

2006

A Synopsis of Melanthiaceae (Liliales) with Focus on Character Evolution in Tribe Melanthieae

Wendy B. Zomlefer
University of Georgia

Walter S. Judd
University of Florida

W. Mark Whitten
University of Florida

Norris H. Williams
University of Florida

Follow this and additional works at: <http://scholarship.claremont.edu/aliso>



Part of the [Botany Commons](#)

Recommended Citation

Zomlefer, Wendy B.; Judd, Walter S.; Whitten, W. Mark; and Williams, Norris H. (2006) "A Synopsis of Melanthiaceae (Liliales) with Focus on Character Evolution in Tribe Melanthieae," *Aliso: A Journal of Systematic and Evolutionary Botany*: Vol. 22: Iss. 1, Article 44. Available at: <http://scholarship.claremont.edu/aliso/vol22/iss1/44>

A SYNOPSIS OF MELANTHIACEAE (LILIALES) WITH FOCUS ON CHARACTER EVOLUTION IN TRIBE MELANTHIEAE

WENDY B. ZOMLEFER,^{1,4} WALTER S. JUDD,² W. MARK WHITTEN,³ AND NORRIS H. WILLIAMS³

¹Department of Plant Biology, University of Georgia, 2502 Miller Plant Sciences, Athens, Georgia 30602-7271, USA;

²Department of Botany, University of Florida, PO Box 118526, Gainesville, Florida 32611-8526, USA
(wjudd@botany.ufl.edu); ³Department of Natural Sciences, Florida Museum of Natural History, University of Florida,
PO Box 117800, Gainesville, Florida 32611-7800, USA (whitten@fmnh.ufl.edu), (orchid@fmnh.ufl.edu)

⁴Corresponding author (wendyz@plantbio.uga.edu)

ABSTRACT

Melanthiaceae s.l. comprises five tribes: Chionographideae, Heloniadeae, Melanthieae, Parideae, and Xerophylleae—each defined by distinctive autapomorphies. The most morphologically diverse tribe Melanthieae, now with seven genera, had not been subject to rigorous phylogenetic character study prior to the current series of investigations that also include an overview of the family. Data from our publications and studies underway are here assessed and integrated, providing a useful overview of Melanthiaceae, and especially of Melanthieae. The results of parsimony analyses of ITS (nuclear ribosomal) and *trnL*-F (plastid) DNA sequence data correlate with potentially synapomorphic phenotypic characters for genera of Melanthieae, including habit form, rootstock type, bulb shape, inflorescence structure, indumentum type, tepal shape, nectary morphology, and ovary position. Sequence data also correlate well with the pattern of variation in chromosome number. The molecular and morphological data support generic recircumscription in Melanthieae and also validate several generalizations concerning character evolution within the tribe, as well as among the tribes of the family.

Key words: *Amianthium*, character evolution, ITS, Liliales, Melanthiaceae, *Schoenocaulon*, *Stenanthium*, *Trillium*, *trnL*-F, *Veratrum*, *Zigadenus*.

INTRODUCTION

Recent molecular studies over the past decade (e.g., Chase et al. 1995a, b, 2000; Rudall et al. 2000; Soltis et al. 2000; Hilu et al. 2003; Davis et al. 2004) have resulted in reevaluation of monocot phylogeny, particularly of the polyphyletic Liliaceae s.l., the “petaloid” or “lilioid monocots”—so named because the flowers have conspicuous petaloid tepals and, therefore, superficially resemble true lilies (species of *Lilium* L.). These reassessments include revision of Melanthiaceae, a family with a long history of problematic circumscription (comprehensive summaries in Zomlefer 1997a and Zomlefer et al. 2001). Before availability of DNA sequence data, the most contemporary treatment of the family by Dahlgren and associates (Dahlgren and Clifford 1982; Dahlgren et al. 1985) divided the family into six tribes, some now shown to be misplaced and/or polyphyletic (Table 1). As defined here, Melanthiaceae sensu the Angiosperm Phylogeny Group II (APG II 2003) comprise 11–16 genera (ca. 154–201+ spp.) of predominately woodland and/or alpine perennial herbs occurring mainly in the temperate to Arctic zones of the Northern Hemisphere, with one species of *Schoenocaulon* A. Gray extending into South America (Table 2). The family likely arose during the Cretaceous (estimated age ca. 46–62 million years), a hypothesis postulated by Vinnersten and Bremer (2001). Many taxa exhibit “Tertiary” disjunct biogeographical patterns, as for example *Helonias* L. s.l. (Appalachians/eastern Asia), *Trillium* L. (eastern/western North America/eastern Asia), *Xerophyllum* Michx. (eastern/western North America), and sister-pair *Chamaelirium* Willd./*Chionographis* Maxim. (Appalachians/

eastern Asia; Zomlefer 1996, 1997a; see also Li 1952; Wood 1971; Wu 1983).

Melanthiaceae are divided into five well-defined tribes: Chionographideae, Heloniadeae, Melanthieae, Xerophylleae, and the segregate family Trilliaceae as tribe Parideae (Table 2). Alternatively, other taxonomists have suggested segregate familial status for these morphologically distinct “tribal” clades: Chionographideae, Heloniaceae s.s. or s.l. (the latter including Chionographideae), Xerophyllaceae (Takhtajan 1994, 1997) along with the segregate Trilliaceae—leaving a very restricted Melanthiaceae s.s. consisting of only tribe Melanthieae (see Zomlefer 1997a). Currently, the expanded circumscription has the morphological support of extrorse anthers and ovaries often with three distinct styles (Rudall et al. 2000) and merits further study. Table 2 summarizes the salient features of these monophyletic tribes, including hypothesized synapomorphies.

The relationship of the tribes, shown in Fig. 1, has been strongly supported by a series of independent investigations of higher level taxa incorporating *rbcL*, *atpB*, *matK*, 18S rDNA, and *trnL*-F molecular data (e.g., Chase et al. 1993, 1995a, b, 2000; Duvall et al. 1993; Fuse and Tamura 2000; Rudall et al. 2000; Soltis et al. 2000; Zomlefer et al. 2001; Hilu et al. 2003; Davis et al. 2004), as well as cladistic analyses of morphological characters (Goldblatt 1995). These studies place Melanthiaceae in the Liliales, sister to the Liliaceae/Smilacaceae s.l. clade (Rudall et al. 2000; Soltis et al. 2000). Within Melanthiaceae (Fig. 1), Melanthieae is sister to the rest of the family, and Parideae (Trilliaceae) and Xerophylleae comprise a clade sister to the Heloniadeae/Chionographideae clade.

Table 1. Circumscription of Melanthiaceae (and Trilliaceae) sensu Dahlgren and associates (Dahlgren and Clifford 1982; Dahlgren et al. 1985), showing the subsequent placement of these genera by APG II (2003). See Zomlefer (1997a–c, 1999) and Reveal and Zomlefer (1998) for summaries. ? = genus tentatively included by Dahlgren.

Dahlgren Tribe (if in Melanthiaceae), Family, Order	Angiosperm Phylogeny Group II Tribe (if in Melanthiaceae), Family, Order
1. Chionographideae, Melanthiaceae, Liliales – <i>Chamaelirium</i> , <i>Chionographis</i>	1. Chionographideae, <u>Melanthiaceae</u> , Liliales
2. Melanthieae, Melanthiaceae, Liliales – <i>Amianthium</i> , <i>Melanthium</i> , <i>Schoenocaulon</i> , <i>Stenanthium</i> , <i>Veratrum</i> , <i>Zigadenus</i> s.l.	2. Melanthieae, <u>Melanthiaceae</u> , Liliales
3. Narthecieae, Melanthiaceae, Liliales – <i>Aletris</i> , <i>Helonias</i> , <i>Heloniopsis</i> , <i>Lophiola</i> ?, <i>Metanarthecium</i> , <i>Narthecium</i> , <i>Nietneria</i>	–NA–, Nartheciaceae, Dioscoreales – <i>Aletris</i> , <i>Lophiola</i> , <i>Metanarthecium</i> , <i>Narthecium</i> , <i>Nietneria</i>
4. Petrosavieae, Melanthiaceae, Liliales – <i>Petrosavia</i> , <i>Protolirion</i>	3. Heloniadeae, <u>Melanthiaceae</u> , Liliales – <i>Helonias</i> , <i>Heloniopsis</i> –NA–, Petrosaviaceae, incertae sedis
5. Tofieldieae, Melanthiaceae, Liliales – <i>Harperocallis</i> ?, <i>Pleea</i> , <i>Tofieldia</i>	–NA–, Tofieldiaceae, Alismatales
6. Xerophylleae, Melanthiaceae, Liliales – <i>Xerophyllum</i>	4. Xerophylleae, <u>Melanthiaceae</u> , Liliales
–NA–, Trilliaceae, Dioscoreales – <i>Daiswa</i> , <i>Kinugasa</i> , <i>Medeola</i> ?, <i>Paris</i> , <i>Scoliopus</i> ?, <i>Trillium</i>	5. Parideae, <u>Melanthiaceae</u> , Liliales – <i>Daiswa</i> , <i>Kinugasa</i> , <i>Paris</i> , <i>Trillium</i>

Heloniadeae/Chionographideae Clade

Heloniadeae (or Heloniadaceae s.s.) are characterized by the synapomorphic spinulate pollen, gynobasic style, and possibly also a specific karyology ($x = 17$) with chromosomes having a particular size range (2.0–5.0 μ), secondary constrictions, and centromere position [longest 10 pairs, subtelocentric; shortest pair, metacentric; remaining six pairs, submetacentric; see Utech (1980) for details]. Chionographideae (or Chionographidaceae) have the synapomorphies of four-porate pollen and with clavate sculpturing and possibly also imperfect flowers (Hara 1968; Meagher and Antonovics 1982), plus a putative base chromosome number of $x = 6$ (Zomlefer 1997a). Heloniadeae and Chionographideae (or Heloniadaceae s.l.) are linked as a clade morphologically by intact pollen, ebracteate flowers, and cuboidal calcium oxalate crystals (Goldblatt 1995; Table 2).

Parideae/Xerophylleae Clade

The infrageneric phylogeny of Parideae has been recently extensively investigated via cladistic analyses of morphological and molecular data (e.g., Kato et al. 1995a, b; Kawano and Kato 1995; Osaloo and Kawano 1999; Osaloo et al. 1999; Fukuda 2001; Farmer and Schilling 2002). Evident morphological autapomorphies for this distinctive tribe include the unusual habit (a simple stem terminating in a relatively large, solitary flower subtended by a single whorl of net-veined leaves or leaf-like bracts; Fig. 1), the differentiated perianth of calyx and corolla, the unusual fruit (see Discussion), and arillate seeds. The monophyly of Parideae is also supported by a unique karyology with a basic complement of five, morphologically similar chromosomes ($n = 5$) comprising the large genome size of the $2n$, $3n$, $4n$, $6n$, and $8n$ plants of the tribe (summary in Zomlefer 1996).

Autapomorphies for the monogeneric Xerophylleae (*Xerophyllum*) include several anatomical features, including a thick pericycle of two or three cell layers, in addition to

several unique characters of the highly modified, sclerified leaf: annular thickenings on the mesophyll cells, two distinct phloem poles in the vascular bundles, and sunken stomata that lack aperture lips (Ambrose 1975). A morphological synapomorphy is the rootstock comprising a bulb terminating a stout rhizome (Table 2; Fig. 1)

Parideae, often traditionally maintained as segregate family Trilliaceae (e.g., Hutchinson 1959, 1973; Dahlgren et al. 1985; Takhtajan 1997; Tamura 1998), are embedded within Melanthiaceae as sister to Xerophylleae (summary in Zomlefer 1996). Presently, no morphological synapomorphies for the clade comprising these two tribes are known. However, Xerophylleae are linked morphologically with Melanthieae by a raphide-styloid combination, a bulb plus rhizome rootstock, and a unique susceptibility to certain rust fungi (Table 2; Goldblatt 1995; Zomlefer 1997a). Additional study is needed to reconcile these morphological and molecular results, particularly to carefully examine characters supporting the presumed phylogenetic relationship of Parideae and Xerophylleae.

Melanthieae

Systematists have long recognized Melanthieae (properly designated “Veratreae” when within Liliaceae s.l.), as a cohesive and natural group. As listed in Table 2 (details in Zomlefer 1997a), the tribe is validated by several potential synapomorphies, including unique alkaloids (“veratrum alkaloids”), distinctive floral anatomy, bulbs, conspicuous tepal nectaries, andromonoecism, unusual anther dehiscence, operculate pollen (Colasante and Rudall 2000), and incompletely fused carpels maturing into a “ventricidal” capsular fruit type (splitting along the ventral sutures). A base chromosome number of $x = 8$ has also been postulated as potentially synapomorphic for the tribe (detailed below under Discussion).

The focus of our studies has been the infrageneric phy-

Table 2. Critical characters for the tribes of the Melanthiaceae s.l. sensu APG II (2003). Chart derived and updated from Zomlefer (1996, 1997a) and Zomlefer et al. (2001). Refer to Tanaka (1997a–e, 1998) concerning the expanded circumscription of *Helionias*. Generic circumscriptions within Parideae follow Farmer and Schilling (2002); see also Takhtajan (1983), Mitchell (1987, 1988), and Li (1984, 1986, 1998) concerning the *Paris* L.–*Daiswa* complex. * = potential autapomorphies; ** = potential synapomorphies.

APG II (2003)	Melanthiaceae				
	Heloniadaceae s.l.		Melanthiaceae s.s.	Xerophyllaceae	Trilliaceae
Segregate Families	Heloniadaceae s.s.	Chionographidaceae		Xerophylleae	Parideae
Tribes	Heloniadeae ("Heloniaceae")	Chionographideae	Melanthiaceae ("Veratreae" in Liliaceae)		
Distribution	Eastern N America + eastern Asia	Eastern N America + eastern Asia	Mainly Northern Hemisphere (1 sp. in S America)	Eastern N America + western N America	Eastern N America, western N America + Eurasia
Genera (number of species)	<i>Helonias</i> (incl. <i>Heloniopsis</i> , <i>Ypsilandra</i> ; 9)	<i>Chamaelirium</i> (1), <i>Chionographis</i> (4–5)	<i>Amianthium</i> (1), <i>Anticlea</i> (ca. 11); <i>Schoenocaulon</i> (24), <i>Stenanthium</i> (2–3), <i>Veratrum</i> (incl. <i>Melanthium</i> ; 17–45), <i>Toxicoscordion</i> (ca. 8); <i>Zigadenus</i> s.s. (1)	<i>Xerophyllum</i> (2)	<i>Daiswa</i> (10–15), <i>Kinugasa</i> (1), <i>Paris</i> (5–24), <i>Pseudotrillium</i> (1), <i>Trillidium</i> (1), <i>Trillium</i> (41–43+)
Base chromosome no. (x)	17* [2n = 34]	Probably 6* [2n = 12?, 24, 42]	8*, 10, 11 [2n = 16, 20, 22, 32, 52?, 64, 80, 96]	15 [2n = 30]	5* [2n = 10, 15, 20, 30, 40]
C ₂ CaO ₄ crystal type	Cuboidal**	Cuboidal**, ± raphides	Raphides and styloids**	Raphides and styloids**	Cuboidal*
Rootstock	Rhizome	Rhizome	Bulb with/without rhizome**	Bulb with rhizome**	Rhizome
Sexual condition of flowers	Perfect	Perfect and/or imperfect*: andromonoecism; also dioecism, gynodioecism	Perfect or perfect + staminate: andromonoecism*	Perfect	Perfect
Perianth morphology	Tepals Distinct	Tepals Distinct	Tepals Distinct to basally connate	Tepals Distinct	Calyx + corolla* Distinct
Nectary type	None or perigonal	None	Perigonal* (sometimes reduced)	None	Perigonal, septal, or none
Anther thecae fusion	Apically/totally confluent	Distinct or confluent	Confluent	Distinct	Distinct
Anther dehiscence	Longitudinal slits	Longitudinal slits	Opening into valvate, peltate discs*	Longitudinal slits	Longitudinal slits
Pollen morphology	1-sulcate Intectate** Spinulate*	4-porate* Intectate** Clavate*	1-sulcate or operculate* Tectate Reticulate	1-sulcate Tectate Reticulate	1-sulcate or inaperturate Tectate Ornamentation various
Ovary position	Superior	Superior	Superior to 1/2-inferior	Superior	Superior
Carpel fusion (style number)	Syncarpous (1 or 3)	Syncarpous or carpels coherent (3)	More or less syncarpous or carpels weakly coherent (3)	Carpels coherent (3)	Syncarpous or carpels distinct apically (1, 3, or 10)
Fruit type	Loculicidal capsule	Loculicidal capsule or septicidal-like loculicidal capsule	Septicidal ("ventricidal") capsule*	Loculicidal capsule	Baccate/non-baccate*, indehiscent or dehiscent (dehiscence various)
Other potential apomorphies	Ebracteate inflorescence** Gynobasic style*	Ebracteate inflorescence**	Susceptibility to 2 rust fungi** Veratrum alkaloids* Dorsal composite vascular bundles in flower*	Susceptibility to 2 rust fungi** Thick pericycle (2–3 cell rows)* Highly modified leaf* Stems with reduced leaves*	Single whorl of net-veined leaves at stem apex* Solitary flower* Distinct karyology* Arillate seeds*

logeny of Melanthieae, the most morphologically diverse tribe in the family, and investigation of evolutionary patterns of character states. Until our current analyses, the circumscription of the constituent core genera of Melanthieae (*Amianthium* A. Gray, *Schoenocaulon*, *Stenanthium* (A. Gray) Kunth, *Veratrum* L., *Melanthium* L., *Zigadenus* L. s.l.) had not been subject to rigorous character analyses, and their intergeneric relationships were also unresolved.

Zigadenus complex.—Our study began with examination of *Zigadenus* s.l., a heterogeneous, non-monophyletic grouping, i.e., not defined by synapomorphies (Zomlefer 1997a). Taxonomists had long grappled with defining this assemblage, often by erecting a number of variously defined segregate genera: *Amianthium* (Gray 1837), *Anticlea* (Kunth 1843), *Oceanoros* (Small 1903), *Toxicoscordion* (Rydberg 1903), and *Tracyanthus* (Small 1903). Contemporary botanists typically have accepted only one segregate, a monotypic *Amianthium*, with the remaining ca. 19 species maintained in *Zigadenus* s.l. (e.g., in *Flora of North America*: Schwartz 2002; Utech 2002). As part of a study on the tribe, we evaluated the circumscription of the *Zigadenus* complex using

parsimony analyses of ITS (nuclear ribosomal) and *trnL*-F (plastid) DNA sequence data (Zomlefer et al. 2001). The strongly supported cladograms are summarized in the phylogeny shown in Fig. 2. Based on our study, *Stenanthium*, as traditionally defined, is biphyetic (and embedded within *Zigadenus* s.l.), *Zigadenus* s.l. is polyphyletic, and *Amianthium* is a distinct entity only distantly related to the other *Zigadenus* species.

Supported by these results, we now recognize five genera (some with novel circumscription) of the former *Zigadenus* complex: (1) *Amianthium* (monotypic: *A. muscotoxicum* (Walter) A. Gray), (2) *Anticlea* Kunth (including *Stenanthella* Rydb.; ca. 11 spp.), (3) *Stenanthium* (*S. gramineum* (Ker Gawl.) Morong, *Zigadenus densus* (Desr.) Fernald, and *Z. leimanthoides* (A. Gray) A. Gray), (4) *Toxicoscordion* Rydb. (ca. 8 spp.), and (5) *Zigadenus* s.s. (monotypic: *Z. glaberrimus* Michx.). The species of these genera form five strongly supported clades (Fig. 2) that correlate with geographical distribution, chromosome number, and certain morphological characters (Table 3). The nomenclatural consequences are addressed in Zomlefer and Judd (2002). These

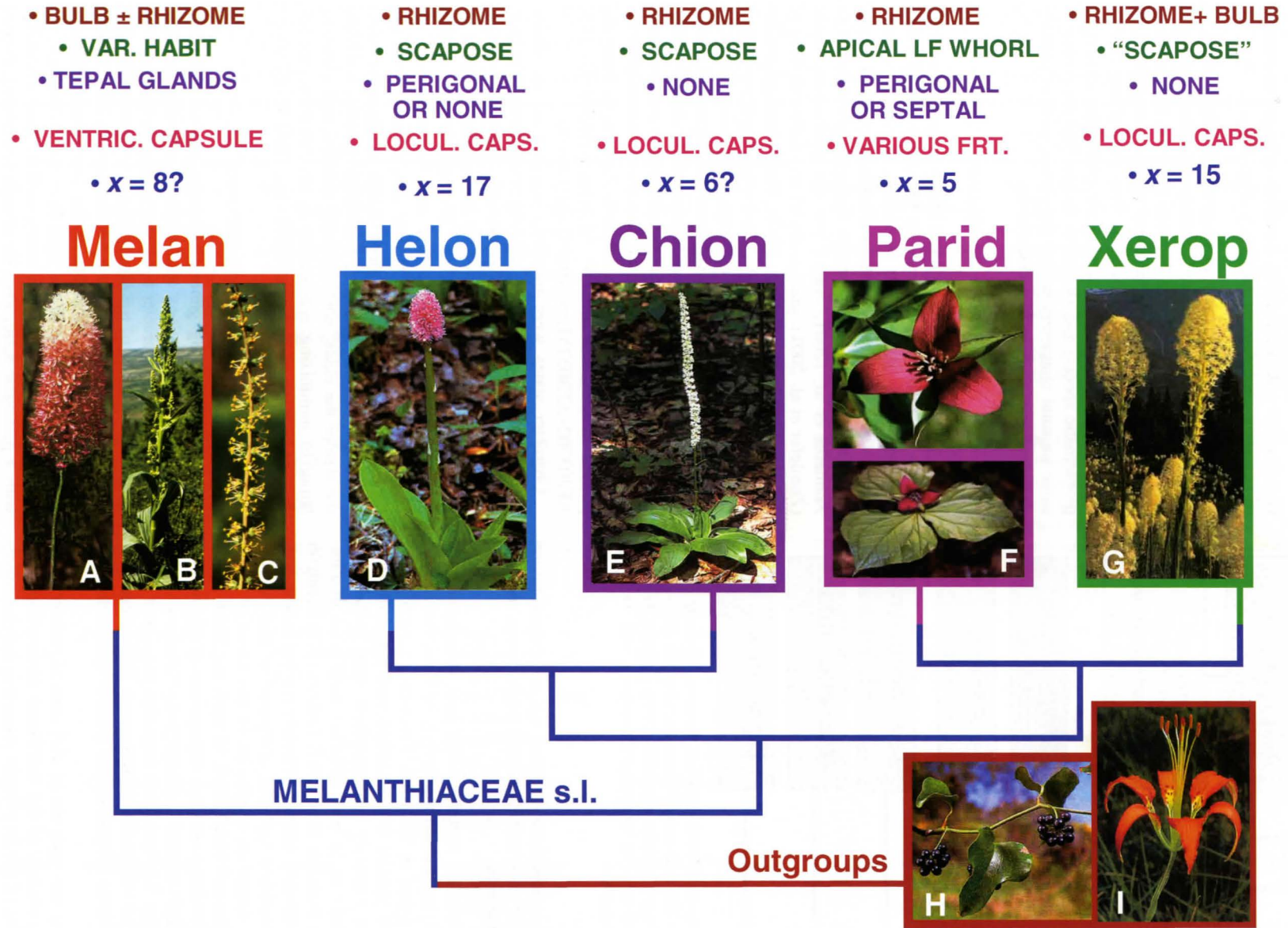


Fig. 1.—Distribution of select characters in Melanthiaceae s.l. (see Table 2). The phylogeny and outgroups are based on analyses of molecular data (Chase et al. 1993, 1995a, b, 2000; Duvall et al. 1993; Fuse and Tamura 2000; Rudall et al., 2000; Soltis et al. 2000; Zomlefer et al. 2001; APG II 2003). Exemplar species: A, *Stenanthium densum* (Desr.) Zomlefer & Judd; B, *Veratrum album*; C, *Schoenocaulon dubium* (Michx.) Small; D, *Helonias bullata* L.; E, *Chamaelirium luteum* (L.) A. Gray; F, *Trillium erectum*; G, *Xerophyllum tenax* (Pursh) Nutt.; H, *Smilax bona-nox* L. (Smilacaceae); I, *Lilium catesbaei* Walt. (Liliaceae). Melan = Melanthieae; Helon = Heloniadeae; Chion = Chionographideae; Parid = Parideae; Xerop = Xerophylleae; Outgroups = Smilacaceae and Liliaceae. Photo credits: A–C, G, Dana G. Griffin, III; D–F, H, I, Wilbur H. Duncan. FRT. = fruit; LF = leaf; LOCUL. CAPS. = loculicidal capsule; VAR. = various; VENTRIC. = ventricidal

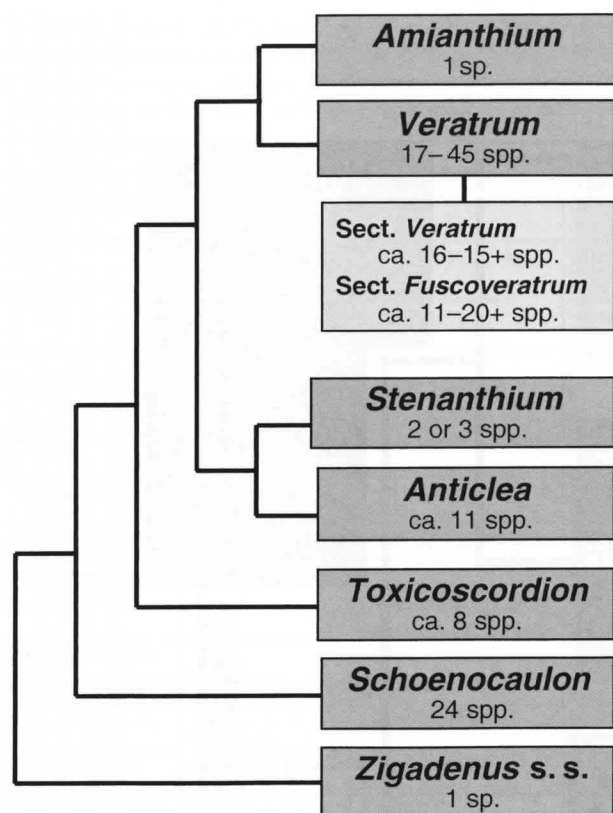


Fig. 2.—Phylogenetic relationships of the seven genera in Melanthieae, based on ITS and *trnL*-F molecular data for 170 samples representing 90 taxa (Zomlefer et al. 2001, 2003, in prep.). *Veratrum* is further divided into two monophyletic sections, sect. *Veratrum* and sect. *Fuscoveratrum*.

data resolved *Amianthium/Veratrum* s.l. and *Stenanthium/Anticlea* as sister taxa, and *Zigadenus glaberrimus*, as sister to the rest of the tribe.

Veratrum/Melanthium complex.—We next investigated the infrageneric phylogeny and monophyly of *Veratrum* s.l., the most diverse genus in the tribe. *Veratrum*, a problematic group of 20–45 species with a complicated taxonomic history, has been variously circumscribed with *Melanthium* submerged totally or in part (detailed summaries in Zimmerman 1958; Kupchan et al. 1961; Bodkin 1978; Zomlefer 1997a). Contemporary authors generally recognize both genera, with *Melanthium* typically composed of two to four eastern North American species as in the *Flora of North America* (Bodkin and Utech 2002; McNeal and Shaw 2002). We sought to evaluate whether segregation of *Melanthium* (however defined) created a paraphyletic *Veratrum*. In addition, *Veratrum* s.l. had also formally (Loesener 1926, 1927, 1928) and informally (Zimmerman 1958) been subdivided into several subgenera and sections (all of doubtful monophyly).

According to our analyses of ITS data (Zomlefer et al. 2003), the recognition of the traditional *Melanthium* with any combination of the four North American species makes the rest of *Veratrum* paraphyletic, and we concluded that the *Veratrum/Melanthium* complex is best treated conservatively as one monophyletic genus, divided into two sections (and

two subsections) that are supported by several morphological synapomorphies. The two morphologically distinct subsections of *Veratrum*, sect. *Veratrum* and sect. *Fuscoveratrum* O. Loes., are indicated in Fig. 2 and below in our discussion of character evolution in the family (Fig. 3, 4).

Schoenocaulon.—Currently in progress (Zomlefer et al. in prep.) are morphological and ITS analyses of the species and infraspecific taxa in the last genus in the tribe, *Schoenocaulon*. *Schoenocaulon* is a distinctive group, well defined by several synapomorphies (Table 3). Our preliminary results thus far support recircumscription and placement of several problematic species and also allow insight into the evolution some unusual characters within the genus, such as nectary and tepal margin type (see Discussion).

MATERIALS AND METHODS

Our cladograms of Melanthieae in this review paper (Fig. 2–4) is based on cladistic analyses of *trnL*-F and ITS data (Zomlefer et al. 2001, 2003) in addition to current, unpublished studies on *Schoenocaulon* (Zomlefer et al. in prep.). Laboratory protocols and search strategies are detailed in Zomlefer et al. (2001, 2003). For our preliminary study (Zomlefer et al. 2001), plant material was collected fresh or silica dried (Chase and Hills 1991). Herbarium specimens, ranging in age from 2–127 years, provided supplemental material for subsequent, more thorough study involving little-collected taxa. Successful extractions involved leaf blades and/or tepals. Specimens have been carefully chosen to represent variation within species complexes, as well as multiple collections of variable taxa. Sequences and voucher information for all taxa in these publications have been deposited in GenBank (*trnL*-F: AF303663–AF303701; ITS: AF303702–AF303731, AF494297–AF494336).

Character states were manually mapped on our cladograms (Fig. 2–4) so that character state transitions were minimized (i.e., application of parsimony). For our investigations, we recognize taxa above the rank of species based on criteria outlined by Backlund and Bremer (1998) for general principles of classification: first and foremost, they are monophyletic but secondarily, they should have strong statistical support and also be more or less recognizable based on morphological characters. Secondary criteria, including the size of the clade, nomenclatural stability, and issues relating to minimizing redundancy in classification, are addressed in Kellogg and Judd (2002) and APG II (2003).

RESULTS AND DISCUSSION

Besides supporting generic recircumscription in Melanthieae, our investigations also validate several generalizations concerning character evolution within the tribe, as well as among the tribes of the family (Fig. 1). Variation in habit, tepals, and perigonal glands have traditionally been used to distinguish taxa within Melanthieae, but several features, such as the extension of the tepal base into a claw, are not discrete, and some character states, such as those associated with a particular habit, may be strongly correlated. Formal comprehensive cladistic analyses of morphological (and other) characters are in progress (Zomlefer and Judd, in prep.) to confirm putative synapomorphies and to identify addi-

Table 3. Characters defining the seven genera of Melanthiaceae. Modified from Zomlefer et al. (2001) and Zomlefer and Judd (2002). * = possible autapomorphies.

	<i>Amianthium</i> (1 sp.)	<i>Anticlea</i> (ca. 11 spp.)	<i>Schoenocaulon</i> (24 spp.)	<i>Stenanthium</i> (2 or 3 spp.)	<i>Toxicoscordion</i> (ca. 8 spp.)	<i>Veratrum</i> [incl. <i>Melanthium</i>] (17–45 spp.)	<i>Zigadenus</i> s.s. (1 sp.)
Distribution	Southeastern USA (coastal plain and mountains)	Asia; N America to Guatemala	FL, southwestern NM, TX, south to Peru–Venezuela	Southeastern USA (coastal plain and mountains)	Midwestern USA and western N America	N temperate to Arctic Eurasia; temperate N America	Southeastern USA (coastal plain)
Habitat	Acidic coniferous forests and bogs	Acidic and/or al- pine coniferous forests, prairies, calcareous shores, and fens	Barrens, prairies, sandhills, alpine grassland, and pine-oak forests	Acidic coniferous forests and bogs	Acidic and/or alpine coniferous forests, prairies, desert, chaparral, and ser- pentine habitat	Alpine environments, rocky tundra, and rich deciduous forests	Acidic coniferous forests and bogs
Base chromo- some num- ber (<i>x</i>) [Fig. 4]	8 [$2n = 32$]	8 [$2n = 32$]	8 [$2n = 16$]	10* [$2n = 20$]	11* [$2n = 22$]	8 [$2n = 16?$, 32, 64, 80, 96]	26(?)* (uncon- firmed) [$2n =$ 52]
Rootstock type [Fig. 3A]	Bulb, broadly ovoid	Bulb, narrowly ovoid	Bulb covered with dark brown to black fibers*	Bulb, slender (cylin- dric)*	Bulb, ovoid	Bulb + rhizome* (rhi- zome sometimes re- duced)	Rhizome*
Habit [Fig. 3A]	Scapose	Scapose	Scapose	Scapose	Scapose	Leafy-stemmed or more or less scapose	Scapose
Inflorescence type [Fig. 3A]	Racemose; gla- brous	Racemose; gla- brous	Spicate*; glabrous	Racemose (racemes sometimes branched), panicu- late; glabrous	Racemose (racemes sometimes branched); gla- brous	Compound racemes or panicles; floccose pubescent*	Paniculate; gla- brous
Tepal texture, base, margin [Fig. 3B]	Petaloid; obtuse, slightly tapered; entire	Petaloid; cuneate to gradually ta- pered; entire	Petaloid, fleshy, or scarious; cuneate to gradually ta- pered; entire, den- tate, erose*; sometimes auricu- late	Petaloid; cuneate to gradually tapered; entire	Petaloid; conspicu- ously clawed (at least inner 3)*; entire	Petaloid to sepaloid; cuneate to some- times clawed; entire (sometimes undu- late), erose, denticu- late, fimbriate	Petaloid; slightly tapered; entire
Perigonal glands [Fig. 3B]	1; reduced/absent*	1; bilobed	Nectariferous cavi- ty* or 1 ovoid gland	1; obscure (or absent)*	1; obovate*	2, distinct; confluent; marginal (V-shaped) or a transverse band; reduced/absent	2; ovate*
Ovary position	Partly inferior	½-inferior	Superior (flowers hypogynous to perigynous)	Superior to ½-inferior	Superior	Superior to ½-inferior	Superior
Other signifi- cant char- acters	Large seeds with sarcotesta* Unique alkaloids*		Appendaged seeds*			Broadly winged seeds*	Unusual anatomi- cal features*

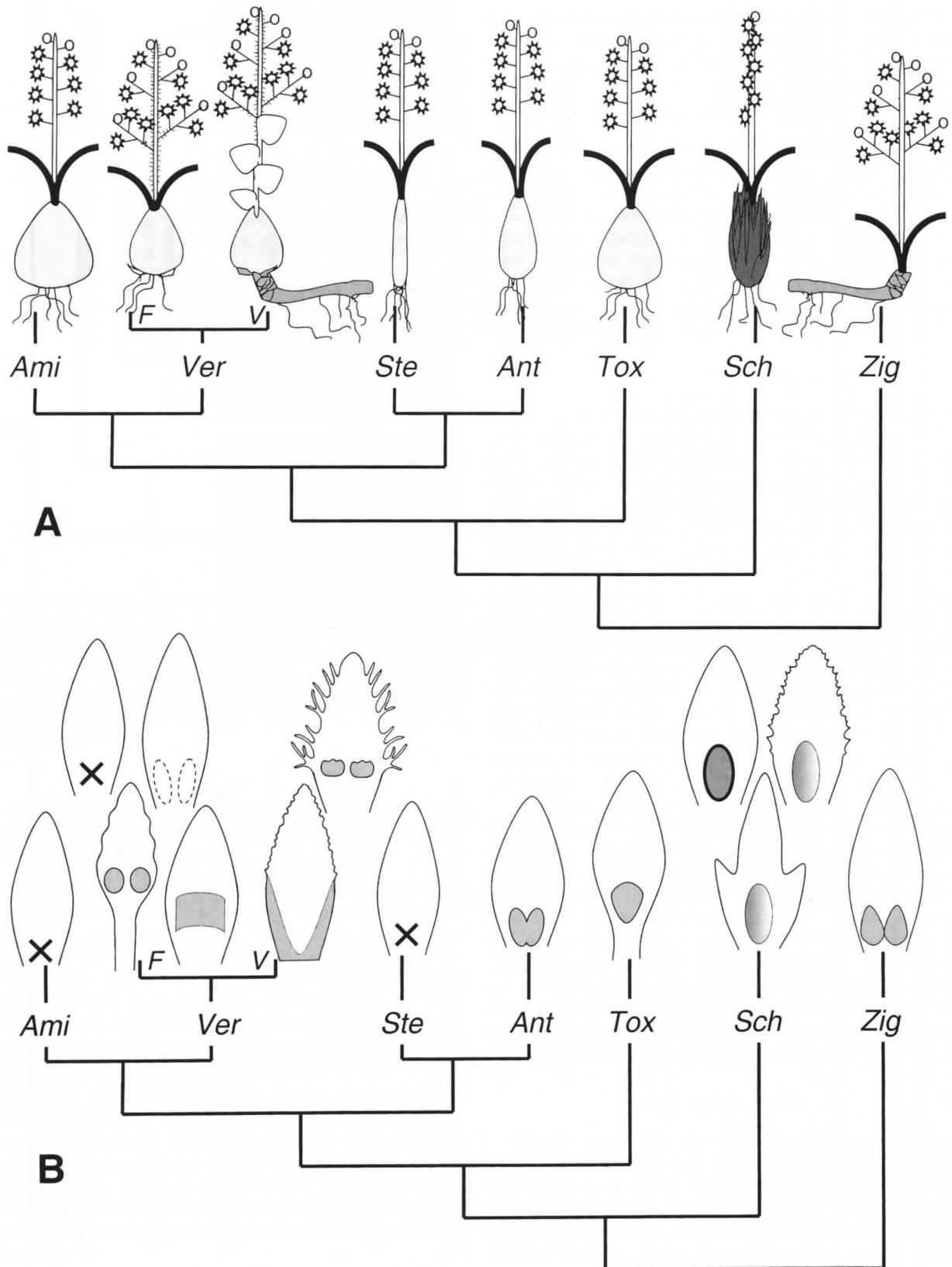


Fig. 3.—Stylized depiction of some examples of morphological characters in Melanthieae. A: Habit (scapose vs. leafy-stemmed; inflorescence type) and rootstock (rhizome and/or bulb). B: Tepals (shape, margin; perigonal gland morphology). *V* = *Veratrum* sect. *Veratrum*; *F* = *Veratrum* sect. *Fuscoveratrum*; *Ami* = *Amianthium*; *Ver* = *Veratrum* s.l.; *Ste* = *Stenanthium*; *Ant* = *Anticlea*; *Tox* = *Toxicoscordion*; *Sch* = *Schoenocaulon*; *Zig* = *Zigadenus* s.s.

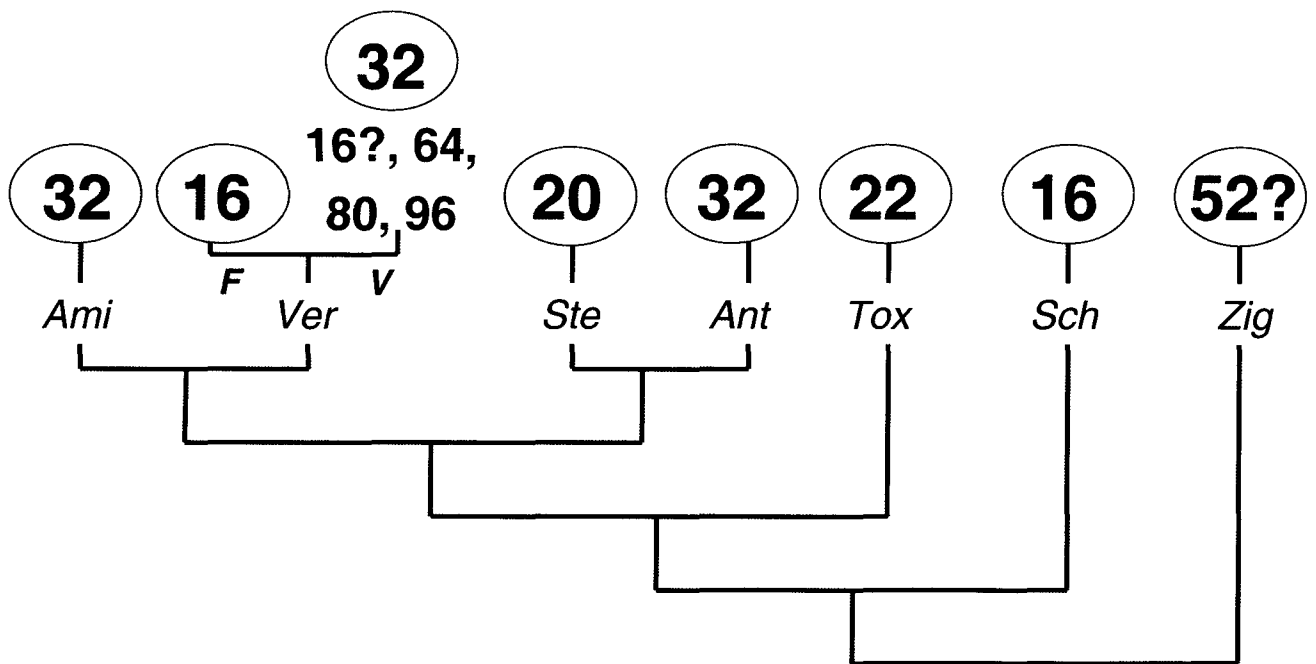


Fig. 4.—Reported chromosome numbers in Melanthiaceae. Data from references summarized in Zomlefer (1997a, 2003). ? = questionable or unverified report; V = *Veratrum* sect. *Veratrum*; F = *Veratrum* sect. *Fuscovratrum*; Ami = *Amianthium*; Ver = *Veratrum* s.l.; Ste = *Stenanthium*; Ant = *Anticlea*; Tox = *Toxicoscordion*; Sch = *Schoenocaulon*; Zig = *Zigadenus* s.s.

tional ones. Our summary here outlines the pattern of a few distinctive exemplar character state changes within Melanthiaceae inferred by hypothesis of phylogeny (Fig. 2–4). Lack of resolution in cladogram topology sometimes prohibited determination of the precise level of universality for particular states, and these uncertainties, along with unequivocal character transitions, are discussed below.

Characters

Rootstock.—The plants of Chionographideae, Heloniadeae, and Parideae have rhizomes (Table 2; Fig. 1)—in contrast to the tunicate bulbs (characterized by an outer coat of membranous leaf bases) that have evolved within Melanthiaceae (Fig. 3A). *Zigadenus* s.s. (sister to the rest of Melanthiaceae) has a bulbless rhizome covered in persistent leaf bases but not developing the tunicate apex, whereas a bulb occurs in all other genera (Ambrose 1975, 1980). The consistently narrow (cylindrical) bulb of *Stenanthium* is apomorphic for the genus (Zomlefer and Judd 2002), as is the distinctive dark fibrous bulb (covered with dark brown to black scales or fibers) for *Schoenocaulon* (Table 3; Zomlefer 1997a; Zomlefer et al. 2001). In *Veratrum* sect. *Veratrum*, the bulb terminates a well-developed rhizome, an unusual arrangement synapomorphic for the genus. A somewhat similar rhizome-bulb combination also characterizes Xerophylleae (Table 2; Fig. 1), but the swollen leaf bases do not encircle the stem as in the bulbs of *Veratrum* (Ambrose 1975). According to our phylogeny (Fig. 1), the rootstock type of Xerophylleae is autapomorphic for this tribe and has been independently derived, a conclusion supported by the morphological differences in the rhizome-bulb configurations of the two clades. The well-developed bulbs of some members of *Veratrum* sect. *Fuscovratrum* (and several spe-

cies of *Schoenocaulon*) terminate a very reduced rhizome. Based on parsimony, the rhizome likely has been secondarily reduced/lost in these taxa (Fig. 3A).

Habit features.—Our phylogeny allows development of hypotheses concerning evolution of some distinctive plant forms in Melanthiaceae (especially within Melanthiaceae), although the appearance of a plant is generally difficult to quantify. For example, an obvious autapomorphy for the Parideae is the unusual habit: a simple stem terminating in a relatively large, solitary flower subtended by a single whorl of net-veined leaves or leaf-like bracts (Fig. 1F). Reduced leaves cover the stem in Xerophylleae (a possible synapomorphy), so the plants appear scapose (Fig. 1G; Zomlefer 1997a). The majority of the remainder of the family are characterized by leafless stems (Fig. 1A, D, E) and the basal leaves, typically with a conspicuous midvein, are generally narrow, sessile, and taper gradually to a sheathing base. These features likely are synapomorphic for Melanthiaceae (or at least in part synapomorphic, as some may have evolved in more inclusive clades; Fig. 1).

Graceful, scapose plants with basal leaves characterize most of Melanthiaceae (Bodkin 1978; Fig. 3A). The robust leafy stems characterizing *Veratrum* sect. *Veratrum* are a striking contrast to typical plant form for the rest of the tribe (Fig. 1B). Several obvious correlated leaf characteristics contribute to this so-called veratrum habit—large, elliptic, sessile blades strongly plicated along several prominent primary veins (conspicuous midvein lacking) and closed, tubular, overlapping basal sheaths forming a hollow pseudostem around the true stem (Zomlefer 1997a). Some members nested within sect. *Fuscovratrum* have evolved some similar features. For example, *V. nigrum* L. has wide sessile leaves that form a weak pseudostem at the plant base, and

V. parviflorum Michx. and *V. woodii* J. W. Robbins have somewhat broad and weakly plaited (but petiolate) leaves. According to our results (Zomlefer et al. 2003), these developments are likely autapomorphic at the species rank. Thus, broad plicated leaves evolved more than once within *Veratrum* but are best developed in sect. *Veratrum*, characterized by the synapomorphic "veratrum habit."

Inflorescence structure also contributes to the overall appearance of a plant. In Parideae, the inflorescence comprises a single terminal flower (Fig. 1F), a character synapomorphic for this tribe. Inflorescences in Chionographideae (Fig. 1E), Heloniadeae (Fig. 1D), and Xerophylleae (Fig. 1G) are racemose and unbranched (congested and umbellate in some species of *Helonias* s.l.). In Melanthieae (Fig. 1A–C, 3A), the racemes may be unbranched (e.g., *Amianthium muscivictim*), once-branched (e.g., *Stenanthium leimanthoides*), or form large paniculate inflorescences [e.g., *Veratrum album* L. (Fig. 1B), *Zigadenus glaberrimus*]. In addition, a spicate inflorescence (flowers sessile to subsessile) is synapomorphic for *Schoenocaulon* (Fig. 1C, 3A), and the floccose pubescence of dendritic hairs covering the inflorescence branches is synapomorphic for *Veratrum* (Fig. 3A).

Tepals.—A perianth differentiated into three foliose sepals and three colorful petals characterizes the Parideae (Fig. 1F), but the other tribes have a perianth of six, generally petaloid tepals [all sepaloid in some Melanthieae, e.g., *Veratrum viride* (L.) Aiton]. As with habit type, certain aspects of tepal morphology are most variable in *Veratrum*. The tepal base is generally cuneate to gradually tapered for most of Melanthieae (Table 3), with the notable exceptions of distinctively clawed tepals characterizing *Toxicoscordion* and some species of *Veratrum* sect. *Fuscovetrum*. According to our cladogram (Fig. 3B), the clawed tepals synapomorphic for *Toxicoscordion* (Zomlefer et al. 2001) likely evolved independently from those in *Veratrum*. In addition, on the basis of parsimony this specialized character either evolved at least twice within *Veratrum* sect. *Fuscovetrum* or may be synapomorphic for the section and lost in certain species (see cladograms in Zomlefer et al. 2003). In sect. *Fuscovetrum*, the degree of filament adnation to the tepal is correlated with tepal shape: arising at the base of unclawed tepals to conspicuously epitepalous on clawed tepals. Additionally, the epitepalous filaments strongly incurve in the species with the most well-differentiated claws [e.g., *V. latifolium* (Desr.) Zomlefer]. These correlations (i.e., of tepal shape and staminal adnation/curvature) are not found in *Toxicoscordion*, reinforcing our hypothesis that clawed tepals evolved in parallel for *Toxicoscordion* and *Veratrum* sect. *Fuscovetrum*.

The tepal margin of most members of the family are entire. In *Veratrum*, however, the entire (sometimes undulate) plesiomorphic condition occurs only in species of sect. *Fuscovetrum* and a synapomorphic nonentire form (erose, denticulate, to deeply fimbriate) diagnoses sect. *Veratrum* (Fig. 3B; Table 3). The erose to dentate tepal margins in most species of *Schoenocaulon* have an independent origin, and according to our preliminary cladograms from ITS data (Zomlefer et al., in prep.), may be synapomorphic for the genus and lost in some species. In addition, several species of *Schoenocaulon* (such as *S. calcicola* Greenm.) have well-

developed hyaline auricles at the tepal base (Fig. 3B; Brinker 1942; Frame 1990).

Perigonal glands.—Nectaries of Melanthieae (Table 2), when present, vary from a generalized nectariferous area or depression at the filament-tepal base junction (some Heloniadeae and most Parideae), septal nectaries (some Parideae), or the well-defined, often fleshy, perigonal glands synapomorphic for Melanthieae. The distinctive melanthioid glands occur on the adaxial surface of the tepals, usually near the base (Leinfellner 1961; Daumann 1970), and vary in configuration depending on the genus (Table 3; Fig. 3B). The plesiomorphic condition for the tribe, i.e., in *Zigadenus* s.s., comprises paired ovate glands (see Fig. 1: outgroup condition = no perigonal glands). Since the hypothesis of a single event is most parsimonious, fused tepal glands are likely a synapomorphic for the rest of the tribe (i.e., for the clade containing all genera except for *Zigadenus*; Fig. 3B). Therefore, the bilobed (partially fused) gland characterizing *Anticlea* is possibly plesiomorphic; the obovate gland shape (but not one gland per tepal) is autapomorphic for *Toxicoscordion*.

In *Schoenocaulon*, nectariferous tissue typically lines a shallow to conspicuous concavity at the tepal base except in *S. officinale* A. Gray, which has a single, oval, and pad-like gland (Zomlefer 1997a). Since our ITS phylogeny (Zomlefer et al. in prep.) strongly supports *S. officinale* as embedded within the genus, the unusual nectariferous pit is synapomorphic for *Schoenocaulon*, and the fleshy nectary of *S. officinale* is autapomorphic for that species.

Several perigonal nectary forms occur in *Veratrum*, including two unique nonsucculent types that have evolved within the genus (Table 3; Fig. 3B). According to our comprehensive sampling (Zomlefer et al. 2003), the marginal and basally confluent (V-shaped) nectariferous zone characterizing most species in sect. *Veratrum* is likely synapomorphic for the section, and the nectariferous lateral band across the median of the tepal in several members of sect. *Fuscovetrum* (*V. maackii* Regel complex and *V. nigrum*) is synapomorphic for or has evolved within this section. Presently, the level of universality is also uncertain for the paired succulent glands present in both sections of *Veratrum* (e.g., *V. fimbriatum* A. Gray in sect. *Veratrum*; *V. woodii* in sect. *Fuscovetrum*) due to unresolved portions of our ITS-based cladogram. These may represent the plesiomorphic condition of the tribe or reversal to the plesiomorphic state.

According to our phylogeny (Fig. 3B), the reduction (or absence) of glands is apomorphic for and independently evolved in *Amianthium* and *Stenanthium*. Reduced/absent glands also occur in some species in *Veratrum* sect. *Fuscovetrum* [e.g., *V. anticleoides* Trautv. & C. A. Mey.) H. Takeda & T. Miyake] and probably represent independent secondary reductions that may be autapomorphic for particular species in some instances (Zomlefer et al. 2003).

Gynoecium fusion and position.—Batsch (1802) first described the Melanthieae (comprising *Helonias*, *Melanthium*, *Nartheicum* Huds., and *Veratrum*), distinguishing them from the rest of the Liliaceae by the apically divergent carpels (i.e., carpels distinct toward apex or the styles free). The family, as now circumscribed, includes plants with various degrees of carpellary fusion (Table 2; Sterling 1980,

1982) ranging from syncarpous (Heloniadeae, some Chionographideae and Parideae) to variously developed apocarpous (e.g., carpels weakly syncarpous to coherent in Melanthieae, basally connate and apically distinct in some Parideae). Partially distinct carpels (including gynoecia with connate ovaries and distinct styles) likely represent a synapomorphy of Melanthieae. This condition may represent a reversal from the fully syncarpous gynoecia of the outgroups (i.e., Alstroemeriaceae, Colchicaceae, Liliaceae s.s., and Smilacaceae).

Ovary position is consistently superior in all tribes (Table 2) except within Melanthieae where partial epigyny has evolved in *Anticlea* and *Stenanthium* (half-inferior), and to a lesser extent, in *Amianthium* (partly inferior) and some *Veratrum* (superior to one-third inferior; Table 3). We had initially suggested the half-inferior ovary as synapomorphic for the *Stenanthium*/*Anticlea* clade (Zomlefer et al. 2001), but a partially inferior ovary may be a synapomorphy for the *Amianthium*/*Veratrum*–*Stenanthium*/*Anticlea* clade (Fig. 2).

Fruit type.—The plesiomorphic loculicidal capsule is characteristic for Heloniadeae, Chionographideae, and Xerophylleae, while Parideae and Melanthieae each have unusual fruits (Fig. 1; Table 2) that deviate from the outgroup condition (loculicidal capsule for Liliaceae, berry for Smilacaceae). [The report of septicidal fruit in Chionographideae by Tamura (1998) is in error: the fruits are loculicidal but may also split deeply along the septa (Zomlefer and Judd, pers. obs.).]

In Parideae, the often colorful fruit varies from baccate to non-fleshy and may be indehiscent (berry-like) or dehiscent (capsule-like) with irregular to regular dehiscence occurring at the base and/or along the septa and/or into the locules (Zomlefer 1996). According to Berg (1958), a few species (e.g., *Trillium erectum* L., *T. undulatum* Willd., *T. camschatcense* Ker-Gawl.) produce a “true berry” (i.e., indehiscent with fleshy mesocarp). The fruit of most members of the tribe, however, do not conform to classical definitions. The baccate fruit of *Daiswa*, for example, has loculicidal dehiscence. In *Trillium*, however, the dehiscent fruits evidently lack a definite type of valvate-dehiscence mechanism, and in some baccate fruits (e.g., *T. maculatum* Rafin.), the mesocarp is thin or mealy and the fleshy tissue comprises succulent placentae plus seed arils (“ariloid berry,” Zomlefer 1994). Baccate (sometimes dehiscent) fruit may be synapomorphic for Parideae, with loculicidal dehiscence evolving within the tribe and synapomorphic for *Daiswa*. The pattern of variation in fruit texture, coloration, and dehiscence in Parideae requires rigorous assessment in relation to various phylogenetic hypotheses postulated by Farmer and Schilling (2002).

The more or less apocarpous gynoecium of all Melanthieae matures into a capsule that is not strictly septicidal: the mature carpels open ventricidally (i.e., along the inner or ventral faces of the carpels) from the apex and base and then along the central column of the ovary—hence, the designation as “ventricidal capsule” by Dahlgren and Clifford (1982) for this unusual synapomorphic dehiscence.

Chromosome number.—Probable base numbers for sister taxa Parideae and Xerophylleae (Table 2; Fig. 1), are five and 15, respectively, and for sister taxa Heloniadeae and

Chionographideae, 17 and possibly six, respectively, (Lowry et al. 1987; Zomlefer 1996, 1997a). A base chromosome number of $x = 8$ is often cited for Melanthieae (Sen 1975; Tamura 1995; Lowry et al. 1987; Zomlefer 1997a), and multiples of this number are prevalent (Fig. 4): *Amianthium* ($2n = 32$), *Anticlea* (including *Stenanthella*; $2n = 32$), *Schoenocaulon* ($2n = 16$), and *Veratrum* (including *Melanthium*; sect. *Veratrum*: $2n = 32, 64, 80, 96$; sect. *Fuscovetrum*: $2n = 16$). Apparent exceptions are the synapomorphic $2n$ numbers of 20 for *Stenanthium* (Zomlefer and Smith 2002) and 22 for *Toxicoscordion* (Zomlefer 2003), as well as an unconfirmed diploid number report of 52 for *Zigadenus* s.s. (Preece 1956), the sister group to remaining Melanthieae.

Due to the small size of the chromosomes (ca. 2.0–4.0 μm in length), the few comprehensive karyological studies (e.g., Lee 1985) lack the detail to infer mechanisms of chromosomal evolution, although these chromosome numbers indicate the prevalence of polyploidy and/or aneuploid variation of the prospective basic number. Polyploidy has been well documented in *Veratrum* sect. *Veratrum* ($2n = 32$). Based on documented secondary pairing of metaphase I bivalents in *V. oxysepalum* Turcz. and *V. stamineum* Maxim., Tokumoto (1940) hypothesized a tetraploid origin for the diploid number of this section. In addition, a polyploid sequence of $2n = 32, 64, 80, 96$ occurs in *V. oxysepalum* (Sokolovskaya 1969; Zhukova 1969; Zhukova and Tikhonova 1971; Zhukova and Petrovsky 1976, 1980). Confirmation of the chromosome number for *Zigadenus glaberrimus* (a possible polyploid) and the reassessment of the base number for the Melanthieae merit further investigation (Zomlefer, in prep.), especially in relation to chromosomal evolution for the other tribes.

Phylogeny as Testable Hypotheses

As discussed above, our hypothesis of generic relationships and circumscription in Melanthieae, based on ITS and *trnL*-F molecular data (Fig. 2), is supported by several phenotypic and chromosomal character states. Our preliminary molecular analyses (Zomlefer et al. 2001) included 30 samples of 29 taxa in the tribe, and subsequently we have sequenced almost all taxa (total: 170 samples of 90+ taxa; Zomlefer et al. 2003 in prep.). The increased sampling for our current investigations represents the complete range of morphological variation, especially within *Veratrum* (Zomlefer et al. 2003) and *Schoenocaulon* (Zomlefer et al. in prep.). All species have resolved within the generic clades as we predicted based on morphology correlated with our preliminary cladogram. For example, the four segregate genera of the former *Zigadenus* complex consistently correlate with four distinct nectary types (Zomlefer et al. 2001; Zomlefer and Judd 2002), thereby supporting the circumscription of *Toxicoscordion* sensu Rydberg (1903) and novel delimitations of *Anticlea* [including *Stenanthium frigidum* (Schldl. & Cham.) Kunth and *S. occidentale* A. Gray] and *Stenanthium* (including *Zigadenus densus* and *Z. leimanthoides*).

Using our phylogeny as a predictive tool, we have also extrapolated the chromosome number for certain taxa in Melanthieae. For example, new chromosome counts strengthen support for the monophyly of *Stenanthium* and *Toxicoscordion*, as circumscribed by Zomlefer and Judd (2002). The

synapomorphic mitotic chromosome number of $2n = 20$, reported for *S. gramineum*, has now been verified for the two *Zigadenus* species transferred to *Stenanthium* (Zomlefer and Smith 2002). The chromosome number $2n = 22$ (or $n = 11$) had been reported for all species now placed in *Toxicoscordion*, except for one anomalous report by Zakhariava and Makushenko (1969) of $2n = 32$ for *T. nuttallii* (A. Gray) Rydb. based on an undescribed and unvouchered plant then growing at the Munich Botanical Garden (original source not cited). Zomlefer (2003) confirmed the mitotic chromosome number of $2n = 22$ for *T. nuttallii* with plants from populations in two counties in Texas, thereby validating the diploid number of 22 as a consistent synapomorphy for the genus.

Although earlier systematists had recognized some morphological characters that correlate with monophyletic groups within Melanthiaceae (e.g., spicate inflorescence for *Schoenocaulon*), many features, such as the non-entire tepals in *Veratrum* sect. *Veratrum*, had not been used to define supraspecific groups. In addition, the pattern of variation of these features had not previously been assessed from a phylogenetic perspective. In our investigations, clarification of polarity and level of universality of these phenotypic and chromosomal characters has supported clades resolved by our molecular analyses. In particular, the major supraspecific clades of Melanthiaceae (and Melanthiaceae) recognized in our studies have morphological, anatomical, chromosomal, and/or chemical synapomorphies and are, thus, easily diagnosable. In our exploration of character evolution within Melanthiaceae, we will continue to examine potentially synapomorphic characters that may increase support of molecular based phylogenies and also facilitate recognition of these taxa.

ACKNOWLEDGMENTS

This paper is a summary of an invited presentation given by WBZ for the Liliales session at The Third International Conference on the Comparative Biology of the Monocotyledons (Rancho Santa Ana Botanic Garden, Claremont, California; 2 April 2003). We are grateful to the curators/collections managers of the following herbaria for loaning material crucial to this continuing project: ARIZ, BRIT, CAS, CICY, F. GH, HAL, IEB, K, KUN, MEXU, MICH, MO, MOR, NMC, NY, PH, RSA, TCD, TEX, TUS, UC, UNLV, UNM, US, WIS, AND XAL. We also thank Kent Perkins for permission to sample specimens at FLAS; Wilbur H. Duncan and Dana G. Griffin III, for the use of their photographs in Fig. 1; David E. Giannasi for reviewing a draft of this manuscript; and two anonymous reviewers for constructive criticisms of the text. The University of Georgia, Department of Plant Biology, generously provided funds to WBZ for travel to CAS, FLAS, GH, MO, NY, UC/JEPS and WIS. Expenses for *Monocots III* for WBZ were covered by the National Park Service [contract agreement J2114-03-0006; PI D. E. Giannasi & CoPI W. B. Zomlefer].

LITERATURE CITED

- AMBROSE, J. D. 1975. Comparative anatomy and morphology of the Melanthioideae (Liliaceae). Ph.D. dissertation. Cornell University, Ithaca, New York.

- . 1980. A re-evaluation of the Melanthioideae (Liliaceae) using numerical analyses, pp. 65–81. In C. D. Brickell, D. F. Cutler, and M. Gregory [eds.], *Petaloid monocotyledons*. Academic Press, London, UK.
- ANGIOSPERM PHYLOGENY GROUP II [APG II]. 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Bot. J. Linn. Soc.* **141**: 399–436.
- BACKLUND, A. AND K. BREMER. 1998. To be or not to be—principles of classification and monophyletic plant families. *Taxon* **47**: 391–400.
- BATSCH, A. J. 1802. *Tabula affinitatum regni vegetabilis*. Landes-Industrie-Comptoir, Weimar, Germany. 286 p.
- BERG, R. 1958. Seed dispersal, morphology, and phylogeny of *Trilium*. *Skr. Norske Vidensk.-Akad. Oslo, Mat.-Naturvidensk. Kl.* **11**: 1–36.
- BODKIN, N. L. 1978. A revision of North American *Melanthium* L. (Liliaceae). Ph.D. dissertation. University of Maryland, College Park.
- , AND F. H. UTECH. 2002. *Melanthium*, pp. 77–79. In Flora of North America Editorial Committee [eds.], *Flora of North America north of Mexico*, Vol. 26. Oxford University Press, New York.
- BRINKER, R. R. 1942. Monograph of *Schoenocaulon*. *Ann. Missouri Bot. Gard.* **29**: 287–315.
- CHASE, M. W., M. R. DUVAL, H. G. HILLS, J. G. CONRAN, A. V. COX, L. E. EGUIARTE, J. HARTWELL, M. F. FAY, L. R. CADDICK, K. M. CAMERON, AND S. HOOT. 1995a. Molecular phylogenetics of Liliaceae, pp. 109–137. In P. J. Rudall, P. J. Cribb, D. F. Cutler, and C. J. Humphries [eds.], *Monocotyledons: systematics and evolution*. Royal Botanic Gardens, Kew, Richmond, Surrey, UK.
- , AND H. G. HILLS. 1991. Silica gel: an ideal material for field preservation of leaf samples for DNA studies. *Taxon* **40**: 215–220.
- , D. E. SOLTIS, R. G. OLMSTEAD, D. MORGAN, D. H. LES, B. D. MISHLER, M. R. DUVAL, R. A. PRICE, H. G. HILLS, Y.-L. QUI, K. A. KRON, J. H. RETTIG, E. CONTI, J. D. PALMER, J. R. MANHART, K. J. SYTSM, H. J. MICHAELS, W. J. KRESS, K. G. KAROL, W. D. CLARK, M. HEDRÉN, B. S. GAUT, R. K. JANSEN, K.-J. KIM, C. F. WIMPEE, J. F. SMITH, G. R. FURNIER, S. H. STRAUSS, Q.-Y. XIANG, G. M. PLUNKETT, P. S. SOLTIS, S. M. SWENSEN, S. E. WILLIAMS, P. A. GADEK, C. J. QUINN, L. E. EGUIARTE, E. GOLENBERG, G. H. LEARN, S. W. GRAHAM, S. C. H. BARRETT, S. DAYANANDAN, AND V. A. ALBERT. 1993. Phylogenetics of seed plants: an analysis of nucleotide sequences from the plastid gene *rbcl*. *Ann. Missouri Bot. Gard.* **80**: 528–580.
- , P. S. SOLTIS, P. J. RUDALL, M. F. FAY, W. H. HAHN, S. SULLIVAN, J. JOSEPH, M. MOLVRAJ, P. J. KORES, T. J. GIVNISH, K. J. SYTSM, AND J. C. PIRES. 2000. Higher-level systematics of the monocotyledons: an assessment of current knowledge and a new classification, pp. 3–16. In K. L. Wilson and D. A. Morrison [eds.], *Monocots: systematics and evolution*. CSIRO Publishing, Collingwood, Victoria, Australia.
- , D. W. STEVENSON, P. WILKIN, AND P. J. RUDALL. 1995b. Monocot systematics: a combined analysis, pp. 695–730. In P. J. Rudall, P. J. Cribb, D. F. Cutler, and C. J. Humphries [eds.], *Monocotyledons: systematics and evolution*. Royal Botanic Gardens, Kew, Richmond, Surrey, UK.
- COLASANTE, M., AND P. J. RUDALL. 2000. *Veratrum album* and *V. nigrum* (Melanthiaceae) in Italy: micromorphology and systematics. *Pl. Biosystems* **134**: 233–240.
- DAHLGREN, R. M. T., AND H. T. CLIFFORD. 1982. *The monocotyledons: a comparative study*. Academic Press, London, UK. 378 p.
- , AND P. F. YEO. 1985. *The families of the monocotyledons*. Springer-Verlag, Berlin, Germany. 520 p.
- DAUMANN, E. 1970. Das Blütennektarium der Monocotyledonen unter besonderer Berücksichtigung seiner systematischen und phylogenetischen Bedeutung. *Feddes Repert.* **80**: 463–590.
- DAVIS, J. I., D. W. STEVENSON, G. PETERSON, O. SEBERG, L. M.

- CAMPBELL, J. V. FREUDENSTEIN, D. H. GOLDMAN, C. R. HARDY, F. A. MICHELANGELI, M. P. SIMMONS, C. D. SPECHT, F. VERGARA-SILVA, AND M. GONDALFO. 2004. A phylogeny of the monocots, as inferred from *rbcL* and *atpA* sequence variation, and a comparison of methods for calculating jackknife and bootstrap values. *Syst. Bot.* **29**: 467–510.
- DUVALL, M. R., M. T. CLEGG, M. W. CHASE, W. D. CLARK, W. J. KRESS, H. G. HILLS, L. E. EGUIARTE, J. F. SMITH, B. S. GAUT, E. A. ZIMMER, AND G. H. LEARN. 1993. Phylogenetic hypotheses for the monocotyledons constructed from *rbcL* data. *Ann. Missouri Bot. Gard.* **80**: 607–619.
- FARMER, S. B., AND E. E. SCHILLING. 2002. Phylogenetic analyses of Trilliaceae based on morphological and molecular data. *Syst. Bot.* **27**: 674–692.
- FRAME, D. M. 1990. A revision of *Schoenocaulon* (Liliaceae–Melanthiaceae). Ph.D. dissertation. City University of New York.
- FUKUDA, I. 2001. Origin and evolution in *Trillium*. 1. The origin of the Himalayan *Trillium govanianum*. *Cytologia* **66**: 105–111.
- FUSE, S., AND M. N. TAMURA. 2000. A phylogenetic analysis of the plastid *matK* gene with emphasis on Melanthiaceae sensu lato. *Pl. Biol.* **2**: 415–427.
- GOLDBLATT, P. 1995. The status of R. Dahlgren's orders Liliales and Melanthiales, pp. 181–200. In P. J. Rudall, P. J. Cribb, D. F. Cutler, and C. J. Humphries [eds.], *Monocotyledons: systematics and evolution*. Royal Botanic Gardens, Kew, Richmond, Surrey, UK.
- GRAY, A. 1837. Melanthacearum Americae septentrionalis revisio. *Ann. Lyceum Nat. Hist. New York* **4**: 105–140.
- HARA, H. 1968. A revision of the genus *Chionographis* (Liliaceae). *J. Jap. Bot.* **43**: 257–267.
- HILU, K. W., T. BORSCH, K. MÜLLER, D. S. SOLTIS, P. S. SOLTIS, V. SAVOLAINEN, M. W. CHASE, M. P. POWELL, L. A. ALICE, R. EVANS, H. SAUQUET, C. NEINHUIS, T. A. B. SLOTTA, J. G. ROHWER, C. S. CAMPBELL, AND L. W. CHATROU. 2003. Angiosperm phylogeny based on *matK* sequence information. *Amer. J. Bot.* **90**: 1758–1776.
- HUTCHINSON, J. 1959. The families of flowering plants, Ed. 2, Vol. 2. Monocotyledons. Clarendon Press, Oxford, UK. 792 p.
- . 1973. The families of flowering plants, Ed. 3. Oxford University Press, UK. 968 p.
- KATO, H., S. KAWANO, R. TERAUCHI, M. OHARA, AND F. H. UTECH. 1995a. Evolutionary biology of *Trillium* and related genera (Trilliaceae) I. Restriction site mapping and variation of chloroplast DNA and its systematic implications. *Pl. Spec. Biol.* **10**: 17–29.
- , R. TERAUCHI, F. H. UTECH, AND S. KAWANO. 1995b. Molecular systematics of the Trilliaceae sensu lato as inferred from *rbcL* sequence data. *Molec. Phylogenet. Evol.* **4**: 184–193.
- KAWANO, S., AND H. KATO. 1995. Evolutionary biology of *Trillium* and related genera (Trilliaceae) II. Cladistic analyses on gross morphological characters, and phylogeny and evolution of the genus *Trillium*. *Pl. Spec. Biol.* **10**: 169–183.
- KELLOGG, E. A., AND W. S. JUDD. 2002. Methods and principles of biological systematics, pp. 13–39. In W. S. Judd, C. S. Campbell, E. A. Kellogg, P. F. Stevens, and M. J. Donoghue, *Plant systematics: a phylogenetic approach*, Ed. 2. Sinauer Associates, Inc., Sunderland, Massachusetts.
- KUNTH, C. S. 1843. Melanthaceae [sic]. *Enumeratio plantarum*, Vol. 4. J. G. Collae, Stuttgart, Germany. 752 p.
- KUPCHAN, S. M., J. H. ZIMMERMAN, AND A. AFONSO. 1961. The alkaloids and taxonomy of *Veratrum* and related genera. *Lloydia* **24**: 1–26.
- LEE, N. S. 1985. A cytotaxonomic study of Korean *Veratrum* species. *Korean J. Pl. Taxon.* **15**: 155–161.
- LEINFELLNER, W. 1961. Zur Kenntnis des Monokotyledonen-Perigons, Vol. 3. Die Perigonblätter einiger weiterer Melanthioideen (*Melanthium*, *Zygadenus* [sic], *Anticlea*, *Toxicoscordion*, *Veratrum* und *Kreysia*). *Österr. Bot. Z.* **108**: 194–210.
- LI, H.-L. 1952. Floristic relationships between eastern Asia and eastern North America. *Trans. Amer. Philos. Soc.* **42**: 371–409.
- LI, H. 1984. The phylogeny of the genus *Paris* L. *Acta Bot. Yunnan.* **6**: 351–362.
- . 1986. A study on the taxonomy of the genus *Paris* L. *Bull. Bot. Res. (Kunming)* **6**: 109–144.
- [ed.]. 1998. The genus *Paris* (Trilliaceae). Science Press, Beijing, China. 203 p.
- LOESENER, O. 1926. Studien über die Gattung *Veratrum* und ihre Verbreitung. *Verh. Bot. Vereins Prov. Brandenburg* **68**: 105–166.
- . 1927. Übersicht über Arten der Gattung *Veratrum*, Teil I. *Repert. Spec. Nov. Regni Veg.* **24**: 61–72.
- . 1928. Übersicht über Arten der Gattung *Veratrum*, Schluss. *Repert. Spec. Nov. Regni Veg.* **25**: 1–10.
- LOWRY, P. P., P. GOLDBLATT, AND H. TOBE. 1987. Notes on the floral biology, cytology and embryology of *Campynemanthe* (Liliales: Campynemataceae). *Ann. Missouri Bot. Gard.* **74**: 573–576.
- MCNEAL, D. W., AND A. D. SHAW. 2002. *Veratrum*, pp. 72–76. In Flora of North America Editorial Committee [eds.], *Flora of North America north of Mexico*, Vol. 26. Oxford University Press, New York.
- MEAGHER, T. R., AND J. ANTONOVICS. 1982. Life history variation in dioecious plant populations: a case study of *Chamaelirium luteum*, pp. 137–154. In H. Dingle and J. Hegmann [eds.], *Evolution and genetics of life histories*. Springer-Verlag, New York.
- MITCHELL, R. J. 1987. *Paris*—Part I. *Plantsman* **9**: 81–89.
- . 1988. *Paris*—Part 2. *Daiswa*. *Plantsman* **10**: 167–190.
- OSALOO, S. K., AND S. KAWANO. 1999. Molecular systematics of Trilliaceae II. Phylogenetic analyses of *Trillium* and its allies using sequences of *rbcL* and *matK* genes of cpDNA and internal transcribed spacers of 18S–26S nrDNA. *Pl. Spec. Biol.* **14**: 75–94.
- , F. H. UTECH, M. OHARA, AND S. KAWANO. 1999. Molecular systematics of Trilliaceae I. Phylogenetic analyses of *Trillium* using *matK* gene sequences. *J. Pl. Res.* **112**: 35–49.
- PREECE, S. J. 1956. A cytotaxonomic study of the genus *Zigadenus*. Ph.D. dissertation, State College of Washington, Pullman.
- REVEAL, J. L., AND W. B. ZOMLEFER. 1998. Two new orders for monocotyledonous plants. *Novon* **8**: 176–177.
- RUDALL, P. J., K. L. STOBART, W.-P. HONG, J. G. CONRAN, C. A. FURNESS, G. C. KITE, AND M. W. CHASE. 2000. Consider the lilies: systematics of Liliales, pp. 347–357. In K. L. Wilson and D. A. Morrison [eds.], *Monocots: systematics and evolution*. CSIRO Publishing, Collingwood, Victoria, Australia.
- RYDBERG, P. A. 1903. Some generic segregations. *Bull. Torrey Bot. Club* **30**: 271–281.
- SCHWARTZ, F. C. 2002. *Zigadenus*, pp. 81–89. In Flora of North America Editorial Committee [eds.], *Flora of North America north of Mexico*, Vol. 26. Oxford University Press, New York.
- SEN, S. 1975. Cytotaxonomy of Liliales. *Feddes Repert.* **86**: 255–305.
- SMALL, J. K. 1903. Flora of the southeastern United States. Publ. by author, New York. 1370 p.
- SOKOLOVSKAYA, A. P. 1969. Correlations between the size of pollen grains and the chromosome number in the far-eastern species of *Veratrum* L. *Bot. Zhurn. (Moscow & Leningrad)* **54**: 563–566.
- SOLTIS, D. E., P. S. SOLTIS, M. W. CHASE, M. E. MORT, D. C. ALBACH, M. ZANIS, V. SAVOLAINEN, W. H. HAHN, S. B. HOOT, M. F. FAY, M. AXTELL, S. M. SWENSEN, L. M. PRINCE, W. J. KRESS, K. C. NIXON, AND J. S. FARRIS. 2000. Angiosperm phylogeny inferred from 18S rDNA, *rbcL*, and *atpB* sequences. *Bot. J. Linn. Soc.* **133**: 381–461.
- STERLING, C. 1980. Comparative morphology of the carpel in the Liliaceae: Helonieae. *Bot. J. Linn. Soc.* **80**: 341–356.
- . 1982. Comparative morphology of the carpel in the Liliaceae: Veratreae. *Bot. J. Linn. Soc.* **84**: 57–77.
- TAKHTAJAN, A. 1983. A revision of *Daiswa* (Trilliaceae). *Brittonia* **35**: 255–270.
- . 1994. Six new families of flowering plants. *Bot. Zhurn. (Moscow & Leningrad)* **79**: 96–97.
- . 1997. Diversity and classification of flowering plants. Columbia University Press, New York. 643 p.

- TAMURA, M. N. 1995. A karyological review of the orders Asparagales and Liliales (Monocotyledonae). *Feddes Repert.* **106**: 83–111.
- . 1998. Melanthiaceae, pp. 369–380. In K. Kubitzki [ed.], *The families and genera of vascular plants*, Vol. 3. Monocotyledons. Springer-Verlag, Berlin, Germany.
- TANAKA, N. 1997a. Taxonomic significance of some floral characters in *Helonias* and *Ypsilandra* (Liliaceae). *J. Jap. Bot.* **72**: 110–116.
- . 1997b. Evolutionary significance of the variation of the floral structure of *Heloniopsis*. *J. Jap. Bot.* **72**: 131–138.
- . 1997c. Phylogenetic and taxonomic studies on *Helonias*, *Ypsilandra* and *Heloniopsis*. I. Comparison of character states (1). *J. Jap. Bot.* **72**: 221–228.
- . 1997d. Phylogenetic and taxonomic studies on *Helonias*, *Ypsilandra* and *Heloniopsis*. I. Comparison of character states (2). *J. Jap. Bot.* **72**: 286–292.
- . 1997e. Phylogenetic and taxonomic studies on *Helonias*, *Ypsilandra* and *Heloniopsis*. II. Evolution and geographical distribution. *J. Jap. Bot.* **72**: 329–336.
- . 1998. Phylogenetic and taxonomic studies on *Helonias*, *Ypsilandra* and *Heloniopsis*. III. Taxonomic revision. *J. Jap. Bot.* **73**: 102–115.
- TOKUMOTO, N. 1940. Polyploidy and secondary pairing in the genus *Veratrum*. *Bot. & Zool.* **8**: 1189–1195.
- UTECH, F. H. 1980. Somatic karyotype analysis of *Helonias bullata* L. (Liliaceae), with a comparison to the Asian *Heloniopsis orientalis* (Thunb.) C. Tanaka. *Ann. Carnegie Mus.* **49**: 153–160.
- . 2002. *Amianthium*, pp. 89–90. In *Flora of North America* Editorial Committee [eds.], *Flora of North America north of Mexico*, Vol. 26. Oxford University Press, UK.
- VINNERSTEN, A., AND K. BREMER. 2001. Age and biogeography of major clades in Liliales. *Amer. J. Bot.* **88**: 1695–1703.
- WOOD, C. E. 1971. Some floristic relationships between the southern Appalachians and western North America, pp. 331–404. In P. C. Holt [ed.], *The distributional history of the biota of the southern Appalachians*, part 2, *Flora*. Virginia Polytechnic Institute and State University, Blacksburg.
- WU, Z. Y. 1983. On the significance of Pacific intercontinental discontinuity. *Ann. Missouri Bot. Gard.* **70**: 577–590.
- ZAKHARIEVA, O. I., AND L. M. MAKUSHENKO. 1969. Chromosome numbers of monocotyledons belonging to the families Liliaceae, Iridaceae, Amaryllidaceae, and Araceae. *Bot. Zhurn. (Moscow & Leningrad)* **54**: 1213–1227.
- ZHUKOVA, P. G. 1969. Chromosome number in certain plant species indigenous to the northeast of the U.S.S.R. IV. *Bot. Zhurn. (Moscow & Leningrad)* **54**: 1985–1990.
- , AND V. V. PETROVSKY. 1976. Chromosome numbers of some western Chokotka plant species, II. *Bot. Zhurn. (Moscow & Leningrad)* **61**: 963–969.
- , AND ———. 1980. Chromosome numbers and taxonomy of some species of the Anyui Mountains. *Bot. Zhurn. (Moscow & Leningrad)* **65**: 651–659.
- , AND A. D. TIKHONOVA. 1971. Chromosome numbers of certain plant species indigenous to the Chukotskiy province. *Bot. Zhurn. (Moscow & Leningrad)* **56**: 868–875.
- ZIMMERMAN, J. H. 1958. A monograph of *Veratrum*. Ph.D. dissertation, University of Wisconsin, Madison.
- ZOMLEFER, W. B. 1994. *Guide to flowering plant families*. University of North Carolina Press, Chapel Hill. 430 p.
- . 1996. The Trilliaceae in the southeastern United States. *Harvard Pap. Bot.* **1**(9): 91–120.
- . 1997a. The genera of Melanthiaceae in the southeastern United States. *Harvard Pap. Bot.* **2**: 133–177.
- . 1997b. The genera of Tofieldiaceae in the southeastern United States. *Harvard Pap. Bot.* **2**: 179–194.
- . 1997c. The genera of Nartheciaceae in the southeastern United States. *Harvard Pap. Bot.* **2**: 195–211.
- . 1999. Advances in angiosperm systematics: examples from the Liliales and Asparagales. *J. Torrey Bot. Soc.* **125**: 58–62.
- . 2003. Documented chromosome numbers 2003: 1. Chromosome number of *Toxicoscordion nuttallii* (Liliales: Melanthiaceae) and clarification of the genus. *Sida* **20**: 1083–1090.
- , AND W. S. JUDD. 2002. Resurrection of segregates of the polyphyletic genus *Zigadenus* s.l. (Liliales: Melanthiaceae) and resulting new combinations. *Novon* **12**: 299–308.
- , AND G. L. SMITH. 2002. Documented chromosome numbers 2002: 1. Chromosome number of *Stenanthium* (Liliales: Melanthiaceae) and its significance in the taxonomy of tribe Melanthieae. *Sida* **20**: 221–226.
- , W. M. WHITTEN, N. H. WILLIAMS, AND W. S. JUDD. 2003. An overview of *Veratrum* (Liliales: Melanthiaceae) and an infrageneric phylogeny based on ITS sequence data. *Syst. Bot.* **28**: 250–269.
- , N. H. WILLIAMS, W. M. WHITTEN, AND W. S. JUDD. 2001. Generic circumscription and relationships in the tribe Melanthieae (Liliales, Melanthiaceae), with emphasis on *Zigadenus*: evidence from ITS and *trnL*-F sequence data. *Amer. J. Bot.* **88**: 1657–1669.