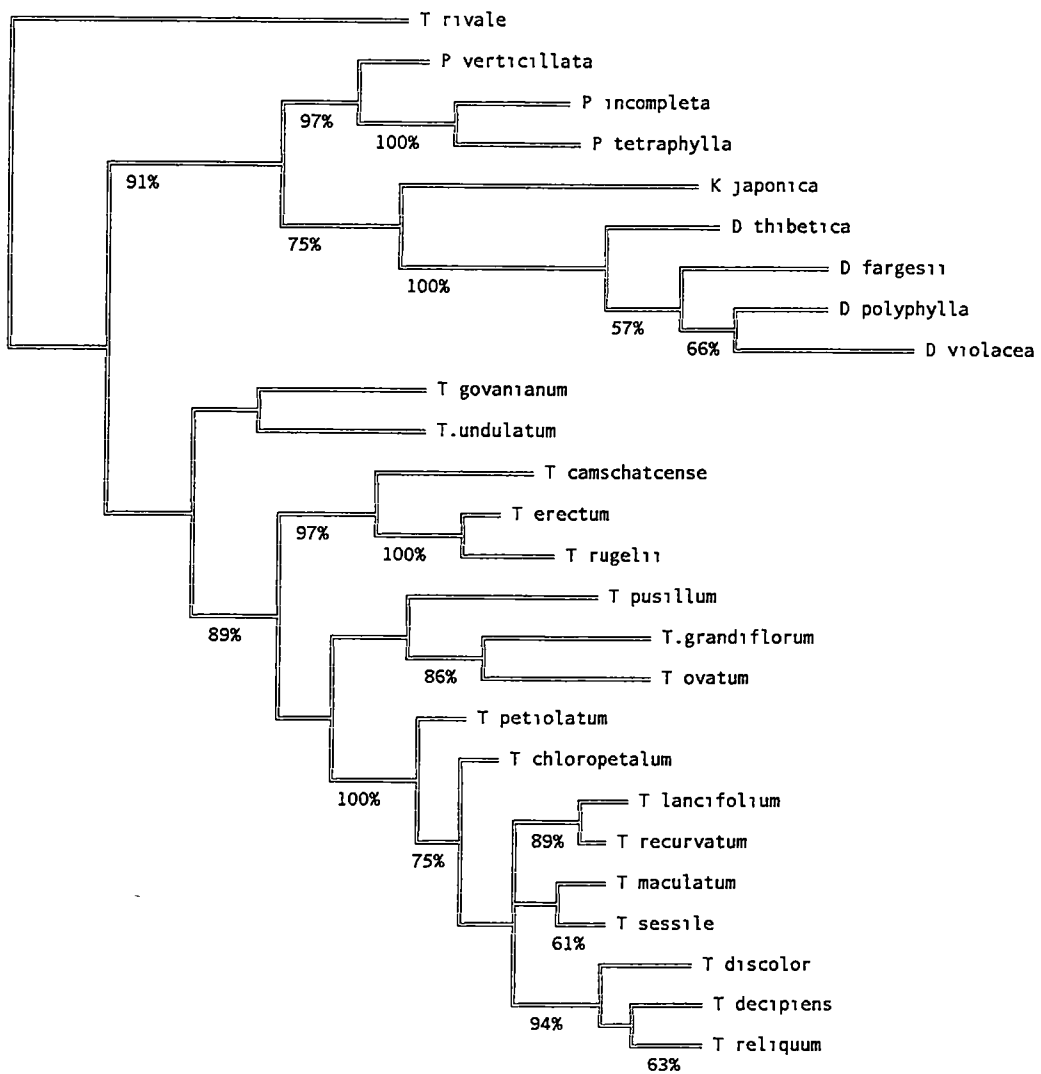


Figure 9. Strict consensus of 3 trees from the combined analysis of Trilliaceae.

Trillium undulatum and *T. govanianum* were basal to the rest of the *Trillium*. Within the "Trillium clade," *T.* subg. *Phyllantherum* was a monophyletic clade supported at 100%; the "Pedicellate group" was a paraphyletic grade consisting of an "Erectum clade" with 97% support and a "Grandiflorum clade" which was supported at 86%.

3.5 Full Morphological Data Set

When the full data set of 86 taxa was analyzed, 1,296 shortest trees were produced with length of 1,785 and a CI of 0.74. This data set included 97 characters of which 80 were variable, and 71 were informative (q.v. Table 9); the same 13 were also excluded (q.v. Section 3.3).

Paris s l (with the basal *T. govanianum*) and *Trillium* were placed as sister taxa in the strict consensus tree produced by the analysis of this data set (Figure 10). *Paris s.s.* was most derived and placed as part of a polytomy in a paraphyletic grade containing *Daiswa*. *Kinugasa japonica* was basal to *Paris s.s.* and served to separate *Paris* and *Daiswa*. In the "Trillium clade," *T. undulatum* was basal with the rest of the *Trillium* forming cohesive clades as part of a polytomy: the "Grandiflorum clade" (with an embedded "Pusillum clade"), the "Erectum clade," and the "Phyllantherum clade."

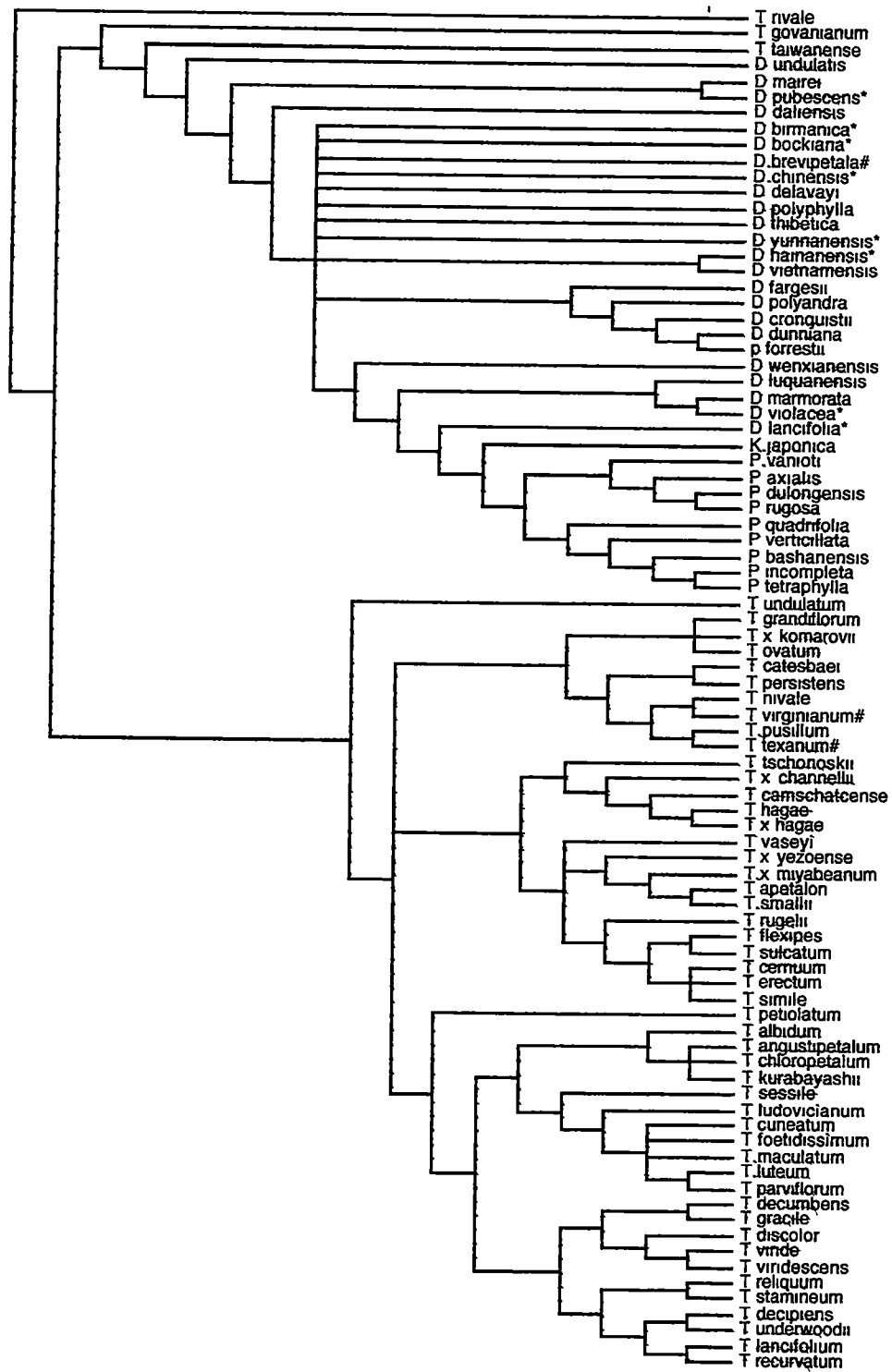


Figure 10. Strict consensus of 1,296 trees from the full morphological analysis.

4.0 DISCUSSION

4.1 *Trillium rivale*

The real surprise of this analysis was the recognition that *Trillium rivale* (**Figure 11**) is distinct from both *Paris* and from *Trillium* (q.v. **Appendix G**). Although traditionally classified as a *Trillium*, *T. rivale* is clearly sister and basal to the remaining taxa in the family Trilliaceae. This status is supported by numerous morphological apomorphies, 138 single base-pair changes, and 5 base-pair indels (**Table 12**).

Although *Trillium rivale* has a strong superficial resemblance to other members of *Trillium*, it is also different in a number of features:

- thick, leathery, cordate leaves,
- spotted petals;
- the seed remains viable even after drying;
- the cotyledon shape is more leaf-like than strap-like;
- faster flowering from seed;
- the pedicel elongates until the fruit is ripe.

Based on the results of this analysis, *T. rivale* should be placed in its own genus, for which the name *Pseudotrillium* is proposed. It can be diagnosed as follows

different from *Trillium* because *T. rivale* has spotted petals and a pedicel that continues to elongate, different from *Trillidium* because *T. rivale* has broad spotted petals rather than narrow purple tepals; different from *Paris s.s.* because of the broad, spotted petals, the thickened rhizome, and the presence of an eliasome on the seed; different from *Kinugasa* because that genus has broad, colored sepals and filiform petals unlike the other genera

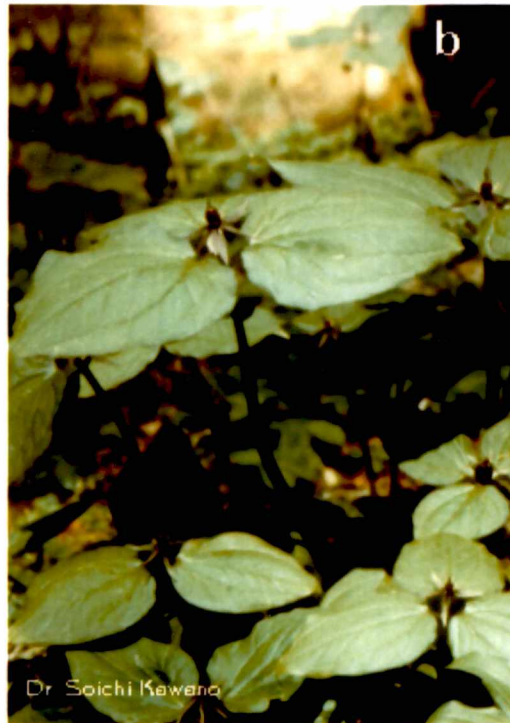


Figure 11. Unique taxa within Trilliaceae. a. *Trillium rivale* b. *T. govanianum* (copyright and used by permission of Dr. Soichi Kawano) c. *Paris japonica* (copyright and used by permission of Dr. V.G. Soukup) d. *T. undulatum*.

Table 12. Support for basal position of *Trillium rivale*.

data set	character	state change
<i>matK</i>	14 absolute base pair changes	
ITS	24 absolute base pair changes	
	5 indels	
morphology	leaf texture	coriaceous to herbaceous
	petal width	average to narrow
	petal color distribution	spotted to throughout
	placentation	combination to axillary
	style presence	present to absent
	fruit type	fleshy capsule to berry
	sepal apex type	with midrib extension to entire
	sepal apices	cuspidate to acuminate
	shape of sepal sides	oblong-elliptic to elliptic
	petal widest point	elliptic ovate to ovate
	shape of petal sides	rhombic-elliptic to elliptic
	filament color	green to purple
	connective color	green to purple
	ovary color	white to yellow-green
	stigma color	creamy white to purple
	fruit color	green to purple

in the family; and different from *Daiswa* because that genus has narrow petals, a dehiscent capsule, and a complete aril covering the seed.

A key to the genera with brief descriptions of each is provided in **Appendix A**.

4.2 *Trillidium govanianum* and *Trillium undulatum*

Trillidium govanianum and *Trillium undulatum* were either shown as basal to *Trillium*, or *Trillidium govanianum* was basal to *Paris s l* and *Trillium undulatum* was basal or near-basal to *Trillium*. depending on which analysis was being considered.

Although they share certain ecological features (both being plants of high altitude *Rhodendron* thickets), morphological data suggest that *Trillidium govanianum* and *Trillium undulatum* are not monophyletic. *Trillium undulatum* and *Trillidium govanianum* share the unusual characters of extrorse anther dehiscence and distinctly petiolate leaves (**Figure 12**) *Trillidium govanianum* shares several diagnostic characters with *Paris s l* including pollen shape (ellipsoidal) and apertures (monosulcate), endosperm type (nuclear), and narrow filiform petals, *Trillium undulatum* shares these character states with *Trillium* rather than *Trillidium* (**Figure 11**)

It is quite probable that long-branch attraction, which is typically characterized by unusually long branches relative to other branches in the tree (Felsenstein, 1978; Huelsenbeck, 1997), occurred between these two taxa, if a tree was generated which placed *Trillidium govanianum* basal to *Paris s l* and *Trillium undulatum* basal to *Trillium*, this tree was often shorter than the strict consensus trees that were generated by Paup* (**q.v. Table 11**) or generally less than 2% longer. Even though it is difficult to test for long

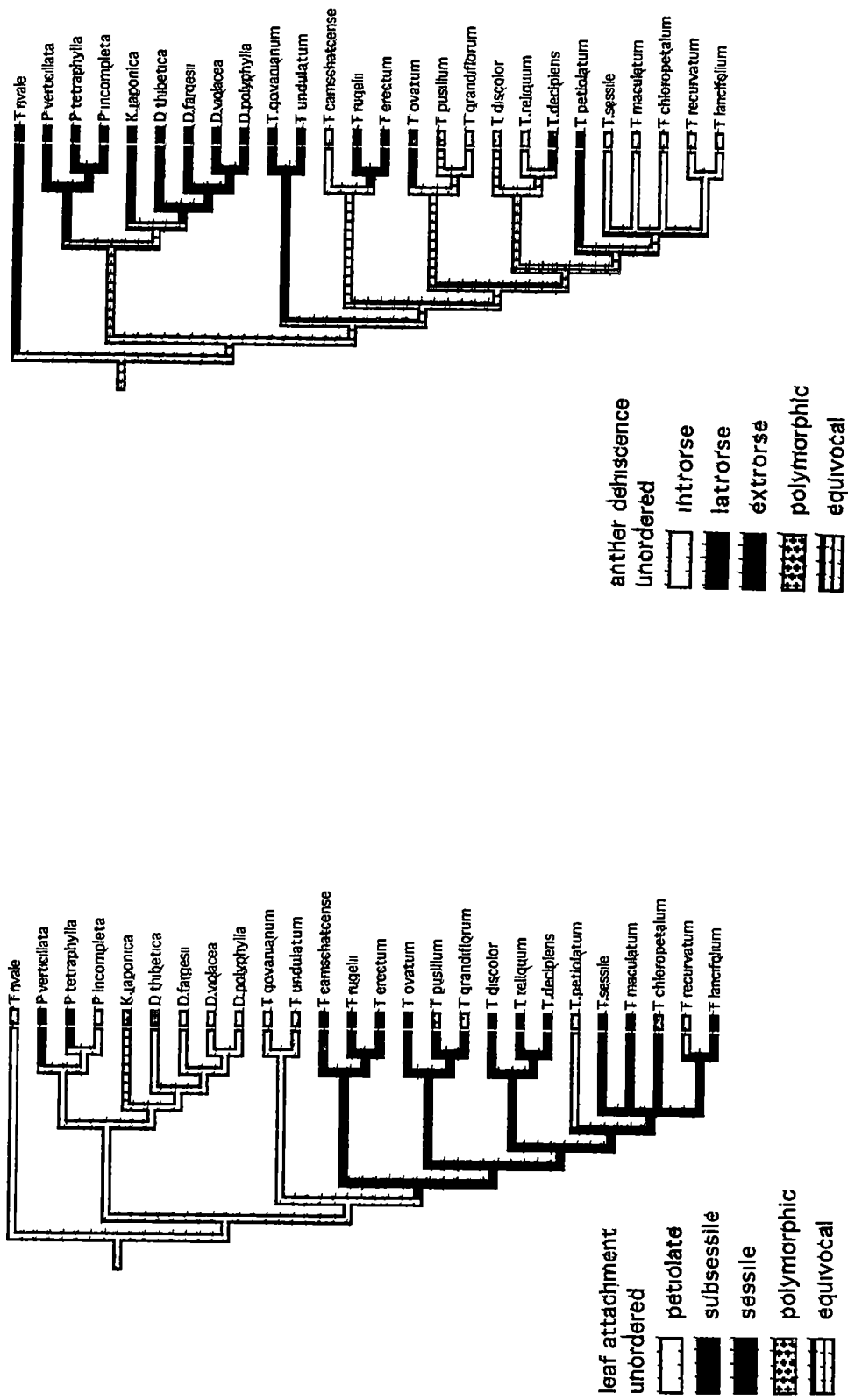


Figure 12. Distribution of petiolate leaves and extrorse anther dehiscence in Trilliaceae.

branch attraction, it can most often be remedied by the addition of more taxa (Graybeal, 1998); witness the placement of *T. pusillum* in both the small and large morphological analyses (Figures 8 and 10): with the addition of more taxa in the "Pusillum clade," the placement of this taxon changed.

4.2 1 *Trillidium govanianum*

Although *Trillidium govanianum* is more similar to *Paris* than to *Trillium*, it is distinct from both on molecular as well as morphological grounds and should be recognized as distinct. It occurs in the Himalayan Mountains, a locale more within the range of *Paris s.l* rather than *Trillium*. It is a trimerous plant like *Trillium* with broad leaves; however, it shares several unusual synapomorphies with *Paris s.l* such as endosperm type, pollen shape and apertures, and narrow filiform petals. *Trillidium govanianum* has a pigmented, tepaloid inflorescence rather than the plesiomorphic condition of having distinct sepals and petals, in *Paris s.l* this usually consists of filiform yellowish-green petals and broad sepals. It also lacks an aril on the seeds; a synapomorphy which is shared with *Paris s.s*, but not *Trillium* (partial aril) or *Daiswa* (enveloping sarcotesta). It is for these reasons that Hara et al. (1978) and Nolte (1994) have revived *Trillidium*. This analysis supports the position that there is sufficient evidence for recognition of *Trillidium* as a distinct genus.

4.2 2 *Trillium undulatum*

Trillium undulatum is clearly a *Trillium* based on both morphology and biogeography. Like *Trillium*, it has broad leaves and trimerous phyllotaxy. It usually has a red, v-shaped pattern at the base of each petal that is unique in Trilliaceae; the coloration of

most petals within Trilliaceae is usually unmarked. It has the relatively rare features within *Trillium* of extrorse anther dehiscence and petiolate leaves. The distribution of *T. undulatum* in the Appalachian Mountains not only places it within the general range of *Trillium* but also in its center of greatest diversity. *Trillium undulatum* also has the spherical, omniaperturate pollen that is typical of *Trillium* species.

4.3 *Paris s.l.*

Paris s.l. was consistently placed as a monophyletic group in all of the analyses. In addition to the traditionally used trait of merosity, *Paris* and *Trillium* can be distinguished by several other characters. Most notable among these are synapomorphies such as narrower leaves, filiform petals, elliptical, monosulcate pollen, and nuclear endosperm of *Paris*. A listing of synapomorphies that defined the *Paris* clade is given in **Table 13**.

The molecular cladistic analyses provided support for the separation of *Paris s.l.* into two sister clades corresponding to *Paris s.s.* and *Kinugasa + Daiswa*. The support for the monophyly of *Daiswa* was provided primarily by the molecular and the combined analysis (**q.v. Figures 7 and 9**), not just from morphology alone. From a molecular standpoint, there were 3 indels and 3 base-pair changes that can be used to separate *Paris* and *Daiswa + Kinugasa* in the ITS sequence. There were several morphological synapomorphies as well (**Table 13**).

The placement of *Kinugasa japonica* with *Daiswa* rather than *Paris* in the molecular and combined analyses was quite surprising. In traditional, morphological classifications, *Kinugasa* has always been aligned with *Paris*; but both ITS and *matK* clearly suggested a

Table 13. Synapomorphies for *Paris*, *Kinugasa* and *Daiswa*.

subgroup	data set	character	state change
including <i>Trillidium</i>	matK	1 absolute base pair change	
	ITS	1 absolute base pair change	
	morphology	petal transverse posture	outcurved to plane
		petal width	average to filiform
		pollen shape	spherical to ellipsoid
		pollen aperture	omniaperturate to monosulcate
		number of locules	1 to 4
		ovary apex	attenuate to crowned
seed arils	incomplete to none		
endosperm type	helobial to nuclear		
excluding <i>Trillidium</i>	matK	2 absolute base pair changes	
	ITS	1 indel	
	morphology	anthocyanins	present to absent
		anther dehiscence	extrorse to lateral
	style presence	absent to present	
<i>Daiswa</i> including <i>Kinugasa</i>	matK	2 absolute base pair changes	
	ITS	2 absolute base pair changes	
<i>Daiswa</i>	matK	1 absolute base pair change	
	ITS	6 absolute base pair changes	
	morphology	number of locules	4 or more to 1
		placentation	axillary to parietal
		fruit type	berry to fleshy capsule
		fruit dehiscence	indehiscent to loculicidal
seed arils	absent to complete		

Table 13. (continued).

subgroup	data set	character	state change
<i>Paris s.l.</i>	<i>matK</i>	1 absolute base pair change	
	ITS	3 absolute base pair changes	
		1 indel	
	morphology	rhizome size	thick to very thin
		ovary apex	crowned to attenuate
<i>Kinugasa</i>	<i>matK</i>	4 absolute base pair change	
	ITS	13 absolute base pair change	
	morphology	rhizome size	thick to very thick
		leaf attachment	petiolate to sessile
		leaf widest point	ovate to obovate
		leaf texture	herbaceous to papery
		sepal form	sepaloid to petaloid
		sepal texture	herbaceous to membranous
		sepal color	green to white
anther dehiscence	lateral to extrorse		

relationship between *Kinugasa* and *Daiswa*, with both exhibiting many of the same indels and base pair changes (Table 13). Morphologically, *Kinugasa* shares several features with *Paris s.s.* such as slender stigmatic branches, an indehiscent berry, and seeds without a sarcotesta; a thick rhizome and angular ovary are characters that it shares with *Daiswa*. Because of the unusual morphology of the species (i.e., the showy, white sepals, and octoploid chromosome count), and the difficulty in aligning it with either *Paris* or *Daiswa*, the separate genus *Kinugasa* should be retained for this species.

Daiswa was usually placed as a monophyletic sister group to *Paris s.s.* Its monophyly was supported by indels, base pair changes, and morphological characters such as leaf width, filament color, stamen color distribution, stigma size, fruit type, fruit dehiscence, and seed arils (Table 13). Of this group of characters, only fruit type and seed arils were listed by Takhtajan (1983) as being diagnostic for *Daiswa*. Because of the recognition of *Kinugasa* as a genus, and because *Paris* and *Daiswa* were clearly separated on a molecular level, it is recommended that *Daiswa* be recognized as distinct from *Paris*.

4.4 *Trillium*

The results of the analyses provided strong support for the monophyly of the "Trillium clade," which was defined by several base pair changes as well as morphological characters (Table 14). Within this clade, the subgroups were not as well defined as those in *Paris s.l.* *Trillium* subg. *Phyllantherum* was a well-defined, monophyletic group; but the pedicellate taxa in the "Trillium clade" usually formed a paraphyletic grade in the smaller analyses.

Table 14. Synapomorphies for *Trillium*.

subgroup	data set	character	state change
<i>Trillium s.l.</i>	ITS	1 absolute base pair change	
	morphology	cotyledon shape placentation	leaf-like to strap-like axillary to parietal
<i>Trillium</i> excluding <i>T. undulatum</i>	matK	1 absolute base pair change	
	ITS	1 absolute base pair change	
	morphology	leaf attachment anther dehiscence	petiolate to sessile extrorse to introrse
<i>T. undulatum</i>	matK	4 absolute base pair changes	
	ITS	3 absolute base pair changes 1 indel	
	morphology	petal color distribution	throughout to geographic
"Grandiflorum group"	morphology	leaf widest point	ovate to ovate-elliptic
		anthocyanins	absent to turning pink with age
		petal apices	acute to obtuse
		pollen ornamentation	granulate to spinulate
"Erectum group"	matK	1 absolute base pair change	
		1 indel	
	ITS	1 absolute base pair change	
	morphology	leaf widest point petal width	ovate to elliptic narrow to average
"Phyllantherum group"	matK	2 absolute base pair changes	
	ITS	3 absolute base pair changes	
		2 indels	
	morphology	pedicel posture	above the leaves to none
		shape of leaf sides	rhombic elliptic to elliptic
		petal color	white to purple
petal transverse posture		outcurved to incurved	
petal vertical posture	divergent to erect		

Trillium subg *Trillium*, which traditionally includes all of the pedicellate taxa, was most cohesive in the large morphological analysis. In that analysis, there were 3 monophyletic groups: the “*erectum* group,” the “*grandiflorum* group” (containing a monophyletic “*pusillum* group”), and the “*phyllantherum* group.” Unfortunately, the “*pusillum* group” was represented only by *T. pusillum* in the molecular analyses, so its coherence as a group in the smaller analyses was difficult to assess. In the large morphological analysis, this group consisted of *T. pusillum* (and its included varieties *virginianum* and *texanum*), *T. nivale*, *T. catesbaei*, and *T. persistens*; this group could also be called the “*delostylis* group” based on Rafinesque’s genus name as all of these taxa exhibit a common style. Clearly, *T. pusillum* itself was distinct from the other *Trillium*. The “*erectum* group” showed up on the molecular as well as combined analyses; the “*grandiflorum* group” was present in the small analyses only with *T. pusillum* excluded or as a polytomy.

Trillium subg *Phyllantherum* was shown to be quite cohesive with character support beyond the single trait of the sessile-flowered habit. Other characters such as leaf apices, petal width, petal transverse posture, and petal vertical posture also helped to define this group. Other characters unique to individual analyses were also apomorphies for this group including leaf bases, stamen transverse posture, anther dehiscence, filament color, and ovary color.

In none of the analyses performed during the course of this work, was *T. pusillum* var. *virginianum*, a sessile-flowered variety of a normally pedicellate plant, ever aligned with the other members of subg. *Phyllantherum*. *Trillium pusillum* var. *virginianum* also exhibits the relatively rare trait of a common style unlike the other members of subg *Phyllantherum*.

Of Freeman's subgroups, the only one that was supported in the results of the phylogenetic analyses was the "*T recurvatum* group" which is composed of *T recurvatum* and *T lancifolium*. The other groups (the "*T sessile* group" and the "*T maculatum* group") were not shown to be cohesive in these analyses (**Figure 13, q.v**, **Section 1.4**)

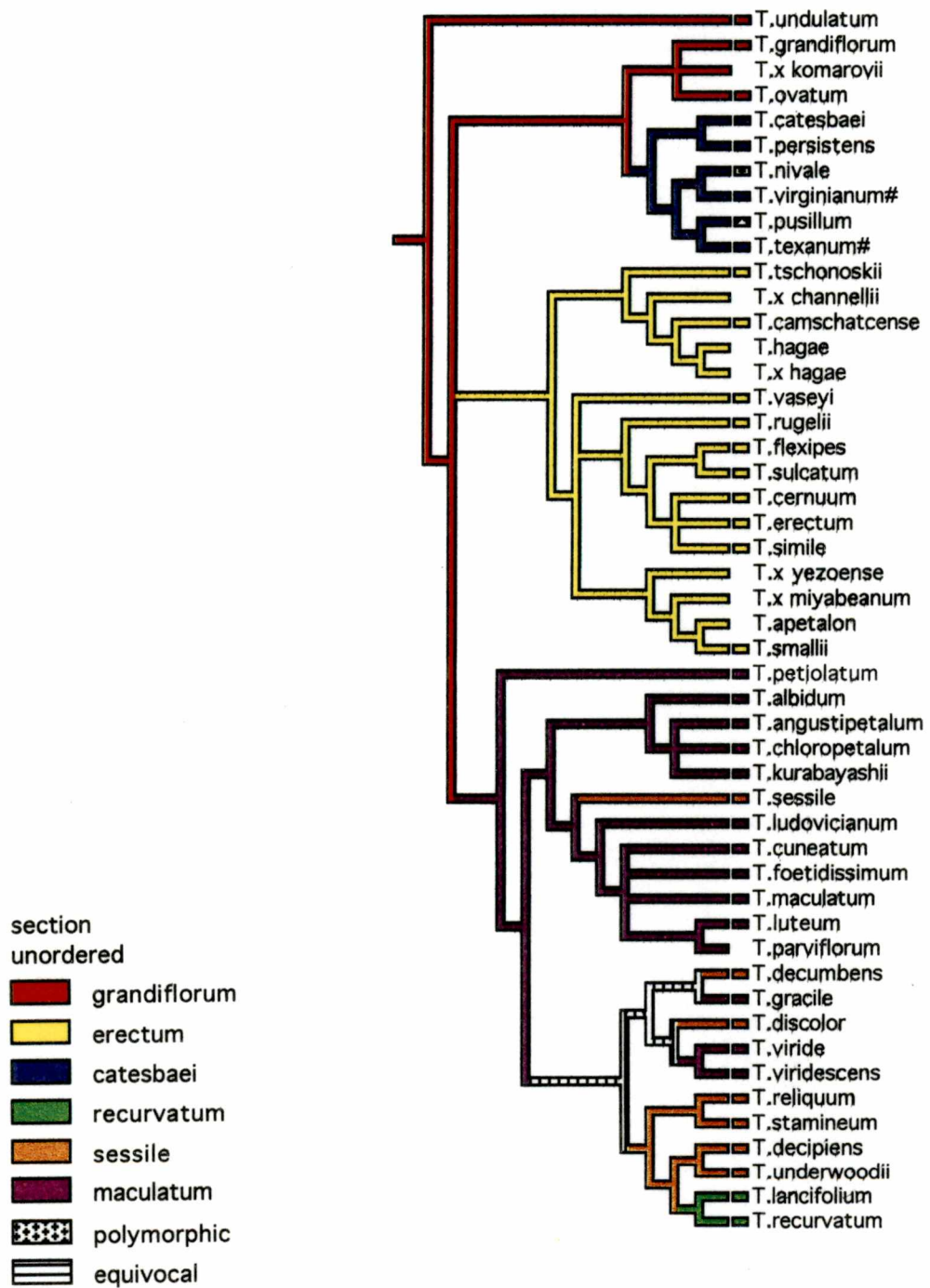


Figure 13. Distribution of traditional subgeneric groupings of *Trillium* on the morphological tree.

5.0 CONCLUSIONS

- *Trillium rivale* is as distinct from *Paris* as it is from *Trillium* and should be placed within its own genus, for which the name *Pseudotrillium* (*nom ined*) is proposed. Differences between *Pseudotrillium* and other Trilliaceae include morphological, molecular, and ecological traits.
- *Trillium govanianum* is distinct from *Trillium* and *Paris* on molecular as well as morphological grounds and should be recognized as distinct at the genus level as *Trillidium govanianum*
- *Trillium* and *Paris s l* are separable based on more than just floral merosity. Characters that serve to separate *Paris* and *Trillium* include molecular characters as well as leaf width and petal width
- *Paris s l* is separable into clades corresponding to *Paris*, *Daiswa*, and *Kinugasa* based primarily on molecular results but also with morphological support. Because *Kinugasa* is morphologically distinct and does not align with either *Paris* or *Daiswa*, all three genera should be retained.
- Because the subgenera within *Trillium* do not separate into distinct, monophyletic, sister clades, the single genus *Trillium* should be retained. Infrageneric classification of subgenus *Trillium* requires further study.
 - Subgenus *Phyllantherum* is a monophyletic, easily recognized grouping
 - Subgenus *Trillium* is not a cohesive group, existing only in smaller groups such as the "erectum group" and the "grandiflorum group" rather than as a whole. This group of taxa requires further study.
- Based on the fact that *Pseudotrillium rivale* is the basal taxon in the family, it appears that the origin for the family is in the Pacific Northwest followed by radiation to Eastern North America and Asia. Because the European species is tetraploid, radiation to Europe probably came from Asia.

6.0 SUGGESTIONS FOR FUTURE WORK

- Extend the sampling to include a molecular analysis of the whole family. Of particular interest to be sequenced are additional species of *Daiswa* and *Paris*; to date, only 8 of some 30 species have been sequenced. In addition, subspecific taxa, particularly in the "*pusillum* group" need to be sequenced. The *matK* gene has been sampled for much of *Trillium*, but current plans do not involve sequencing the whole family (Kawano, 1998). Perhaps sequencing or other molecular analysis could answer some of the questions that exist about certain subspecific taxa, e.g., should the varieties of *T. pusillum* or *D. polyphylla* be treated as varieties or should they be elevated to species status.
- Taxonomic revision of the whole family as a unit. This would allow the taxonomist to look characters across the whole family that have been deemed to be important in various genera. Although taxonomic assessments have been made as a part of this work, it is beyond the scope of this work to determine the validity of taxa (especially within *Daiswa*) or of the correct position of subspecific taxa (e.g., *Trillium pusillum* var. *texanum*).
 - Status of several synonymized taxa; cf *T. catesbaei*, *T. nervosum*, and *T. stylosum*; *T. gleasonii* and *T. flexipes*; *T. lancifolium* and *T. lanceolatum*; and *T. taiwanense* and *P. fargesii* var. *brevipetalata*. There is evidence in the literature that some of these synonymized taxa may indeed be distinct.
 - More detailed morphological study of several taxa including *Trillidium govanianum*, *Kinugasa japonica*, *Trillium undulatum*, the *Trillium pusillum* complex, and the status of *Trillium ovatum* ssp. *hibbersonii*.
- Hybrid status of North American *Trillium*. It is evident that hybridization occurs in nature in *Trillium* in Japan (Haga 1951, 1952, 1956, Haga and Kurabayashi 1953, 1954; Haga et al., 1974). Hybridization evidently occurs in North America as well (Dusek, 1980b; Freeman 1969a, 1975, Case and Case, 1997; personal observation). It would be informative to find molecular markers to define the extent of hybridization as ploidy is not indicative of hybrid status in North American *Trillium*. Hybrid status of *Paris* and *Daiswa* has not been examined even though polyploids exist.
- Pollen and endosperm characters. This would allow the hypothesis that these characters are truly constant across genera to be tested.
- Placentation. The placentation within *Trillium* has been determined to be often neither axile or parietal, but a combination of both. This information would define the extent of this unusual phenomenon.
- Fruit type and dehiscence. Fruit type in *Trillium* is not clearly defined and has not been extensively studied. Are there indeed morphological and anatomical differences between the "normal" berry and the often mentioned "fleshy capsule?"

- Seed germination and cotyledon type. Do those taxa like *Trillium rivale* and *Daiswa* sp exhibit some form of epigeal germination producing a true leaf above ground, or is it just a more leaf-like cotyledon
- Anthocyanin chemistry especially as regards the white trilliums (e.g , *Trillium grandiflorum*) that turn pink with age.

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APPENDICES

APPENDIX A
DESCRIPTIONS OF TRILLIACEAE

APPENDIX A.1

Trilliaceae from the DELTA web site

The Families of Flowering Plants

L. Watson and M. J. Dallwitz



Trilliaceae Lindl.

Alternatively *Parideae* (*Paridaceae*) Dum.

~ *Liliaceae*

Including *Phlebaceae* Dulac (p p)

Excluding *Scoliopus*, *Medeola* (transferred to *Uvulariaceae*)

Habit and leaf form. *Herbs. Plants non-succulent; autotrophic Perennial*, with neither basal nor terminal aggregations of leaves, rhizomatous, or rhizomatous and tuberous. Mesophytic (mostly woodland species) *Leaves whorled (in a single whorl, borne high on the stem)*; 3(–22) per whorl (generally the same number as the perianth whorls); flat; petiolate to sessile; simple. *Lamina* entire; *lanceolate, or oblong to ovate, or obovate; palmately veined to parallel-veined*, cross-venulate; cordate, or attenuate at the base, or cuneate at the base, or rounded at the base. Lamina margins entire; flat.

Leaf anatomy. *Lamina* dorsiventral. The mesophyll containing calcium oxalate crystals. The mesophyll crystals raphides. Minor leaf veins without phloem transfer cells (*Trillium*). Vessels absent.

Stem anatomy. Primary vascular tissue in two or more rings of bundles (often 3). Secondary thickening absent. Xylem without vessels

Root anatomy. Root xylem with vessels. Vessel end-walls scalariform

Reproductive type, pollination. Plants hermaphrodite. Floral nectaries present. Nectar secretion from the perianth, or from the gynoecium, or from the perianth and from the gynoecium. Entomophilous.

Inflorescence, floral, fruit and seed morphology. *Flowers solitary (sessile or pedicellate)*; terminal (on the erect stem); medium-sized (to 'rather large'), regular; 3–5(–8) merous; cyclic; tetracyclic, or pentacyclic, or polycyclic. *Floral receptacle with neither androphore nor gynophore*. Perigone tube absent. Hypogynous disk absent.

Perianth with distinct calyx and corolla, or sepaline, or of 'tepals', 6–18; free; 1 whorled, or 2 whorled (the inner whorl sometimes rudimentary or missing, e.g. *Paris tetraphylla*, *Kinugasa*); usually isomerous; petaloid, or sepaloid and petaloid; without spots, or spotted; similar in the two whorls to different in the two whorls (often different in shape and/or colour); green, or yellow, or white, or purple, persistent. **Calyx** (when regarded as such) 3–5(–10); 1 whorled, polysepalous; regular; *persistent*; imbricate, or contorted. **Corolla** (when the inner whorl thus interpreted) 3–5(–8); *1 whorled*; polypetalous; imbricate, or contorted; regular; green, or white, or yellow, or pink, or purple (etc.); persistent. Petals clawed (sometimes), or sessile; entire

Androecium 6–10(–24). Androecial members free of the perianth, all equal; free of one another; 2(–6) whorled. Androecium exclusively of fertile stamens. **Stamens 6–10(–24); diplostemonous (usually), or triplostemonous, or polystemonous**; oppositiperianthial (often portrayed thus in floral diagrams), or alterniperianthial. Filaments appendiculate (by prologation of the connective), or not appendiculate. **Anthers basifixed**; non-versatile; dehiscent via longitudinal slits; extrorse, or latrorse, or introrse; tetrasporangiate. Microsporogenesis successive. Pollen shed as single grains. Pollen grains aperturate, or nonaperturate (*Trillium*), when aperturate, 1 aperturate; sulcate; 2-celled. *Gynoecium* 3–6(–10) carpelled. Carpels isomeric with the perianth. The pistil 1 celled, or 3–6(–10) celled. **Gynoecium syncarpous; semicarpous to synovarious, or synovarious to synstylovarious; superior**. Ovary 1 locular, or 3–6(–10) locular. *Gynoecium* in *Paris* transverse. Ovary sessile. *Gynoecium* stylate. Styles 1, or 3–6(–10), free, or partially joined; apical. Stigmas dry type; papillate; Group II type (B(ii)). Placentation when unilocular, parietal (the placentas strongly intrusive), when plurilocular, axile. Ovules in the single cavity 20–100 ('many'), 15–50 per locule ('many'), arillate (usually), or non-arillate; anatropous; bitegmic, crassinucellate. Outer integument not contributing to the micropyle. Embryo-sac development *Allium*-type. Polar nuclei fusing only after one has been fertilized, or fusing simultaneously with the male gamete (?). Antipodal cells formed; 3, not proliferating, ephemeral, or persistent. Synergids pear-shaped. Endosperm formation helobial (*Trillium*), or nuclear.

Fruit fleshy to non-fleshy; dehiscent, or indehiscent (when baccate); **a capsule (fleshy, e.g. *Trillium*), or a berry (e.g. *Paris*)**. Capsules when dehiscent, splitting irregularly, or septicidal, or loculicidal, or septicidal and loculicidal. **Seeds copiously endospermic. Embryo rudimentary at the time of seed release to weakly differentiated**. Embryo achlorophyllous (1/1); globose to ovoid. Testa without phytomelan.

Seedling. Hypocotyl internode present (developing into a small tuber). Seedling collar not conspicuous. Cotyledon hyperphyll elongated; assimilatory; dorsiventrally flattened. Coleoptile absent. First leaf dorsiventral. Primary root ephemeral.

Physiology, biochemistry. Not cyanogenic. Proanthocyanidins absent. Flavonols present; kaempferol and quercetin. Ellagic acid absent. Saponins/sapogenins present (steroidal, sometimes poisonous).

Geography, cytology Holarctic and Paleotropical. Temperate. Temperate Eurasia, North America. $2n = 10, 15, 20, 30, 40$ Supposed basic chromosome number of family 5. Ploidy levels recorded 2, 3, 4, 6, and 8

Taxonomy Subclass Monocotyledonae. Superorder Liliiflorae, Dioscoreales. Species 53. Genera 4; *Daiswa*, *Kinugasa*, *Paris*, *Trillium*

Discussed in detail by Zomlefer (1996)

Illustrations • trill856.gif.

Quotations

Small good to anything growing wild,
They were crooking many a trillium
That had budded before the boughs were piled
(Robert Frost, 'Pea Brush')

Cite this publication as. Watson, L., and Dallwitz, M. J (1992 onwards) 'The Families of Flowering Plants. Descriptions, Illustrations, Identification, and Information Retrieval ' Version: 15th October 1998. <http://biodiversity.uno.edu/delta/> Dallwitz (1980), Dallwitz, Paine and Zurcher (1993 onwards, 1998), and Watson and Dallwitz (1991) should also be cited (see References)

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APPENDIX A.2

Key to the genera of Trilliaceae

Key to the genera of Trilliaceae

- 1a. Inflorescence composed of tepals, phyllotaxy trimerous **Trillidium**
- 1b. Inflorescence composed of sepals and petals, phyllotaxy trimerous to numerous 2
- 2a. Sepals showy, white, petaloid; petals filiform or absent **Kinugasa**
- 2b. Sepals herbaceous, green or purplish, petals filiform to broad, or absent .. 3
- 3a. Phyllotaxy mostly trimerous with broad leaves and petals 4
- 3b. Phyllotaxy mostly 4- to 11-merous with narrow leaves and very narrow to filiform petals 6
- 4a. Petals generally spotted, ovate, frequently appearing clawed, leaves cordate to rounded, coriaceous **Pseudotrillium**
- 4b. Petals not spotted, from ovate to obovate, leaves ovate to obovate, herbaceous **Trillium**
- 5a. Flowers sessile, without common style, leaves frequently mottled subgenus **Phyllantherum**
- 5b. Flowers pedicellate, with or without a common style, leaves mostly not mottled subgenus **Trillium**
- 6a. Ovary with axile placentation; seeds with partial green aril or with no aril .. **Paris**
- 6b. Ovary with parietal placentation; seeds with enclosing red or orange sarcotesta **Daiswa**

APPENDIX A.3

The genera within Trilliaceae

The genera within Trilliaceae (adapted from Tamura, 1998).

***Daiswa* Raf.**

Rhizome thick or very thick. Stem erect to 2 m tall. Leaves (3-) 5-14 (-22), narrowly lanceolate or broadly linear to oval, elliptical or obovate (rarely broadly) acuminate to attenuate, usually petiolate (rarely sessile). Flowers pedicellate. Sepals 3-10, linear to lanceolate-oblong or oblanceolate, green (rarely with white veins). Petals 0 or 3-12, long filiform to linear, generally less than 2 mm wide (rarely to 5 mm). Stamens 2 or 3 times number of sepals (rarely 4 or more), dehiscence lateral. Ovary subglobose to ovoid-pyramidal, angular with a disk or crown at apex, placentation parietal, ovules numerous; style thick, branches as many as sepals, linear. Fruit a purple to deep purple loculicidal capsule; sarcotesta scarlet or orange.

***Kinugasa* Tatew. and Sutô**

Rhizome very thick. Stem erect, stout, cylindrical. Leaves (6-) 7-10 (-12), broadly oblanceolate to obovate-oblong, abruptly acuminate, sessile. flowers pedicellate. Sepals 7-10 (-12) lanceolate-oblong, petaloid. Petals equal in number or missing, white, filiform. Stamens twice the number of sepals, dehiscence extrorse. Ovary subglobose, round, green, placentation axile with locules equal to the number of sepals, with a disk (usually white) at the apex; ovules many, style slender, branches equal to number of sepals. Fruit a globose, dark purple berry, seeds elliptical, without aril.

***Paris* L.**

Rhizome linear-creeping (to 5 mm in diameter) or thick. Stem erect. Leaves (3-) 4-12, lanceolate or oblanceolate to elliptical or obovate (rarely broadly), acuminate or attenuate, sessile or subsessile (rarely petiolate) Flowers pedicellate. Sepals 4-5, narrowly lanceolate to oval, green (rarely purplish), patent to reflexed. Petals 0, 4-5, filiform, linear to subulate. Stamens twice the number of sepals, dehiscence latrorse Ovary roundish, green or purple, placentation axile with locules equal to number of sepals, apex usually attenuate, ovules many to several; style slender, branches equal to number of sepals Fruit a purple to black subglobose berry. Seeds globose with aril or without.

***Pseudotrillium* nom ined.**

Rhizome narrow, branching, flattened. Stem erect. Leaves 3, ovate or cordate, coriaceous, glossy, distinctly petiolate, acuminate, often blue-green Flowers pedicellate with pedicel continuing to elongate until fruit ripens. Sepals 3, ovate, generally shorter than petals. Petals 3, broadly ovate often appearing clawed, white to pink weakly or strongly spotted with madder-pink, attenuate to apiculate. Stamens 6 (twice number of sepals) with extrorse dehiscence Ovary weakly angled, pale green, placentation a combination of parietal and axile, stigmas 3. Fruit a greenish-white berry Seeds with an aril.

***Trillidium* Kunth**

Rhizome narrow. Stem erect. Leaves 3, ovate narrowly to broadly, acuminate, rounded to cordate, petiolate. Flowers pedicellate, more or less tepaloid (outer segments occasionally wider than inner), tepals 6, dark purple (outer segments occasionally green), linear, acute, patent to reflexed. Stamens equal to number of

tepals, extrorsely dehiscent. ovary reddish-purple, ovoid-globose with an apical disk
Stigmas 3, slender. Fruit dark purple berry, seeds without aril.

***Trillium* L.**

Rhizome narrow to thick. Stem erect (rarely decumbent) Leaves 3, ovate to obovate, narrow to very broad, acute to obtuse or acuminate, rounded to cuneate, sessile (rarely petiolate), green or mottled. Flowers pedicellate (erect to nodding). Sepals 3, green or greenish-purple, ovate to elliptic. Petals 0 or 3, white, pink, reddish-purple, yellow, green, or bronze broadly ovate to narrowly obovate to linear. Stamens twice number of sepals, dehiscence introrse (lateral, or rarely extrorse) Ovary white, green, purple, round to prominently winged (rarely with an apical disk or crown), placentation axile, parietal or a combination of both. Stigmas equal to number of sepals usually sessile upon the ovary (less frequently united into a short style), branches linear to subulate. Fruit a berry or indehiscent fleshy capsule. Seeds many to numerous, with an aril.

APPENDIX B
ANNOTATED NOMENCLATURE LISTING

	genus	taxa	authority	journal	citation	year	language	Comments
1	<i>Trillium</i>	<i>acuminatum</i>	Raf	Med Repos II	5 361	1808	english	Med Flora II 99 1830
2	<i>Trillium</i>	<i>affine</i>	Rendle	J Bot	39 334	1901	latin	
3	<i>Trillium</i>	<i>albidum</i>	J D Freeman	Brittonia	27(1) 48	1975	latin	
4	<i>Trillium</i>	<i>album</i>	Small	Fl SE US	ed 1, 278	1903	english	have 1913, IK=T rhomboideum v album
5	<i>Trillium</i>	<i>amabile</i>	Miyabe & Tatew	Trans Sapporo Nat Hist Soc	15 137	1938, 1938	latin	
6	<i>Trillium</i>	<i>amabilis</i>	Cogn	Monogr Phan	7 1079	1891		
7	<i>Trillium</i>	<i>ambloopsis</i>	Raf	Medical Flora	2 99	1830	english	Aut Bot descr
8	<i>Trillium</i>	<i>ambloopsis v angustifolium</i>	Raf	Medical Flora	2 99	1830	name	
9	<i>Trillium</i>	<i>ambloopsis v cuneatum</i>	Raf	Medical Flora	2 99	1830	english	
10	<i>Trillium</i>	<i>ambloopsis v incarnatum</i>	Raf	Medical Flora	2 99	1830	name	
11	<i>Trillium</i>	<i>ambloopsis v longifolium</i>	Raf	Medical Flora	2 99	1830	name	
12	<i>Trillium</i>	<i>ambloopsis v pumilium</i>	Raf	Medical Flora	2 99	1830	name	
13	<i>Trillium</i>	<i>ambloopsis v stenopetalum</i>	Raf	Medical Flora	2 99	1830	name	
14	<i>Trillium</i>	<i>ambloopsis v undulatum</i>	Raf	Medical Flora	2 99	1830	name	
15	<i>Trillium</i>	<i>angustifolium</i>	Raf	Medical Flora	2 98	1830	english	Aut Bot 132 nom
16	<i>Trillium</i>	<i>angustifolium v gracile</i>	Raf	Medical Flora	2 98	1830	name	
17	<i>Trillium</i>	<i>angustifolium v maculatum</i>	Raf	Medical Flora	2 98	1830	name	
18	<i>Trillium</i>	<i>angustifolium v roseum</i>	Raf	Medical Flora	2 98	1830	name	
19	<i>Trillium</i>	<i>angustifolium v stenopetalum</i>	Raf	Medical Flora	2 98	1830	name	
20	<i>Trillium</i>	<i>angustipetalum</i>	(Torr) J D Freeman	Brittonia	27(1) 55	1975	c nov	
21	<i>Paris</i>	<i>apetala</i>	Hoffm	Commentat Soc Phys-Med Univ Lit Caes Mosq	1(1) pl 5	1808	latin	IK=incompleta
22	<i>Trillium</i>	<i>apetalon</i>	Makino	Bot Mag, (Tokyo)	24(282) 137	1910	english	
23	<i>Trillium</i>	<i>apetalon f atropurpureocarpa</i>	Makino	J Jap Bot	5 28	1928	english	
24	<i>Trillium</i>	<i>apetalon v atropurpureocarpum</i>	J Samej	Acta Horti Gothob	25 160	1962	d latin	

	genus	taxa	authority	Journal	citation	year	language	Comments
25	<i>Trillium</i>	<i>apetalon v atropurpureocarpum f album</i>	J Samej	Acta Horti Gothob	25 160	1962	d latin	
26	<i>Trillium</i>	<i>apetalon v maximowiczii</i>	(Miyabe & Kudô) Nemoto	Flora of Japan Supplement	1078	1936	c nov	
27	<i>Trillium</i>	<i>apetalon v rubrocarpum</i>	J Samej	Acta Horti Gothob	25 160	1962	d latin	
28	<i>Trillium</i>	<i>apetalon v rubrocarpum f tripetalum</i>	J Samej	Acta Horti Gothob	25 160	1962	d latin	
29	<i>Trillium</i>	<i>apetalon f viridicarpa</i>	Makino	J Jap Bot	5 28	1928	english	
30	<i>Trillium</i>	<i>apetalon f viridipurpureocarpa</i>	Makino	J Jap Bot	5 28	1928	english	
31	<i>Trillium</i>	<i>apetalon v viridipurpureocarpum</i>	(Makino) J Samej	Acta Horti Gothob	25 160	1962	d latin	
32	<i>Paris</i>	<i>aprica</i>	H Lévy	Feddes Reperit Spec Nov Regni Veg	6 265	1909	latin	
33	<i>Paris</i>	<i>arisanensis</i>	Hayata	Icon Pl Formos	9 141	1920	latin	
34	<i>Paris</i>	<i>atrata</i>	H Lévy	Feddes Reperit Spec Nov Regni Veg	12 536	1913	latin	
35	<i>Trillium</i>	<i>atropurpureum</i>	M A Curtis ex Beck	Bot N & M St	361	1833	pro syn	IK=erectum
36	<i>Trillium</i>	<i>atropurpureum</i>	Raf	Aut Bot	134	1840	latin	
37	<i>Paris</i>	<i>axialis</i>	H Li	Acta Bot Yunnan	6(3) 273	1984	latin	
38	<i>Paris</i>	<i>axialis v rubra</i>	H H Zhou, K Y Wu & R Tao	Acta Bot Yunnan	13(4) 421	1991	d latin	
39	<i>Trillium</i>	<i>balduianum</i>	Raf	Aut Bot	135	1840	latin	
40	<i>Paris</i>	<i>bashanensis</i>	F T Wang & Ts Tang	Fl Repub Popul Sin	15 250	1988	d latin	
41	<i>Paris</i>	<i>biondii</i>	Pamp	Nuovo Giorn Bot Ital	17 241	1910	latin	
42	<i>Daiswa</i>	<i>birmanica</i>	Takht	Brittonia	35(3) 259	1983	latin	
43	<i>Paris</i>	<i>birmanica</i>	(Takht) H Li & Nollie	Edinb J Bot	54(3) 351	1997	c nov	
44	<i>Paris</i>	<i>bockiana</i>	Diels in Engl	Bot Jahrb Syst	29 253	1901	latin	
45	<i>Daiswa</i>	<i>bockiana</i>	(Diels) Takht	Brittonia	35(3) 267	1983	c nov	
46	<i>Paris</i>	<i>brachysepala</i>	Pamp	Nuovo Giorn Bot Ital	n s 22 266	1915	latin	
47	<i>Trillium</i>	<i>brevipes</i>	Raf	Aut Bot	134	1840	latin	
48	<i>Trillium</i>	<i>brevipetalum</i>	Raf	Medical Flora	2 100	1830	english	
49	<i>Trillium</i>	<i>brevipetalum v latifolium</i>	Raf	Medical Flora	2 100	1830	name	
50	<i>Trillium</i>	<i>brevipetalum v roseum</i>	Raf	Medical Flora	2 100	1830	name	
51	<i>Trillium</i>	<i>californicum</i>	Kellogg	Proc Calif Acad Sci	2 50	1863	english	IK=ovatum
52	<i>Trillium</i>	<i>camschatcense</i>	Ker Gawl	Bot Mag	22 sub t 855	1805	english	IK="in obs "
53	<i>Trillium</i>	<i>camschatcense</i>	Vorosch in Vorob Priamur	Opred Rast Primoor	124	1966	name	Also Fl Sovet Daljn Vost p 126

	genus	taxa	authority	journal	citation	year	language	Comments
54	<i>Trillium</i>	<i>camschatcense</i> v <i>kurlense</i>	(Tatew) H Nakai & KOJI Ito	J Jap Bot	66(1) 56	1991	c nov	
55	<i>Trillium</i>	<i>camschatcense</i> f <i>plenum</i>	(J Samej) H Nakai & KOJI Ito	J Jap Bot	66(1) 55	1991	c nov	
56	<i>Trillium</i>	<i>camschatcense</i> f <i>polyphyllum</i>	(J Samej) H Nakai & KOJI Ito	J Jap Bot	66(1) 55	1991	c nov	
57	<i>Trillium</i>	<i>camschatcense</i> v <i>soyanum</i>	(J Samej) H Nakai & KOJI Ito	J Jap Bot	66(1) 56	1991	c nov	
58	<i>Trillium</i>	<i>camschatcense</i> f <i>violaceum</i>	(Miyabe & Tatew) H Nakai & KOJI Ito	J Jap Bot	66(1) 55-56	1991	c nov	
59	<i>Trillium</i>	<i>camschatcense</i> v <i>tschonoskii</i>	(Maxim) V N Vorosch in Skiortsov	Florist issl v rozn Ra?onak h SSSR	159	1985		
60	<i>Trillium</i>	<i>camschatcense</i> v <i>camtschatcense</i>	Pall ex Pursh	Fl Am Sept	1 246	1814	pro syn	IK=erectum?, q v kamtschatcense, listed as synonymy, credits to Pallas in Herb Lambert
61	<i>Trillium</i>	<i>caesbaei</i>	Elliott	Sketch	1 429	1817	latin	IK=stylosum
62	<i>Trillium</i>	<i>caesbaei</i> v <i>incarnatum</i>	Raf	Medical Flora	2 101	1830	name	
63	<i>Trillium</i>	<i>caesbaei</i> v <i>obovatum</i>	Raf	Medical Flora	2 101	1830	name	
64	<i>Paris</i>	<i>cavaleriei</i>	H Lévy & Vaniot	Nouv Contrib Liliac etc Chine	20	1906	latin	
65	<i>Trillium</i>	<i>cernuum</i>	L	Species Plantarum	339	1753	latin	
66	<i>Trillium</i>	<i>cernuum</i>	Michx	Fl bor-amer	1 216	1803	latin	IK=stylosum, credits to L
67	<i>Trillium</i>	<i>cernuum</i>	W P C Barton	Fl N Am	2 13, 1 40	1821- 1823	english	IK=erectum, syn cernuum of Pursh, Elliott, Nuttall, non L, catesby, Michaux non Walter
68	<i>Trillium</i>	<i>cernuum</i> B <i>atrorubens</i>	A W Wood in E T Cox	Rep Geol Survey Ind	2 282-287	1871	english	
69	<i>Trillium</i>	<i>cernuum</i> v <i>declinatum</i>	(A Gray) Farwell	Rep Michigan Acad Sci	21 363	1920	c nov	
70	<i>Trillium</i>	<i>cernuum</i> v <i>declinatum</i> f <i>billingtonii</i>	Farw	Rep Michigan Acad Sci	21 364	1920	c nov	
71	<i>Trillium</i>	<i>cernuum</i> v <i>declinatum</i> f <i>walpolei</i>	Farw	Rep Michigan Acad Sci	21 363	1920	c nov	
72	<i>Trillium</i>	<i>cernuum</i> f <i>lalondei</i>	Cay & J Cay	Naturaliste Canad	113(3) 327	1984	d latin	
73	<i>Trillium</i>	<i>cernuum</i> v <i>macranthes</i>	A J Eames & Wiegand as by R J Mitchell	Plantisman	12 44	1990	M rank	should be macranthum
74	<i>Trillium</i>	<i>cernuum</i> v <i>macranthum</i>	A J Eames & Wiegand	Rhodora	25 191	1923	latin	

	genus	taxa	authority	Journal	citation	year	language	Comments
75	<i>Trillium</i>	<i>cernuum f marginatum</i>	Cay & J Cay	Naturaliste Canad	113(3) 326	1984	d latin	
76	<i>Trillium</i>	<i>cernuum v terra-novae</i>	B Boivin	Rhodora	55 101	1953	latin	
77	<i>Trillium</i>	<i>cernuum v typicum</i>	Wherry	Bartonia	23 49	1945	name	
78	<i>Trillium</i>	<i>cernuum v typicum f tangerae</i>	Wherry	Bartonia	23 49	1945	latin	
79	<i>Trillium</i>	<i>cernuum f viride</i>	Cay & J Cay	Naturaliste Canad	113(3) 326	1984	d latin	
80	<i>Trillium</i>	<i>chandleri</i>	Farw	Rep Michigan Acad Sci	20 158	1918	english	
81	<i>Trillium</i>	<i>chandleri f foliaceum</i>	Farw	Rep Michigan Acad Sci	20 158	1918	english	
82	<i>Trillium</i>	<i>chandleri f gladiwizii</i>	Farw	Rep Michigan Acad Sci	20 158	1918	english	
83	<i>Trillium</i>	<i>chandleri f palaceum</i>	Farw	Rep Michigan Acad Sci	20 158	1918	english	
84	<i>Trillium</i>	<i>chandleri f plenum</i>	Farw	Rep Michigan Acad Sci	20 159	1918	english	
85	<i>Trillium</i>	<i>chandleri f subulatum</i>	Farw	Rep Michigan Acad Sci	20 158	1918	english	
86	<i>Trillium</i>	<i>channellii</i>	Fukuda, J.D. Freeman & Itou	Novon	6(2) 164	1966	d latin	
87	<i>Paris</i>	<i>chinensis</i>	French	Nouv Arch Mus Hist Nat	ser 2, 10 97	1888	latin	
88	<i>Daiswa</i>	<i>chinensis</i>	(Franch) Takht	Brittonia	35(3) 259-262	1983	c nov	
89	<i>Daiswa</i>	<i>chinensis s brachysepala</i>	(Pamp) Takht	Brittonia	35(3) 262	1983	c nov	
90	<i>Daiswa</i>	<i>chinensis s chinensis</i>	(Franch) Takht	Brittonia	35(3) 262	1983	c nov	
91	<i>Trillium</i>	<i>chloropetalum</i>	(Torr) Howell	Fl N W Amer	1 661	1902	english	
92	<i>Trillium</i>	<i>chloropetalum v angustipetalum</i>	(Torr) Munz	Aliso	4 88	1958	c nov	
93	<i>Trillium</i>	<i>chloropetalum v giganteum</i>	(Hook & Arn) Munz	Aliso	4 88	1958	c nov	
94	<i>Trillium</i>	<i>chloropetalum s giganteum</i>	(Hook & Arn) E Murray	Kalmia	14 20	1914	c nov	IK=sessile v giganteum
95	<i>Paris</i>	<i>christii</i>	H Lévy	Bull Acad Int Geogr Bot	12 255	1903	latin	IK=D cronquistii
96	<i>Trillium</i>	<i>cleavlandicum</i>	Swallow	Class Book	ed 2, 546	1847	name	IK cites Wood, Wood cites Swallow
97	<i>Trillium</i>	<i>confusum</i>	Dusek	Bull Amer Rock Gar Soc	38 164-165	1980	english	
98	<i>Trillium</i>	<i>crassifolium</i>	Piper	Erythea	7 104	1899	english	
99	<i>Paris</i>	<i>crispa</i>	H Li	Acta Bot Yunnan	5 13	1992	name	name only in abstract text specifies p rugosa

	genus	taxa	authority	Journal	citation	year	language	Comments
100	<i>Daiswa</i>	<i>cronquistii</i>	Takht	Brittonia	35 262-263	1983	latin	
101	<i>Paris</i>	<i>cronquistii</i>	(Takhtajan) H Li emend H Li	Bull Bot Res NE Forest Inst	6(1) 112	1986	latin	
102	<i>Daiswa</i>	<i>cronquistii</i>	Takhtajan as by H Li	Acta Bot Yunnan	6(4) 357	1984	SOV	should be <i>cronquistii</i>
103	<i>Paris</i>	<i>cronquistii</i>	(Takht) H Li	Acta Bot Yunnan	6(4) 357	1984	c nov.	
104	<i>Paris</i>	<i>cronquistii</i> v <i>xichouensis</i>	H Li	Bull Bot Res NE Forest Inst	6(1) 113	1986	d latin	IK=D dahurica
105	<i>Trillium</i>	<i>crustica</i>	Lapham	n/a		unpub		
106	<i>Trillium</i>	<i>cuneatum</i>	Raf	Aut Bot	133	1840	latin	
107	<i>Trillium</i>	<i>cuneatum f luteum</i>	(Muhl) H E Ahles as by R J Mitchell	Plantisman	11.133	1989	M authority	should be J D Freeman
108	<i>Trillium</i>	<i>cuneatum f luteum</i>	J D Freeman	Brittonia	27(1) 36	1975	latin	
109	<i>Trillium</i>	<i>cuneatum v luteum</i>	(Muhl) H E Ahles	Flora of the Carolinas	p 290	1964	english	syn <i>T luteum</i> -- not IDd as c nov
110	<i>Paris</i>	<i>dahurica</i>	Fisch ex Turcz	Bull Soc Imp Naturalistes Moscou	27(2) 105	1854	latin	IK=polyphylla
111	<i>Paris</i>	<i>dahurica</i>	Fisch ex Turcz	Bull Soc Imp Naturalistes Moscou	27(2) 105	1854	latin	refs P dahurica Fish in litt
112	<i>Paris</i>	<i>daisua</i>	Buch-Ham ex D Don	Prod Fl Nep	49	1825	pro syn	
113	<i>Paris</i>	<i>daisua</i>	Buch-Ham ex D Don	Plantisman	10 111	1988	SOV	should be <i>daisua</i> -- is this SOV or corrected spelling?
114	<i>Paris</i>	<i>dalenensis</i>	H Li & V G Soukup	Acta Bot Yunnan	5 15	1992	latin	
115	<i>Paris</i>	<i>debeauxii</i>	H Lev	Nouv Contrib Liliac etc Chine	21	1906	latin	
116	<i>Trillium</i>	<i>decepiens</i>	J D Freeman	Brittonia	27(1) 17	1975	latin	
117	<i>Trillium</i>	<i>declinatum</i>	(A Gray) Gleason	Bull Torrey Bot Club	33 389	1906	english	
118	<i>Trillium</i>	<i>declinatum</i>	Raf	Aut Bot	135	1840	latin	
119	<i>Trillium</i>	<i>declinatum f walpolei</i>	(Farw) Friesner	Buller Univ Bot Stud	3(29) 34	1929	c nov	desc Proc Ind Acad Sci 24,1924(1925), p 315, but not named there
120	<i>Trillium</i>	<i>decumbens</i>	Harb	Biltmore Bot Stud	1 158	1902	english	
121	<i>Paris</i>	<i>delavayi</i>	Franch	Journ de Bot	190	1898	latin	
122	<i>Daiswa</i>	<i>delavayi</i>	(Franch) Takht	Brittonia	35 269-270	1983	c nov	
123	<i>Paris</i>	<i>delavayi v ovalifolia</i>	H Li	Bull Bot Res NE Forest Inst	6(1) 115	1986	d latin	
124	<i>Paris</i>	<i>delavayi v petiolata</i>	(Baker ex C H Wright) H Li	Vasc Pl Hengduan Mount	2 2469	1994	c nov	
125	<i>Trillium</i>	<i>discolor</i>	Chapm	Fl of S U S	478	1860	english	cites to Wray
126	<i>Trillium</i>	<i>discolor</i>	T W Ray ex Hook	Bot Mag	pl t 3097	1831	latin	
127	<i>Trillium</i>	<i>divaricatum</i>	Raf	Medical Flora	2 102	1830	english	

	genus	taxa	authority	journal	citation	year	language	Comments
128	<i>Paris</i>	<i>dulongensis</i>	H Li & Kurita	Acta Bot Yunnan	5 14-15	1992	latin	
129	<i>Paris</i>	<i>dunniana</i>	H Lev	Faddes Rept. Spec Nov Regni Veg	9 78	1910	latin	
130	<i>Daiswa</i>	<i>dunniana</i>	(H. Lev) Takht	Brittonia	35(3) 257	1983	e nov	
131	<i>Trillium</i>	<i>erectum</i>	L	Species Plantarum	340	1753	latin	
132	<i>Trillium</i>	<i>erectum</i>	Stell in Pallas	Neue Nord Beytr Phys Geogr erd-Volkerbeschreib	2 300	1781	name	
133	<i>Trillium</i>	<i>erectum</i>	L as by D Dietrich	Syn Pl	2 1212	1840	SOV	should be erectum
134	<i>Trillium</i>	<i>erectum B alba</i>	A W Wood	Class Book	p 705	1866	english	
135	<i>Trillium</i>	<i>erectum f albiflorum</i>	R Hofm	Proc Boston Soc Nat Hist	36 244	1922	d latin	
136	<i>Trillium</i>	<i>erectum B album</i>	Ker Gawl	Bot Mag	pl 1027	1807	english	
137	<i>Trillium</i>	<i>erectum f album</i>	(Pursh) T S Patrick	n/a	9 76	unpub	unpub	no name given -- refs Michaux
138	<i>Trillium</i>	<i>erectum album</i>	Clute	Amer Bot (Binghampton)		1905	name	
139	<i>Trillium</i>	<i>erectum v album</i>	A Gray in Perry	Narr Exp of Am Squad to China Seas & Japan	2 320	1856	english	variety or trinomial ??? -- syn for erectum v japonicum, credits to Pursh
140	<i>Trillium</i>	<i>erectum v album</i>	Lodd in L H Bailey	Stand Cycl Hort	6 3382	1917	english	
141	<i>Trillium</i>	<i>erectum B album</i>	(Michx) Pursh	Fl Am Sept	1 245	1817	english	
142	<i>Trillium</i>	<i>erectum A atropurpureum</i>	(Michx) Pursh	Fl Am Sept	1 245	1817	english	
143	<i>Trillium</i>	<i>erectum v blandum</i>	Jennison	Rhodora	40 486	1938	latin	
144	<i>Trillium</i>	<i>erectum f brevipedicellatum</i>	Louis-Marie	Rev Oka Agron Inst Agric	14 150	1940	d latin	
145	<i>Trillium</i>	<i>erectum v cahnae</i>	Farw	Amer Midl Naturalist	9 266	1925	english	
146	<i>Trillium</i>	<i>erectum f cahnae</i>	(Farw) Louis-Marie	Rev Oka Agron Inst Agric	14 153	1940	d latin	
147	<i>Trillium</i>	<i>erectum v declinatum</i>	A Gray	Manual	523	1867	english	
148	<i>Trillium</i>	<i>erectum v flavum</i>	Torr	Fl NY	2 296	847	english	
149	<i>Trillium</i>	<i>erectum v giganteum</i>	Louis-Marie	Rev Oka Agron Inst Agric	14 151	1940	d latin	
150	<i>Trillium</i>	<i>erectum f horizontale</i>	Louis-Marie	Rev Oka Agron Inst Agric	14 110	1940	french	
151	<i>Trillium</i>	<i>erectum v horizontale</i>	Louis-Marie	Rev Oka Agron Inst Agric	14 151	1940	latin	
152	<i>Trillium</i>	<i>erectum v japonicum</i>	A Gray	Mem Amer Acad Arts	6 413	1859	latin	
153	<i>Trillium</i>	<i>erectum v japonicum florepleno</i>	A Gray in L H Bailey	Stand Cycl Hort	3 3382	1935	pro syn	
154	<i>Trillium</i>	<i>erectum v japonicum flore rubro</i>	A Gray	Mem Amer Acad Arts	413			Not here!! Source is Miyabe and Kudo

	genus	taxa	authority	journal	citation	year	language	Comments
155	<i>Trillium</i>	<i>erectum f luteum</i>	Louis-Marie	Rev Oka Agron Inst Agric	14 150	1940	d latin	
156	<i>Trillium</i>	<i>erectum f nigrescens</i>	Louis-Marie	Rev Oka Agron Inst Agric	14 151	1940	d latin	
157	<i>Trillium</i>	<i>erectum v ochroleucum</i>	Hook ex J Macoun	Cat Can Pl	4 49	1888	name	
158	<i>Trillium</i>	<i>erectum f pallidandrum</i>	Vict & J Rousseau	Rev Oka Agron Inst Agric	33 66	1929	d latin	
159	<i>Trillium</i>	<i>erectum f parviflorum</i>	Louis-Marie	Rev Oka Agron Inst Agric	14 150	1940	d latin	
160	<i>Trillium</i>	<i>erectum f parvum</i>	Louis-Marie	Rev Oka Agron Inst Agric	14 150	1940	d latin	
161	<i>Trillium</i>	<i>erectum G petalis ochroleucthis</i>	Hook	Fl bor -amer	2 180	1840	name	cites Bot Mag t 3250
162	<i>Trillium</i>	<i>erectum f polymerum</i>	Vict	Contr Inst Univ Montreal	14 30	1929	d latin	
163	<i>Trillium</i>	<i>erectum f rubrostratum</i>	Louis-Marie	Rev Oka Agron Inst Agric	14 151	1940	d latin	
164	<i>Trillium</i>	<i>erectum rubrum</i>	Clute	Amer Bot (Binghampton)	9 76	1905	name	
165	<i>Trillium</i>	<i>erectum f sessiloides</i>	B Bovin	Rhodora	55 102	1953	latin	
166	<i>Trillium</i>	<i>erectum v simile</i>	(Gleason) Ihara	J Geobot	25(4) 143	1978	c nov	
167	<i>Trillium</i>	<i>erectum v sulcatum</i>	Barksd	J Elisha Mitchell Sci Soc	54 280	1938	english	
168	<i>Trillium</i>	<i>erectum v tschonoskii</i>	Yamam	J Soc Trop Agric	10 177	1938	pro syn	
169	<i>Trillium</i>	<i>erectum v vaseyi</i>	(Harb) H E Ahles	J Elisha Mitchell Sci Soc	80 172	1964	c nov	
170	<i>Trillium</i>	<i>erectum v vaseyi f simile</i>	(Gleason) H E Ahles	J Elisha Mitchell Sci Soc	80 172	1964	c nov	
171	<i>Trillium</i>	<i>erectum v viridiflorum</i>	Curtis	Bot. Mag	60 tab 3250	1833	english	no author given
172	<i>Trillium</i>	<i>erectum f viridiflorum</i>	(Curtis) Peattie	J Elisha Mitchell Sci Soc	42 203	1927	c nov	
173	<i>Trillium</i>	<i>erythrocarpum</i>	Ker Gawl	Bot. Mag	t 855	1805	latin	
174	<i>Trillium</i>	<i>erythrocarpum</i>	Michx	Fl bor -amer	1 216	1803	latin	
175	<i>Trillium</i>	<i>erythrocarpum B clevelandicum</i>	A W Wood	Class Book	546	1847	english	
176	<i>Paris</i>	<i>fargesii</i>	Franch	Journ de Bot	190	1898	latin	
177	<i>Daiswa</i>	<i>fargesii</i>	(Franch) Takht	Brittonia	35(3) 264	1983	c nov	
178	<i>Daiswa</i>	<i>fargesii v brevipetala</i>	T C Huang & K C Yang	Taiwania	33 123, f 1	1988	d latin	
179	<i>Paris</i>	<i>fargesii v brevipetala</i>	(T C Huang & K C Yang) T C Huang & K C Yang	Taiwania	34(1) 52	1989	name	IK=D fargesii v brevipetala, lists T taiwanense as SYN!!
180	<i>Paris</i>	<i>fargesii v latipetala</i>	H Li & V G Soukup	Acta Bot. Yunnan	5 17-18	1992	d latin	

	genus	taxa	authority	journal	citation	year	language	Comments
181	Paris	<i>fargesii</i> v <i>petiolata</i>	(Baker ex C H Wright) F T Wang & Ts Tang	Fl Repub Popul Sin	15 91	1978	c nov	
182	Paris	<i>fargesii</i> v <i>brevipetala</i>	(T C Huang & K C Yang) H Li	Genus Paris (Trilliaceae)	50	1998	c nov	
183	Trillium	<i>flavum</i>	Raf	Medical Flora	2 100	1830	english	Aut Bot 133, desc
184	Trillium	<i>flexipes</i>	Raf	Aut Bot	133	1840	latin	
185	Trillium	<i>flexipes</i> f <i>walpolei</i>	(Farw.) Fernald	Rhodora	46(541) 17	1944	c nov	
186	Trillium	<i>foetidissimum</i>	J D Freeman	Brittonia	27(1) 31	1975	latin	
187	Trillium	<i>foetidissimum</i> f <i>luteum</i>	J D Freeman	Brittonia	27(1) 32	1975	latin	
188	Trillium	<i>foetidum</i>	Salisb	Parad Lond	t 35 i t 35	1805	latin	
189	Paris	<i>formosana</i>	Hayata	J Coll Sci Imp Univ Tokyo	30 367	1911	latin	
190	Daiswa	<i>forrestii</i>	Takht	Brittonia	35(3) 268	1983	latin	
191	Paris	<i>forrestii</i>	(Takht) H Li	Acta Bot Yunnan	6(4) 359	1984	c nov	IK=D forestii
192	Paris	<i>franchetiana</i>	H Lev	Bull Acad Int Geogr Bot	12 256	1903	latin	
193	Paris	<i>fauchiana</i>	H Léves by F T Wang & Ts Tang	Fl Repub Popul Sin	15 92	1978	SOV	should be franchetiana
194	Trillium	<i>giganteum</i>	(Hook & Arn) A Heller	Bull S Calif Acad Sci	2 67	1903	c nov	
195	Trillium	<i>giganteum</i> v <i>angustipetalum</i>	(Torr) R R Gates	Ann Missouri Bot Gard	4 51	1917	c nov	
196	Trillium	<i>giganteum</i> v <i>chloropetalum</i>	(Torr) R R Gates	Ann Missouri Bot Gard	4 50	1917	c nov	
197	Paris	<i>gigas</i>	H Lev & Vaniot	Nouv Contrib Liliac etc Chine	20	1906	latin	
198	Trillium	<i>glaucum</i>	Raf as by R J Mitchell	Plantisman	12 44	1990	SOV	should be glaucum
199	Trillium	<i>glaucum</i>	Raf	Medical Flora	2 102	1830	english	
200	Trillium	<i>gleasonii</i>	Fernald	Rhodora	34 21	1932	english	
201	Trillium	<i>gleasonii</i> f <i>billingtonii</i>	(Farw) Louis-Marie	Rev Oka Agron Inst Agric	14 153	1940	d latin	
202	Trillium	<i>gleasonii</i> f <i>walpolei</i>	(Farw) Deam	Fl Indiana	323	1940	c nov	
203	Trillium	<i>gleasonii</i> f <i>walpolei</i>	(Farw) Louis-Marie	Rev Oka Agron Inst Agric	14 153	1940	d latin	
204	Trillium	<i>govenianum</i>	Wall as by L H Bailey	Stand Cycl Hort	6 3382	1917	SOV	should be govenianum
205	Trilicium	<i>govanianum</i>	Kunth	Enum Pl	5 120	1850	latin	IK=Trillium govanianum
206	Trillium	<i>govanianum</i>	Wall in Royle	Illust Bot Himal	384, t 93, f 1	1828	latin	Wall Cat n 812
207	Trillium	<i>gracile</i>	J D Freeman	Sida	3 289	1969	latin	
208	Trillium	<i>gracile</i> f <i>luteum</i>	J D Freeman	Sida	3 290	1969	latin	

209	genus	taxa	authority	Journal	citation	year	language	Comments
209	<i>Trillium</i>	<i>grandiflorum</i>	Hook	Fl bor -amer	2 180	1840	name	credits to Salisbury
210	<i>Trillium</i>	<i>grandiflorum</i>	(Michx) Salisb	Parad Lond	t 1	1817	latin	
211	<i>Trillium</i>	<i>grandiflorum f</i> <i>carpellare</i>	Dans	Naturaliste Canad	72 145	1945	d latin	
212	<i>Trillium</i>	<i>grandiflorum f</i> <i>chandleri</i>	Vict	Contr Inst Univ Montréal	14 30	1929	c nov	
213	<i>Trillium</i>	<i>grandiflorum f</i> <i>dimerum</i>	Louis-Marie	Rev Oka Agron Inst Agric	14 146	1940	d latin	
214	<i>Trillium</i>	<i>grandiflorum f</i> <i>divisum</i>	Louis-Marie	Rev Oka Agron Inst Agric	14 148	1940	d latin	
215	<i>Trillium</i>	<i>grandiflorum v elatior</i>	Raf	Medical Flora	2 100	1830	name	
216	<i>Trillium</i>	<i>grandiflorum f</i> <i>elongatum</i>	Louis-Marie	Rev Oka Agron Inst Agric	14 148	1940	d latin	
217	<i>Trillium</i>	<i>grandiflorum f</i> <i>fasciatum</i>	Louis-Marie	Rev Oka Agron Inst Agric	14 112	1940	french	describes chandleri????
218	<i>Trillium</i>	<i>grandiflorum f</i> <i>linoides</i>	(Raf) Vict	Contr Inst Univ Montréal	14 30	1929	c nov	
219	<i>Trillium</i>	<i>grandiflorum v</i> <i>longifolium</i>	Raf	Medical Flora	2 100	1830	name	
220	<i>Trillium</i>	<i>grandiflorum v</i> <i>macroptium</i>	Raf	Medical Flora	2 100	1830	name	
221	<i>Trillium</i>	<i>grandiflorum v</i> <i>minimum</i>	Coleman	Kent Sci Inst Misc Publ	2 40	1874	english	
222	<i>Trillium</i>	<i>grandiflorum v</i> <i>obovatum</i>	(Pursh) Farw	Ann Rep Comm Parks & Boulev , Detroit	11 53	1900	c nov	
223	<i>Trillium</i>	<i>grandiflorum v</i> <i>obovatum</i>	Raf	Medical Flora	2 100	1830	name	
224	<i>Trillium</i>	<i>grandiflorum v</i> <i>obovatum f albiflorum</i>	Farw	Rep Michigan Acad Sci	21 364	1920	english	
225	<i>Trillium</i>	<i>grandiflorum v</i> <i>obovatum f virescens</i>	Farw	Rep Michigan Acad Sci	20 157	1919	english	
226	<i>Trillium</i>	<i>grandiflorum v</i> <i>orbiculare</i>	Farw as by Louis-Marie	Rev Oka Agron Inst Agric	114 111	1940	M rank	should be forma orbiculare
227	<i>Trillium</i>	<i>grandiflorum f</i> <i>orbiculare</i>	Farw	Rep Michigan Acad Sci	20 157	1918	english	
228	<i>Trillium</i>	<i>grandiflorum v</i> <i>parviflorum</i>	Raf	Medical Flora	2 100	1830	name	
229	<i>Trillium</i>	<i>grandiflorum v</i> <i>parvum</i>	R R Gates	Ann Missouri Bot Gard	4 58	1917	d latin	
230	<i>Trillium</i>	<i>grandiflorum f</i> <i>petalotum</i>	Louis-Marie	Rev Oka Agron Inst Agric	14 149	1940	d latin	
231	<i>Trillium</i>	<i>grandiflorum f</i> <i>polymerum</i>	Vict	Contr Inst Univ Montreal	14 31	1929	d latin	

	genus	taxa	authority	journal	citation	year	language	Comments
232	<i>Trillium</i>	<i>grandiflorum</i> v <i>pumilum</i>	Raf	Medical Flora	2 100	1830	name	
233	<i>Trillium</i>	<i>grandiflorum</i> f <i>regressum</i>	Louis-Marie	Rev Oka Agron Inst Agric	14 149	1940	d latin	
234	<i>Trillium</i>	<i>grandiflorum</i> f <i>rhodanthum</i>	R G Johnson	Castanea	34 329	1969	d latin	
235	<i>Trillium</i>	<i>grandiflorum</i> v <i>rhomboidum</i>	Raf	Medical Flora	2 100	1830	name	
236	<i>Trillium</i>	<i>grandiflorum</i> f <i>roseum</i>	Farw	Rep Michigan Acad Sci	21 364	1920	english	
237	<i>Trillium</i>	<i>grandiflorum</i> v <i>roseum</i>	hort ex L H Bailey	Stand Cycl Hort	6 3382	1917	english	GCI claims Hubbard
238	<i>Trillium</i>	<i>grandiflorum</i> v <i>roseum</i>	Raf	Medical Flora	2 100	1830	name	Aut Bot 134 1840, descr
239	<i>Trillium</i>	<i>grandiflorum</i> v <i>spatulatum</i>	Farw as by Louis-Marie	Rev Oka Agron Inst Agric	14 111	1940	M rank	should be forma spatulatum
240	<i>Trillium</i>	<i>grandiflorum</i> f <i>spatulatum</i>	Farw	Rep Michigan Acad Sci	20 157	1918	english	
241	<i>Trillium</i>	<i>grandiflorum</i> f <i>striatum</i>	Louis-Marie	Rev Oka Agron Inst Agric	14 147	1940	d latin	
242	<i>Trillium</i>	<i>grandiflorum</i> v <i>variegatum</i>	E F Sm	Bot Gaz (London)	4 181	1879	english	
243	<i>Trillium</i>	<i>grandiflorum</i> f viride	Farw	Rep Michigan Acad Sci	20 157	1918	english	
244	<i>Trillium</i>	<i>hagae</i> (hybrd (3x))	Miyabe & Tatew	Trans Sapporo Nat Hist Soc	14 189	1936	pro sp	
245	<i>Trillium</i>	<i>hagae</i> (6x)	Miyabe & Tatew	Trans Sapporo Nat Hist Soc	14 189	1936	latin	
246	Paris	<i>hainanensis</i>	Merr	Philipp J Sci	23(3) 238	1923	latn	
247	Daiswa	<i>hainanensis</i>	(Merr.) Takht	Brittonia	35(3) 258	1983	c nov	
248	Daiswa	<i>hainanensis</i> s <i>vietnamensis</i>	Takht	Brittonia	35(3) 2259	1983	latin	
249	Paris	<i>hamifer</i>	H Lev	Feddes Reperit Spec Nov Regni Veg	12 288	1913	latin	
250	<i>Trillium</i>	<i>hamosum</i>	Raf	Medical Flora	2 101	1830	english	IR=T cernuum
251	Paris	<i>henryi</i>	Diels in Engl	Bot Jahrb Syst	29 252	1901	latin	
252	Paris	<i>hexaphylla</i>	Cham	Linnaea	6 586	1831	latin	IK says p 568
253	Paris	<i>hexaphylla</i> v <i>manshurica</i>	(Kom.) B H Vorosh	Bull Glavn Bot Sad	84 31	1972	c nov	IK=P manshurica

	genus	taxa	authority	journal	citation	year	language	Comments
254	Paris	<i>hexaphylla f purpurea</i>	Miyabe & Tatew	Trans Sapporo Nat Hist Soc	15 137	1938	d latin	
255	<i>Trillium</i>	<i>hibbersonii</i>	L Wiley	Rare Wildflowers of N.A.	440-447	1969	english	
256	Paris	<i>hookeri</i>	H Lev	Feddes Reperit Spec Nov. Regni. Veg	7 231	1909	latin	
257	<i>Trillium</i>	<i>hugeri</i>	Small	Fl SE US	277	1913	english	
258	<i>Trillium</i>	<i>hugeri f flava</i>	Peattie	J Elisha Mitchell Sci Soc	42 199	1929	english	
259	Paris	<i>imperialis</i>	Jacquem ex Hook f	Fl Brit India	6 362	1892	pro syn	IK=polyphylla
260	Paris	<i>incompleta</i>	M Bieb	Fl Taur Cauc	1 306	1808	latin	
261	<i>Trillium</i>	<i>isanthum</i>	Raf	Medical Flora	2 98	1830	english	IF=T sessile
262	<i>Trillium</i>	<i>isanthum v albiflorum</i>	Raf	Medical Flora	2 98	1830	name	
263	<i>Trillium</i>	<i>isanthum v parviflorum</i>	Raf	Medical Flora	2 98	1830	name	
264	Paris	<i>japonica</i>	(Franch & Sav) Franch	Mem Soc Phil Paris	291	1889	latin	
265	Kinugasa	<i>japonica</i>	(Franch & Sav) Tatew & Suto	Trans Sapporo Nat Hist Soc	14 36	1935	latin	
266	Kinugasa	<i>japonica v tomentosa</i>	Miyabe & Tatew	Trans Sapporo Nat Hist Soc	14 189	1936	d latin	
267	<i>Trilidium</i>	<i>japonicum</i>	Franch & Sav	Enum Pl Jap	2 525	1877	latin	
268	<i>Trillium</i>	<i>japonicum</i>	(Franch & Sav) Matsun	Enum Sci Names	298	1895	name	IK=Trilidium japonicum
269	<i>Trillium</i>	<i>kamtschaticum</i>	Pall ex Miyabe	Flora Kuriles	265	1890	english	credits to Pallas ex Pursh
270	<i>Trillium</i>	<i>kamtschaticum</i>	Miyabe & Tatew	Flora Hokkaido & Saghalin	3 343	1932	name	credits to Pursh
271	<i>Trillium</i>	<i>kamtschaticum v kurlense</i>	Tatew in Miyabe & Kudó	Flora Hokkaido & Saghalin	3 343	1932	d latin	
272	<i>Trillium</i>	<i>kamtschaticum f plenum</i>	J Samej	Acta Horti Gothob	25(6) 162	1962	d latin	In Trillium Garden 9 (1961) w/ Japanese description. nom illegit
273	<i>Trillium</i>	<i>kamtschaticum f polyphyllum</i>	J Samej	Acta Horti Gothob	25(6) 162	1962	d latin	
274	<i>Trillium</i>	<i>kamtschaticum s rhombifolium</i>	(Kom) E Murray	Kalmia	13 32	1983	c nov	IK=T rhombifolium
275	<i>Trillium</i>	<i>kamtschaticum v rhombifolium</i>	(Kom) E Murray	Kalmia	13 32	1983	c nov	IK=T rhombifolium
276	<i>Trillium</i>	<i>kamtschaticum v soyanum</i>	J Samej	Acta Horti Gothob	25(6) 162	1962	d latin	
277	<i>Trillium</i>	<i>kamtschaticum f violaceum</i>	Miyabe & Tatew	Trans Sapporo Nat Hist Soc	16(1) 7	1939	d latin	
278	<i>Trillium</i>	<i>kamtschaticum</i>	Ledeb	Fl Rossica	4 121	1853	pro syn	IK=T obovatum, Pallas in herb Lambert (fide Pursh).

	genus	taxa	authority	journal	citation	year	language	Comments
279	<i>Trillium</i>	<i>komarovii</i> (hybrid)	H Nakai & KOJI Ito	J Jap Bot	66(1) 56	1991	n nov	based on <i>T rhombifolium</i> Kom nom illegit
280	<i>Trillium</i>	<i>kurabayashii</i>	J D Freeman	Brittonia	27(1) 56	1975	latin	
281	<i>Trillium</i>	<i>kurabayashii f luteum</i>	V G Soukup	Phytologia	50(4) 290	1982	latin	
282	<i>Paris</i>	<i>kwantungensis</i>	R H Miao	Acta Sci Nat Univ Sunvatseni	3 74	1982	latin	
283	<i>Paris</i>	<i>lanceolata</i>	Hayata as by H Li	Bull Bot Res NE Forest Inst	6(1) 124	1985	SOV	should be <i>lanceifolia</i>
284	<i>Trillium</i>	<i>lanceolatum</i>	Boykin ex S Watson	Proc Amer Acad Arts	14 274	1879	pro syn	IK=T recurvatum
285	<i>Trillium</i>	<i>lanceolatum v rectistamineum</i>	R R Gates	Ann Missouri Bot Gard	4 48	1917	english	
286	<i>Paris</i>	<i>lanceifolia</i>	Hayata	Bot Mag., (Tokyo)	20 52	1906	latn	
287	<i>Dauswa</i>	<i>lanceifolia</i>	(Hayata) Takht	Brittonia	35(3) 266	1983	c nov	
288	<i>Trillium</i>	<i>lanceifolium</i>	Raf	Aut Bot	132	1840	latin	
289	<i>Trillium</i>	<i>latifolium</i>	Raf	Medical Flora	2 97, 101 f 91	1830	english	IK=T cernuum
290	<i>Trillium</i>	<i>liriodes</i>	Raf	Medical Flora	2 100	1840	english	
291	<i>Trillium</i>	<i>liriodes f albomarginatum</i>	Farw	Rep Michigan Acad Sci	20 157	1918	english	
292	<i>Trillium</i>	<i>liriodes v crassaule</i>	Raf	Medical Flora	2 101	1830	name	
293	<i>Trillium</i>	<i>liriodes f giganteum</i>	Farw	Rep Michigan Acad Sci	20 157	1918	english	
294	<i>Trillium</i>	<i>liriodes v longepetiolatum</i>	Farw	Rep Michigan Acad Sci	20 158	1918	english	
295	<i>Trillium</i>	<i>liriodes v longepetiolatum f variegatum</i>	(E F Smith) Farw	Rep Michigan Acad Sci	20 158	1918	c nov	
296	<i>Trillium</i>	<i>liriodes v longepetiolatum f vegetum</i>	Farw	Rep Michigan Acad Sci	20 158	1918	english	
297	<i>Trillium</i>	<i>liriodes v longifolium</i>	Raf	Medical Flora	2 101	1830	name	
298	<i>Trillium</i>	<i>liriodes v maculatum</i>	Raf	Medical Flora	2 101	1830	name	
299	<i>Trillium</i>	<i>liriodes v parviflorum</i>	Raf	Medical Flora	2 101	1830	name	
300	<i>Trillium</i>	<i>liriodes v pumitum</i>	Raf	Medical Flora	2 101	1830	name	
301	<i>Trillium</i>	<i>liriodes v roseum</i>	Raf	Medical Flora	2 101	1830	name	
302	<i>Trillium</i>	<i>liriodes v longepetiolatum f subsessile</i>	Farw	Amer Midl Naturalist	11 51	1928	english	
303	<i>Trillium</i>	<i>liriodes v undulatum</i>	Raf	Medical Flora	2 101	1830	name	
304	<i>Trillium</i>	<i>liriodes f unguilatum</i>	Farw	Rep Michigan Acad Sci	20 158	1918	english	

	genus	taxa	authority	journal	citation	year	language	Comments
305	<i>Trillium</i>	<i>longiflorum</i>	Raf	Medical Flora	2 97	1830	english	
306	<i>Trillium</i>	<i>longiflorum</i> v <i>atropurpureum</i>	Raf	Medical Flora	2 98	1830	name	
307	<i>Trillium</i>	<i>longiflorum</i> v <i>latifolium</i>	Raf	Medical Flora	2 98	1830	name	
308	<i>Trillium</i>	<i>longiflorum</i> v <i>maculatum</i>	Raf	Medical Flora	2 98	1830	name	
309	<i>Trillium</i>	<i>longiflorum</i> v <i>parvifolium</i>	Raf	Medical Flora	2 98	1830	name	
310	<i>Trillium</i>	<i>longiflorum</i> v <i>pumilum</i>	Raf	Medical Flora	2 98	1830	name	
311	<i>Trillium</i>	<i>longiflorum</i> v <i>rubricaulis</i>	Raf	Medical Flora	2 98	1830	name	
312	<i>Trillium</i>	<i>longiflorum</i> v <i>undulatum</i>	Raf	Medical Flora	2 98	1830	name	
313	<i>Paris</i>	<i>longistigmata</i>	H Li	Acta Bot Yunnan	6(3) 275	1984	latin	
314	<i>Trillium</i>	<i>ludovicianum</i>	Harb	Biltmore Bot Stud	1 23	1901	english	
315	<i>Paris</i>	<i>luquanensis</i>	H Li	Acta Bot Yunnan	4(4) 353	1982	latin	
316	<i>Trillium</i>	<i>luteum</i>	(Muhl.) Harb	Biltmore Bot Stud	1 21	1901	english	
317	<i>Trillium</i>	<i>luteum</i> v <i>latipetalum</i>	R R Gates	Ann Missouri Bot Gard	4 46	1917	english	
318	<i>Trillium</i>	<i>maculatum</i>	Raf	Medical Flora	2 103	1830	english	IK=T sessile
319	<i>Trillium</i>	<i>maculatum</i> f <i>luteum</i>	J D Freeman	Brittonia	27(1) 29	1975	latin	
320	<i>Trillium</i>	<i>maculatum</i> f <i>simulans</i>	J D Freeman	Brittonia	27(1) 29	1975	latin	
321	<i>Paris</i>	<i>mairei</i>	H Lev	Feddes Reperit Spec Nov Regni Veg	11 302	1912	latin	
322	<i>Paris</i>	<i>manshurica</i>	Korn	Fl URSS	4 748	1935	latin	
323	<i>Paris</i>	<i>manshurica</i>	Korn	Key Pl Far East Reg USSR	1 385	1931	russian	
324	<i>Paris</i>	<i>marchandii</i>	H Lev	Feddes Reperit Spec Nov Regni Veg	12 533	1913	latin	
325	<i>Paris</i>	<i>marmorata</i>	Stearn	Bull Brit Mus (Nat Hist) Bot	2(3) 79	1956	latin	
326	<i>Trillium</i>	<i>medium</i>	Raf	Medical Flora	2 102	1830	english	IK=T cernuum
327	<i>Trillium</i>	<i>medium</i> v <i>gracile</i>	Raf	Medical Flora	2 102	1830	name	
328	<i>Trillium</i>	<i>medium</i> v <i>grandiflorum</i>	Raf	Medical Flora	2 102	1830	name	
329	<i>Trillium</i>	<i>medium</i> v <i>pubicum</i>	Raf	Medical Flora	2 102	1830	name	
330	<i>Trillium</i>	<i>medium</i> v <i>undulatum</i>	Raf	Medical Flora	2 102	1830	name	
331	<i>Trillium</i>	<i>membranaceum</i>	Raf	Medical Flora	2 98	1830	english	
332	<i>Trillium</i>	<i>membranaceum</i> v <i>ellipticum</i>	Raf	Medical Flora	2 98	1830	name	

	genus	taxa	authority	journal	citation	year	language	Comments
333	<i>Trillium</i>	<i>membranaceum</i> v <i>obovatum</i>	Raf	Medical Flora	2 98	1830	name	
334	<i>Trillium</i>	<i>membranaceum</i> v <i>parvifolium</i>	Raf	Medical Flora	2 98	1830	name	
335	<i>Paris</i>	<i>mercieri</i>	H Lev	Bull Acad Int Geogr Bot	12 255	1903	latin	
336	<i>Paris</i>	<i>wercieri</i>	H Lev as by H LI	Bull Bot Res NE Forest Inst	6(1) 119	1985	SOV	should be mercieri
337	<i>Trillium</i>	<i>myabebeanum (hybrid)</i>	Tatew ex J Samej	Acta Horti Gothob	25 166	1962	latin	
338	<i>Trillium</i>	<i>myabebeanum f</i> <i>albiflorum</i>	V G Soukup	Phytologia	50(4) 290	1982	d latin	
339	<i>Trillium</i>	<i>mybeanum</i> v <i>atropurpureocarapum</i>	J Samej	Acta Horti Gothob	25 166	1962	d latin	
340	<i>Trillium</i>	<i>morii</i>	Hayata	Icon Pl Formos	7 41	1918	latin	
341	<i>Trillium</i>	<i>nervosum</i>	Elliott	Sketch	1 429	1817	latin	IK=T stylosum
342	<i>Trillium</i>	<i>nivale</i>	Riddell	Syn Fl W St	93	1835	english	
343	<i>Trillium</i>	<i>nutans</i>	Raf	Medical Flora	2 99	1830	english	IK=T erectum
344	<i>Trillium</i>	<i>nutans v album</i>	Raf	Medical Flora	2 99	1830	name	
345	<i>Trillium</i>	<i>nutans v</i> <i>atropurpureum</i>	Raf	Medical Flora	2 99	1830	name	
346	<i>Trillium</i>	<i>nutans v bicolor</i>	Raf	Medical Flora	2 99	1830	english	
347	<i>Trillium</i>	<i>nutans v flexuosum</i>	Raf	Medical Flora	2 99	1830	name	
348	<i>Trillium</i>	<i>nutans v obovatum</i>	Raf	Medical Flora	2 99	1830	name	
349	<i>Trillium</i>	<i>nutans v</i> <i>rhombioidum</i>	Raf	Medical Flora	2 99	1830	name	
350	<i>Trillium</i>	<i>nutans v undulatum</i>	Raf	Medical Flora	2 99	1830	name	
351	<i>Trillium</i>	<i>obcordatum</i>	Raf	Medical Flora	2 101	1830	english	IK=T grandiflorum
352	<i>Paris</i>	<i>obovata</i>	Ledeb.	ic Pl Ross	1 6	1829	latin	
353	<i>Paris</i>	<i>obovata f purpurea</i>	(Miyabe & Tatew) Honda	Nom Pl Japan , ed amend	358	1957	name	
354	<i>Trillium</i>	<i>obovatum</i>	Hook	Fl bor -amer	2 180	1840	latin	IK=T ovatum credits 2 Pursh
355	<i>Trillium</i>	<i>obovatum</i>	Kom	Key Pl Far East Reg USSR	1 385	1931	russian	credits to Pursh
356	<i>Trillium</i>	<i>obovatum</i>	Kunth	Enum Pl	5 124	1833	latin	credits to Pursh
357	<i>Trillium</i>	<i>obovatum</i>	Pursh	Fl Am Sept	1 245	1814	latin	IK=T erectum, GCJ=T grandiflorum
358	<i>Paris</i>	<i>octaphylla</i>	Hoffm	Hort Mosq	27	1808	latin	IK=incompleta
359	<i>Trillium</i>	<i>oregonum (hybrid)</i>	Dusek	Bull Amer Rock Gar Soc	38 168	1980	english	
360	<i>Trillium</i>	<i>ovatum</i>	Pursh	Fl Am Sept	1 245	1814	latin	
361	<i>Trillium</i>	<i>ovatum f hibbersonii</i>	T M C Taylor & Szczaw	Syesis	7 250	1974	d latin	PUBL 1975
362	<i>Trillium</i>	<i>ovatum f maculosum</i>	Case & R B Case	Trilliurns	118	1997	d latin	
363	<i>Trillium</i>	<i>ovatum v oettingeri</i>	Case & R B Case	Trilliurns	118	1997	M rank	should be subspecies oettingeri

	genus	taxa	authority	journal	citation	year	language	Comments
364	<i>Trillium</i>	<i>ovatum s oettingeri</i>	Munz & Thorne	Aliso	8(1) 15	1973	latin	
365	<i>Trillium</i>	<i>ovatum v stenosepalum</i>	R R Gates	Ann Missouri Bot Gard	4 61	1917	latin	
366	<i>Trillium</i>	<i>ozarkianum</i>	E J Palmer & Steyer	Ann Missouri Bot Gard	22 504	1935	latin	
367	<i>Trillium</i>	<i>pallasii</i>	Hulten	Kongl Svenska Vetensk -Akad Handl	Serres III, 5, 1 252	1927	latin	
368	<i>Trillium</i>	<i>parviflorum</i>	V G Soukup	Brittonia	32(3) 330	1980	latin	
369	<i>Trillium</i>	<i>pendulum</i>	Muhl	Cat Pl Am Sept	38	1813	english	
370	<i>Trillium</i>	<i>pendulum</i>	Willd	Ges Naturf Fr Neue Schr	3 421	1801	latin	IK=T erectum
371	<i>Paris</i>	<i>pentatolia</i>	P Renault	Fl Dep Orne	26	1803-4	french	IK=quadrifolia
372	<i>Trillium</i>	<i>persistens</i>	W H Duncan	Rhodora	73(794) 244	1971	latin	
373	<i>Trillium</i>	<i>petalosum</i>	Pursh as by Louis-Marie	Rev Oka Agron Inst Agrc	14 113	1940	french	dates 1840 and credits to Pursh
374	<i>Paris</i>	<i>petiolata</i>	Baker ex C H Wright	J Linn Soc Bot	36 145	1903	latin	
375	<i>Paris</i>	<i>petiolata v membranacea</i>	C H Wright	J Linn Soc Bot	36 145	1903	latin	
376	<i>Trillium</i>	<i>petiolatum</i>	Pursh	Fl Am Sept	1 244	1814	latin	
377	<i>Trillium</i>	<i>petiolatum f luteum</i>	V G Soukup	Phytologia	50(4) 290	1982	latin	
378	<i>Trillium</i>	<i>pictum</i>	Pursh	Fl Am Sept	1 244	1814	latin	IK=T erythrocarpum
379	<i>Trillium</i>	<i>pictum v roseum</i>	Raf	Medical Flora	2 99	1830	name	
380	<i>Trillium</i>	<i>pictum v undulatum</i>	Raf	Medical Flora	2 99	1830	name	
381	<i>Paris</i>	<i>pintaensis</i>	H Lev	Feddes Reperit Spec Nov Regni Veg	6 265	1909	latin	
382	<i>Paris</i>	<i>polyandra</i>	S F Wang	Bull Bot Res NE Forest Inst	5(1) 169	1985	latin	
383	<i>Paris</i>	<i>polyphylla</i>	Sm in Rees	Cyclop	26 no 2	1819	english	
384	<i>Daiswa</i>	<i>polyphylla</i>	(Sm) Raf	Fl Tell	4 18	1838	c nov	
385	<i>Paris</i>	<i>polyphylla v alba</i>	H Li & R J Mitchell	Bull Bot Res NE Forest Inst	6(1) 123	1986	d latin	
386	<i>Daiswa</i>	<i>polyphylla v alba</i>	(H Li & R J Mitchell) R J Mitchell	Plantsman	10 179	1988	c nov	
387	<i>Paris</i>	<i>polyphylla v appendiculata</i>	H Hara	Fl E Himalaya	410	1966	d latin	
388	<i>Paris</i>	<i>polyphylla v appendiculata</i>	H Hara as by H Li	Acta Bot Yunnan	6(4) 352	1984	SOV	should be polyphylla appendiculata

	genus	taxa	authority	Journal	citation	year	language	Comments
389	Paris	<i>polyphylla v brachystemon</i>	Franch	Journ de Bot	12 191	1898	latin	
390	Paris	<i>polyphylla v chinensis</i>	(Franch) H Hara	J Fac Sci Univ Tokyo, Sect 3, Bot	10(10) 176	1969	c nov	
391	Paris	<i>tetraphylla f corollata</i>	M Mizushima	J Jap Bot	27 145. f 1	1952	d latin	
392	Paris	<i>polyphylla s fargesii</i>	(Franch) H Hara	J Fac Sci Univ Tokyo, Sect 3, Bot	10(10) 177	1969	c nov	
393	Paris	<i>polyphylla v latifolia</i>	F T Wang & C Y Chang in F T Wang & Ts Tang	Fl Repub Popul Sin	15 250,94	1978	d latin	
394	Paris	<i>polyphylla f latifolia</i>	(F T Wang & C Y Chang) H Li	Bull Bot Res NE Forest Inst	6(1) 125	1986	c nov	IK=P polyphylla v latifolia
395	Paris	<i>polyphylla f macrosepala</i>	H Li	Bull Bot Res NE Forest Inst	6(1) 127	1986	d latin	
396	Paris	<i>polyphylla s marmorata</i>	(Stearn) H Hara	J Fac Sci Univ Tokyo, Sect 3, Bot	10(10) 176	1969	c nov	
397	Paris	<i>polyphylla s marmorata</i>	(Stearn) Hara as by H Li	Bull Bot Res NE Forest Inst	6(1) 130	1986	SOV	should be polyphylla s marmorata
398	Paris	<i>polyphylla v minor</i>	S F Wang	Bull Bot Res NE Forest Inst	8(3) 139	1988	latin	
399	Paris	<i>polyphylla v nana</i>	H Li	Bull Bot Res NE Forest Inst	6(1) 123	1986	d latin	
400	Paris	<i>polyphylla v platipetala</i>	Franch as by H Li	Bull Bot Res NE Forest Inst	6(1) 119	1986	SOV	should be polyphylla latipetala
401	Paris	<i>polyphylla v platipetala</i>	Franch	Journ de Bot	12 191	1898	latin	
402	Paris	<i>polyphylla v pseudothibetica</i>	H Li	Bull Bot Res NE Forest Inst	6(1) 126	1986	d latin	
403	Paris	<i>polyphylla v pseudothibetica f macrosepala</i>	H Li	Bull Bot Res NE Forest Inst	6(1) 127	1986	d latin	
404	Paris	<i>polyphylla v pubescens</i>	Hand-Mazz	Akad Wiss Wien Sitzungsber, Math-Naturwiss Kl, Abt 1	62 145	1925	latin	
405	Paris	<i>polyphylla v stenophylla</i>	Franch	Nouv Arch Mus Hist Nat	ser 2 10 97	1888	latin	
406	Paris	<i>polyphylla v stenophylla f latifolia</i>	(F T Wang & C Y Chang) H Li	Bull Bot Res NE Forest Inst	6(1) 125	1986	c nov	
407	Paris	<i>polyphylla v thibetica</i>	(Franch) H Hara	J Fac Sci Univ Tokyo, Sect 3, Bot	10(10) 176	1969	c nov	
408	Paris	<i>polyphylla v apetala</i>	(Hand-Mazz) F T Wang & Ts Tang	Fl Repub Popul Sin	15 95	1978	c nov	not identified as a c nov, but used as one
409	Paris	<i>polyphylla v kwantungensis</i>	(R H Miao) S C Chen & S Yun Liang	Acta Phytotax Sin	33(5) 490	1995		

	genus	taxa	authority	journal	citation	year	language	Comments
410	Paris	<i>polyphylla</i> v <i>yunnanensis</i> f <i>velutina</i>	H Li & Nolte	Edinb J Bot	54(3) 352	1997	d latin	
411	Paris	<i>polyphylla</i> v <i>wallichii</i>	H Hara	Fl E Himalaya	3rd Rep 134	1975	latin	
412	Paris	<i>polyphylla</i> v <i>yunnanensis</i>	(Franch) Hand -Mazz	Symbolae Sinica	7 1216	1936	c nov	
413	Daiswa	<i>pubescens</i>	(Hand -Mazz) Takht	Brittonia	35(3) 268	1993	c nov	
414	Paris	<i>pubescens</i>	(Hand -Mazz) F T Wang & Ts Tang	Fl Replib Popul Sin	15 96	1978	c nov	
415	Trillium	<i>pumilum</i>	Pursh	Fl Am Sept	1 245	1814	latin	IK=T pusillum
416	Trillium	<i>pumilum</i>	Raf	Med Repos II	5 354	1808	name	
417	Trillium	<i>purpureum</i>	Kin ex Elliott	Sketch	1 430	1817	latin	Gates says 'in'
418	Trillium	<i>pusillum</i> v <i>monticola</i>	Reveal as by Case & R B Case	Trilliums	126	1997	SOV	should be monticulium
419	Trillium	<i>pusillum</i>	Michx	Fl bor -amer	1 215	1803	latin	
420	Trillium	<i>pusillum</i> v <i>alabamicum</i>	J D Freeman & C J Garrett	M S thesis	47	1982	d latin	
421	Trillium	<i>pusillum</i> v <i>monticulium</i>	Bodkin & Reveal	Brittonia	34(2) 141	1982	d latin	
422	Trillium	<i>pusillum</i> v <i>ozarkanum</i>	(E J Palmer & Steyerm.) Steyerm	Rhodora	62 130	1960	name	
423	Trillium	<i>pusillum</i> v <i>texanum</i>	(Buckley) C F Reed	Phytologia	50(4) 279, 283	1982	c nov	IK=T texanum
424	Trillium	<i>pusillum</i> v <i>texanum</i>	(Buckley) Reveal & C R Broome	Castanea	46(1) 56	1981	c nov	IK=T texanum
425	Trillium	<i>pusillum</i> v <i>georgianum</i>	D L Jacobs & R L Jacobs	Trilliums in wood & gard	54	1997	english	
426	Trillium	<i>pusillum</i> v <i>kentuckianum</i>	D L Jacobs & R L Jacobs	Trilliums in wood & gard	54	1997	english	
427	Trillium	<i>pusillum</i> v <i>virginianum</i>	Fernald	Rhodora	45 397	1943	latin	
428	Trillium	<i>pusillum</i> v <i>virginianum</i>	Fernald emend Cabe	Castanea	60(1) 9-11	1995	latin	
429	Paris	<i>quadrifolia</i>	L	Species Plantarum	367	1753	latin	
430	Paris	<i>quadrifolia</i>	L as by H Li	Bull Bot Res NE Forest Inst	6(1) 134	1986	SOV	should be quadrifolia
431	Paris	<i>quadrifolia</i> v <i>dahurica</i>	(Fisch) Franch	Nouv Arch Mus Hist Nat	ser 2 10 96	1888	french	
432	Paris	<i>quadrifolia</i> v <i>hexaphylla</i>	(Cham) B Fedtsch	Trudy Glavn Bot Sada	31 121	1912	russian	
433	Paris	<i>quadrifolia</i> B <i>obovata</i>	(Ledeb) Regel & Tiling	Fl Ajan	121	1858	latin	
434	Paris	<i>quadrifolia</i> B <i>obovata</i>	(Ledeb) Regel & Tiling as by Li	Bull Bot Res NE Forest Inst	6(1) 137	1986	SOV	should be quadrifolia obovata

	genus	taxa	authority	Journal	citation	year	language	Comments
435	Paris	<i>quadrifolia</i> v <i>setchuanensis</i>	Franch	Journ de Bot	12 191	1898	latin	
436	Paris	<i>quadrifolia</i> v <i>angustiovata</i>	D Z Ma & H L Liu	Fl Ningxianensis	2 523	1988		
437	Paris	<i>quadrifolia</i> v <i>orientalis</i>	(L) Kuntze					presented in Tropicos without reference
438	Paris	<i>quadrifolius</i>	L as by Himpel	Fl Eisass-Lothr	276	1891	SOV	
439	Trillium	<i>rectistamineum</i>	H St John	Rhodora	22 79	1920	c nov	should be <i>quadrifolia</i> , IK= <i>quadrifolia</i>
440	Trillium	<i>recurvatum</i>	L C Beck	Amer J Sci	Ser L, 11 178	1826	english	IK=T lanceolatum v rectistamineum
441	Trillium	<i>recurvatum f</i> <i>esepatum</i>	J D Freeman & Heineke	Rhodora	89(857) 17	1987	latin	
442	Trillium	<i>recurvatum f</i> <i>foliosum</i>	Steyerm	Rhodora	61 124	1959	d latin	
443	Trillium	<i>recurvatum s</i> <i>lanceolatum</i>	(S Watson) E Murray	Kalmia	13 32	1983	c nov	IK=T recurvatum v lanceolatum
444	Trillium	<i>recurvatum ?</i> <i>lanceolatum</i>	S Watson	Proc Amer Acad Arts	14 273	1879	english	
445	Trillium	<i>recurvatum v luteum</i>	Friesner as by R J Mitchell	Plantisman	11 143	1989	M rank	should be forma <i>luteum</i>
446	Trillium	<i>recurvatum f luteum</i>	Clute	Amer Bot (Binghampton)	28 79	1922	english	
447	Trillium	<i>recurvatum f luteum</i>	Friesner	Butler Univ Bot Stud	3 29,31	1929	english	
448	Trillium	<i>recurvatum v</i> <i>maculatum</i>	Raf	Medical Flora	2 98	1830	name	
449	Trillium	<i>recurvatum v</i> <i>obovatum</i>	Raf	Medical Flora	2 98	1830	name	
450	Trillium	<i>recurvatum f</i> <i>petaloideum</i>	Steyerm	Rhodora	61 124	1959	d latin	
451	Trillium	<i>recurvatum v</i> <i>sessilifolium</i>	Raf	Medical Flora	2 98	1830	name	
452	Trillium	<i>recurvatum f shayi</i>	E J Palmer & Steyerm	Ann Missouri Bot Gard	22 504	1935	d latin	
453	Trillium	<i>recurvatum v</i> <i>undulatum</i>	Raf	Medical Flora	2 98	1830	name	
454	Trillium	<i>reflexum</i>	Clute	Amer Bot (Binghampton)	28 78	1922	name - sov?	should be <i>recurvatum?</i>
455	Trillium	<i>reflexum</i>	Raf	Western Minerva	41	1821	name	
456	Trillium	<i>reliquum</i>	J D Freeman	Brittonia	27(1) 21	1975	latin	
457	Trillium	<i>reliquum f luteum</i>	J D Freeman	Brittonia	27(1) 21	1975	latin	
458	Trillium	<i>revolutum</i>	Raf	Western Minerva	41	1821	name	

	genus	taxa	authority	Journal	citation	year	language	Comments
459	<i>Trillium</i>	<i>rhombifolium</i>	Vorosch in Vorob	Opred Rast Primor Primur	124	1966	SOV	lists rhombifolium in synonymy
460	<i>Trillium</i>	<i>rhombifolium</i>	Korn	Fl URSS	4 748	1935	latin	
461	<i>Trillium</i>	<i>rhombifolium</i>	Raf	Aut Bot	133	1840	latin	
462	<i>Trillium</i>	<i>rhomboidum</i>	Michx	Fl bor-amer	1 215	1803	latin	IK=T erectum, T grandiflorum
463	<i>Trillium</i>	<i>rhomboidum B album</i>	Michx	Fl bor-amer	1-215	1803	latin	
464	<i>Trillium</i>	<i>rhomboidum A atropurpureum</i>	Michx	Fl bor-amer	1 215	1803	latin	
465	<i>Trillium</i>	<i>rhomboidum G grandiflorum</i>	Michx	Fl bor-amer	1 216	1803	latin	
466	<i>Trillium</i>	<i>rivale</i>	S Watson	Proc Amer Acad Arts	20 378	1885	english	
467	<i>Trillium</i>	<i>roseum</i>	Hort ex L H Bailey	Stand Cycl Hort	6 3382	1917	pro syn	
468	<i>Trillium</i>	<i>roseum</i>	Hort ex Steud	Nom	ed II 2 710	1840	name	
469	<i>Trillium</i>	<i>rotundifolium</i>	Raf	Medical Flora	2 97	1830	english	
470	<i>Trillium</i>	<i>rotundifolium v flexicaule</i>	Raf	Medical Flora	2 98	1830	name	
471	<i>Trillium</i>	<i>rotundifolium v maculatum</i>	Raf	Medical Flora	2 98	1830	name	
472	<i>Trillium</i>	<i>rotundifolium v orbiculatum</i>	Raf.	Medical Flora	2 98	1830	name	
473	<i>Trillium</i>	<i>rotundifolium v pallidum</i>	Raf	Medical Flora	2 98	1830	name	
474	<i>Trillium</i>	<i>rotundifolium v rubricaulis</i>	Raf	Medical Flora	2 98	1830	name	
475	<i>Trillium</i>	<i>rotundifolium v undulatum</i>	Raf	Medical Flora	2 98	1830	name	
476	<i>Trillium</i>	<i>rugelii</i>	Rendle	J Bot	39 331 pl 46	1901	latin	
477	<i>Trillium</i>	<i>rugelii f atrovenosum</i>	T S Patrick	n/a		unpub	unpub	
478	<i>Paris</i>	<i>rugosa</i>	H Li & Kurita	Acta Bot Yunnan	5 13	1992	latin	
479	<i>Trillium</i>	<i>scouleri</i>	Rydb in/ex Gleason	Bull Torrey Bot Club	33 394	1906	english	
480	<i>Trillium</i>	<i>sessile</i>	Elliott	Sketch	1 427	1817	latin	credits to no one, just like cernuum
481	<i>Trillium</i>	<i>sessile</i>	L	Species Plantarum	340	1753	latin	
482	<i>Trillium</i>	<i>sessile G angustipetalum</i>	Torr	Pac RR Rep	4 151	1857	latin	ref's Emory's Rep Mexican Boond Commis (ined)
483	<i>Trillium</i>	<i>sessile G boreale</i>	Nutt	Trans Amer Philos Soc	5 154	1835	english	read on 4 April 1834, published 1835
484	<i>Trillium</i>	<i>sessile G californicum</i>	S Watson	Proc Amer Acad Arts	14 273	1879	english	
485	<i>Trillium</i>	<i>sessile D chloropetalum</i>	Torr	Pac RR Rep	4(Bot) 151	857	latin	
486	<i>Trillium</i>	<i>sessile s giganteum</i>	(Hooker & Arnott) Murray	Katma	12 25	1982	c nov	

	genus	taxa	authority	journal	citation	year	language	Comments
487	<i>Trillium</i>	<i>sessile B giganteum</i>	Hook & Arn	Bot Beechy Voyages	402	1840	d latin	
488	<i>Trillium</i>	<i>sessile v giganteum</i>	Torr. in L.H. Bailey	Stand Cycl Hort	6 3381	1917	pro syn	
489	<i>Trillium</i>	<i>sessile B luteum</i>	Muhl	Cat Pl Am Sept	38	1813	english	
490	<i>Trillium</i>	<i>sessile f luteum</i>	(Muhl) Peattie	J Elisha Mitchell Sci Soc	42 197	1927	english	
491	<i>Trillium</i>	<i>sessile f luteum</i>	E J Palmer & Steyer	Ann Missouri Bot Gard	22 503	1935	name	credits to Peattie
492	<i>Trillium</i>	<i>sessile v nuttallii</i>	S Watson	Proc Amer Acad Arts	14 273	1879	english	
493	<i>Trillium</i>	<i>sessile B praecox</i>	Nutt	Trans Amer Philos Soc	5 154	1835	english	
494	<i>Trillium</i>	<i>sessile v rubrum</i>	hort ex L.H. Bailey	Stand Cycl Hort	6 3381	1917	english	
495	<i>Trillium</i>	<i>sessile v vindescens</i>	(Nutt) Trel in Branner & Coville	Rep Ark Geol Surv	1888 v 4 225	1891	c nov	
496	<i>Trillium</i>	<i>sessile f viridiflorum</i>	L K Beyer	Torreya	27 83	1927	english	
497	<i>Trillium</i>	<i>sessile v wrayi</i>	S Watson	Proc Amer Acad Arts	14 273	1879	english	
498	<i>Paris</i>	<i>setchuensis</i>	(Franch) Barkalov	Sosud Rast Sovet Dal'nego Vostoka	3 171	1988	c nov	IK=P quadrifolia v setchuensis
499	<i>Trillium</i>	<i>simile</i>	Gleason	Bull. Torrey Bot Club	33 391	1906	english	
500	<i>Trillium</i>	<i>simile f rubrotinctum</i>	T S Patrick ex D L Jacobs & R L Jacobs	Trilliums in wood & gard	57	1997	english	
501	<i>Trillium</i>	<i>smallii</i>	Maxim	Melanges Biol bull Phys-math Acad Imp Sci Saint-Petersbourg	2 862	1883	latin	
502	<i>Trillium</i>	<i>smallii A apetalon</i>	(Makino) Takeda	Kozan-shokubutusu shashin zushu	2 79	1932	c nov	
503	<i>Trillium</i>	<i>smallii f atropurpureocarpa</i>	(Makino) Honda	Nom Pl Japan	482	1939	name	
504	<i>Trillium</i>	<i>smallii v atropurpureocarpum</i>	J Samej	Acta Horti Gothob	25 165	1962	d latin	
505	<i>Trillium</i>	<i>smallii v maximowiczii</i>	Miyabe & Kudō	Flora Hokkaido & Saghalin	3 344-245	1932	d latin	
506	<i>Trillium</i>	<i>smallii f viridicarpa</i>	Honda	Nom Pl Japan	520	1939	name	
507	<i>Trillium</i>	<i>smallii f viridipureocarpa</i>	(Makino) Honda	Nom Pl Japan	482		name	
508	<i>Trillium</i>	<i>spatulatum</i>	Raf	Medical Flora	2 101	1830	english	IK=T erectum
509	<i>Trillium</i>	<i>stramineum</i>	Harb as by Louis-Marie	Rev Oka Agron Inst Agric	14 113	1940	SOV	should be stamineum
510	<i>Trillium</i>	<i>stamineum</i>	Harb	Biltmore Bot Stud	1 23	1901	english	
511	<i>Trillium</i>	<i>stamineum f luteum</i>	J D Freeman	Brittonia	27(1) 26	1975	latin	
512	<i>Trillium</i>	<i>stenanthes</i>	Raf	Aut Bot	132	1840	latin	

	genus	taxa	authority	Journal	citation	year	language	Comments
513	<i>Trillium</i>	<i>stylosum</i>	Nutt	Gen Am	1 239	1818	english	
514	<i>Trillium</i>	<i>stylosum</i>	A W Wood	Class Book	705	1866	english	
515	<i>Trillium</i>	<i>sulcatum</i>	T S Patrick	Brittonia	36(1) 27	1984	latin	
516	<i>Trillium</i>	<i>sulcatum f. albotescens</i>	T S Patrick	Brittonia	36(1) 30	1984	latin	
517	<i>Paris</i>	<i>taiungensis</i>	S S Ying	Quart J Chinese Forest	8(4) 139	1975	latin	
518	<i>Trillium</i>	<i>tawanense</i>	S S Ying	J Jap Bot	64(6) 154	1989	latin	
519	<i>Paris</i>	<i>tetraphylla</i>	A Gray	Mem Amer Acad Arts	6(1) 412	1858-59	latin	Article titled "On the Botany of Japan"
520	<i>Paris</i>	<i>tetraphylla v angustifolia</i>	Miq	Ann Mus Bot Lugduno-Batavum	3 147	1867	latin	
521	<i>Paris</i>	<i>tetraphylla v penduliflora</i>	Murata & T Yamanaka	Acta Phytotax Geobot	17 52	1957	d latin	
522	<i>Paris</i>	<i>tetraphylla f penduliflora</i>	(Murata & T Yamanaka) H Hara	J Fac Sci Univ Tokyo, Sect 3, Bot	Sec 3, Vol X(10), p 163	1969	c nov	
523	<i>Paris</i>	<i>tetraphylla v sessiliflora</i>	Makino	Bot Mag, (Tokyo)	26 395	1912	english	
524	<i>Paris</i>	<i>tetraphylla f sessiliflora</i>	(Makino) H Hara	Bot Mag, (Tokyo)	52 513	1938	c nov	
525	<i>Paris</i>	<i>tetraphylla v yakusimensis</i>	Masam	Mem Fac Sci Taihoku Imp Univ	11 558	1934	d latin	
526	<i>Trillium</i>	<i>texanum</i>	Buckley	Proc Acad Nat Sci Philadelphia	1860 443	1861	english	IK=T pusillum
527	<i>Daiswa</i>	<i>thibetica</i>	(Franch) Takht	Brittonia	35 265-266	1983	c nov	
528	<i>Paris</i>	<i>thibetica</i>	Franch	Nouv Arch Mus Hist Nat	Ser II 10 184	1887-88	latin	
529	<i>Paris</i>	<i>thibetica v apetalata</i>	Hand -Mazz	Akad Wiss Wien Sitzungsber, Math -Naturwiss Kl, Abt 1	62 149	1925	latin	
530	<i>Trillium</i>	<i>tinctorum</i>	Raf	Medical Flora	2 98	1830	english	
531	<i>Paris</i>	<i>trifolia</i>	P Renault	Fl Dep Orne	26	1803-4	french	IK=quadrifolia
532	<i>Trillium</i>	<i>tschonoskii</i>	Maxim	Melanges Biol bull Phys-math Acad Imp Sci Saint-Petersbourg	2 862	1883	latin	
533	<i>Trillium</i>	<i>tschonoskii</i>	Maxim as by Honda	Norm Pl Japan	482	1932	SOV	should be tschonoskii
534	<i>Trillium</i>	<i>tschonoskii v atrotubens</i>	Miyabe & Tatew	Trans Sapporo Nat Hist Soc	7 190	1936	d latin	this one is in vol 14 *not* 7
535	<i>Trillium</i>	<i>tschonoskii f cryptopetalum</i>	Makino as by J Sarnel	Acta Horti Gothob	25 163	1962	M rank	should be variety

	genus	taxa	authority	journal	citation	year	language	Comments
536	<i>Trillium</i>	<i>ischnoskii</i> v <i>cryptopetalum</i>	Makino	Bot Mag , (Tokyo)	24(262) 138	1910	english	
537	<i>Trillium</i>	<i>ischnoskii</i> v <i>himalaicum</i>	H Hara	J Jap Bot	44(12) 373	1969	latin	
538	<i>Trillium</i>	<i>ischnoskii</i> f <i>morii</i>	(Hayata) Masum	List Vasc Pl Taiwan	135	1954	c nov	FIND SOURCE!! This is VARIETY
539	<i>Trillium</i>	<i>ischnoskii</i> f <i>morii</i>	(Hayata) Yamam	J Soc Trop Agric	10 177	1938	c nov	
540	<i>Trillium</i>	<i>ischnoskii</i> f violaceum	Makino	Bot Mag , (Tokyo)	27 115	1913	english	
541	<i>Trillium</i>	<i>underwoodii</i>	Small	Bull. Torrey Bot Club	24 172	1897	english	
542	<i>Trillium</i>	<i>underwoodii</i> v <i>luteum</i>	J F Macbr	Contr Gray Herb	n ser 56 19	1918	c nov	
543	<i>Paris</i>	<i>undulata</i>	H L I	Acta Bot Yunnan	5 16-17	1992	name	name only in abstract text specifies <i>P undulatis</i>
544	<i>Paris</i>	<i>undulatis</i>	H L I & V G Soukup	Acta Bot Yunnan	5 16-17	1992	latin	
545	<i>Trillium</i>	<i>undulatum</i>	Kin ex Elliott	Sketch	1 430	1817	latin	
546	<i>Trillium</i>	<i>undulatum</i>	Wild	Ges Naturf Fr Neue Schr	3 422	1801	latin	IK=T erythrocarpum
547	<i>Trillium</i>	<i>undulatum</i>	Raf	Med Repos II	II 5 354	1808	name	Med Fl 1830 desc, Med Rep II, nom, Journ. Bot nom, Aut Bot 1840 nom
548	<i>Trillium</i>	<i>undulatum</i> f <i>cleavelandicum</i>	(Swallow) Fernald	Rhodora	45 517	1943	c nov	GCI credits to Wood Fernald cites "Swallow ex Wood" in synonymy
549	<i>Trillium</i>	<i>undulatum</i> f <i>enotatum</i>	T S Patrok	Rhodora	87(850) 157	1985	d latin	
550	<i>Trillium</i>	<i>undulatum</i> f <i>polymerum</i>	Vict ex Louis-Marie	Rev Oka Agron Inst Agric	14 152	1940	d latin	
551	<i>Trillium</i>	<i>undulatum</i> v <i>pubescens</i>	Kartesz?	Synonymized Plants			name	Kartesz lists the name w/o authority in the First Edition of his checklist
552	<i>Trillium</i>	<i>undulatum</i> f <i>striatum</i>	Louis-Marie	Rev Oka Agron Inst Agric	14 152	1940	latin	
553	<i>Trillium</i>	<i>unguiculatum</i>	Nutt	Trans Amer Philos Soc	5 154	1837	latin	IK=T recurvatum
554	<i>Trillium</i>	<i>unguiculatum</i>	Raf	Medical Flora	2 98	1830	english	First Cat Bot Gard 1824, nom, Med Fl 1830 descr
555	<i>Trillium</i>	<i>unguiculatum</i> v <i>crassicaule</i>	Raf	Medical Flora	2 99	1830	name	
556	<i>Trillium</i>	<i>unguiculatum</i> v <i>maculatum</i>	Raf	Medical Flora	2 99	1830	name	
557	<i>Trillium</i>	<i>unguiculatum</i> v <i>undulatum</i>	Raf	Medical Flora	2 99	1830	name	
558	<i>Paris</i>	<i>vanotii</i>	H Lévy	Nouv Contrib Liliac etc Chine	21	1906	latin	correct spelling should be <i>vanotii</i> -- it is listed as <i>vanoti</i> in text
559	<i>Trillium</i>	<i>vaseyi</i>	Harb	Biltmore Bot Stud	1 24	1901	english	
560	<i>Trillium</i>	<i>vaseyi</i> f <i>album</i>	House	Muhlenbergia	6 73	1910	english	
561	<i>Trillium</i>	<i>vaseyi</i> f <i>elegans</i>	T S Patrick ex D L Jacobs & R L Jacobs	Trilliums in wood & gard	58	1997	english	

	genus	taxa	authority	Journal	citation	year	language	Comments
562	<i>Trillium</i>	<i>vaseyi</i> v <i>simile</i>	(Gleason) Barksd	J Elisha Mitchell Sci Soc	54 285	1938	c nov	
563	<i>Trillium</i>	<i>venosum</i>	R R Gates	Ann Missour Bot Gard	4 66	1917	latin	
564	<i>Paris</i>	<i>verticillata</i>	M Bleb	Fl Taur Cauc	3 287	1819	latin	
565	<i>Paris</i>	<i>verticillata</i> s <i>manchurica</i>	(Kom) Kitag	Lineam-Fl Mansh	140	1939	c nov	
566	<i>Paris</i>	<i>verticillata</i> v <i>manshurica</i>	(Kom) H Hara	Bot Mag, (Tokyo)	52 514	1938	c nov	
567	<i>Paris</i>	<i>verticillata</i> v <i>manshurica</i>	(Kom) Kitag as by R J Mitchell	Plantsman	9 86	1987	M rank	should be subspecies
568	<i>Paris</i>	<i>verticillata</i> v <i>obovata</i>	(Ledeb) H Hara	J Fac Sci Univ Tokyo, Sect 3, Bot Norm Pl Japan	Ill, 10(10) 165 481	1969	c nov	
569	<i>Paris</i>	<i>verticillata</i> f <i>purpurea</i>	(Miyabe & Tatew) Honda			1939	name	
570	<i>Paris</i>	<i>verticillata</i> v <i>nigra</i>	Y N Lee	Flora of Korea	935	1998	latin	3rd edition, photo #2948
571	<i>Paris</i>	<i>verticillata</i> f <i>viridis</i>	Nakai	Iconogr Pl Asiae Orient	5(2) 492, t 153	1952	latin	
572	<i>Paris</i>	<i>verticillata</i> v <i>setchuensis</i>	(Franch) Hand -Mazz	Symbolae Sinica	7(5) 1214	1936	c nov	
573	<i>Paris</i>	<i>vietnamensis</i>	(Takht) H Li	Acta Bot Yunan	6(4) 357	1984	c nov	
574	<i>Paris</i>	<i>violacea</i>	H Lev	Feddes Repert Spec Nov Regni Veg	11 302	1912	latin	
575	<i>Daiswa</i>	<i>violacea</i>	(H Lev) Takht	Brittonia	35 266-267	1983	c nov	
576	<i>Trillium</i>	<i>virgimanum</i>	(Fernald) C F Reed	Phytologia	50 279,283	1982	c nov	IK=T pusillum v virgimanum
577	<i>Trillium</i>	<i>viride</i>	L C Beck	Amer J Sci	Ser 1 11 178	1826	english	IK=T sessile
578	<i>Trillium</i>	<i>viride</i> v <i>luteum</i>	(Muhl) Gleason	Phytologia	4 23	1952	c nov	
579	<i>Trillium</i>	<i>virescens</i>	Nutt	Trans Amer Philos Soc	5 155	1834	latin	
580	<i>Paris</i>	<i>wenxianensis</i>	Z X Peng & R N Zhao	Acta Bot Bor -Occid Sin	6(2) 133	1986	latin	
581	<i>Paris</i>	<i>yakusimensis</i>	(Masam) Masam	Bull Soc Bot France	83 696	1936/ 1937	name	
582	<i>Trillium</i>	<i>yezoense</i> (<i>hybrid</i>)	Tatew ex J Samej	Acta Horti Gothob	25 167	1962	latin	
583	<i>Trillium</i>	<i>yezoense</i> v <i>atropurpureocarpum</i>	J Samej	Acta Horti Gothob	25 167	1962	d latin	
584	<i>Paris</i>	<i>yunnanensis</i>	Franch	Mem Soc Phil Paris	24 290	1888	latin	
585	<i>Daiswa</i>	<i>yunnanensis</i>	(Franch) Takht	Brittonia	35(3) 257	1983	c nov	

APPENDIX C

MORPHOLOGICAL CHARACTERS AND THEIR STATES

This data set was generated when a non-trilliaceous species (e.g., *Medeola virginica* or *Amianthium muscaetoxicum*) was being used as an outgroup. With the use of *Trillium rivale* as outgroup, several of these characters are no longer necessary.

C.1 Hybrid Status

1 - yes	2 - no
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This character was not used in the morphological analysis. It was included in the data set because of the recognized Japanese hybrids. "No" is the assumed state.

C.2 Flowering Time

1 - February	2 - March	3 - April	4 - May
5 - June	6 - July	7 - August	

This is another character that was not used in the analysis, but was included so that the existence of any correlations between the groups and flowering time could be examined. There is no assumed state for this character.

C.3. Chromosome Number

1 - $2n = 10$	2 - $2n = 15$	3 - $2n = 20$
4 - $2n = 30$	5 - $2n = 40$	

This character was included because of the prevalence of polyploids in the Asiatic *Trillium*, as well as *Paris s l.* To date only scattered occurrences of triploids have been reported from North America. " $2n = 10$ " is the assumed state for this character.

C.4 Geographic Area

1 - China	2 - western North America	3 - eastern North America
4 - Europe	5 - northern Asia	6 - southern Asia

This character was included to analyze the geographical distribution particularly among the North American *Trillium*. Northern Asia includes Russia, Japan, and Korea (i.e., countries north of China), whereas southern Asia includes countries south of China. There is no assumed state for this character.

C.5. Genus

1 - outgroup	2 - <i>Trillium</i>	3 - <i>Paris s l</i>
--------------	---------------------	----------------------

This character was included so that currently accepted genera could be mapped onto the final tree topology. There is no assumed state for this character.

C.6 Subgenus

1 - outgroup	2 - <i>Trillium</i>	3 - <i>Phyllantherum</i>
4 - <i>Paris</i>	5 - <i>Kinugasa</i>	6 - <i>Daiswa</i>

As with the character Genus, and the two following characters, this character was included so that traditional groupings could be mapped onto the final tree topology. There is no assumed state for this character.

C.7. Section

1 - outgroup	2 - <i>grandiflorum</i>	3 - <i>erectum</i>	4 - <i>catesbaei</i>
5 - <i>recurvatum</i>	6 - <i>sessile</i>	7 - <i>maculatum</i>	8 - <i>paris</i>
9 - <i>axiparis</i>	10 - <i>kinugasa</i>	11 - <i>daiswa</i>	12 - <i>dunniana</i>
13 - <i>marmorata</i>	14 - <i>fargesiana</i>	15 - <i>thibetica</i>	

There is no assumed state for this character.

C.8 Rafinesque's genera

1 - outgroup	2 - <i>Paris</i>	3 - <i>Daiswa</i>
4 - <i>Phyllantherum</i>	5 - <i>Trillium</i>	6 - <i>Delostylis</i>

This character was added *post priori* when the distribution of the genera was examined. From the initial trees produced, it appeared as if Rafinesque's generic groupings might have some validity. There is no assumed state for this character.

C.9. Plant Type

1 - herb	2 - vine
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This character was used to separate non-trilliaceous outgroups from the ingroup. "Herb" is the only state currently used for this character.

C.10. Foliaceousness

1 - scapose	2 - leafy	3 - subscapose
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This character was used to separate the non-trilliaceous outgroups from the ingroup. "Subscapose" would be used if a plant was basally leafy (for instance) with leaves diminishing in size up the stem. Note that this character only refers to the amount rather than placement (C.23) of the leaves. "Scapose" is the only state currently used for this character.

C.11 Plant Sexuality

1 - bisexual	2 - dioecious	3 - polygamous
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This character was used to separate the non-trilliaceous outgroups from the ingroup "Bisexual" is the only state currently used for this character

C 12 Inflorescence Type

1 - solitary	2 - simple umbel	3 - raceme	4 - panicle of racemes
5 - panicle	6 - spike	7 - cyme	

This character was used to separate the non-trilliaceous outgroups from the ingroup "Solitary" is the only state currently used for this character

C 13 Number of Flowers

1 - one	2 - more than one
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This character was used to separate the non-trilliaceous outgroups from the ingroup. "One" is the only state currently used for this character

C 14 Flower Composition

1 - tepals	2 - sepals + petals
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This character was used to separate the non-trilliaceous outgroups from the ingroup. "Sepals plus petals" is the only state currently used for this character

C 15 Pedicel Vertical Posture

1 - erect	2 - above the leaves	3 - horizontal
4 - below the leaves	5 - none	

This character covers both presence/absence of a pedicel as well as vertical orientation. There is a great deal of variation in pedicel posture among *Trillium*. "Above the leaves" is the assumed state for this character, "none" is assumed for *Trillium* subg *Phyllantherum*.

C.16. Root Type

1 - rhizome	2 - bulb	3 - tuber	4 - fibrous
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This character was used to separate the non-trilliaceous outgroups from the ingroup "Rhizome" is the only state currently used for this character

C 17 Rhizome Size

1 - very thin (to 5 mm)	2 - slender (5 - 10 mm)	3 - thick (1 - 2.5 cm)	4 - very thick (over 2.5 cm)
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This character illustrates the difference in rhizome sizes between *Paris* and *Daiswa* and within *Trillium*. Measurements were not available for all rhizome diameters, but descriptive phrases such as "thick" and "very thick" were used. There is no assumed state for this character.

C 18 Stem Habit

1 - erect	2 - partially decumbent	3 - decumbent
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This character illustrates the variation in the stem habit in sessile-flowered *Trillium*. "Erect" is the assumed state for this character.

C.19. Plant vestiture

1 - glabrous	2 - puberulent	3 - pubescent	4 - pilose
5 - papillose	6 - scabrous	7 - striate	

This character illustrates the variation in pubescence within the family. "Glabrous" is the assumed state for this character.

C.20 Stem Color

1 - green	2 - yellowish-green	3 - reddish-purple	4 - greenish-purple
5 - purplish	6 - brownish-green	7 - reddish	8 - green over purple
9 - purple-tinged			

This character illustrates the variation in stem color. Unfortunately, much collapsing of similar colors into "meta-colors" must occur in order to keep the number of character states to an informative minimum. For instance, "yellowish green" includes colors such as "greenish-yellow," "yellow-green," and "green-yellow." "Green" is the assumed state for this character.

C 21 Stem Color Distribution

1 - throughout	2 - geographic	3 - suffused
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Even though color is an important field character, the phylogenetic significance of such a subjective measure is doubtful. Color patterning or distribution as a character was developed as a way to include color information that might be more informative phylogenetically. "Geographic" is used to refer to a color pattern that is segregated by area of the plant under consideration; "suffused" refers to a blending of colors. "Throughout" is the assumed state for this character.

C 22 Leaf Number

1 - two	2 - three	3 - four	4 - five
5 - six	6 - seven	7 - eight	8 - nine
9 - ten	10 - eleven and up		

Because merosity was the traditional separating character between *Trillium* and *Paris s l*, merosity characters were included in the initial analysis. These characters were later removed to discern their impact on the analysis. There is no assumed state for this character for *Paris s l*, "three" is the assumed state for *Trillium*.

C.23 Leaf Location

1 - terminal	2 - cauline	3 - basal	4 - reduced cauline
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This character was used to separate the non-trilliaceous outgroups from the ingroup. Note that this character refers only to placement rather than amount (cf foliaceousness, C.10) of leaves that the plant possesses. "Terminal" is the only state currently used for this character.

C 24 Leaf Arrangement

1 - whorled	2 - alternate	3 - opposite	4 - spirally inserted
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This character was used to separate the non-trilliaceous outgroups from the ingroup. "Whorled" is the only state currently used for this character.

C 25 Leaf Number of Whorls

1 - one	2 - more than one	3 - none
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This character was used to separate the non-trilliaceous outgroups from the ingroup. "One" is the only state currently used for this character.

C 26. Leaf Attachment

1 - petiolate	2 - subsessile	3 - sessile
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This character illustrates the variation in leaf attachment within the family. There is no assumed state for this character.

C 27 Leaf Shape: Widest Point

1 - ovate ($\frac{1}{4}$)	2 - elliptic-ovate	3 - elliptic/ rhombic/ oblong ($\frac{1}{2}$)
4 - elliptic-obovate	5 - obovate ($\frac{3}{4}$)	

The plane shape characters were the most difficult to model accurately. A given shape is actually composed of three different measures resulting in one shape: the location of the widest point between the stem and apex, the actual width of the leaf (length to width ratio), and the curvature of the sides. This character defines the location of the widest point of the leaf: whether it is ovate (approximately $\frac{1}{4}$ of the distance from the stem to the apex), elliptic/rhombic/oblong (widest in the center), obovate (approximately $\frac{3}{4}$ of the distance) or somewhere in-between. There is no assumed state for this character.

C 28 Leaf Shape Width

1 - linear	2 - narrow	3 - average
4 - broad	5 - very broad	6 - depressed or transverse

This character is the second part of the plane shape. The relative width is determined either by leaf length and width measures or descriptive terms. These values are then based on the IAPT plane shape chart (Systematics Association Committee for Descriptive Terminology, 1962). There is no assumed state for this character.

C 29 Leaf Shape: Sides

1 - elliptic (curved)	2 - oblong-elliptic	3 - oblong (parallel)
4 - oblong-rhombic	5 - rhombic (straight)	6 - rhombic-elliptic

This character is the last of the leaf plane shape characters. There is no assumed state for this character.

C 30 Leaf Margin

1 - entire	2 - undulate	3 - serrulate
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This character was used to separate the non-trilliaceous outgroups from the ingroup. "Entire" is the only state currently used for this character.

C.31 Leaf Color Distribution

1 - throughout	2 - mottled	3 - geographic	4 - suffused
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This character allows the modeling of specific patterns of variegation in the leaves. "Throughout" is the assumed state for this character.

C 32 Leaf Color

1 - green	2 - more or less purple mottled	3 - green with maroon hue	4 - green with small brownish spots
5 - green with white variegation on veins	6 - mottled	7 - mottled with dark green	8 - green with spots of light green
9 - multiple shades of green	A - shades of green beside pale midrib	B - dark green spots on mottled background	C - dark green between veins with pale midrib

This character illustrates the various patterns of variegation between the sessile-flowered *Trillium* as well as several species of *Paris l*. "Green" is the assumed state for this character

C 33 Leaf Lower Surface

1 - pubescent on veins	2 - scabrous on veins	3 - glossy	4 - dull
5 - purple	6 - purple nerves	7 - glabrous	8 - pubescent

This character illustrates the different lower leaf surfaces in Trilliaceae. "Glabrous" is the assumed state for this character.

C 34. Leaf Apex Type

1 - entire	2 - with sinuses	3 - with mid-rib, midvein, or vein extension
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This character groups the different kinds of leaf apices. It was believed that the fewer number of states might be more phylogenetically informative. "Entire" is the assumed state for this character.

C 35 Leaf Apices

1 - acuminate	2 - acute	3 - obtuse	4 - rounded
5 - emarginate	6 - sub-acute	7 - cuspidate	8 - blunt
9 - attenuate			

This character illustrates the variety of leaf apices in the family. There is no assumed state for this character

C 36 Leaf Base Type

1 - entire	2 - with sinuses
------------	------------------

As in leaf apex type (C 34), this character groups the different types of leaf bases into fewer, more phylogenetically informative characters "Entire" is the assumed state for this character

C 37 Leaf Bases

1 - cuneate	2 - sheathing	3 - obtuse	4 - rounded
5 - attenuate	6 - hastate	7 - cordate	

This character illustrates the variety of leaf bases in the family as well as separates the non-trilliaceous outgroups from the ingroup There is no assumed state for this character

C 38 Leaf Texture

1 - herbaceous	2 - membranous	3 - papery
4 - rugose	5 - coriaceous	

This character illustrates the various leaf textures within the family. There is no assumed state for this character.

C 39 Number Main Nerves

1 - many	2 - three	3 - five	4 - seven
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This character illustrates the differences in vascular pattern of the leaves. There is no assumed state for this character

C 40 Bracts

1 - absent	2 - present
------------	-------------

This character was used to separate the non-trilliaceous outgroups from the ingroup. "Absent" is the only state currently used for this character

C 41 Sepal Form

1 - normal	2 - petaloid
------------	--------------

This character was used primarily to separate the non-trilliaceous outgroups from the ingroup "Normal" is the assumed state for this character.

C 42 Sepal Fusion

1 - separate	2 - fused
--------------	-----------

This character was used to separate the non-trilliaceous outgroups from the ingroup "Separate" is the only state currently used for this character

C 43 Sepal Number

1 - three	2 - four	3 - five	4 - six
5 - seven	6 - eight	7 - nine	8 - ten

This character illustrates the variety in merosity in the family "Three" is the assumed state for *Trillium* for this character, *Paris s l* has no assumed state

C 44 Sepal. Widest Point

1 - ovate (¼)	2 - elliptic-ovate	3 - elliptic/ rhombic/ oblong (½)
4 - elliptic-obovate	5 - obovate (¾)	

Like "leaf shape," "sepal shape" has been broken down into component characters (see C 27-C 29) There is no assumed state for this character

C 45 Sepal Width

1 - narrow	2 - average	3 - broad
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This character was the second part of "sepal shape " There is no assumed state for this character

C 46. Sepal Sides

1 - elliptic (curved)	2 - oblong-elliptic	3 - oblong (parallel)
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This character was the third part of "sepal shape." There is no assumed state for this character

C 47 Sepal Duration

1 - persistent	2 - deciduous
----------------	---------------

This character was used primarily to separate the non-trilliaceous outgroups from the ingroup "Persistent" is the assumed state for this character

C 48 Sepal Texture

1 - herbaceous	2 - membranous
----------------	----------------

This character was used primarily to separate the non-trilliaceous outgroups from the ingroup "Herbaceous" is the assumed state for this character

C.49 Sepal Color

1 - reddish-purple	2 - yellow	3 - purple	4 - purplish-green
5 - red	6 - green	7 - reddish green	8 - yellowish-green
9 - white	A - white with green veins	B - greenish with red or purple veins	C - greenish, purple basally
D - greenish, reddish-purple basally	E - greenish-brown	F - greenish with red veins	G - greenish with reddish-purple margins
H - greenish with purple margins	I - green with white veins		

This character illustrates the variation within sepal color Like stem color, C.20, there is much collapsing of colors into "meta-colors. "Green" is the assumed state for this character

C.50 Sepal Color Distribution

1 - throughout	2 - suffused	3 - marginal
4 - mottled	5 - geographic	

Like stem color and leaf color (C 21 and C.31), color patterning or distribution was included as a way to include phylogenetically informative color information "Throughout" is the assumed state for this character

C 51 Sepal Apices

1 - acuminate	2 - acute	3 - obtuse	4 - rounded
5 - acuminate-rounded	6 - sub-acute	7 - cuspidate	8 - emarginate
9 - caudate	A - blunt	B - attenuate	

This character illustrates the variation within the family There is no assumed state for this character.

C 52 Sepal Apex Type

1 - entire	2 - mid-rib, midvein, or vein extension
------------	---

This character groups the leaf apices into what may be a more phylogenetically informative character "Entire" is the assumed state for this character.

C.53. Petal Form

1 - normal	2 - foliaceous	3 - staminoid	4 - none
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This character was used primarily to separate the non-trilliaceous outgroups from the ingroup "Normal" is the assumed state for this character

C 54 Petal Presence

1 - present	2 - absent
-------------	------------

This character and character C 55 are the two characters that are used to identify those taxa with no petals. In the case of all other petal characters, those are listed in the data matrix as "missing" "Present" is the assumed state for this character

C 55 Petal Number

1 - zero	2 - three	3 - four	4 - five
5 - six	6 - seven	7 - eight	

This character was used to illustrate the variety in petal merosity "Three" is the assumed state for *Trillium* for this character, there is no assumed state for *Paris s l*

C.56 Petal Fusion

1 - separate	2 - fused
--------------	-----------

This character was used to separate the non-trilliaceous outgroups from the ingroup "Separate" is the only currently used state for this character

C 57. Petal Widest Point

1 - ovate (¼)	2 - elliptic-ovate	3 - elliptic/ rhombic/ oblong (½)
4 - elliptic-obovate	5 - obovate (¾)	

Like leaf shape (C 27-29) and sepal shape (C 44-46), petal shape has been separated into its component parts. There is no assumed state for this character.

C 58 Petal. Width

1 - filiform	2 - linear	3 - narrow
4 - average	5 - broad	6 - very broad

This character was the second part of the petal shape character. There is no assumed state for this character

C 59 Petal: Sides

1 - elliptic (curved)	2 - oblong-elliptic	3 - oblong (parallel)	4 - rhombic-elliptic
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This character was the third part of the petal shape character. There is no assumed state for this character.

C.60 Petal Duration

1 - persistent	2 - deciduous
----------------	---------------

This character was used primarily to separate the non-trilliaceous outgroups from the ingroup. "Persistent" is the assumed state for this character

C 61 Petal Color

1 - white	2 - yellow	3 - cream	4 - pink
5 - red	6 - purple	7 - bronze	8 - green
9 - reddish-purple	A - greenish-yellow	B - purplish-black	C - brownish-purple
D - greenish-purple	E - purple with a greenish claw	F - yellow with a greenish claw	G - green with a purple claw
H - yellow with a purple claw	I - yellow-green with a purple claw	J - white spotted with rose	K - white with purple basally
L - white with a basal red "V"	M - olive	N - purplish green with a purple claw	

This character illustrates the variety of petal color (and to a lesser extent color patterning) within the family. Like stem color, there has been collapsing of colors into "meta-colors". There is no assumed state for this character

C.62 Petal Color Distribution

1 - throughout	2 - spotted	3 - geographic
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Because of the large number of petal colors (and color patterning) this character was developed to more clearly illustrate these states "Throughout" is the assumed state for this character.

C.63 Petal Anthocyanins

1 - yes	2 - no	3 - white fading to pink
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Because of the broad range of colors, it was felt that perhaps the presence or absence of anthocyanin pigments might be more phylogenetically informative than "red" or "white" In addition to mere presence or absence, there are also those white trilliums that turn pink as they age There is no assumed state for this character

C.64 Petal Transverse Posture

1 - incurved	2 - plane	3 - recurved
4 - undulate	5 - outcurved	

Like plane shape, posture or attitude cannot be adequately represented in just one character The three parts of attitude are transverse (ends to the middle), vertical (relative to the vertical axis), and longitudinal (sides to the center) This character illustrates the variety of petal postures Recurved denotes a petal more curved back on itself rather than just curved away from the vertical axis There is no assumed state for this character

C.65 Petal Vertical Orientation

1 - erect	2 - divergent (upwards)	3 - horizontal
4 divergent (downward)	5 - declined	

This character was the second part of petal posture. There is no assumed state for this character.

C.66 Petal Longitudinal Posture

1 - straight	2 - twisted
--------------	-------------

This character was the third part of petal posture "Straight" is the assumed state for this character.

C 67. Petal Apices

1 - acuminate	2 - acute	3 - obtuse	4 - rounded
5 - blunt	6 - sub-acute	7 - cuspidate	8 - apiculate
9 - emarginate	A - mucronate		

This character illustrates the various petal apices in the family (q v C 35, C.51) There is no assumed state for this character

C 68 Petal Apex Type

1 - entire	2 - midrib, midvein, or vein extension
------------	--

This character, like the others (C 34, C 52) groups the apices by type. "Entire" is the assumed state for this character

C 69 Stamen form

1 - normal	2 - petaloid-abortive
------------	-----------------------

This character was used to separate the non-trilliaceous outgroups from the ingroup "Normal" is the only state currently used for this character

C 70 Stamen Number

1 - zero	2 - 1x sepals	3 - 2x sepals
4 - 3x sepals	5 - 4x sepals	

This character illustrate the variety in numbers of whorls of stamens "2x" is the assumed state for *Trillium* for this character, there is no assumed state for *Paris s l*

C 71 Stamen Fusion

1 - free	2 - adnate to tepal
----------	---------------------

This character was used to separate the non-trilliaceous outgroups from the ingroup "Free" is the only state currently used for this character.

C 72 Stamen Transverse Posture

1 - straight	2 - incurved	3 - slightly recurved
--------------	--------------	-----------------------

Like petal posture (C 64), stamen posture was divided into its component parts. This character was the first There is no assumed state for this character.

C.73 Stamen Vertical Posture

1 - erect	2 - spreading
-----------	---------------

This character is the second part of stamen posture. There is no assumed state for this character.

C.74 Anther Dehiscence

1 - introrse	2 - latrorse	3 - extrorse
--------------	--------------	--------------

This character illustrates the variety of dehiscence in the family. Unlike other families or genera, this is not always constant within Trilliaceae. There is no assumed state for this character.

C.75 Pollen Shape

1 - spherical	2 - ellipsoid	3 - irregular
---------------	---------------	---------------

This character has been found to be diagnostic between *Paris s.l.* and *Trillium*. "Spherical" is the assumed state for *Trillium* for this character, "ellipsoid" is the assumed state for *Paris s.l.* It was pollen shape that helped solidify the position of *Trillidium* as a valid genus. When the position of *Trillium rivale* came under suspicion, pollen grains from *T. rivale*, *T. govonianum*, *T. sulcatum*, and *P. polyphylla* were examined with a Scanning Electron Microscope (SEM) (Figure C.1). *T. rivale* has the spherical pollen of *Trillium*, but *T. govonianum* clearly has ellipsoidal, monosulcate pollen.

C.76 Pollen Aperture

1 - omniaperturate	2 - monosulcate
--------------------	-----------------

This character was used to separate the non-trilliaceous outgroups from the ingroup as well as separate *Trillium* and *Paris, s.l.* "Omniaperturate" is the assumed state for *Trillium* for this character, "monosulcate" is the assumed state for *Paris s.l.* (q.v. Figure C.1).

C.77 Pollen Ornamentation

1 - granulate	2 - echinate	3 - corrugate	4 - verrucate
5 - spinulate	6 - clavate	7 - foveolate	8 - reticulate
9 - psilate	A - gemmate		

This character has been found to be taxonomically informative, but it has not been sampled widely enough across the family to be very phylogenetically informative. There is no assumed state for this character.

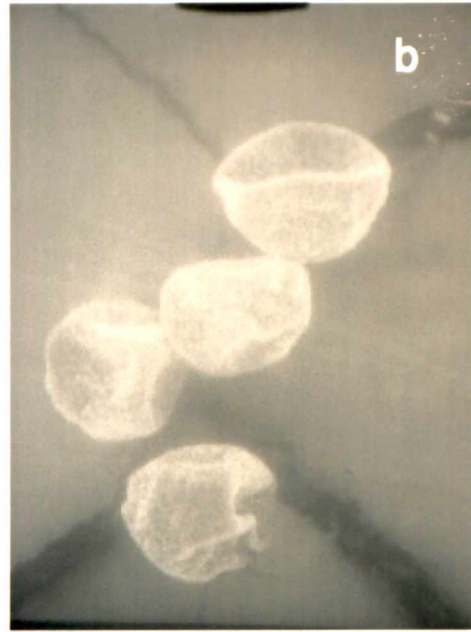


Figure C1. SEM images of pollen from Trilliaceae. a. *Trillium rivale* b. *Trillium sulcatum*
c. *Trillidium govanianum* d. *Paris polyphylla*.

C 78 Connective Prolongation

1 - none	2 - acute	3 - truncate	4 - dilated
5 - round	6 - emarginate	7 - obtuse	

This character illustrates the various shapes of connective prolongation in the family. This character is taxonomically important. There is no assumed state for this character.

C 79. Filament Color

1 - green	2 - purple	3 - whitish-purple	4 - reddish-purple
5 - whitish-green	6 reddish-purplish-brown	7 - pinkish-white	8 - greenish-yellow
9 - white	A - pink	B - brown	C - yellow

This character illustrates the variety in the family. There is no assumed state for this character.

C 80. Pollen Color

1 - yellow	2 - orange	3 - olive	4 - brownish
5 - olive-orange	6 - purple	7 - greyish-purple	8 - pink
9 - yellowish pale purple	A - green	B - maroon	C - orange-yellow

This character illustrates the variety in the family. There is no assumed state for this character.

C 81. Connective Color

1 - green	2 - pink	3 - purple	4 - pinkish-purple
5 - reddish-purple	6 - brown	7 - whitish-green	8 - white
9 - reddish-purplish-brown			

This character illustrates the variety in the family. There is no assumed state for this character.

C.82 Stamen Color Distribution

1 - throughout	2 - pollen different	3 - all different
----------------	----------------------	-------------------

Because of extreme variability in color, this character was used to examine color distribution patterns rather than actual colors. "Throughout" is the assumed state for this character.

C 83. Pistil Form

1 - normal	2 - abortive
------------	--------------

This character was used to separate the non-trilliaceous outgroups from the ingroup. "Normal" is the only state currently used for this character.

C 84. Ovary Position

1 - inferior	2 - superior
--------------	--------------

This character was used to separate the non-trilliaceous outgroups from the ingroup. "Superior" is the only state currently used for this character

C.85 Number of Locules

1 - one	2 - three	3 - four to ten
---------	-----------	-----------------

This character and placentation (C 86) were used to examine the variety within the family. These characters are diagnostic in separating *Paris* and *Daiswa*, there is no consistency within *Trillium*. There is no assumed state for this character

C 86 Placentation

1 - axile	2 - parietal	3 - combination
-----------	--------------	-----------------

In *Paris* and *Daiswa*, placentation and number of locules are correlated, this is not the case in *Trillium*. Due to reports of "variable placentation" in *Trillium* (Zomlefer, 1994, 1996) serial sections were made of various *Trillium* ovaries (Figure C.2). In most of the ovaries that were examined, apically, basally, or both, placentation was obviously axile, but in the center of the ovary, placentation was parietal. Traditionally in *Trillium*, placentation was reported to be axile because Liliaceae have axile placentation. There is no assumed state for this character

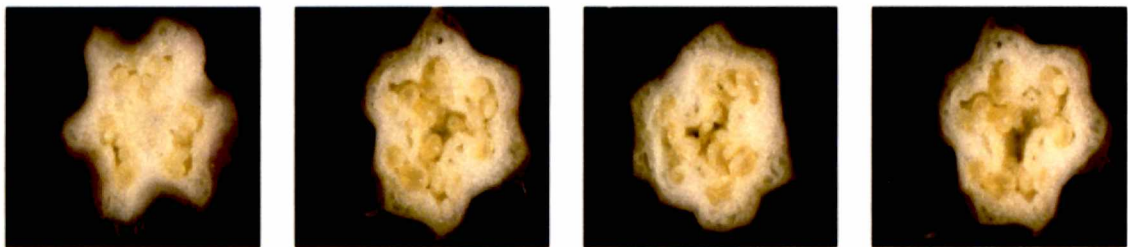
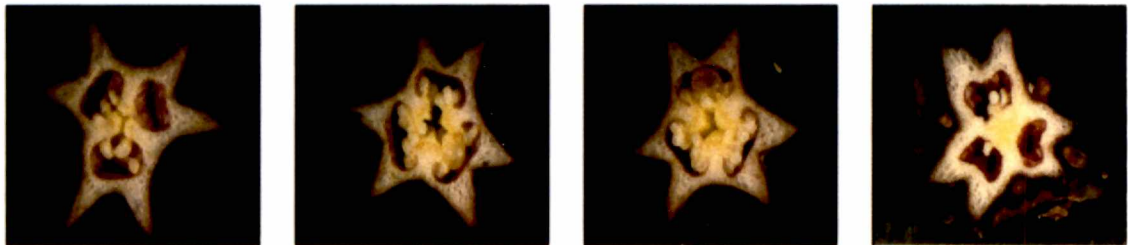
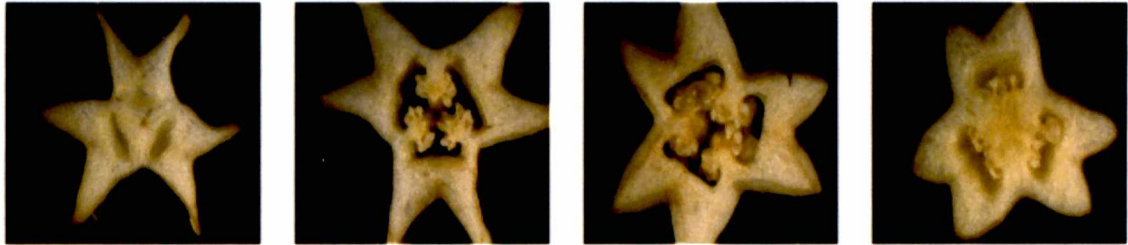
C 87. Ovary Shape

1 - conical	2 - angular-ovoid	3 - ovoid	4 - ellipsoid
5 - obovoid	6 - flask-shaped	7 - subglobose	8 - oval-globose
9 - fusiform	A - ovate-conical		

This character illustrates the variety of shapes within the family. This character has been used taxonomically within pedicellate *Trillium*. There is no assumed state for this character.

Apex

Base



Apex

Base

Figure C2. Examples of placentation in *Trillium*. top: *Trillium sulcatum* middle: *T. sulcatum*
bottom: *T. cuneatum*

C.88 Ovary Cross-section Shape

1 - round	2 - ridged	3 - angled	4 - winged
-----------	------------	------------	------------

This character illustrates the taxonomically important ovary cross-section shape **Figure C.2** also illustrates the difference between "winged" versus "ridged." There is no assumed state for this character

C 89 Ovary Ribs

1 - zero	2 - two	3 - three	4 - four
5 - five	6 - six	7 - seven	

This character illustrates the variety in numbers of ribs or wings There is no assumed state for this character.

C 90. Ovary Apex

1 - truncate	2 - crowned	3 - attenuate	4 - obtuse
--------------	-------------	---------------	------------

This character can be used to separate *Paris* from *Daiswa*; within *Trillium*, there is not a great deal of variety. There is no assumed state for this character

C 91 Style Presence

1 - present	2 - absent
-------------	------------

Many *Paris s l* exhibit a common style, whereas most *Trillium* do not "Absent" is the assumed state for this character

C 92 Stigma Number

1 - three	2 - four	3 - five	4 - six
5 - eight	6 - ten	7 - seven	

This character illustrates the stigmatic merosity "Three" is the assumed state for *Trillium* for this character, *Paris s l* has no assumed state

C 93 Stigma Shape

1 - linear-subulate	2 - subulate
---------------------	--------------

This character illustrates stigma shape which can be important taxonomically in *Trillium* There is no assumed state for this character

C 94 Stigma Vertical Posture

1 - divergent	2 - erect
---------------	-----------

This character, like petal posture and stamen posture, has been divided into its component parts. It illustrates the orientation of the stigmatic branches. There is no assumed state for this character.

C 95 Stigma Transverse Posture

1 - incurved	2 - straight	3 - recurved
--------------	--------------	--------------

This character is the second part of stigma posture. There is no assumed state for this character.

C 96 Stigma Duration

1 - deciduous	2 - persistent
---------------	----------------

This character was used to separate the non-trillaceous outgroups from the ingroup. "Persistent" is the only state currently used for this character.

C 97 Stigma Size

1 - very thin	2 - thin	3 - average	4 - thick
---------------	----------	-------------	-----------

This character illustrates the variation in stigma size within the family. There is no assumed state for this character.

C 98 Ovary color

1 - yellowish-white	2 - green	3 - purple	4 - pink
5 - cream yellow	6 - white	7 - reddish-purple	8 - purplish-brown
9 - yellow-green	A - reddish-purplish-brown over green-red	B - green over purple	C - purple over green
D - purple over yellow	E - purple over white	F - pink over white	G - green with purple disk
H - green with yellow disk	I - green with white disk	J - yellow with black disk	

Like other color characters, there has been grouping into "meta-colors" in this character. This character illustrates the variation in color as well as some color patterning. There is no assumed state for this character.

C 99. Ovary Color Distribution

1 - throughout	2 - spotted	3 - striped	4 - geographic
----------------	-------------	-------------	----------------

This character, like the other color distribution characters, was chosen in the hope that it would be more phylogenetically informative than a long list of colors. "Throughout" is the assumed state for this character.

C 100 Stigma Color

1 - green	2 - purple	3 - yellowish-green	4 - creamy white
5 - yellow	6 - yellowish-white	7 - pink	8 - black
9 - brownish-violet	A - reddish-purplish-brown	B - brown	C - purple out, green in
D - purple-brown out, yellow in	E - purple out, yellow in	F - white, basally pink	G - green out, yellow in
H - pinkish-orange	I - red		

This character illustrates the variation in the family. There is no assumed state for this character.

C 101 Stigma Color Distribution

1 - throughout	2 - banded	3 - geographic
----------------	------------	----------------

This character was assumed to be more phylogenetically informative than color alone. "Throughout" is the assumed state for this character.

C 102 Pistil Color Distribution

1 - throughout	2 - geographic by part	3 - all different
----------------	------------------------	-------------------

This character was assumed to be more phylogenetically informative than color alone. "Throughout" is the assumed state for this character.

C.103 Fruit Type

1 - berry	2 - capsule	3 - fleshy capsule
-----------	-------------	--------------------

This much debate about fruit type in Trilliaceae. The fruit in *Daiswa* is loculicidally dehiscent, but it is not a true capsule. Some people have called this type of fruit a fleshy capsule. In *Trillium*, the fleshy capsule is often mentioned, but it does not exhibit true dehiscence, rather the fruit ruptures as if enlarging too rapidly, or it abscises from the plant rupturing in the process. There is no assumed state for this character.

C 104 Fruit Dehiscence

1 - indehiscent	2 - basally dehiscent	3 - septicidal	4 - irregular
5 - loculicidal	6 - dehiscent	7 - decay	

This character was used to separate the non-trilliaceous outgroups from the ingroup as well as illustrate the various types of dehiscence that have been reported on Trilliaceae. There is no assumed state for this character.

C 105. Fruit Shape

1 - conical	2 - angular-ovoid	3 - ovoid
4 - globose	5 - obovoid	6 - elliptic

This character illustrates the variety of fruit shapes in the family. There is no assumed state for this character.

C.106 Fruit Color

1 - green	2 - maroon	3 - greenish-yellow	4 - rusty red
5 - greenish-white	6 - red	7 - black	8 - bluish-black
9 - brown	A - purple	B - green with purple dots	C - purplish-green
D - greenish-brown	E - green with brown ribs	F - black-purple	G - white
H - pink			

This character illustrates the variety of fruit colors in the family. There is no assumed state for this character.

C 107 Fruit Color Distribution

1 - throughout	2 - mottled	3 - spotted
4 - striped	5 - geographic	

This character was assumed to be more phylogenetically informative than color alone. "Throughout" is the assumed state for this character.

C 108 Seed Arils

1 - incomplete	2 - absent	3 - complete
----------------	------------	--------------

This character is taxonomically important in the family. "Incomplete" is the assumed state for *Trillium*, there is no assumed state for *Paris s l* for this character.

C 109 Endosperm Development

1 - helobial	2 - nuclear
--------------	-------------

This character is diagnostic within the family "Helobial" is assumed for *Trillium*, "nuclear" is assumed for *Paris s l* for this character

C 110 Cotyledon Shape

1 - strap-like	2 - leaf-like
----------------	---------------

This character was determined to be diagnostic in separating *Trillium* from *Paris s l*. (Figure C.3) At this time, it is not know if the leaf-like cotyledon is a true cotyledon, or if it is a true leaf emerging after some sort of epigeal germination. "Strap-like" is assumed for *Trillium*, "leaf-like" is assumed for *Paris s.l*



Figure C3. Examples of cotyledon shape in Trilliaceae. a. *Trillium sulcatum* b. *Paris yunnanensis* c. *Trillium rivale*. Photographs b and c courtesy of Dr. Carl Denton.

APPENDIX D
PAUP* INPUT FILES

APPENDIX D.1

ITS sequence data

#NEXUS
 [ITS-6-1276959946 -- data title]

begin data,
 dimensions ntax=26 nchar=641,
 format datatype=dna missing=-,

```

matrix
[
[
T rivale 1234567890
T govanianum tccagatcgcgaatatgacc 2 sgaagactgtgaactcgtta 4 cggaa-tg-tcgattctgg 6 sgaaggttcgtcttgaagcc 8 aa-tgcccc-tgcccc--tt
D fargesii tccagatacgaatatgtggc 3 sgaagactgtgaactcgtga 5 cggaa-tg-tcgattccgg 7 sgaaggttcgtcccgaagcc 9 aa-tgcccc-ttcccc--tt
D polyphylla tccagatacgaatatgtgct 4 sgaagattgtgaactcgtga 6 sgaaggttcgtcccgaagcc 8 aa-tgcccc-tacacccctt
D thibetica tccagatacgaatatgtgct 5 sgaagattgtgaactcgtga 7 sgaaggttcgtcccgaagcc 9 aa-tgcccc-tacacccctt
D violacea tccagatacgaatatgtgct 6 sgaagattgtgaactcgtga 8 sgaaggttcgtcccgaagcc 0 aa-tgcccc-tacacccctt
K japonica tccagatacgaatatgtgct 7 sgaagattgtgaactcgtga 9 sgaaggttcgtcccgaagcc aa-tgcccc-tacacccctt
P incompleta tccagatacgaatatgtgct 8 sgaagattgtgaactcgtga aa-tgcccc-tacacccctt
P tetraphylla tccagatacgaatatgtgct 9 sgaagattgtgaactcgtga aa-tgcccc-tacacccctt
P verticillata tccagatacgaatatgtgct aa-tgcccc-tacacccctt
T chloropetalum tccagatacgaatatgtgct aa-tgcccc-tacacccctt
T discolor tccagatacgaatatgtgct aa-tgcccc-tacacccctt
T lancifolium tccagatacgaatatgtgct aa-tgcccc-tacacccctt
T maculatum tccagatacgaatatgtgct aa-tgcccc-tacacccctt
T petiolatum tccagatacgaatatgtgct aa-tgcccc-tacacccctt
T recurvatum tccagatacgaatatgtgct aa-tgcccc-tacacccctt
T sessile tccagatacgaatatgtgct aa-tgcccc-tacacccctt
T camschatcense tccagatacgaatatgtgct aa-tgcccc-tacacccctt
T erectum tccagatacgaatatgtgct aa-tgcccc-tacacccctt
T grandiflorum tccagatacgaatatgtgct aa-tgcccc-tacacccctt
T ovatum tccagatacgaatatgtgct aa-tgcccc-tacacccctt
T pusillum tccagatacgaatatgtgct aa-tgcccc-tacacccctt
T rugellii tccagatacgaatatgtgct aa-tgcccc-tacacccctt
T undulatum tccagatacgaatatgtgct aa-tgcccc-tacacccctt
]
]
Begin ITS-1

```

```

100
1234567890 ]
[
T rivale attcagcgcagcatgcbctca agaacgagtagtgaatgc
T govamanum acccggcgcagcagcgcgtca agaacgagtagtgaatgc
D fargesii cctggcgcgcagcagcgcgtca agaacgagtagtgaatgc
D polyphylla actcggcgcgcagcagcgcgtca agaacgagtagtgaatgc
D thibetica actcggcgcgcagcagcgcgtca agaacgagtagtgaatgc
D violacea actcggcgcgcagcagcgcgtca agaacgagtagtgaatgc
K japonica actcggcgcgcagcagcgcgtca agaacgagtagtgaatgc
P incompleta accgagcgcgcagcagcgcgtca agaacgagtagtgaatgc
P tetraphylla accgagcgcgcagcagcgcgtca agaacgagtagtgaatgc
P verticillata accgagcgcgcagcagcgcgtca agaacgagtagtgaatgc
T chloropetalum accgagcgcgcagcagcgcgtca agaacgagtagtgaatgc
T decipiens accgagcgcgcagcagcgcgtca agaacgagtagtgaatgc
T discolor accgagcgcgcagcagcgcgtca agaacgagtagtgaatgc
T lancifolium accgagcgcgcagcagcgcgtca agaacgagtagtgaatgc
T maculatum accgagcgcgcagcagcgcgtca agaacgagtagtgaatgc
T petiolatum accgagcgcgcagcagcgcgtca agaacgagtagtgaatgc
T recurvatum accgagcgcgcagcagcgcgtca agaacgagtagtgaatgc
T reliquum accgagcgcgcagcagcgcgtca agaacgagtagtgaatgc
T sessile accgagcgcgcagcagcgcgtca agaacgagtagtgaatgc
T camschatcense accgagcgcgcagcagcgcgtca agaacgagtagtgaatgc
T erectum accgagcgcgcagcagcgcgtca agaacgagtagtgaatgc
T grandiflorum accgagcgcgcagcagcgcgtca agaacgagtagtgaatgc
T ovatum accgagcgcgcagcagcgcgtca agaacgagtagtgaatgc
T pusillum accgagcgcgcagcagcgcgtca agaacgagtagtgaatgc
T rugelii accgagcgcgcagcagcgcgtca agaacgagtagtgaatgc
T undulatum accgagcgcgcagcagcgcgtca agaacgagtagtgaatgc

```



```

300
1234567890 ]
[
T rivale          2 3 4 5 6 7 8 9 0 ]
T gavananum     2 3 4 5 6 7 8 9 0 ]
D fargesii      2 3 4 5 6 7 8 9 0 ]
D polyphylla    2 3 4 5 6 7 8 9 0 ]
D thibetica     2 3 4 5 6 7 8 9 0 ]
D violacea      2 3 4 5 6 7 8 9 0 ]
K japonica      2 3 4 5 6 7 8 9 0 ]
P incompleta    2 3 4 5 6 7 8 9 0 ]
P tetraphylla   2 3 4 5 6 7 8 9 0 ]
P verticillata 2 3 4 5 6 7 8 9 0 ]
T chloropetalum 2 3 4 5 6 7 8 9 0 ]
T decipiens     2 3 4 5 6 7 8 9 0 ]
T discolor      2 3 4 5 6 7 8 9 0 ]
T lancifolium   2 3 4 5 6 7 8 9 0 ]
T maculatum     2 3 4 5 6 7 8 9 0 ]
T petiolatum    2 3 4 5 6 7 8 9 0 ]
T recurvatum    2 3 4 5 6 7 8 9 0 ]
T reliquum      2 3 4 5 6 7 8 9 0 ]
T sessile       2 3 4 5 6 7 8 9 0 ]
T camtschaticense 2 3 4 5 6 7 8 9 0 ]
T erectum       2 3 4 5 6 7 8 9 0 ]
T grandiflorum  2 3 4 5 6 7 8 9 0 ]
T ovatum        2 3 4 5 6 7 8 9 0 ]
T pusillum      2 3 4 5 6 7 8 9 0 ]
T rugelii       2 3 4 5 6 7 8 9 0 ]
T undulatum     2 3 4 5 6 7 8 9 0 ]

```



```

600 [
1234567890 2 3 4 ]
ataactccaa----- --gaaggttgcc--tgca c
gc---ccctt-gtgcacc cagtaggttgcc--tgca c
D ganesii gc---ccctt-gtgcacc cagtaggttgcc--tgta t
D polyphylla gc---ccctt-atgcacc caacaaggttgcc--tgta c
D thibetica ga---ccctt-gtgcacc cagcaaggttgcc--tgta t
D violacea gc---ccctt-atgcacc caacaaggttgcc--tgta t
K japonica tc---ccctt-gtgcacc caataggttagc--tgca c
P incompleta gc---ccctt-gtgcacc cagtaggttgcc--tgca a
P tetraphylla gc---ccctt-gtgcacc cagtaggttgcc--tgca a
P verticillata gc---ccctt-gtgcacc cagtaggttgcc--tgca a
T chloropetalum g---ccctt-gtgcacc cagtaggttgcc--tgca c
T decipiens g---ccctt-gtgcacc cagtaggttgcc--tgca c
T discolor g---ccctt-gtgcacc cagtaggttgcc--tgca c
T lancifolium g---ccctt-gtgcacc cagtaggttgcc--tgca c
T maculatum g---ccctt-gtgcacc cagtaggttgcc--tgca c
T petiolatum g---ccctt-gtgcacc cagtaggttgcc--tgca c
T recurvatum g---ccctt-gtgcacc cagtaggttgcc--tgca c
T reliquum g---ccctt-gtgcacc cagtaggttgcc--tgca c
T sessile g---ccctt-gtgcacc cagtaggttgcc--tgca c
T camschatcense gg---ccctt-ggacacc cagtaggttgcc--tgaa c
T erectum gg---ccctt-gtgcacc cagtaggttgcc--tgaa c
T grandiflorum ga---ccctt-gtgcacc cagtaggttgcc--tgca c
T ovatum gc---ccctt-gtgcacc cagtaggttgcc--tgca c
T pusillum gc---ccctt-gtgcacc cagtaggttgccgtgaa c
T rugelii gg---ccctt-gtgcacc cagtaggttgcc--tgaa c
T undulatum gc---ccctt-gtgcacc cagtaggttgcc--tgca c
, end,

```

```

begin paup,
  set torder=right,
  set OutRoot=Monophyl,
  Defaults bootstrap nreps=1000 search=Heuristic TreeFile=its boot,
  Defaults ConTree strict=yes MajRule=yes Indices=yes TreeFile=its consensus,
  Defaults Describe Plot=both BrLens=yes ChgList=yes Apol1st=yes,
  log file=its log,
end,

```

APPENDIX D.2

***matK* sequence data**

```

#nexus
[matk data from DDBJ]

begin data,
  dimensions ntax=26 nchar=1578,
  format datatype=dna interleave missing=-,
matrix
[
1234567890
atggaagaattacaattaca 2 aggatatttagaaaaagatg 3 aggatatttagaaaaagatg 4 aggatatttagaaaaagatg 5 gattcggcaacaaaacttc 6 ctataccgcttataatttc 7 ctataccgcttataatttc 8 aggtataattacacacttg 9 aggtataattacacacttg 0
T rivale
T govarianum
D fargesii
D polyphylla
D thibetica
D violacea
K japonica
P incompleta
P tetraphylla
P verticillata
T chloropetalum
T decipiens
T discolor
T lancifolium
T maculatum
T petiolatum
T recurvatum
T reliquum
T sessile
T camtsatcense
T erectum
T grandiflorum
T ovatum
T pusillum
T rugelii
T undulatum
1234567890
atggaagaattacaattaca 2 aggatatttagaaaaagatg 3 aggatatttagaaaaagatg 4 aggatatttagaaaaagatg 5 gattcggcaacaaaacttc 6 ctataccgcttataatttc 7 ctataccgcttataatttc 8 aggtataattacacacttg 9 aggtataattacacacttg 0
[

```



```

300
1234567890
}
[
I
T rivale          1 2 3 4 5 6 7 8 9 0
T govananum      1 2 3 4 5 6 7 8 9 0
D fargesii       1 2 3 4 5 6 7 8 9 0
D polyphylla     1 2 3 4 5 6 7 8 9 0
D thibetica      1 2 3 4 5 6 7 8 9 0
D violacea       1 2 3 4 5 6 7 8 9 0
K japonica       1 2 3 4 5 6 7 8 9 0
P incompleta     1 2 3 4 5 6 7 8 9 0
P tetraphylla    1 2 3 4 5 6 7 8 9 0
P verticillata   1 2 3 4 5 6 7 8 9 0
T chloropetalum  1 2 3 4 5 6 7 8 9 0
T decipiens      1 2 3 4 5 6 7 8 9 0
T discolor       1 2 3 4 5 6 7 8 9 0
T lancifolium    1 2 3 4 5 6 7 8 9 0
T maculatum      1 2 3 4 5 6 7 8 9 0
T petiolatum     1 2 3 4 5 6 7 8 9 0
T recurvatum     1 2 3 4 5 6 7 8 9 0
T reliquum       1 2 3 4 5 6 7 8 9 0
T sessile        1 2 3 4 5 6 7 8 9 0
T camtsatcense  1 2 3 4 5 6 7 8 9 0
T erectum        1 2 3 4 5 6 7 8 9 0
T grandiflorum   1 2 3 4 5 6 7 8 9 0
T ovatum         1 2 3 4 5 6 7 8 9 0
T pusillum       1 2 3 4 5 6 7 8 9 0
T rugelii        1 2 3 4 5 6 7 8 9 0
T undulatum      1 2 3 4 5 6 7 8 9 0
300
1234567890
}
]

```


900
 1234567890
 T rivale tttcttgataaaagaaatgga aatgttaccttgtaaatctc tggcaataatcattttcactt ttggtctaaaccatacagga
 T gowanum tctctgataaaagaaatgga aatgttaccttgtaaatctc tggcaataatcattttcactt ttggtctaaaccatacagga
 D fargesii tctctgataaaagaaatgga aatgttaccttgtaaatctc tggcaataatcattttcactt ttggtctaaaccatacagga
 D polyphylla tctctgataaaagaaatgga aatgttaccttgtaaatctc tggcaataatcattttcactt ttggtctaaaccatacagga
 D thibetica tctctgataaaagaaatgga aatgttaccttgtaaatctc tggcaataatcattttcactt ttggtctaaaccatacagga
 D violacea tctctgataaaagaaatgga aatgttaccttgtaaatctc tggcaataatcattttcactt ttggtctaaaccatacagga
 K japonica tctctgataaaagaaatgga aatgttaccttgtaaatctc tggcaataatcattttcactt ttggtctaaaccatacagga
 P incompleta tctctgataaaagaaatgga aatgttaccttgtaaatctc tggcaataatcattttcactt ttggtctaaaccatacagga
 P tetraphylla tctctgataaaagaaatgga aatgttaccttgtaaatctc tggcaataatcattttcactt ttggtctaaaccatacagga
 P verticillata tctctgataaaagaaatgga aatgttaccttgtaaatctc tggcaataatcattttcactt ttggtctaaaccatacagga
 T chloropetalum tctctgataaaagaaatgga aatgttaccttgtaaatctc tggcaataatcattttcactt ttggtctaaaccatacagga
 T decipiens tctctgataaaagaaatgga aatgttaccttgtaaatctc tggcaataatcattttcactt ttggtctaaaccatacagga
 T discolor tctctgataaaagaaatgga aatgttaccttgtaaatctc tggcaataatcattttcactt ttggtctaaaccatacagga
 T lancifolium tctctgataaaagaaatgga aatgttaccttgtaaatctc tggcaataatcattttcactt ttggtctaaaccatacagga
 T maculatum tctctgataaaagaaatgga aatgttaccttgtaaatctc tggcaataatcattttcactt ttggtctaaaccatacagga
 T petiolatum tctctgataaaagaaatgga aatgttaccttgtaaatctc tggcaataatcattttcactt ttggtctaaaccatacagga
 T recurvatum tctctgataaaagaaatgga aatgttaccttgtaaatctc tggcaataatcattttcactt ttggtctaaaccatacagga
 T reliquum tctctgataaaagaaatgga aatgttaccttgtaaatctc tggcaataatcattttcactt ttggtctaaaccatacagga
 T sessile tctctgataaaagaaatgga aatgttaccttgtaaatctc tggcaataatcattttcactt ttggtctaaaccatacagga
 T camtschatcense tctctgataaaagaaatgga aatgttaccttgtaaatctc tggcaataatcattttcactt ttggtctaaaccatacagga
 T erectum tctctgataaaagaaatgga aatgttaccttgtaaatctc tggcaataatcattttcactt ttggtctaaaccatacagga
 T grandiflorum tctctgataaaagaaatgga aatgttaccttgtaaatctc tggcaataatcattttcactt ttggtctaaaccatacagga
 T ovatum tctctgataaaagaaatgga aatgttaccttgtaaatctc tggcaataatcattttcactt ttggtctaaaccatacagga
 T pusillum tctctgataaaagaaatgga aatgttaccttgtaaatctc tggcaataatcattttcactt ttggtctaaaccatacagga
 T rugelii tctctgataaaagaaatgga aatgttaccttgtaaatctc tggcaataatcattttcactt ttggtctaaaccatacagga
 T undulatum tctctgataaaagaaatgga aatgttaccttgtaaatctc tggcaataatcattttcactt ttggtctaaaccatacagga
 900
 1234567890
 [


```

1500
1234567890
[ [ rivale          2 3 4 5 6 7 ]
  [ govorianum    2 3 4 5 6 7 ]
  [ fargesii      2 3 4 5 6 7 ]
  [ polyphylla    2 3 4 5 6 7 ]
  [ thibetica     2 3 4 5 6 7 ]
  [ violacea      2 3 4 5 6 7 ]
  [ japonica      2 3 4 5 6 7 ]
  [ incompleta    2 3 4 5 6 7 ]
  [ tetraphylla   2 3 4 5 6 7 ]
  [ verticillata  2 3 4 5 6 7 ]
  [ chloropetalum 2 3 4 5 6 7 ]
  [ discipiens    2 3 4 5 6 7 ]
  [ discolor      2 3 4 5 6 7 ]
  [ lancifolium   2 3 4 5 6 7 ]
  [ maculatum     2 3 4 5 6 7 ]
  [ recurvatum    2 3 4 5 6 7 ]
  [ reliquum      2 3 4 5 6 7 ]
  [ sessile       2 3 4 5 6 7 ]
  [ erectum       2 3 4 5 6 7 ]
  [ grandiflorum  2 3 4 5 6 7 ]
  [ ovatum        2 3 4 5 6 7 ]
  [ pusillum      2 3 4 5 6 7 ]
  [ rugelii       2 3 4 5 6 7 ]
  [ undulatum     2 3 4 5 6 7 ]
1500
1234567890
] ]

```

```

end,

```

```

begin paup,
  log file=matk log,
  set torder=right,
  set OutRoot=Monophyl,
  Defaults bootstrap nreps=1000 search=Heuristic TreeFile=its boot,
  Defaults ConTree strict=yes MajRule=yes Indices=yes TreeFile=matk consensus,
  Defaults Describe Plot=both BrLens=yes ChgList=yes ApoList=yes,
  log file=matk log,
end,

```

APPENDIX D.3
Morphological data

#NEXUS

BEGIN DATA,
DIMENSIONS NTAX=86 NCHAR=110,

[Trilliaceae taxa 14.22 -- 14 Dec 1999]
FORMAT SYMBOLS= " 123456789ABCDEFGHIJKLMNO" MISSING=? GAP=- INTERLEAVE ,
OPTIONS MSTAXA=POLYMORPH ,

[ZAP set non-morphological characters]
options zap="1-8",

[ZAP set numbers of plant parts -- leaves, sepals, petals, stamens, stigma]
options zap="22 43 55 70 92";

CharStateLabels

- 1 hybrid_status/ yes no,
- 2 flowering_time/ February March April May June July August,
- 3 chromosome_number/ '2n=10' '2n=15' '2n=20' '2n=30' '2n=40',
- 4 geographical_area/ east_Asia western_North_America
eastern_North_America Europe,
- 5 genus/ outgroup Trillium Paris,
- 6 subgenus/ outgroup Trillium Phyllantherum Paris Kinugasa Daiswa,
- 7 section/ outgroup grandiflorum erectum catesbaei
recurvatum sessile maculatum
paris axiparis kinugasa
daiswa dunniana marmorata fargesiana tibetica,
- 8 Rafinesque/ outgroup Paris Daiswa Phyllantherum Trillium Delostylis,
- 9 PLANT_type/ herbs vines,
- 10 foliaceousness/ scapose leafy,
- 11 plant_sexuality/ bisexual dioecious,
- 12 INFLORESCENCE_type/ solitary simple_umbel,
- 13 FLOWERS_#/ one more_than_one,
- 14 composition/ tepals 'sepals + petals',
- 15 PED_vertical_posture/ erect above_the_leaves horizontal
below_the_leaves none,
- 16 root_type/ rhizome bulb,
- 17 rhizome_size/ very_thin slender thick very_thick,
- 18 STEM_habit/ erect partially_decumbent decumbent,
- 19 vestiture/ glabrous puberulent pubescent pilose papillose scabrous
striate,
- 20 stem_color/ green 'yellowish-green' reddish_purple greenish_purple
purplish brownish-green reddish_green_over_purple
purple_tinged,
- 21 stem_distribution/ throughout geographic suffused,
- 22 LEAF_number/ two three four five six seven eight nine ten
eleven_and_up,
- 23 leaf_location/ terminal cauline,
- 24 leaf_arrangement/ whorled spirally_inserted,
- 25 #_whorls/ one more_than_two none,
- 26 leaf_attachment/ petiolate subsessile sessile,
- 27 'leaf_widest_point'/ 'ovate_(25)' 'elliptic-ovate_(375)'
'elliptic-rhombic-oblong_(5)'
'elliptic-obovate_(675)' 'obovate_(75)',
- 28 'leaf_width_(LxW)'/ linear narrow average broad very_broad
depressed_or_transverse,

29 'leaf_sides'/ 'elliptic_(curved)' 'oblong-elliptic'
 'oblong_(parallel)' 'oblong-rhombic'
 'rhombic_(straight)' 'rhombic-elliptic',
 30 leaf_margin/ entire undulate,
 31 leaf_distribution/ throughout mottled geographic suffused,
 32 leaf_color/ green more_or_less_purple_mottled green_w_maroon_hue
 small_brownish_spots white_variegation_on_veins mottled
 mottled_w_dk_green spots_of_lt_green
 multiple_shades_of_green shades_of_green_beside_pale_mid
 dk_green_spots_on_mottled_backg
 dk_green_between_veins_w_pale_m,
 33 leaf_lower_surface/ pubescent_on_veins scabrous_on_veins glossy dull
 purple purple_nerves glabrous pubescent,
 34 apex_type/ entire sinus 'mid-rib,_midvein_or_vein_exten',
 35 apices/ acuminate acute obtuse rounded emarginate 'sub-acute'
 cuspidate blunt attenuate,
 36 base_type/ entire with_sinusus,
 37 bases/ cuneate sheathing obtuse rounded attenuate hastate cordate,
 38 leaf_texture/ herbaceous membranous papery rugose coriaceous,
 39 #_main_nerves/ many three five seven,
 40 BRACTS/ absent present,
 41 SEPAL_form/ normal petaloid,
 42 sepal_fusion/ separate fused,
 43 sepal_number/ three four five six seven eight nine ten,
 44 'sepal_widest_point'/ 'ovate_(25)' 'elliptic-ovate_(375)'
 'elliptic-rhombic-oblong_(5)'
 'elliptic-obovate_(625)' 'obovate_(75)',
 45 'sepal_width_(LxW)'/ narrow average broad,
 46 'sepal_sides'/ 'elliptic_(curved)' 'oblong-elliptic'
 'oblong_(parallel)',
 47 sepal_duration/ persistent deciduous,
 48 sepal_texture/ herbaceous membranous,
 49 sepal_color/ reddish_purple yellow purple purplish_green red green
 reddish_green yellowish_green white white_w_green_veins
 greenish_w_red_or_purple_veins
 'greenish,_purple_basally'
 'greenish,_reddish-purple_basall' greenish_brown
 'greenish,_w_red_veins' greenish_w_reddish_purple_margi
 greenish_w_purple_margins green_w_white_veins,
 50 sepal_distribution/ throughout suffused marginal mottled geographic,
 51 sepal_apices/ acuminate acute obtuse rounded 'acuminate-rounded'
 'sub-acute' cuspidate emarginate caudate blunt
 attenuate,
 52 sepal_apex_type/ entire 'mid-rib,_midvein_or_vein',
 53 PETAL_form/ normal foliaceous staminoïd none,
 54 petal_presence/ present absent,
 55 petal_number/ zero three four five six seven eight,
 56 petal_fusion/ separate fused,
 57 'petal_widest_point'/ 'ovate_(25)' 'elliptic-ovate_(375)'
 'elliptic-rhombic-oblong_(5)'
 'elliptic-obovate_(625)' 'obovate_(.75)',
 58 'petal_width_(LxW)'/ filiform linear narrow average broad
 very_broad,
 59 'petal_sides'/ 'elliptic_(curved)' 'oblong-elliptic'
 'oblong_(parallel)' 'rhombic-elliptic',
 60 petal_duration/ persistent deciduous,

61 petal_color/ white yellow cream pink red purple bronze green
'reddish-purple' 'greenish-yellow' 'purplish-black'
brownish_purple 'greenish-purple'
purple_w_greenish_claw
yellow_w_greenish_claw green_w_purple_claw
yellow_w_purple_claw 'yellow-green_w_purple_claw'
white_spotted_w_rose white_w_purple_basally
white_w_basal_red_V olive purplish_green_w_purple_cl,
62 petal_distribution/ throughout spotted geographic,
63 anthocyanins/ yes no fading_to_pink,
64 petal_transverse_posture/ incurved plane recurved undulate
outcurved,
65 petal_vertical_orientation/ erect divergent horizontal divergent
declined,
66 petal_longitudinal_posture/ straight twisted,
67 petal_apices/ acuminate acute obtuse rounded blunt 'sub-acute'
cuspidate apiculate emarginate mucronate,
68 petal_apex_type/ entire 'mid-rib, midvein_or_vein_extens',
69 STAMEN_form/ normal 'petaloid-abortive',
70 stamen_number/ zero 1X 2X_sepals 3X 4X,
71 stamen_fusion/ free adnate_to_tepal,
72 stamen_transverse_posture/ straight incurved slightly_recurved,
73 stamen_vertical_posture/ erect spreading,
74 ANTHERS_dehiscence/ introrse lateral extrorse,
75 POLLEN_shape/ spherical ellipsoid irregular,
76 pollen_aperture/ omniaperturate monosulcate,
77 pollen_ornamentation/ granulate echinate corrugate verrucate
spinulate clavate foveolate reticulate psilate
gemmate,
78 CONNECTIVE_prolongation/ not_prolonged acute truncate dilated round
emarginate obtuse,
79 FILAMENT_color/ green purple whitish_purple reddish_purple
whitish_green 'red-purple-brown' pinkish_white
greenish_yellow white pink brown yellow,
80 pollen_color/ yellow orange olive brownish 'olive-orange' purple
greyish_purple pink yellowish_pale_purple green maroon
'orange-yellow',
81 connective_color/ green pink purple pinkish_purple reddish_purple
brown whitish_green white 'red-purple-brown',
82 stamen_distribution/ throughout pollen_different all_different,
83 PISTIL_form/ normal abortive,
84 OVARY_position/ inferior superior,
85 #_locules/ one three four_to_ten,
86 placentation/ axillary parietal combination,
87 ovary_shape/ conical 'angular-ovoid' ovoid ellipsoid obovoid
'flask-shaped' subglobose 'oval-globose' fusiform
'ovate-conical',
88 'ovary_X-section_shape'/ round ridged angled winged,
89 ovary_ribs/ zero two three four five six seven,
90 ovary_apex/ truncate crowned attenuate obtuse,
91 STYLE_presence/ present absent,
92 STIGMA_number/ three four five six eight ten seven,
93 shape/ linear 'linear-subulate' subulate,
94 'vertical_posture(orie)/ divergent erect,
95 stigma_transverse_posture/ incurved straight recurved,
96 stigma_duration/ deciduous persistent,
97 stigma_size/ very_thin thin average thick,

98 ovary_color/ yellowish_white green purple pink cream_yellow
 white 'reddish-purple' purplish_brown yellow_green
 'red-purple-brown_over_green-red' green_over_purple
 purple_over_green purple_over_yellow purple_over_white
 pink_over_white green_w_purple_disk green_w_yellow_disk
 'green_w_white_disk-green_w_white' yellow_w_black_disk
 'red-purple-brown' black,
 99 ovary_distribution/ throughout spotted striped geographic,
 100 stigma_color/ green purple yellowish_green creamy_white yellow
 yellowish_white pink black 'green_and_purple-red'
 'brownish-violet' 'red-purple-brown' brown
 'purple_out,_green_in' 'brown-purple_out,_yellow_in'
 'purple_out,_yellow_in' 'white,_basally_pink'
 'green_out,_yellow_in' 'pinkish-orange' red,
 101 stigma_distribution/ throughout banded geographic,
 102 PISTIL_distribution/ throughout geographic_by_part all_different,
 103 FRUIT_type/ berry capsule fleshy_capsule,
 104 fruit_dehiscence/ indehiscent basally_absciscent septicidal irregular
 loculicidal dehiscence,
 105 fruit_shape/ conical 'angular-ovoid' ovoid globose obovoid
 elliptic,
 106 fruit_color/ green maroon greenish_yellow rusty_red greenish_white
 red black 'bluish-black' brown purple
 green_w_purple_dots 'purplish-green' 'greenish-brown'
 green_w_brown_ribs 'black-purple' white pink,
 107 fruit_color_distribution/ throughout mottled spotted striped
 geographic,
 108 SEED_arils/ incomplete absent complete,
 109 endosperm_development/ helobial nuclear,
 110 cotyledon_shape/ strap_like leaf_like,
 ;


```

BEGIN ASSUMPTIONS,
  OPTIONS DEFTYPE=unord PolyTcount=MINSTEPS ,
  CHARSET non_morf = 1-8
  CHARSET insufficient = 37 64-67 72 77 79-81 85-86 89-90 93-94 100 105,
  CHARSET subjective = 17 88 97,
  CHARSET numbers = 22 43 55 70 92,
  CHARSET color = 20 32 49 61 79-81 98 100 106,
  CHARSET problematic = 33 90 103-104,

  TAXSET OutGroup = 1,
  TAXSET Paris = 2-34
  TAXSET sessile = 35-57
  TAXSET pedicellate = 58-86,

  EXSET del_non_morf = 1-8, 37 64-67 72 77 79-81 85-86 89-90 93-94 100 105,
  EXSET del_insufficient = 17 88 97,
  EXSET del_subjective = 22 43 55 70 92,
  EXSET del_color = 20 32 49 61 79-81 98 100 106
  EXSET del_problematic = 33 90 103-104,

END,

begin paup
log file=morphology log
set torder=right,
set OutRoot=Monophyl,
Defaults bootstrap nreps=1000 search=heuristic TreeFile=morphology boot,
Defaults ConfTree strict=yes MajorRule=yes Indices=yes TreeFile=morphology consensus,
Defaults Describe Plot=both BrLens=yes ChgList=yes ApoList=yes,
end,

```

APPENDIX D.4

Listing of Indels

Table D1. Indels for the ITS gene sequence data set.

number	location	sequence	taxa
1	bp45	'aat' 'a-t'	<i>T camschatcense</i>
2	bp48	'gah' 'g-h'	all except <i>T rivale</i> and <i>T undulatum</i>
3	bp49	'ahc' 'a-c'	all except <i>T undulatum</i>
4	bp50	'ahc' 'a-c'	all except <i>Paris s l</i>
5	bp82	'aat' 'a-t'	<i>T pusillum</i>
6	bp89	'cct' 'c-t'	<i>T pusillum</i>
7	bp96	'ccmt' 'c--t'	<i>Daiswa</i>
8	bp144	'yrg' 'y-g'	<i>T govanianum</i> , <i>P incompleta</i> , <i>P tetraphylla</i> , <i>T camschatcense</i>
9	bp145	'rgk' 'r-k'	<i>Paris s s</i> , <i>Trillium</i> except for <i>T rivale</i> and <i>T govanianum</i>
10	bp197	'atr' 'a-r'	all except <i>T camschatcense</i>
11	bp202	'rgc' 'r-c'	sessile-flowered <i>Trillium</i>
12	bp205	'cya' 'c-a'	all except <i>D violacea</i>
13	bp209	'ygt' 'y-t'	all except <i>P incompleta</i>
14	bp215	'twg' 't-g'	<i>D fargesii</i> , <i>D polyphylla</i> , <i>D violacea</i> , and <i>T ovatum</i>
15	bp218	'shy' 's-y'	all except <i>D polyphylla</i> and <i>D violacea</i>
16	bp219	'hyg' 'h-g'	all except <i>D fargesii</i>
17	bp232	'btggt' 'b--t'	<i>T rivale</i>
18	bp449	'g ktsra a' 'g ----- a'	all except <i>T rivale</i>
19	bp492	'cct' 'c-t'	<i>T camschatcense</i>
20	bp502	'gagg' 'g--g'	all except <i>T rivale</i>
21	bp518	'gtk' 't--k'	<i>P tetraphylla</i>
22	bp525	'tatg' 't--g'	<i>P incompleta</i>
23	bp601	'dna' 'd-a'	all except <i>D fargesii</i> and sessile-flowered <i>Trillium</i>
24	bp602	'n aact c' 'n ---- c'	<i>T rivale</i>
25	bp611	'wtg' 'w-g'	sessile-flowered <i>Trillium</i>
26	bp612	't gkgacaccca m' 't ----- m'	all except <i>T rivale</i>
27	bp634	'ygct' 'y--t'	<i>T pusillum</i>

Table D2. Indels for the *matK* gene sequence data set.

number	location	sequence	taxa
1	bp15	'a ttacag g' 'a ----- g'	<i>T rivale</i> , <i>Paris s s</i> , pedicellate <i>Trillium</i> except for <i>T govanianum</i>
2	bp51	'a caaaay t' 'a ----- t'	all except for <i>T pusillum</i>
3	bp119	'a tataaa t' 'a ----- t'	<i>T decipiens</i> and <i>T reliquum</i>
4	bp390	'a caaata c' 'a ----- c'	<i>T erectum</i> and <i>T rugelii</i>
5	bp607	'a atttka t' 'a ----- t'	<i>T camschatcense</i> , <i>T erectum</i> and <i>T rugelii</i>
6	bp626	'a atctat t' 'a ----- t'	all except for <i>T petiolatum</i> and <i>T reliquum</i>
7	bp810	'a atagat g' 'a ----- g'	<i>T maculatum</i>

APPENDIX E
TAXA COMPARISONS

Table E1. Trilliaceae versus Liliaceae *sensu stricto*

character	Trilliaceae	Liliaceae
roots	rhizomes	bulbs
leaves	petiolate	not petiolate
venation	palmate & reticulate	parallel
stele	eustele	atactostele
oxalate raphids	present	absent
inflorescence	solitary	cyme or raceme
perianth	sepals & petals	tepals
spotted tepals	absent	present
anthers	basifixed	dorsifixed
style	free	simple
parietal cell tissue	present	absent
ovary type	Allium type	Fritillaria type
nucellus	crassinucellate	teninucellate
embryo sac development	mono- or bi-sporic	tetraspore
polar nuclei	fusing post/simult	fusing prior
fruit	berry or fleshy capsule	dry capsule
endosperm	other	not starchy or little
embryo axis	straight	curved
cotyledon sheath	open	closed
steroid saponins	present	absent
mesophyll crystals	raphids	druses, solitary prismatic
leaves	verticillate	some verticillate
symmetry	actin (radial)	actin & zygo.
nectaries	tepal or septal	tepal
petiole	present or absent	absent
dehiscence	introrse, extrorse, lateral	introrse
placentation	parietal, axile or both	axile
embryo type	rudimentary	linear or rudimentary
endosperm formation	nuclear or helobial	nuclear
embryogeny	onagrad	onagrad, asterad, chenopodiad
stigma	dry	wet or dry
connective prolongation	present or absent	absent
arils	present or absent	absent
flower	hypogynous	hypogenous
ptyxis	supervolute	supervolute
stem vessels	absent	absent
leaf vessels	absent	absent
stipules	absent	absent
microsporogenesis	successive	successive
antipodal cells	not proliferating	not proliferating
gynoecium	syncarpous	syncarpous
habit	autotrophic, perennial herbs	autotrophic, perennial herbs

Table E2. Trilliaceae versus Melanthiaceae

character	Trilliaceae	Melanthiaceae
leaves	petiolate & terminal	basal & sheathing
leaves	verticillate	spirally inserted
venation	palmate & reticulate	parallel
stele	eustele	atactostele
oxalate raphids	present	absent
inflorescence	solitary	panicle, raceme, spike
perianth	sepals & petals	tepals
ovary type	Allium type	Polygonum type
nucellus	crassinucellate	crassinucellate
polar nuclei	fusing post/simultaneously	fusing prior
fruit	berry or fleshy capsule	ventricidal capsule
endosperm	other	not starchy or little
embryo type	rudimentary	linear
embryogeny	onagrad	asterad
antipodal cells	not proliferating	proliferating
gynoecium	syncarpous	apocarpous
roots	rhizomes	rhizome or bulb
nectaries	tepal or sepal	sepal (external)
petiole	present or absent	absent
dehiscence	introrse, extrorse, lateral	extrorse
placentation	parietal, axile or both	axile
endosperm formation	nuclear or helobial	helobial
connective prolongation	present or absent	absent
arils	present or absent	absent
symmetry	actinomorphic (radial)	actinomorphic (radial)
style	free (fused carpels)	free (separate carpels)
spotted tepals	absent	absent
anthers	basifixed	basifixed
stigma	dry	dry
ptyxis	supervolute	supervolute
stem vessels	absent	absent
leaf vessels	absent	absent
stipules	absent	absent
habit	autotrophic, perennial herbs	autotrophic, perennial herbs
embryo sac development	mono- or bi-sporic	mono- or bi-sporic
embryo axis	straight	straight
cotyledon sheath	open	open
steroid saponins	present	present
mesophyll crystals	raphids	raphids

Table E3. Trilliaceae versus *Dioscorea*

character	Trilliaceae	Dioscorea
chromosome number	2n = 10	2n = 60
plant type	herb	vine
foliaceousness	scapose	leafy
plant sexuality	monoclinous	dioecious
inflorescence type	solitary	panicle or spike
number of flowers	one	more than one
flower composition	petals + sepals	tepals
stem habit	erect	twining
leaf location	terminal	cauline
number of whorls	one	more than two or none
sepal and petal form	normal	petaloid
sepal and petal fusion	free	fused
ovary position	superior	inferior
fruit type	berry or fleshy capsule	capsule
number of leaves	three to more than 11	more than 11
leaf arrangement	whorled	whorled, opposite, alternate
petal anthocyanins	present or absent	absent
stamen form	normal	normal or abortive
pistil form	normal	normal or abortive
number of locules	one or three	three
placentation	axile, parietal, or combination	axile
style presence	present or absent	present
seed arils	absent, incomplete, present	absent
sepal and petal number	three to more than eleven	three
root type	rhizome	rhizome
leaf margin	entire	entire
bracts	absent	absent

Table E4. Trilliaceae versus *Medeola* and *Scoliopus*

character	Trilliaceae	<i>Medeola</i>	<i>Scoliopus</i>
chromosome number	2n = 10	2n = 14	2n = 14
inflorescence type	solitary	simple umbel	simple umbel
flower number	one	more than one	more than one
leaf number	three to more than 11	x in the first whorl	two
leaf location	terminal	cauline	basal
leaf arrangement	whorled	spirally inserted	opposite
flower composition	sepals plus petals	tepals	sepals plus petals
root type	rhizome	tuber	rhizome
stem habit	erect to decumbent	erect	decumbent
leaf attachment	sessile to petiolate	sessile to petiolate	sessile
leaf color distribution	throughout, mottled or geographic	throughout	mottled
bracts	absent	present	absent
sepal and petal form	normal	petaloid	normal
sepal and petal number	three to 11 or more	three	three
(base merosity)			
sepal and petal duration	persistent	deciduous	deciduous
anthocyanins	present or absent	absent	present
stamen number	2x-4x base merosity	2x base merosity (6)	1x base merosity (3)
stamen fusion	free	free	adnate to sepal
anther dehiscence	introrse, latrorse, extrorse	extrorse	extrorse
number of locules	one or three	one	one
placentation	axile, parietal, or combination	parietal	parietal
style presence	absent or present	absent	present
stigma duration	persistent	deciduous	persistent
fruit type	berry or fleshy capsule	berry	capsule
seed arils	absent, incomplete or present	absent	absent
endosperm development	nuclear (<i>Paris</i>) helobial (<i>Trillium</i>)	nuclear	nuclear
plant type	herb	herb	herb
foliaceousness	scapose	scapose	scapose
plant sexuality	monoclinous	monoclinous	monoclinous
sepal and petal fusion	free	free	free
ovary position	superior	superior	superior

Table E5. Trilliaceae versus *Amianthium*, *Veratrum*, and *Xerophyllum*

character	Trilliaceae	<i>Amianthum</i>	<i>Veratrum</i>	<i>Xerophyllum</i>
foliaceousness	scapose	subscapose	scapose or leafy	leafy
plant sexuality	monoclinous	monoclinous	polygamous	monoclinous
inflorescence type	solitary	raceme	panicle of racemes	raceme
number of flowers	one	many	many	many
flower composition	sepals + petals	tepals	tepals	tepals
root type	rhizome	bulb	bulb	bulb
leaf location	terminal	basal and reduced cauline	cauline or basal	cauline or basal
leaf arrangement	whorled	spirally inserted	spirally inserted	spirally inserted or alternate
bracts	absent	present	present	present or absent
sepal and petal form	normal	petaloid	petaloid	petaloid
sepal and petal fusion	separate	separate	separate or fused	separate or fused
anthocyanin pigments	present or absent	absent	absent or present	absent
sepal fusion	free	free	adnate to tepal	free
anther dehiscence	introrse, extrorse, latrorse	introrse	extrorse	extrorse
pollen shape	spherical (<i>Trillium</i>) ellipsoid (<i>Paris</i>)	ellipsoid	unknown	ellipsoid
pollen aperture	omniaperturate (<i>Trillium</i>) monosulcate (<i>Paris</i>)	monosulcate	monosulcate	monosulcate
number of locules	one or three	three	three	three
placentation	axile, parietal or combination	axile	axile	axile
fruit type	berry or fleshy capsule	capsule	capsule	capsule
seed arils	complete, incomplete, or absent	absent	absent	absent
ovary position	superior	superior	superior	superior
sepal and petal duration	persistent	persistent	persistent	persistent
plant type	herb	herb	herb	herb

APPENDIX F
PRELIMINARY ANALYSES

This section outlines the reasoning behind the use of *Trillium* (*Pseudotrillium*) *rivale* as the outgroup for the cladistic analyses. It was chosen as the outgroup based on its obvious basal placement in the molecular analyses, its unusual placement in the morphological analysis, and the fact that use of potential outgroups outside the family gave unsatisfactory results. When *T. rivale* was used as the outgroup, there were fewer shortest trees, and the consensus trees from these were better resolved than when other potential outgroups were used.

The problem of potential outgroups being too dissimilar was particularly severe in the morphological analyses. For example, when *Amianthium* was used as the outgroup its dissimilar morphology compared to *Trillium* necessitated the addition of several (approximately 15) characters. It is estimated that initial analyses of Trilliaceae with the morphological data set probably produced more than 100,000 shortest trees. With PAUP 3.1.1, the maximum of 32,760 trees was reached quickly, with PAUP*, over 80,000 trees were saved before overloading the system to the point where it could no longer continue, and there were still over 70,000 trees to swap. In the resulting consensus tree, a grade was present with many of the internal clades as expected (e.g., *T.* subg. *Phyllantherum*, *Paris* s.s.) However, *T. rivale* was basal to the clade containing *Paris* s.l. rather than clustering with any of the *Trillium* (**Figure F1**).

Analyses of molecular data gave a strong indication that *T. rivale* was basal within Trilliaceae, but they also showed that there were problems with trying to use an outgroup outside of the family. Dr. Soichi Kawano reported that with *Paris polyphylla* as the outgroup in a *matK* analysis, *T. rivale* was most basal followed by the rest of the *Paris* s.l. taxa. When I made an analysis with the *matK* sequences using *Veratrum maackii* as outgroup, in excess of 250,000 trees were produced. The strict consensus of the first

250,000 trees is given in **Figure F2**. *Trillium rivale* was basal to all other taxa in this tree. As in the morphological analysis, several well defined species groups were evident. Unlike the *matK* data, the ITS sequence data produced only 6 trees, but there were fewer taxa involved in this analysis. With *V. maackii* as outgroup, ITS sequences could not be reliably aligned because of the amount of dissimilarity between it and all Trilliaceae. The ingroup taxa, however, were relatively easy to align to one another. As with the *matK* sequences, with *V. maackii* as outgroup in the ITS analysis, *T. rivale* was placed in a basal position relative to the rest of the ingroup taxa (**Figure F3**)

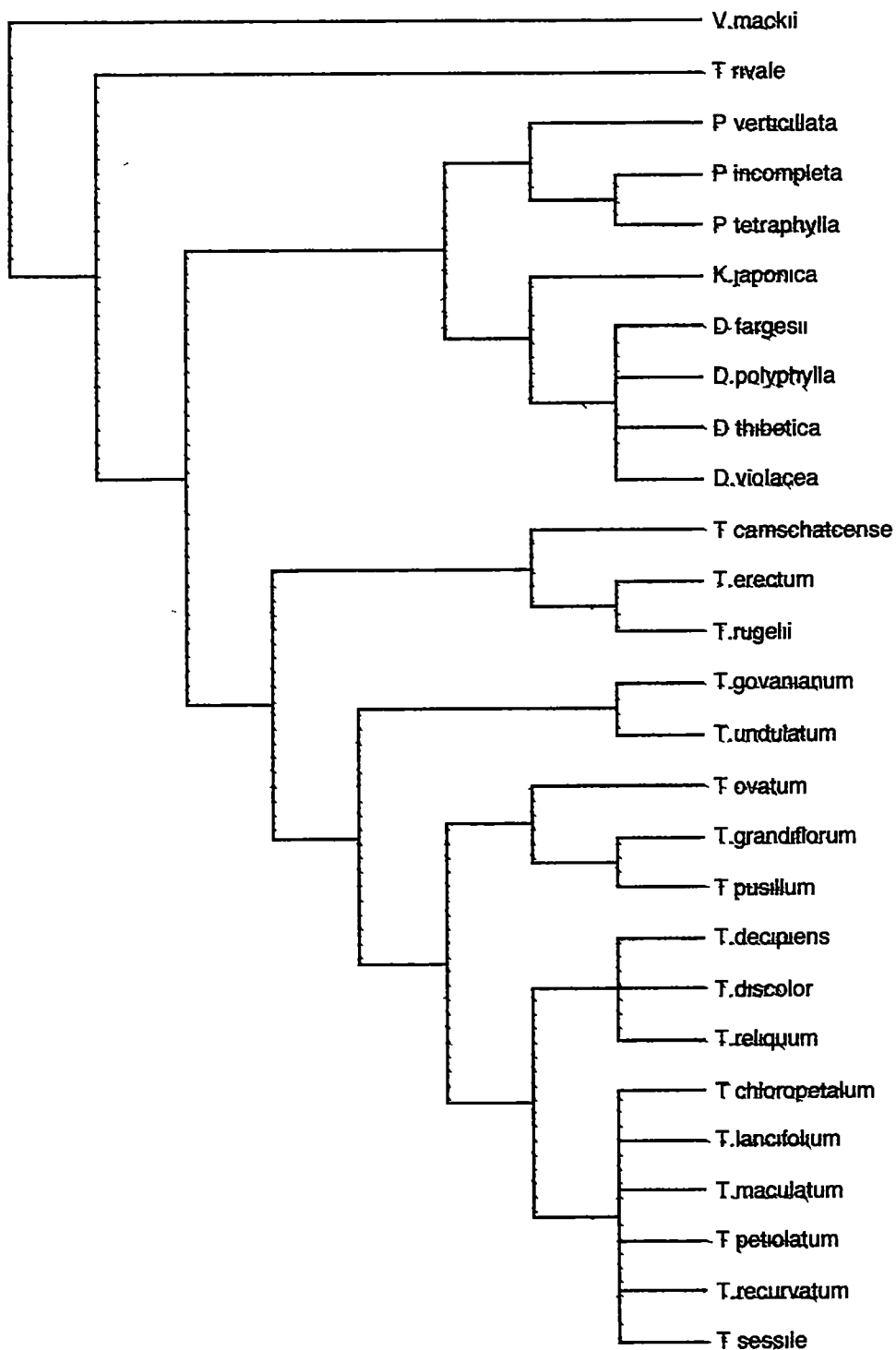


Figure F1. Strict consensus tree from the ITS analysis of Trilliaceae with *V. maackii* as outgroup.

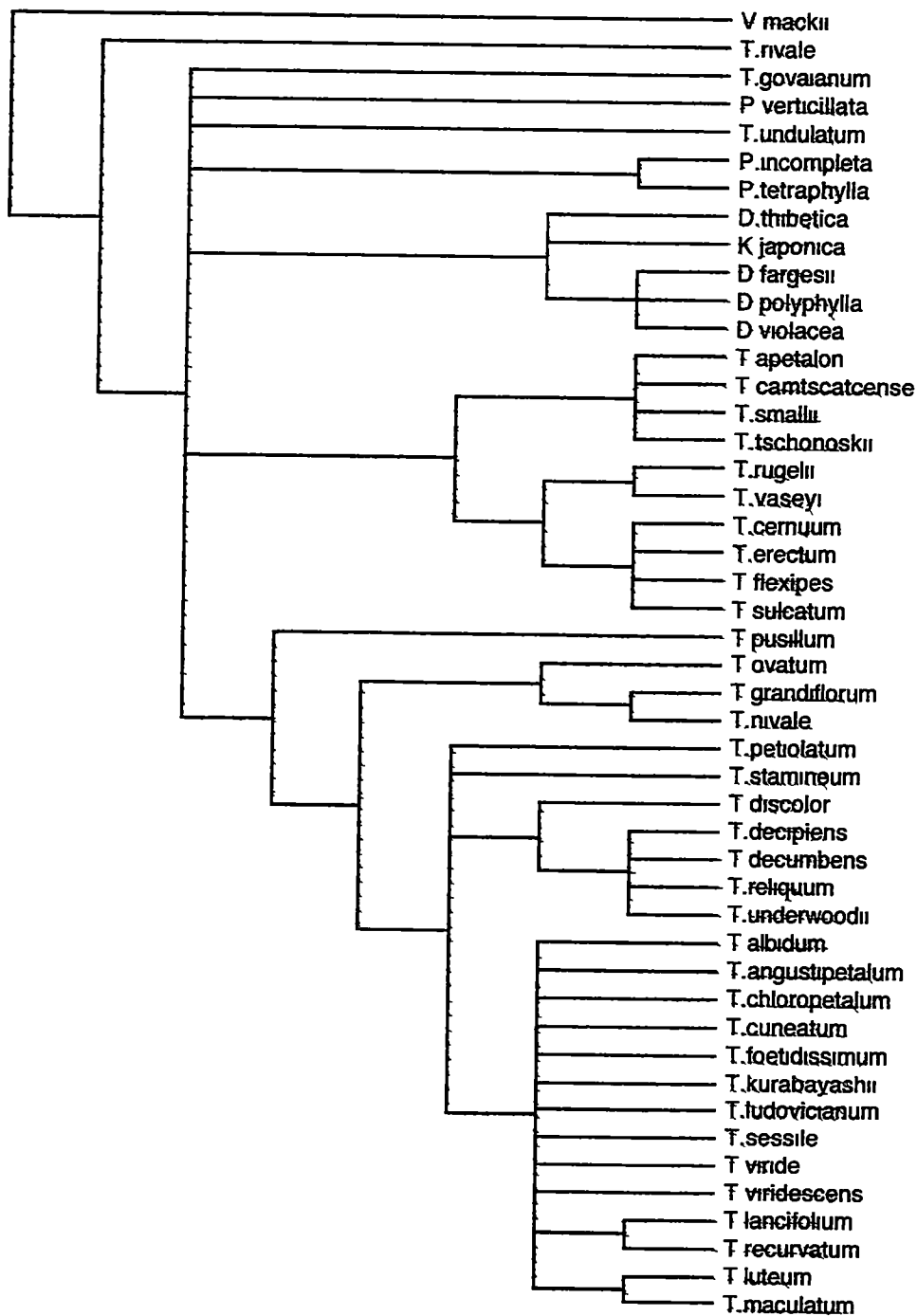


Figure F2. Strict consensus tree from the full *matK* molecular analysis of Trilliaceae with *V. maackii* as outgroup.

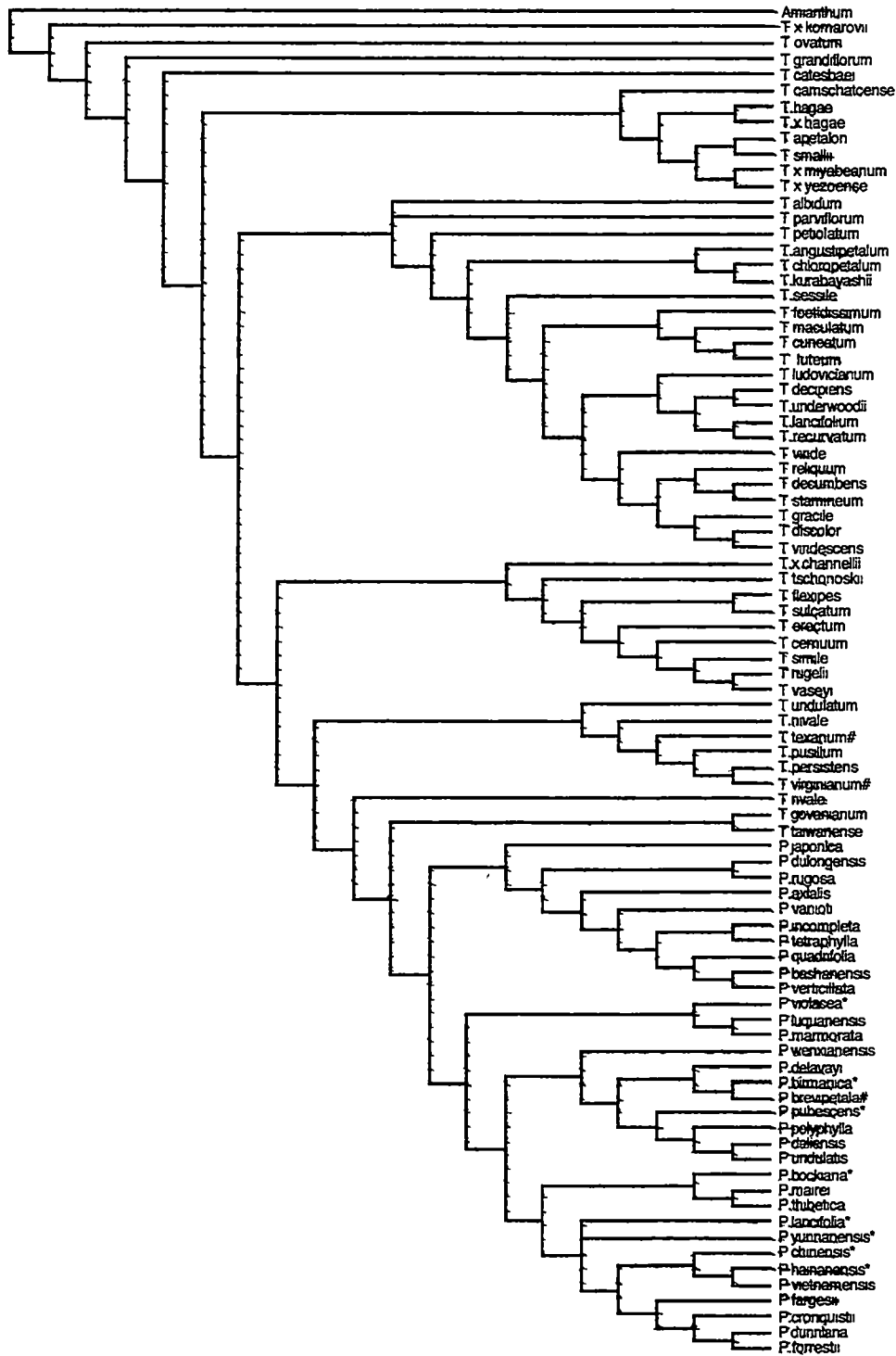


Figure F3. Strict consensus tree from the earlier morphological analysis of Trilliaceae with *A. muscaetoxicum* as outgroup.

APPENDIX G
FULL ANALYSIS

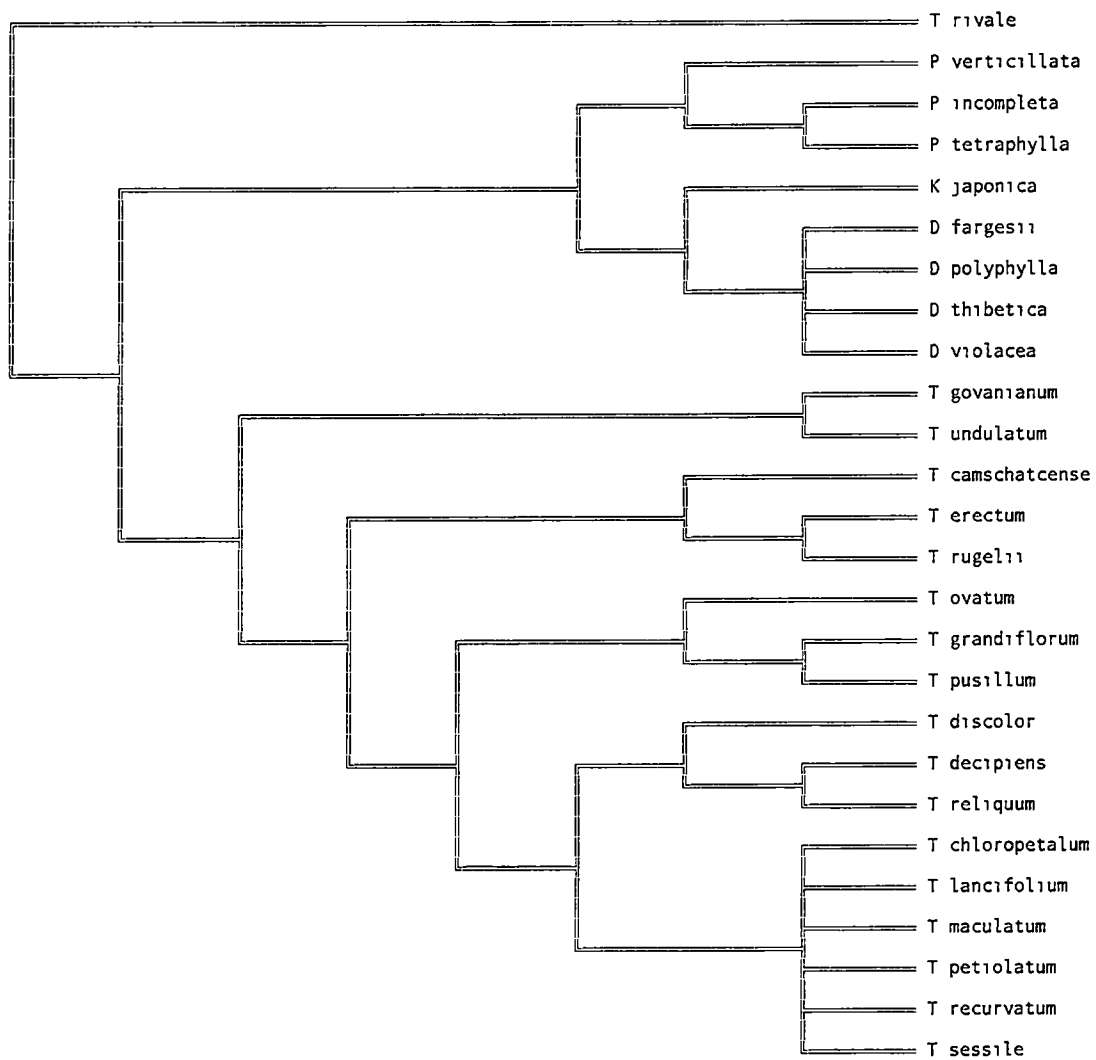
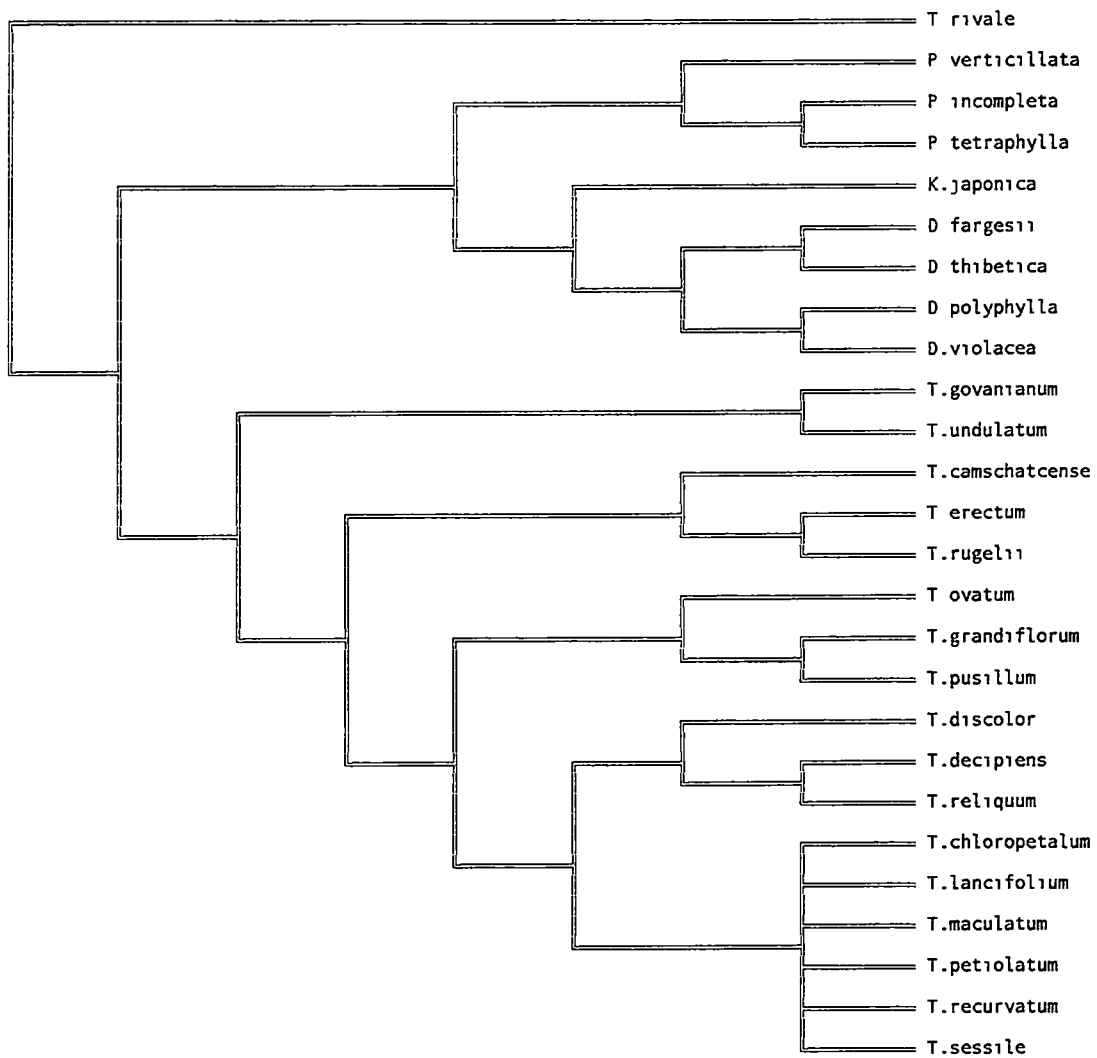


Figure G1. Strict consensus tree from the ITS analysis of Trilliaceae.

3



Heuristic search completed
 Total number of rearrangements tried = 5603
 Score of best tree(s) found = 2755.66433

Figure G2. Maximum likelihood tree from the ITS analysis of Trilliaceae.

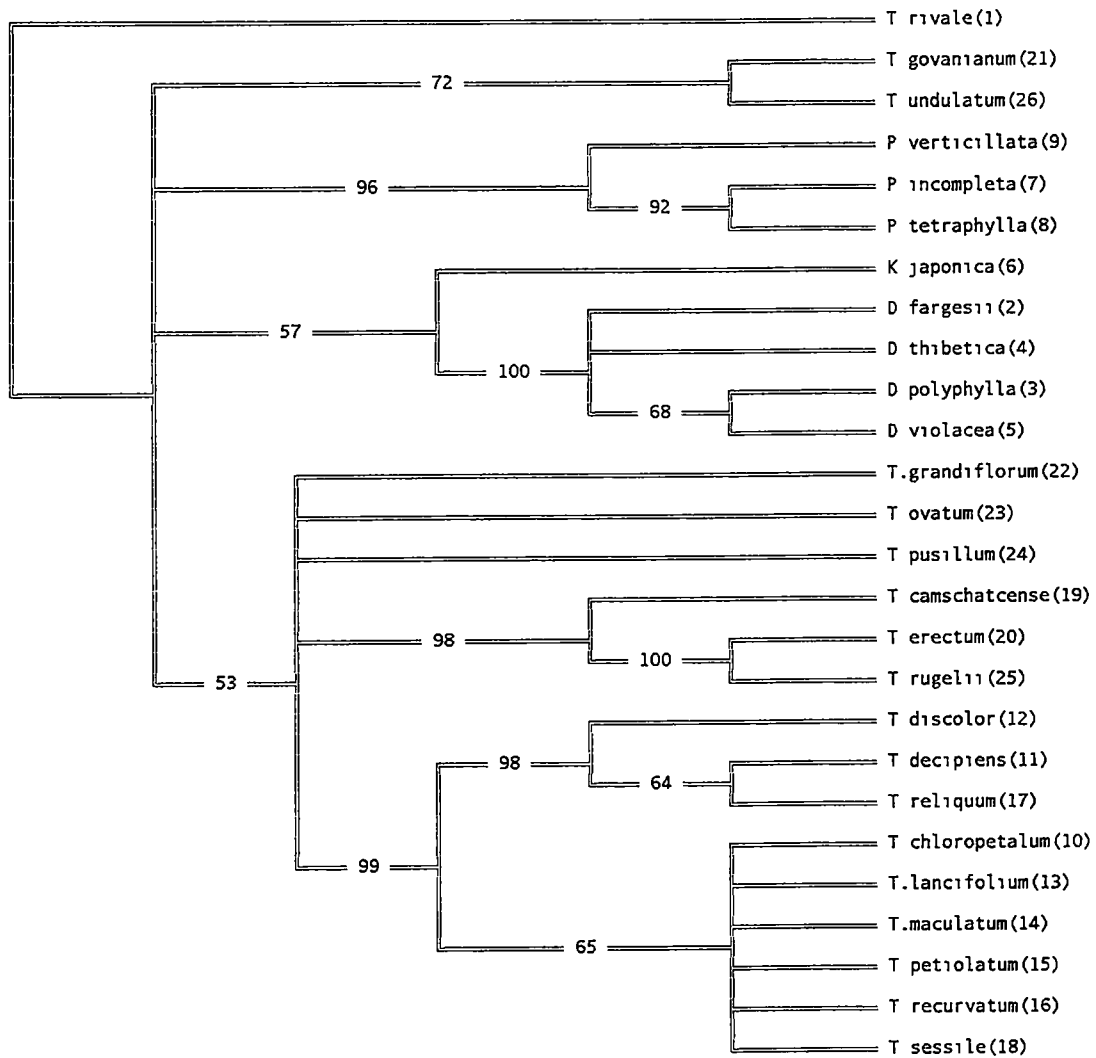


Figure G3. Bootstrap tree from the ITS analysis of Trilliaceae.

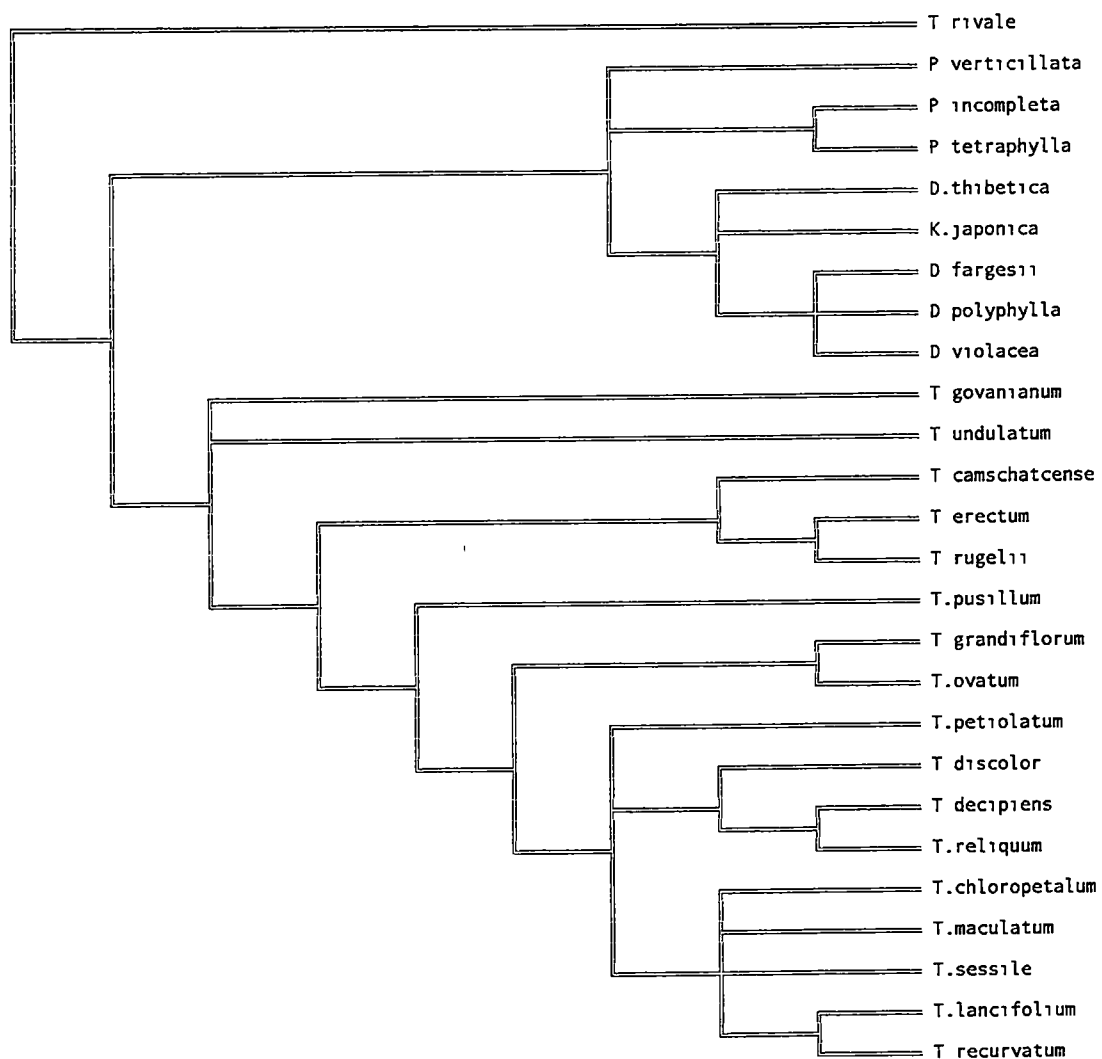
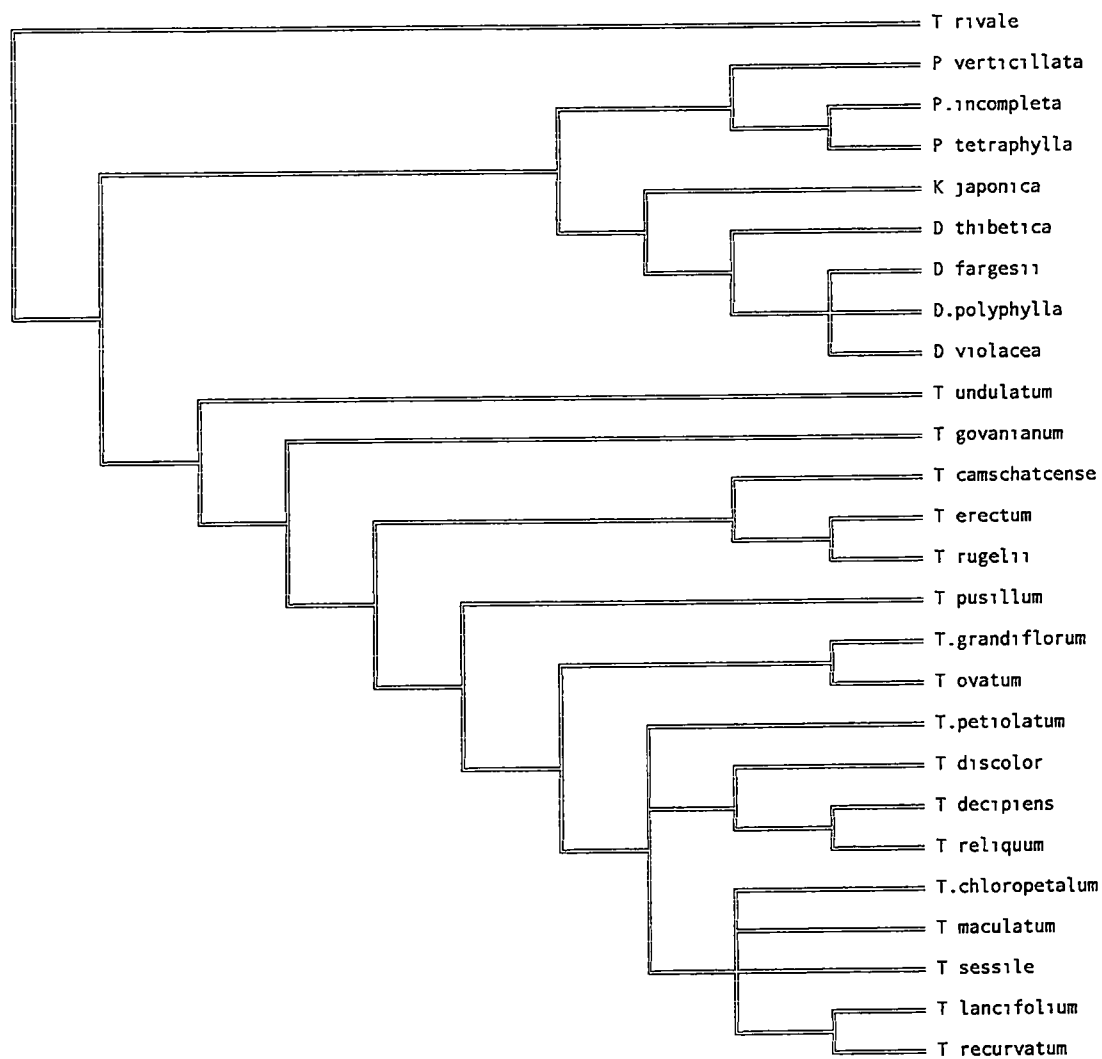


Figure G4. Strict consensus tree from the *matK* analysis of Trilliaceae.



Heuristic search completed
 Total number of rearrangements tried = 6624
 Score of best tree(s) found = 2941 08701

Figure G5. Maximum likelihood tree from the *matK* analysis of Trilliaceae.

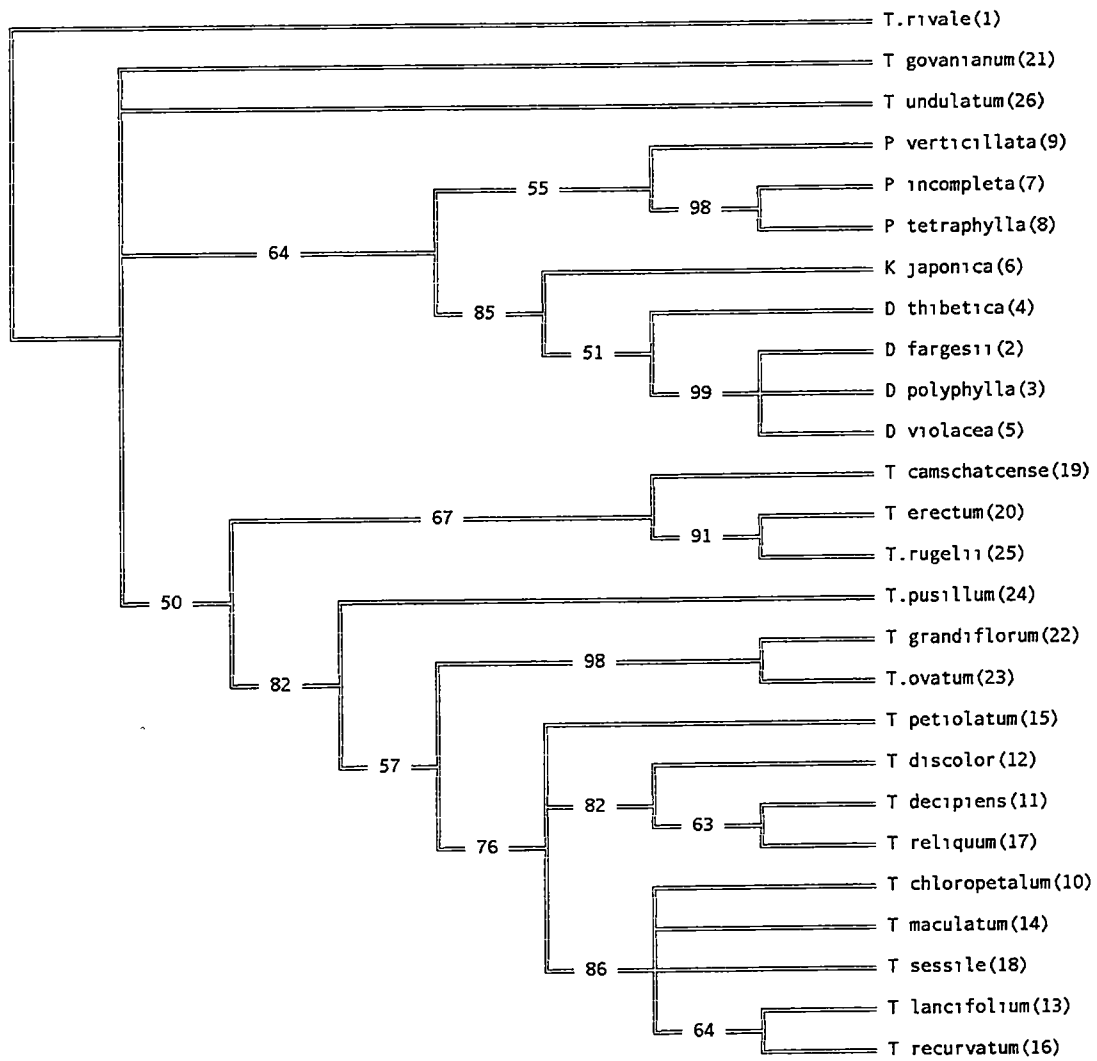


Figure G6. Bootstrap tree from the *matK* analysis of Trilliaceae.

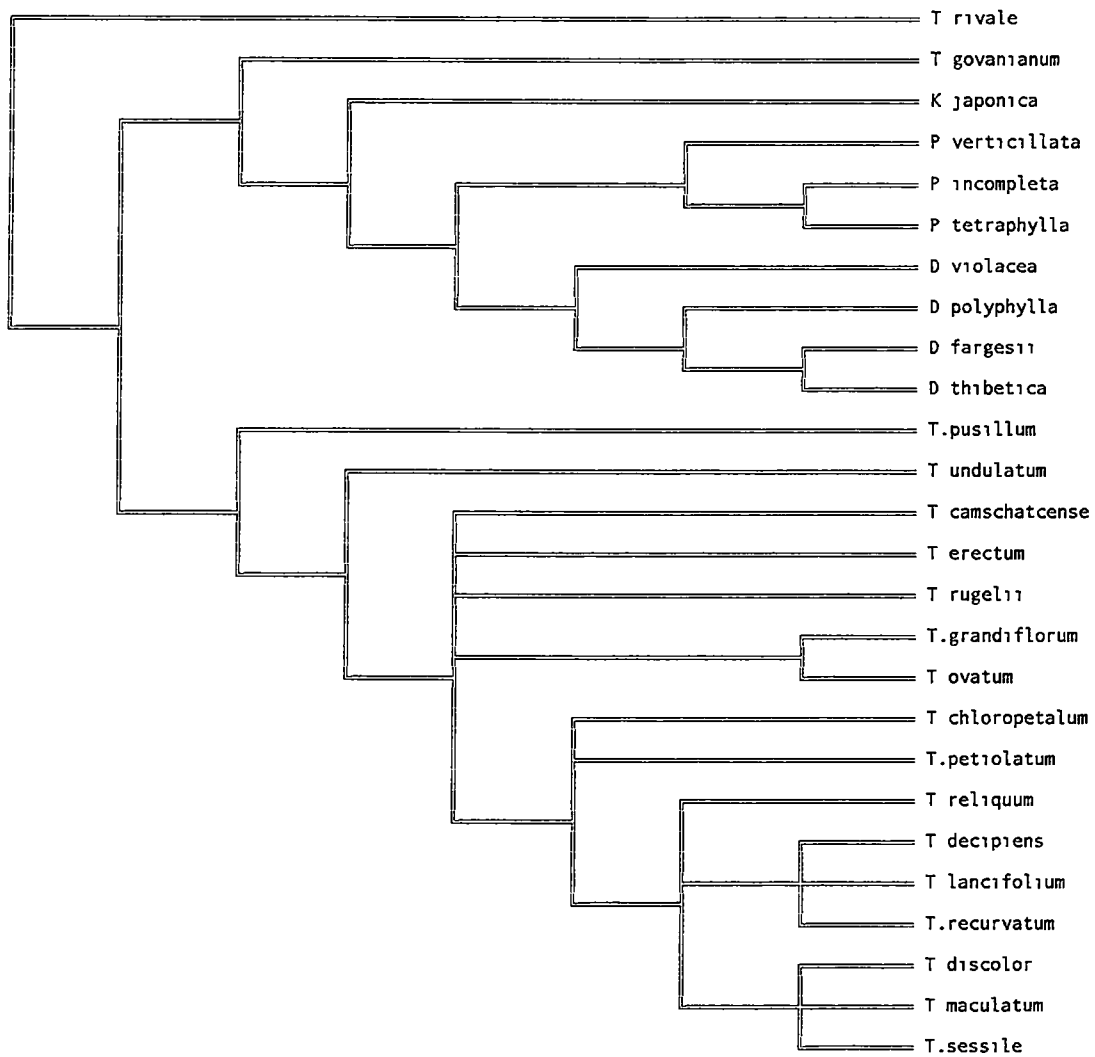


Figure G7. Strict consensus from the small morphological analysis of Trilliaceae.

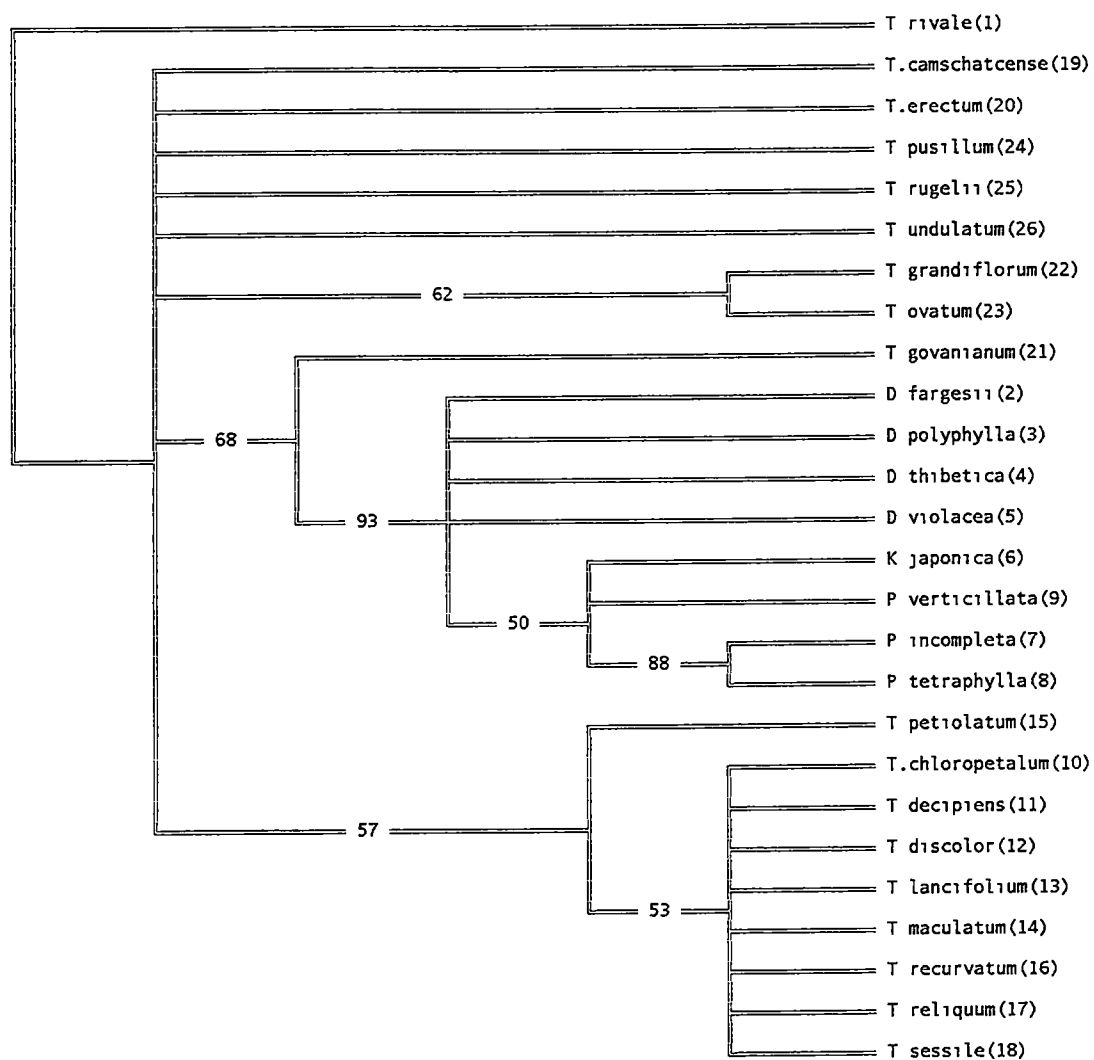


Figure G8. Bootstrap from the small morphological analysis of Trilliaceae.

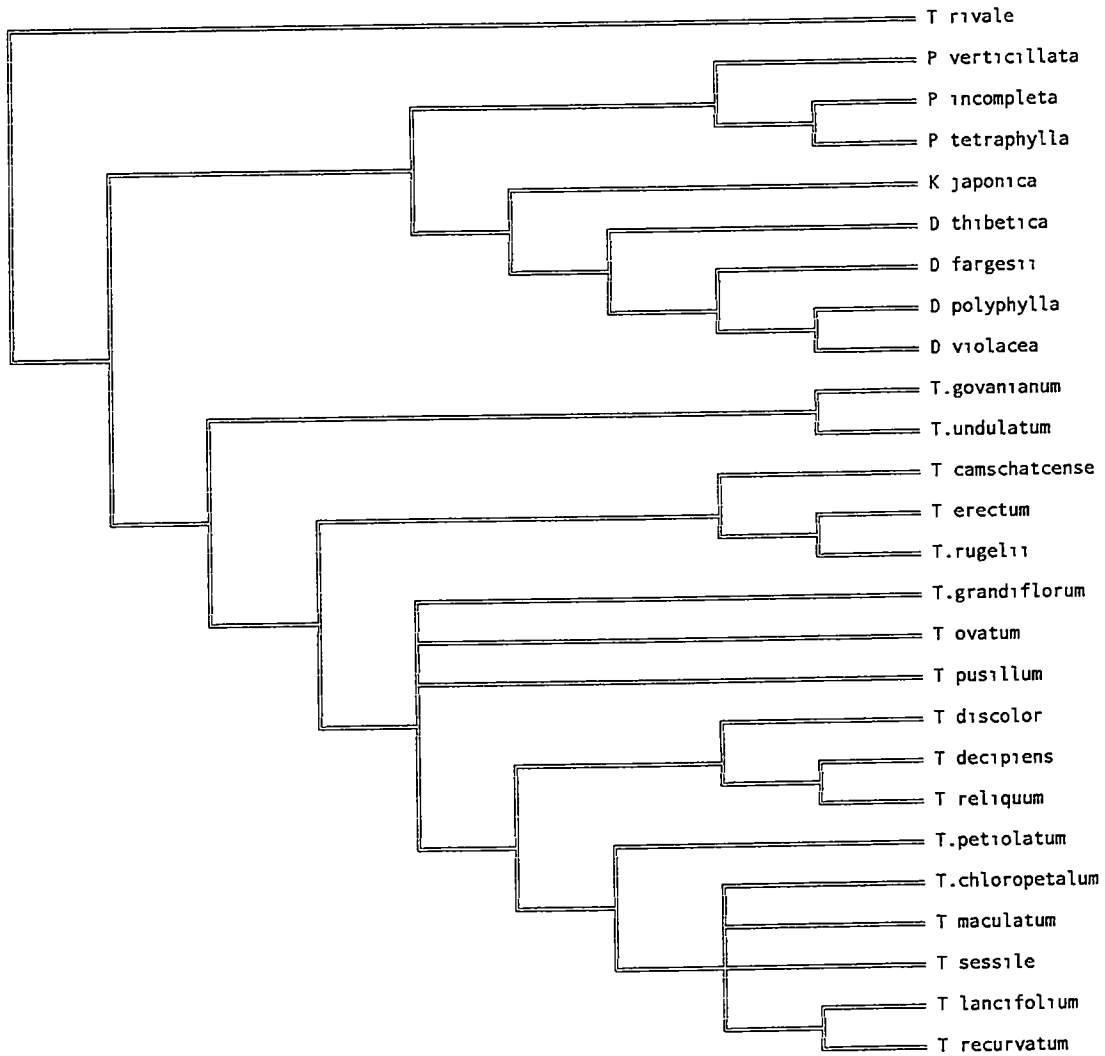
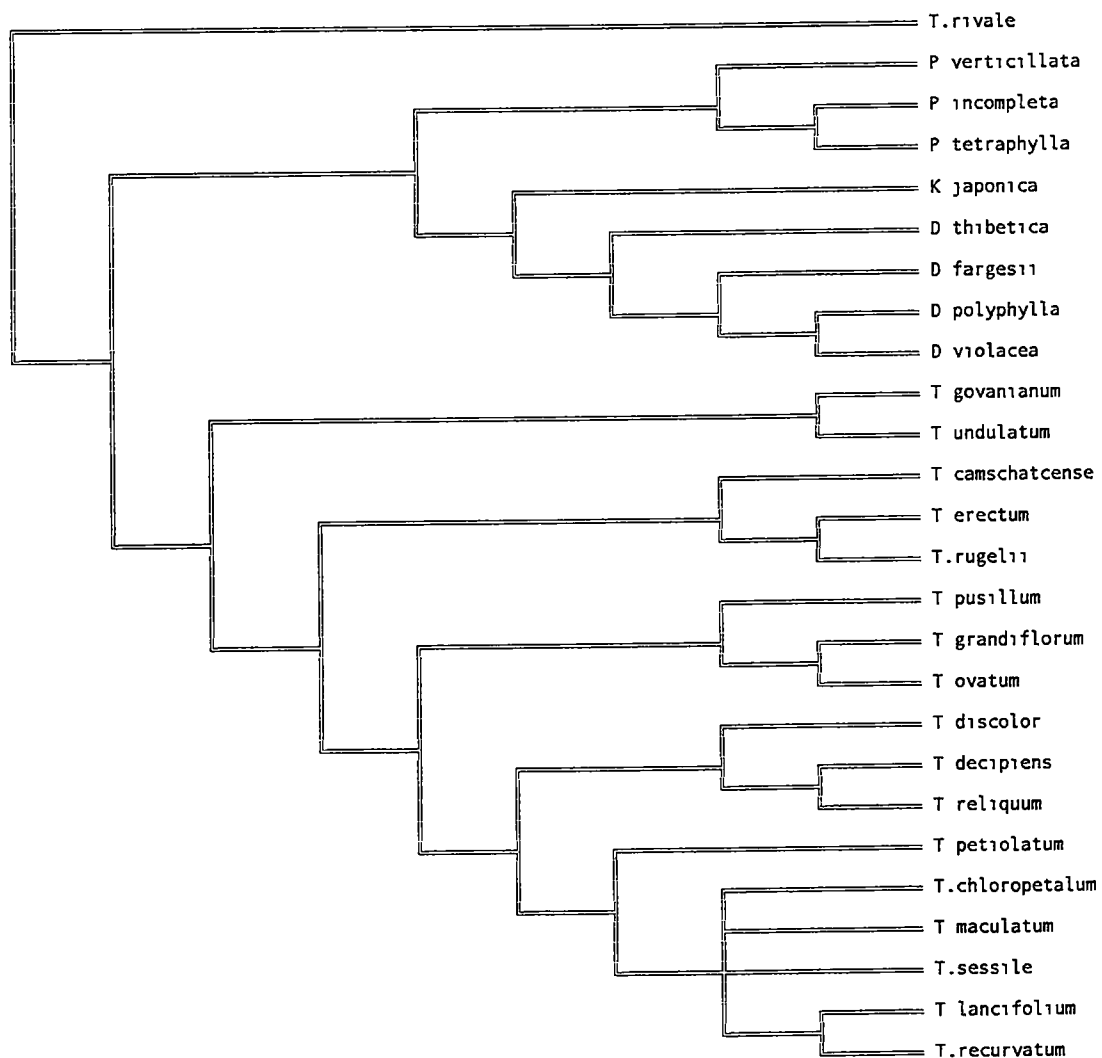


Figure G9. Strict consensus tree from the ITS-*matK* analysis of Trilliaceae.



Heuristic search completed
 Total number of rearrangements tried = 5772
 Score of best tree(s) found = 6013.46004

Figure G10. Maximum likelihood tree from the ITS-*matK* analysis of Trilliaceae.

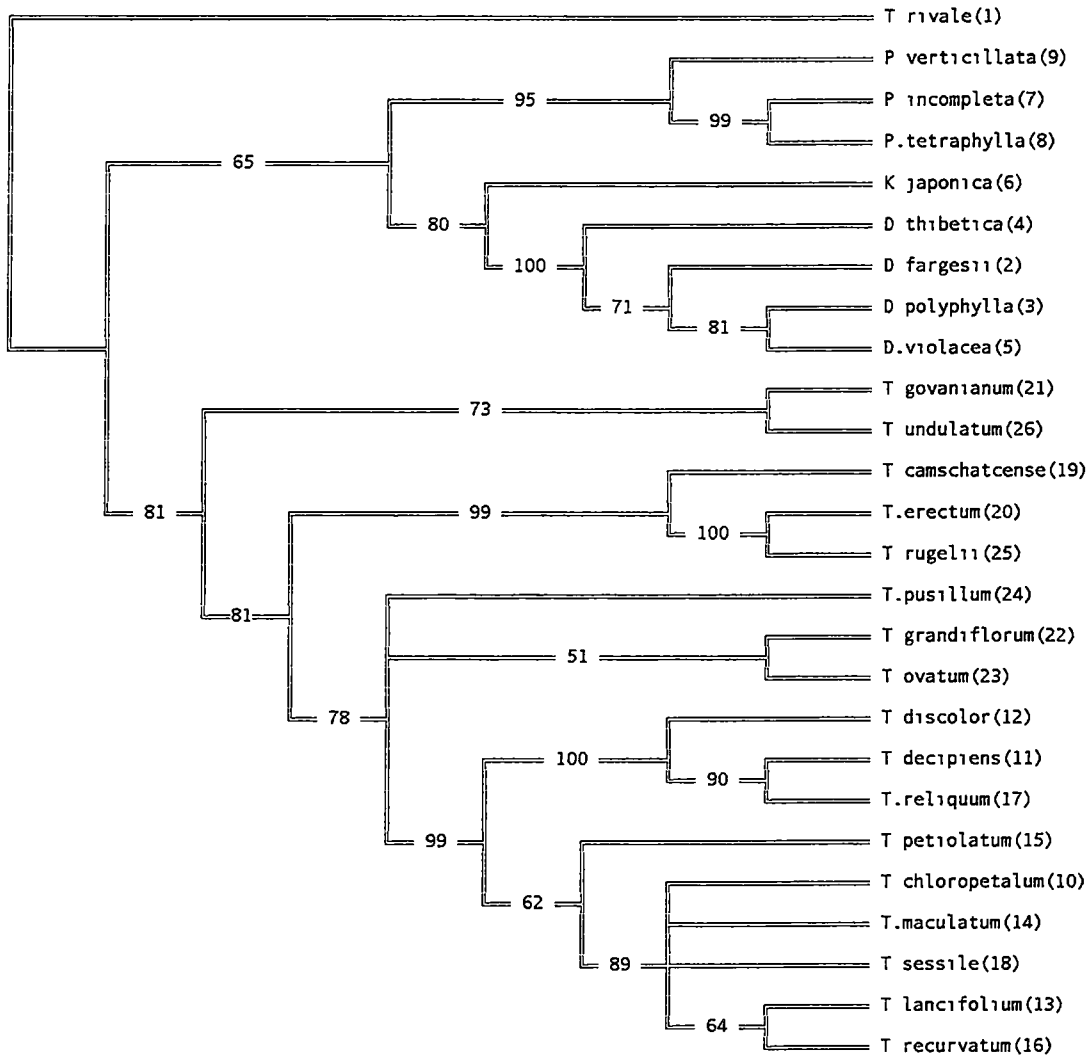


Figure G11. Bootstrap tree from the ITS-*matK* analysis of Trilliaceae.

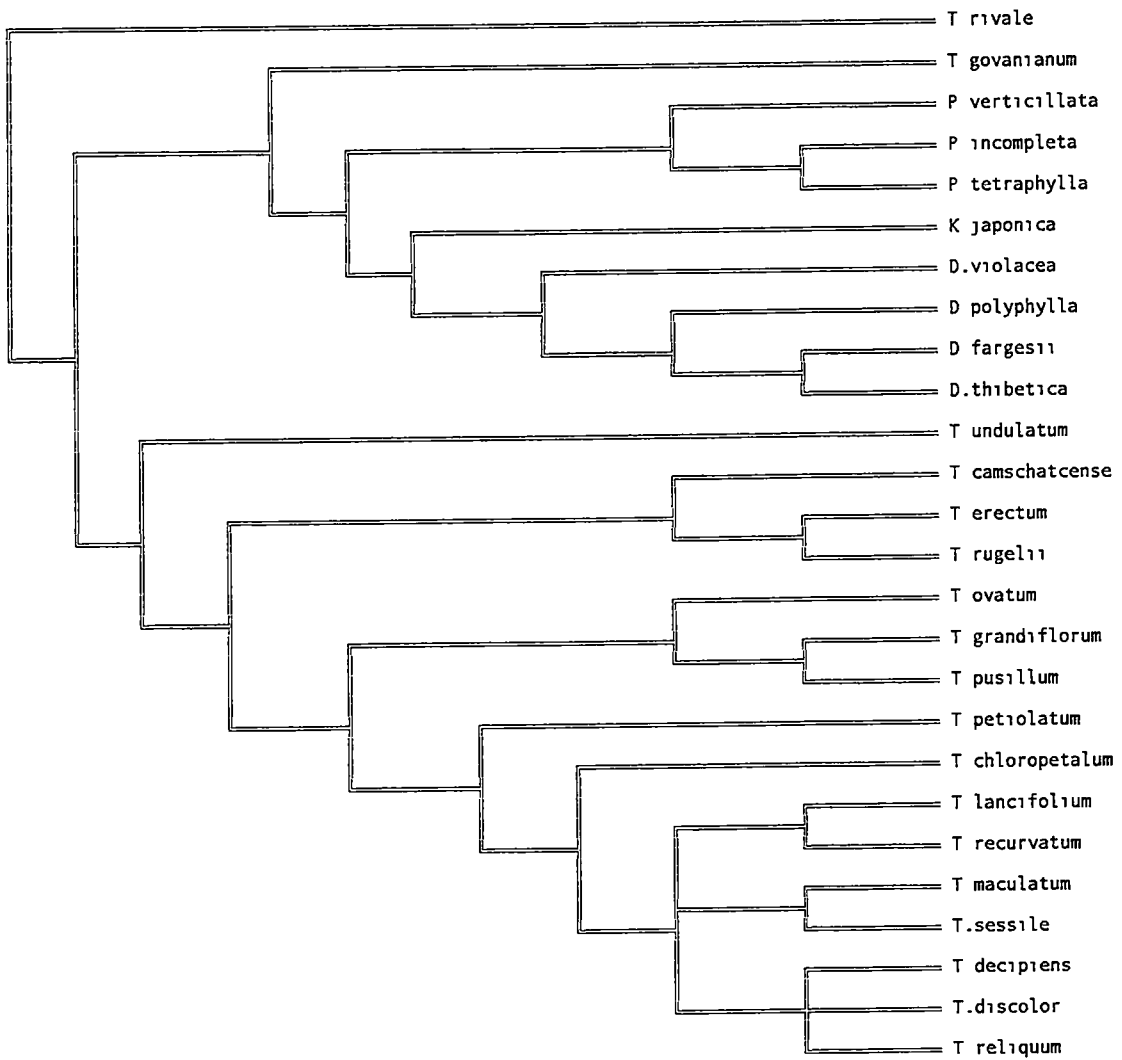


Figure G12. Strict consensus tree from the ITS-morphological analysis of Trilliaceae.

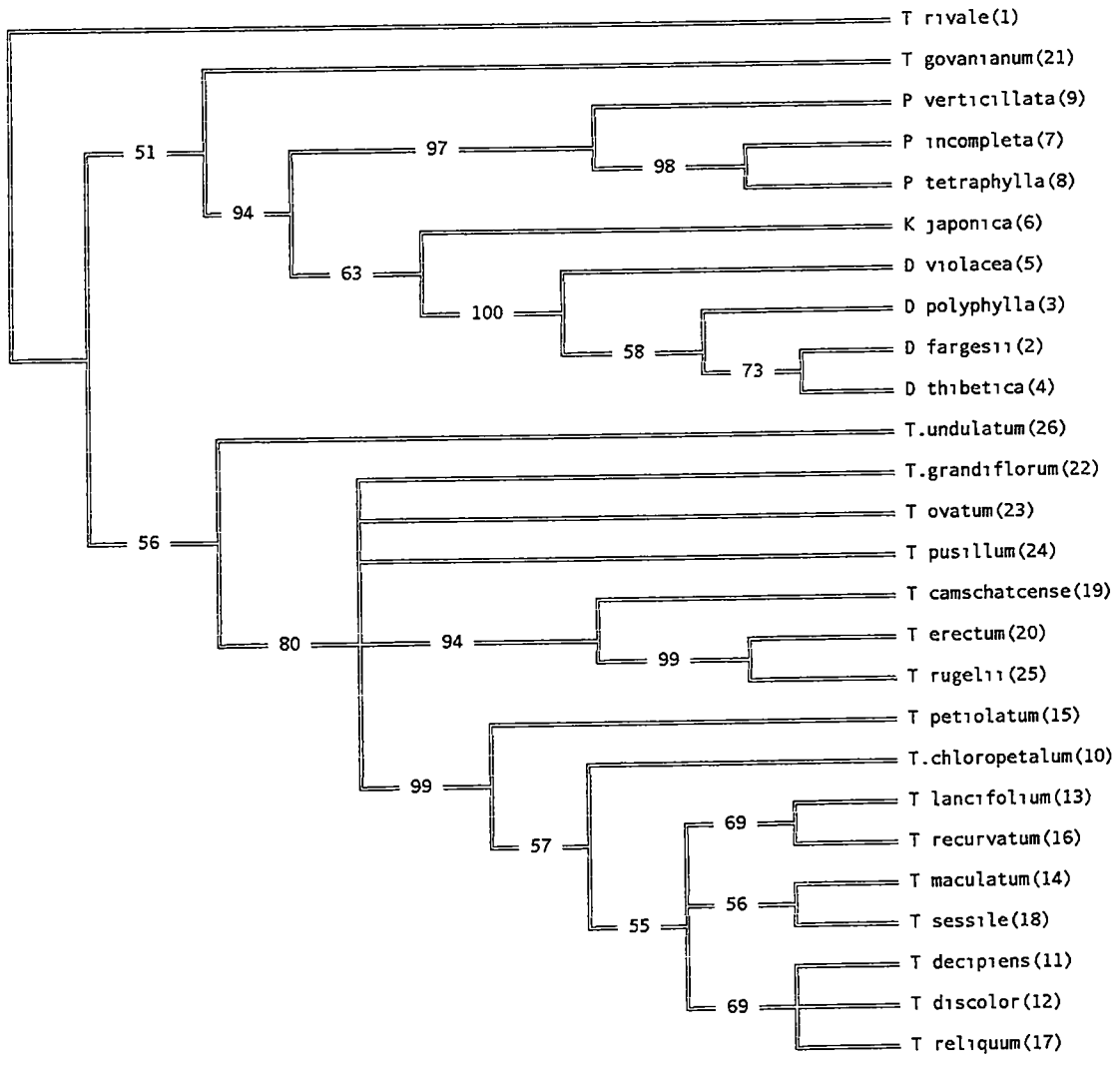


Figure G13. Bootstrap tree from the ITS-morphological analysis of Trilliaceae.

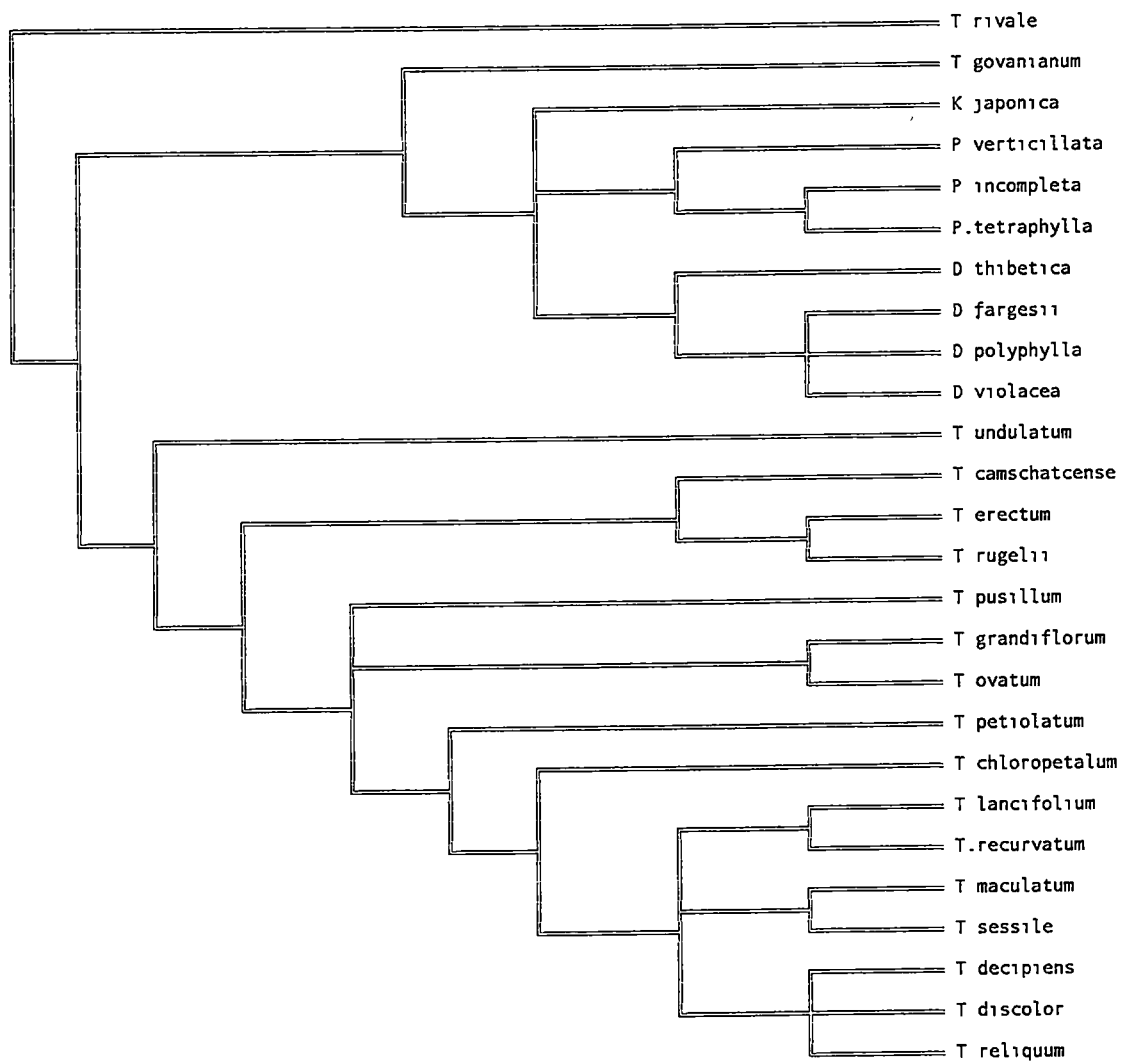


Figure G14. Strict consensus tree from the *matK*-morphological analysis of Trilliaceae.

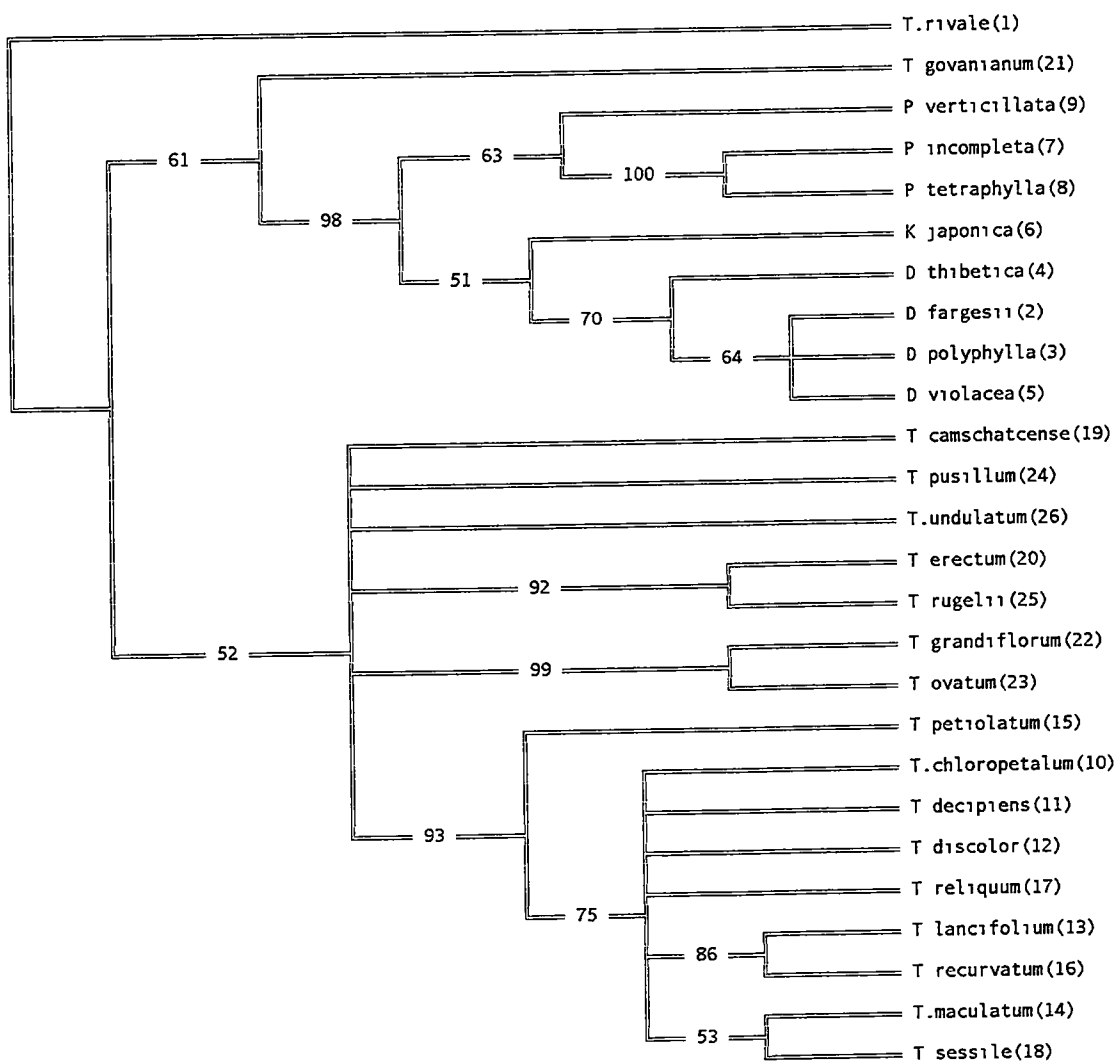


Figure G15. Bootstrap tree from the *matK*-morphological analysis of Trilliaceae.

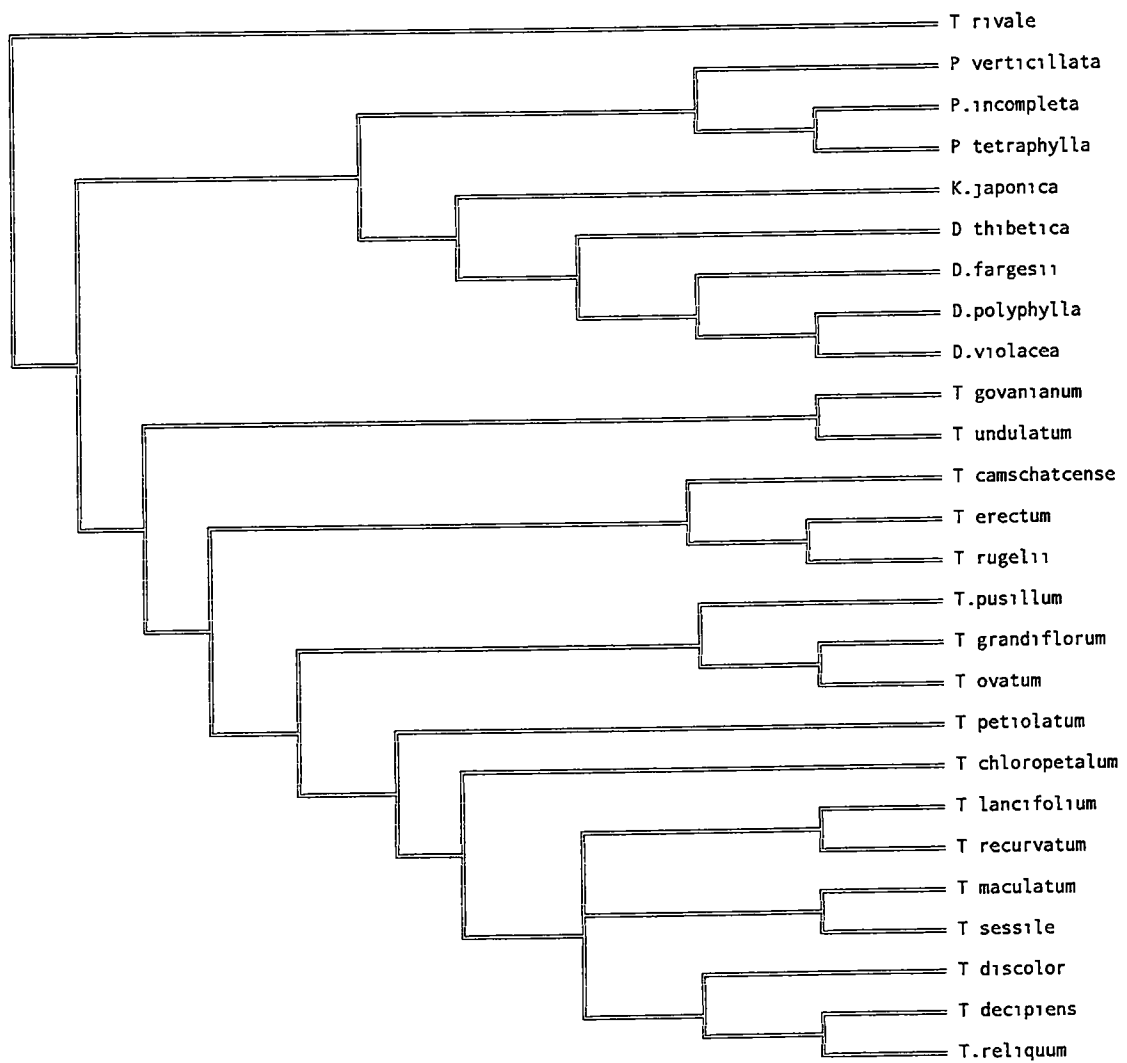


Figure G16. Strict consensus tree from the combined analysis of Trilliaceae.

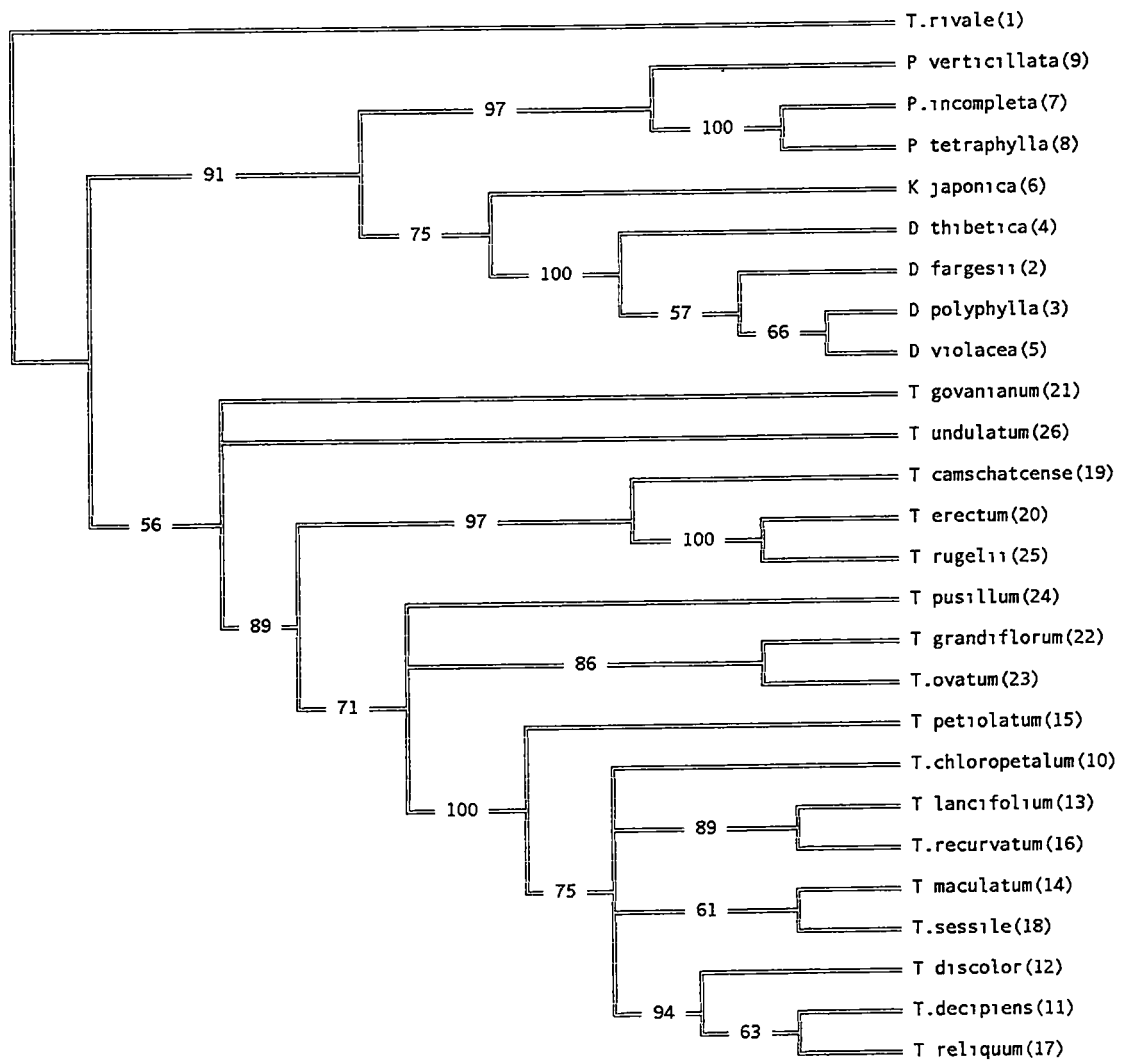


Figure G17. Bootstrap tree from the combined analysis of Trilliaceae.

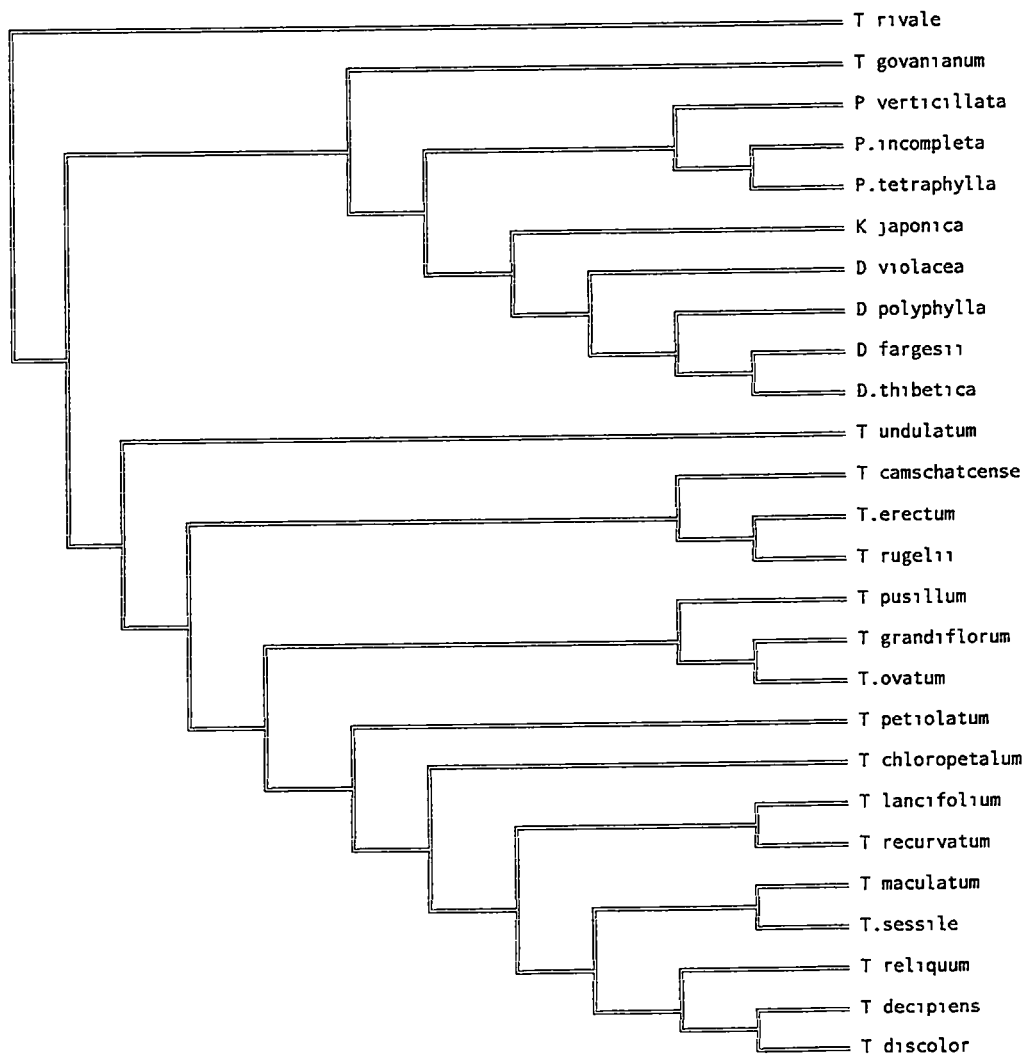


Figure G18. Putative correct tree for Trilliaceae.

VITA

Susan Baker Farmer was born in Chattanooga, Tennessee on 30 July 1953 and moved to Knoxville approximately two years later where she has lived ever since. She graduated 16th in her class from Halls High School in June, 1971 and entered the University of Tennessee that fall. She graduated in 1978 with a B.A. in Computer Science and worked for a reliability assessment and risk engineering firm for a number of years before she is married to John Farmer, Jr. of Clinton, Tennessee and the mother of Thomas. After having spent many years with the spring flora of the region, she entered the Master's program at the University of Tennessee where she attended graduate classes, carried out research, and taught Biology for non-majors. She was awarded her Masters of Science in Botany in May, 2000.

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