Resurrection of Segregates of the Polyphyletic Genus *Zigadenus* s.l. (Liliales: Melanthiaceae) and Resulting New Combinations

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Abstract. Reinstatement of segregate genera and the accompanying recombinations for species in the former polyphyletic *Zigadenus* complex allow for a revised, practical taxonomy that defines monophyletic groups and reflects phylogenetic relationships within tribe Melanthieae (Melanthiaceae). Nine new species combinations result from recircumscription of *Zigadenus* Michaux and *Stenanthium* (A. Gray) Kunth and from recognition of *Anticlea* Kunth and *Toxicoscordion* Rydberg. The genus *Stenanthella* Rydberg and the basionyms for *Stenanthium leimanthoides* (A. Gray) Zomlefer & Judd (*Amianthium leimanthoides* A. Gray) and *Anticlea sachalinensis* (F. Schmidt) Zomlefer & Judd (*Stenanthium sachalinense* F. Schmidt) are lectotypified.

Key words: *Amianthium*, Liliales, Melanthiaceae, *Stenanthium*, *Zigadenus*.

The Melanthiaceae sensu the Angiosperm Phylogeny Group (APG, 1998) comprise 11 to 16 genera (ca. 154–201+ spp.; Zomlefer et al., 2001) 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* extending into South America). Of concern here are certain taxa of the tribe Melanthieae (Zomlefer et al., 2001): *Amianthium* (1 sp.), *Stenanthium* (3–5 spp.), and *Zigadenus* (19 spp.). The poorly defined genus *Stenanthium* s.l. has sometimes been divided into two genera: *Stenanthella* (2–4 spp.) and a monotypic *Stenanthium* (*S. gramineum*; see Rydberg, 1900; Gleason, 1952; Utech, 1987a, b). Taxonomists have divided *Zigadenus* into several segregate genera (summaries in Rydberg, 1903; Gates, 1918; Preece, 1956; Zomlefer, 1997). However, contemporary botanists have typically accepted only one segregate—a monotypic *Amianthium* (Utech, 1986)—with the remaining species maintained in *Zigadenus* s.l. (as in Walsh, 1940; Preece, 1956; Schwartz, 1994, 2002).

As part of a study on the tribe Melanthieae (Zomlefer et al., 2001), the circumscription of the *Zigadenus* complex was evaluated using parsimony analyses of ITS (nuclear ribosomal) and *trn*L-F (plastid) DNA sequence data. Based on the cladograms resulting from this study, *Stenanthium* is biphyletic (and embedded within *Zigadenus*), the traditional *Zigadenus* s.l. is polyphyletic, and *Amianthium* is a distinct entity only distantly related to the other *Zigadenus* species. The species of these genera form five strongly supported clades that correlate with geographical distribution, chromosome number, and certain morphological characters (Table 1). Therefore, we recognize five genera (some with novel circumscription): (1) *Amianthium* (monotypic: *A. muscitoxicum*), (2) *Anticlea* (including *Stenanthella*; ca. 11 spp.), (3) *Stenanthium* (*Stenanthium gramineum*, *Zigadenus densus*, and *Z. leimanthoides*), (4) *Toxicoscordion* (ca. 8 spp.), and (5) *Zigadenus* s. str. (monotypic: *Z. glaberrimus*).

The nomenclatural consequences of these results include reinstatement of two segregate taxa (*Anticlea* and *Toxicoscordion*), redefinition of *Zigadenus* and *Stenanthium*, and nine recombinations. For convenience, we include a key and concise treatment of all five genera, as well as a list of species (Table 2). Although a complete revision of these genera and an investigation of species-level issues are not the focus of this paper, some problematic species complexes are mentioned in the generic commentaries. Table 3 cross-indexes the combinations accepted in this paper with familiar *Zigaden-*

Table 1. Characters defining the five segregates of the *Zigadenus* complex. Modified from Zomlefer et al. (2001); chromosome numbers from numerous references cited in Zomlefer (1997). * = possible autapomorphies.

Species no.	*Amianthium* 1	*Anticlea* ca. 11	*Stenanthium* 2 or 3	*Toxicoscordion* ca. 8	*Zigadenus* s. str. 1
Distribution	SE U.S. (Coastal Plain and mountains)	Asia; North America to Guatemala	SE U.S. (Coastal Plain and mountains)	Midwestern U.S. and western North America	SE U.S. (Coastal Plain)
Habitat	Acidic coniferous forests and bogs	Acidic and/or alpine coniferous forests, prairies, calcareous shores and fens	Acidic coniferous forests and bogs	Acidic and/or alpine coniferous forests, prairies, desert, chaparral, serpentine vegetation	Acidic coniferous forests and bogs
Base chromosome number (x)	8	8	10*	11*	26(?)* (unconfirmed; see discussion)
Rootstock	Broadly ovoid bulb	Narrowly ovoid bulb	Slender (cylindrical) bulb*	Ovoid bulb	Rhizome*
Tepal base	Obtuse and slightly tapered	Cuneate to gradually tapered	Cuneate to gradually tapered	Conspicuously clawed*	Slightly tapered
Gland(s) per tepal; shape	1, reduced/absent*	1; bilobed*	1; obscure (or absent)*	1; obovate*	2; ovate*
Ovary position	Partly inferior	½-inferior	Superior to ½-inferior	Superior	Superior
Other significant characters	Large seeds with sarcotesta* Unique alkaloids*				Unusual anatomical features*
Additional commentary	Historically considered closely related to (or included within) *Zigadenus* s.l.	Wide distribution Includes *Stenanthella* Rydberg	Includes *Oeanoros* Small, *Tracyanthus* Small *Zigadenus densus* and *Z. leimanthoides* perhaps conspecific	Includes the well-known poisonous *Zigadenus* spp. ("death camas")	Type species

Table 2. Segregate genera of the *Zigadenus* complex reflecting the clades supported by morphological and molecular data (Zomlefer et al., 2001). This list includes nine new combinations indicated here with an asterisk.

1. *Amianthium* A. Gray
   A. muscitoxicum (Walter) A. Gray
2. *Anticlea* Kunth
   A. elegans (Pursh) Rydberg
   **A. frigida* (Schlechtendal & Chamisso) Zomlefer & Judd
   **A. hintoniorum* (B. L. Turner) Zomlefer & Judd
   **A. mogollonensis* (W. J. Hess and Sivinski) Zomlefer & Judd
   **A. neglecta* (Espejo, A. R. López-Ferrari & Ceja) Zomlefer & Judd
   **A. occidentalis* (A. Gray) Zomlefer & Judd
   **A. sachalinensis* (F. Schmidt) Zomlefer & Judd
   A. sibirica (L.) Kunth
   A. vaginata Rydberg
   A. virescens (Kunth) Rydberg
   A. volcanica (Bentham) J. G. Baker
3. *Stenanthium* (A. Gray) Kunth
   S. gramineum (Ker Gawler) Morong
   **S. densum* (Desrousseaux) Zomlefer & Judd
   **S. leimanthoides* (A. Gray) Zomlefer & Judd
4. *Toxicoscordion* Rydberg
   T. brevibracteatus (M. E. Jones) R. R. Gates
   T. exaltatum (Eastwood) A. Heller
   **T. fontanum* (Eastwood) Zomlefer & Judd
   T. fremontii (Torrey) Rydberg
   T. micranthum (Eastwood) A. Heller
   T. nuttallii (A. Gray) Rydberg
   T. paniculatum (Nuttall) Rydberg
   T. venenosum (S. Watson) Rydberg
5. *Zigadenus* Michaux
   Z. glaberrimus Michaux

us and *Stenanthium* species names (in alphabetical order) used in current literature.

1. Amianthium A. Gray, Ann. Lyceum Nat. Hist. New York 4: 121. 1837, nom. cons. TYPE: *Amianthium muscitoxicum* (Walter) A. Gray, typ. cons. [basionym: *Melanthium muscaetoxicum* Walter].

Chrosperma Rafinesque, Neogenyton 3. 1825, nom. rej. TYPE: *Melanthium laetum* W. Aiton.

Endocles Salisbury, Gen. Pl. 51. 1866. TYPE: not designated.

Salient features. Ovoid bulb, obtuse (slightly narrowed but not clawed) tepal bases, reduced/absent tepal glands, partly inferior ovary, large seeds with a reddish to purple sarcotesta, distinctive alkaloids; base chromosome number $x = 8$.

Distribution. Southeastern United States (coastal plain and mountains) in acidic coniferous forests and bogs.

Beyond the lack of glands (Utech, 1986) and the distinctive seeds, this genus is characterized by amianthine, a unique alkaloid, and also jervine, a veratrum alkaloid, evidently not found in other species of the *Zigadenus* complex (Neuss, 1953; Kupchan et al., 1961). *Amianthium* has been considered closely related to *Zigadenus* s.l. (see Zomlefer, 1997); however, molecular data (Zomlefer & Perkins, 1999; Zomlefer et al., 2001) strongly support the separation of *Amianthium* as only distantly related to other *Zigadenus* species. As circumscribed here (and in most current literature), this genus comprises one species, *Amianthium muscitoxicum* (Walter) A. Gray. The preferred spelling "*muscitoxicum*" rather than "*muscaetoxicum*" for the specific epithet is supported by the ICBN (Greuter et al., 2000), Article 60, Recommendation 60G.

2. Anticlea Kunth, Enum. Pl. 4: 191. 1843. *Geiseleria* Kunth, Abh. Königl. Akad. Wiss. Berlin 3. 1842, nom. illeg., non *Geiseleria* Klotzsch 1843 (Euphorbiaceae). TYPE: *Anticlea sibirica* (L.) Kunth (lectotype, designated by Pfeiffer, 1873: 219).

Stenanthella Rydberg, Bull. Torrey Bot. Club 27: 530. 1900. Syn. nov. TYPE: *Stenanthella occidentalis* (A. Gray) Rydberg (lectotype, designated here).

Although Rydberg (1900) included two species in his new genus *Stenanthella*, *Stenanthella occidentalis* (A. Gray) Rydberg and *Stenanthella sachalinensis* (F. Schmidt) Rydberg, he based his description of *Stenanthella* on cited specimens of

Table 3. The species of the polyphyletic genera *Zigadenus* s.l. and *Stenanthium* s.l., typically employed in contemporary floras (e.g., Ahles, 1968; Hitchcock et al., 1969; Cronquist et al., 1977; Gleason & Cronquist, 1991; McNeal, 1993; Kartesz, 1994; Schwartz, 2002), are listed in alphabetical order with the recombination advocated in this paper (**boldface**), including nine new combinations. For completeness, the monotypic genus *Amianthium*, a segregate of the *Zigadenus* complex, is also included; its segregate status is supported by Zomlefer et al. (2001). Only three species (*Amianthium muscitoxicum*, *Stenanthium gramineum*, and *Zigadenus glaberrimus*) are retained in their traditional genera; *Amianthium* and *Zigadenus* are monospecific.

Amianthium muscitoxicum (Walter) A. Gray
Stenanthium frigidum (Schlechtendal & Chamisso) Kunth = ***Anticlea frigida*** (Schlechtendal & Chamisso) Zomlefer & Judd
Stenanthium gramineum (Ker Gawler) Morong
Stenanthium occidentale A. Gray = ***Anticlea occidentalis*** (A. Gray) Zomlefer & Judd
Stenanthium sachalinense F. Schmidt = ***Anticlea sachalinensis*** (F. Schmidt) Zomlefer & Judd
Zigadenus brevibracteatus (M. E. Jones) H. M. Hall = ***Toxicoscordion brevibracteatus*** (M. E. Jones) R. R. Gates
Zigadenus densus (Desrousseaux) Fernald = ***Stenanthium densum*** (Desrousseaux) Zomlefer & Judd
Zigadenus elegans Pursh = ***Anticlea elegans*** (Pursh) Rydberg
Zigadenus exaltatus Eastwood = ***Toxicoscordion exaltatum*** (Eastwood) A. Heller
Zigadenus fontanus Eastwood = ***Toxicoscordion fontanum*** (Eastwood) Zomlefer & Judd
Zigadenus fremontii (Torrey) Torrey ex S. Watson = ***Toxicoscordion fremontii*** (Torrey) Rydberg
Zigadenus glaberrimus Michaux
Zigadenus hintoniorum B. L. Turner = ***Anticlea hintoniorum*** (B. L. Turner) Zomlefer & Judd
Zigadenus leimanthoides (A. Gray) A. Gray = ***Stenanthium leimanthoides*** (A. Gray) Zomlefer & Judd
Zigadenus micranthus Eastwood = ***Toxicoscordion micranthum*** (Eastwood) A. Heller
Zigadenus mogollonensis W. J. Hess & Sivinski = ***Anticlea mogollonensis*** (W. J. Hess & Sivinski) Zomlefer & Judd
Zigadenus neglectus Espejo, A. R. López-Ferrari & Ceja = ***Anticlea neglecta*** (Espejo, A. R. López-Ferrari & Ceja) Zomlefer & Judd
Zigadenus nuttallii (A. Gray) S. Watson = ***Toxicoscordion nuttallii*** (A. Gray) Rydberg
Zigadenus paniculatus (Nuttall) S. Watson = ***Toxicoscordion paniculatum*** (Nuttall) Rydberg
Zigadenus sibiricus (L.) A. Gray = ***Anticlea sibirica*** (L.) Kunth
Zigadenus vaginatus (Rydberg) J. F. Macbride = ***Anticlea vaginata*** Rydberg
Zigadenus venenosus S. Watson = ***Toxicoscordion venenosum*** (S. Watson) Rydberg
Zigadenus virescens (Kunth) J. F. Macbride = ***Anticlea virescens*** (Kunth) Rydberg
Zigadenus volcanicus Bentham = ***Anticlea volcanica*** (Bentham) Baker

S. occidentalis. Therefore, we select this species as the lectotype.

Salient features. Narrowly ovoid bulb, cuneate to gradually narrowed (but not clawed) tepal bases, one bilobed gland per tepal, half-inferior ovary; base chromosome number $x = 8$.

Distribution. Asia, North America south to Guatemala in acidic and/or alpine coniferous forests, prairies, calcareous shores and fens.

The segregate genus *Anticlea* (Kunth, 1843; Rydberg, 1903) has been more recently considered as *Zigadenus* sect. *Anticlea* (Kunth) Bentham by Preece (1956) and Schwartz (2002). The one bilobed gland per tepal is an autapomorphy for this taxon. Resurrection of *Anticlea* involves six new combinations with species formerly placed in *Stenanthella* and *Zigadenus* s.l. (Table 2). *Stenanthella*, a *Stenanthium* segregate (Rydberg, 1900), shares little morphologically with *Stenanthium* s. str. but has the diagnostic features of *Anticlea*, including the distinctive nectaries and half-inferior ovary. In addition, *Stenanthella occidentalis* (*Stenanthium occidentale*) resolves in the *Anticlea* clade in the molecular study by Zomlefer et al. (2001).

Anticlea includes the only Asian species in the *Zigadenus* complex (*A. sibirica* and *A. sachalinensis*), the Guatemalan *A. volcanica*, and the widespread and variable North American species *A. elegans* and *A. virescens* and their segregates (*A. vaginata* and *A. hintoniorum*, *A. mogollonensis*, and *A. neglecta*, respectively). The latter are discussed in detail by Turner (1992), Hess and Sivinski (1995), and Frame et al. (1999). Further study of these taxa is needed to evaluate the current specific and infraspecific delimitations and to suggest biologically meaningful taxon circumscriptions. *Stenanthium rhombipetalum* (never formally transferred to *Stenanthella*) has been reduced in synonymy under *Anticlea occidentalis* by Utech (1987a). In addition, the North American *A. occidentalis* and the Asian *A. sachalinensis* may be conspecific (Kupchan et al., 1961), a situation that merits further study.

Anticlea frigida (Schlechtendal & Chamisso) Zomlefer & Judd, comb. nov. Basionym: *Veratrum frigidum* Schlechtendal & Chamisso, Linnaea 6: 46. 1831. *Zigadenus frigidus* (Schlechtendal & Chamisso) D. Don, Edinburgh New Philos. J. 13(26): 233. 1832. *Stenanthium frigidum* (Schlechtendal & Chamisso) Kunth, Enum. Pl. 4: 190. 1843. TYPE: Mexico. Veracruz: Mt. Orizaba, *F. Deppe & C. J. W. Schiede 983* (holotype, HAL; isotypes, HAL, MO).

Utech (1987b: 207) listed "fragment GH!" as a "type" specimen (category of type not specified). However, the handwritten notation on this fragment packet, "*Veratrum frigidum* Cham.! & Schlech." followed by "Schiede" lacks detail to positively identify it as *Deppe & Schiede 983*.

Anticlea hintoniorum (B. L. Turner) Zomlefer & Judd, comb. nov. Basionym: *Zigadenus hintoniorum* B. L. Turner, Phytologia 72: 378. 1992. TYPE: Mexico. Nuevo León: Mpio. Galeana, Cerro Potosí, *G. B. Hinton 17200* (holotype, TEX).

Anticlea mogollonensis (W. J. Hess & Sivinski) Zomlefer & Judd, comb. nov. Basionym: *Zigadenus mogollonensis* W. J. Hess & Sivinski, Sida 16: 390. 1995. TYPE: U.S.A. New Mexico: Catron Co., Mogollon Mts., Gila National Forest, *W. J. Hess 2212* (holotype, MOR; isotypes, NY; also ARIZ, NCU, NMC, OKLA, SMU, US not seen).

Anticlea neglecta (Espejo, A. R. López-Ferrari & Ceja) Zomlefer & Judd, comb. nov. Basionym: *Zigadenus neglectus* Espejo, A. R. López-Ferrari & Ceja, in D. M. Frame et al., Acta Bot. Mex. 48: 47. 1999. TYPE: Mexico. Guanajuato: Mpio. Xichú, Puerto del Manzanar, Sierra de Xichú, *E. Ventura & E. López 9560* (holotype, UAMIZ not seen; isotype, IEB.)

Anticlea occidentalis (A. Gray) Zomlefer & Judd, comb. nov. Basionym: *Stenanthium occidentale* A. Gray, Proc. Amer. Acad. Arts 8: 405. 1873. *Stenanthella occidentalis* (A. Gray) Rydberg, Bull. Torrey Bot. Club 27: 531. 1900. TYPE: Rocky Mountains, Palliser's British North American Exploratory Expedition, 1858, *E. Bourgeau s.n.* (lectotype, designated by Utech (1987a), GH; isolectotypes, NY; also B, K not seen).

Stenanthium rhombipetalum Suksdorf, Werdenda 1: 6. 1923. TYPE: U.S.A. Washington: Skamania Co., Cape Horn, *W. Suksdorf 10,466* (lectotype, designated by Utech (1987a), GH; isolectotypes, MO, NY; also DS, UC, WTU not seen).

Anticlea sachalinensis (F. Schmidt) Zomlefer & Judd, comb. nov. Basionym: *Stenanthium sachalinense* F. Schmidt, Reis. Amur-Land., Bot. 188. 1868. *Stenanthella sachalinensis* (F. Schmidt) Rydberg, Bull. Torrey Bot. Club 27: 530. 1900. TYPE: Russia. "Ins. Sachalin" [Sakhalin Island]: Ktausi, 11 July 1860, *F. Schmidt s.n.* (lectotype, designated here, LE; photograph of lectotype, GA).

In his protologue, Schmidt (1868: 188) cited four collections from different localities on Sakhalin Island in 1860: "Dui" (June, flowering), "Adngiwo" (July, flowers withered/fallen), "Ktausi" (11 July, immature fruit), and "Manue" (August, flowers withered/fallen). We have selected a specimen at LE, the principal depository of his collections (Stafleu & Cowan, 1985). Other probable isolectotypes (at GH, LE, and NY) have only "Ins. Sachalin, Exped Fr. Schmidt" on the labels.

3. Stenanthium (A. Gray) Kunth, Enum. Pl. 4: 189. 1843, nom. cons. *Veratrum* subg. *Stenanthium* A. Gray, Ann. Lyceum Nat. Hist. New York 4: 119. 1837. *Anepsa* Rafinesque, Fl. Tellur. 2: 31. 1836 [1837]. TYPE: *Stenanthium angustifolium* (Pursh) Kunth [basionym: *Veratrum angustifolium* Pursh].

Stenanthium gramineum (Ker Gawler) Morong is synonymous with, and has priority over, *S. angustifolium* (Pursh) Kunth. *Veratrum angustifolium*, described by Pursh (1814) and transferred to *Stenanthium* by Kunth (1843), is the same plant previously described by Gawler (1813), *Helonias graminea* Ker Gawler, subsequently transferred to *Stenanthium* by Morong (Britton et al., 1894). There is also some confusion in the literature concerning *Anepsa*. Rafinesque (1836) based *Anepsa* on four species—two transferred from *Veratrum* and *Stenanthium* (synonyms indicated by Rafinesque, 1836: 2: 31), as well as two others with unknown affinity (see Cowley et al., 2001): (1) *Anepsa carinata* Rafinesque [*Veratrum angustifolium* Pursh = *Stenanthium gramineum* (Ker Gawler) Morong; see Zomlefer, 1997]; (2) *Anepsa latifolia* Rafinesque (*Veratrum parviflorum* Michaux); (3) *Anepsa spicata* Rafinesque (species of unknown affinity); and (4) *Anepsa graminifolia* (species of unknown affinity). *Anepsa*, a genus of mixed elements, has consequently been considered a nomenclatural syn-

onym of *Stenanthium* (Greuter et al., 2000) and of *Veratrum* (Cowley et al., 2001). However, when Rafinesque (1836: 4: 27) stated in a later part of the same work ". . . his [Gray's] *Stenanthium* S. G. [subgenus] of *Veratrum* is my G. [genus] *Anepsa*," he provided a nom. and stat. nov. for *Veratrum* subg. *Stenanthium*, and the type of this subgenus (*V. angustifolium*) is, therefore, the type of *Anepsa* (K. Gandhi, pers. comm.).

Tracyanthus Small, Fl. S.E. U.S. 250. 1903. Syn. nov. TYPE: *Tracyanthus angustifolius* (Michaux) Small.
Oceanoros Small, Fl. S.E. U.S. 252. 1903. Syn. nov. TYPE: *Oceanoros leimanthoides* (A. Gray) Small.

Salient features. Slender bulb, cuneate to gradually and slightly narrowed (but not clawed) tepal bases, 1 obscure (or lacking) gland per tepal, superior to half-inferior ovary; base chromosome number $x = 10$ (reported only for *S. gramineum*).

Distribution. Southeastern United States (coastal plain and mountains) in acidic coniferous forests and bogs.

Until the molecular investigation (Zomlefer et al., 2001), the relationship of *Stenanthium* s.l. to *Zigadenus* s.l. was unknown, although in phenetic analyses by Ambrose (1975, 1980) *S. gramineum* clustered with several *Zigadenus* species. The results of Zomlefer et al. (2001) strongly support a markedly different circumscription of the traditional *Stenanthium*: the type element, *Stenanthium gramineum*, forms a clade with *Zigadenus densus* and *Z. leimanthoides* (while the species of the *Stenanthium* segregate *Stenanthella* resolve with *Anticlea*). Autapomorphies for this expanded concept of *Stenanthium* are a slender (cylindrical) bulb, loss/reduction of the tepal glands, and possibly also a base chromosome number of $x = 10$ (reported only for *S. gramineum*; Miller, 1930; Satô, 1942).

Therefore, this new definition of *Stenanthium* necessitates the transfer of two former *Zigadenus* species, *Stenanthium densum* and *S. leimanthoides*. These taxa have been separated from the rest of the *Zigadenus* complex as segregate genera (*Oceanoros* and *Tracyanthus*; Small, 1903) and considered within *Zigadenus* as "section *Oceanoros*" (Preece, 1956; Schwartz, 2002). (As of this writing, this sectional name has not been validly published.) Traditionally, plant size and inflorescence type have been used to distinguish these two sympatric and closely related species: specimens of *Stenanthium leimanthoides* at FLAS, GA, GH, MO, and NY are strikingly much more robust plants with compound racemose inflorescences in comparison to the more delicate *S. densum* with unbranched racemes (W. Zomlefer, pers. obs.). However, field studies of intergrading populations by McDearman (1984) suggest that these two taxa are likely conspecific (summary in Zomlefer, 1997). Some authors have placed *S. leimanthoides* in synonymy with *S. densum* (M. MacRoberts, pers. comm.; Schwartz, 2002; Sorrie & Weakley, 2001); varietal status of *S. leimanthoides* has also been suggested (R. Wunderlin, pers. comm.). The status of *S. leimanthoides* merits additional systematic study, as well as determination of the chromosome number.

Stenanthium densum (Desrousseaux) Zomlefer & Judd, comb. nov. Basionym: *Melanthium densum* Desrousseaux, in Lamarck, Encycl. 4: 26. 1796 [1797]. *Zigadenus densus* (Desrousseaux) Fernald, Rhodora 42: 254. 1940. TYPE: U.S.A. Carolina: no date, *J. Fraser s.n.* (holotype, P-LA, microfiche 6207.654: III.3).

Helonias angustifolia Michaux, Fl. Bor.-Amer. 1: 212. 1803. *Amianthium angustifolium* (Michaux) A. Gray, Ann. Lyceum Nat. Hist. New York 4: 124. 1837. *Zigadenus angustifolius* (Michaux) S. Watson, Proc. Amer. Acad. Arts 14: 280. 1879. *Tracyanthus angustifolius* (Michaux) Small, Fl. S.E. U.S. 251. 1903. TYPE: U.S.A. "Basse Carolina" [South Carolina]: "in herbosis et fruticetis sylvarum humidis Carolinae inferioris," no date, *J. Fraser s.n.* (holotype, P-MICHX, microfiche 6211.48: I.2).

See Fernald (1940) for details about the types for both basionyms.

Stenanthium leimanthoides (A. Gray) Zomlefer & Judd, comb. nov. Basionym: *Amianthium leimanthoides* A. Gray, Ann. Lyceum Nat. Hist. New York 4: 125. 1837. *Zigadenus leimanthoides* (A. Gray) A. Gray, Manual (ed. 2) 476. 1856. *Oceanoros leimanthoides* (A. Gray) Small, Fl. S.E. U.S. 252, 1328. 1903. TYPE: U.S.A. New Jersey: Camden Co., "the other side of Haddington," 20 July 1837, *E. M. Durand s.n.* (lectotype, designated here, GH; isolectotype, NY).

Gray (1837) cited three collections in his protologue (see discussion of these paratypes in Walsh, 1940, and Preece, 1956). Preece (1956) chose the Durand specimen at GH as a "lectotype" in his unpublished dissertation, and we here follow his decision.

Paratypes. U.S.A. **North Carolina:** Burke Co., Table Mountain, 1835, *M. A. Curtis s.n.* (GH, NY). **Louisiana:** Orleans Co., New Orleans, 1834, [Dr.] *Ingalls s.n.* (NY).

4. **Toxicoscordion** Rydberg, Bull. Torrey Bot. Club 30: 272. 1903. TYPE: *Toxicoscordion intermedium* (Rydberg) Rydberg.

Chitonia Salisbury, Gen. Pl. 51. 1866, nom. illeg., non *Chitonia* D. Don 1823 (Melastomataceae).

Chitonia has often been cited as a synonym for *Zigadenus* s.l. (Walsh, 1940; Preece, 1956; Cowley et al., 2001). Baker (1880) adopted this name as the basis for erecting *Zigadenus* sect. *Chitonia* (Salisbury) Baker and included species of *Toxicoscordion* and *Stenanthium*. Salisbury (1866) did not mention any species in the protologue or in his discussion of the genus. No specimens are labeled *Chitonia* or *Zigadenus* among Salisbury's few remaining collections at BM (R. Vickery, pers. comm.), the repository of his collections (Stafleu & Cowan, 1985). Although the tepal glands are not mentioned, the description of the plant (Salisbury, 1866: 51) from the "west coast of North America" with "petals attenuated into a . . . claw" best agrees with the characteristics of *Toxicoscordion*.

Salient features. Ovoid bulb, conspicuously clawed tepal bases, 1 obovate gland per tepal, superior ovary; base chromosome number $x = 11$.

Distribution. Midwestern United States and western North America in acid and/or alpine coniferous forests, prairies, desert, chaparral, or serpentine vegetation.

Molecular and morphological data resolve *Toxicoscordion* as distinct from the rest of the *Zigadenus* complex (Zomlefer et al., 2001). In their unpublished dissertations, both Preece (1956) and Schwartz (1994) treated this taxon as *Zigadenus* sect. *Chitonia* (Salisbury) Baker (see also Schwartz, 2002). The resurrection of *Toxicoscordion* requires one new combination (*T. fontanum*), a species described within *Zigadenus* by Eastwood (1937), long after Rydberg (1903) had erected the segregate *Toxicoscordion* and had transferred the appropriate contemporary *Zigadenus* species (Table 2). Autapomorphies include conspicuously clawed tepals (especially the inner three), one obovate gland per tepal, and a base chromosome number of 11 (Zomlefer et al., 2001). A citation of $2n = 32$ for *T. nuttallii* (Fedorov, 1969; Moore, 1971, 1973), originally reported by Zakharieva and Makushenko (1969), is based on an undescribed and unvouchered plant then growing at the Munich Botanical Garden (original source not cited); this "*Zigadenus*" species was likely an *Anticlea* ($x = 8$).

The species of *Toxicoscordion* (Table 2), restricted to midwestern–western North America, include the well known poisonous "death camas" plants of the rangelands such as *T. nuttallii*, *T. paniculatum*, and *T. venenosum* (see Marsh et al., 1915, 1926). Further study is needed to determine appropriate specific and infraspecific limits within the variable *T. micranthum–T. fremontii* species complexes, as well as the overlapping *T. paniculatum–T. venenosum* complex. For example, in an isozyme study of these species (Schwartz, 1994), the monophyly of *T. paniculatum* is suspect because the five sampled populations were separated from each other in UPGMA cluster analyses and distance Wagner trees.

Toxicoscordion fontanum (Eastwood) Zomlefer & Judd, comb. nov. Basionym: *Zigadenus fontanus* Eastwood, Leafl. W. Bot. 2: 41. 1937. *Zigadenus micranthus* Eastwood var. *fontanus* (Eastwood) O. S. Walsh ex McNeal, Phytologia 73: 308. 1992. TYPE: U.S.A. California: Marin Co., Bootjack, Mt. Tamalpais, *J. T. Howell 12656* (holotype, CAS).

5. Zigadenus Michaux, Fl. Bor.-Amer. 1: 214, t. 22. 1803. TYPE: *Zigadenus glaberrimus* Michaux.

Salient features. Rhizome (no bulb), slightly (and more or less gradually) narrowed tepal bases, 2 ovate glands per tepal, superior ovary, unusual anatomical features; base chromosome number $x = 26$(?).

Distribution. Southeastern United States (coastal plain) in acidic coniferous forests and bogs.

Zigadenus, as defined here, comprises only *Zigadenus glaberrimus* (the type and the only species in the protologue), a circumscription advocated historically by several botanists (e.g., Rydberg, 1903; Small, 1903, 1933; Gates, 1918). Molecular data (Zomlefer & Perkins, 1999; Zomlefer et al., 2001) confirm a monospecific circumscription of *Zigadenus* and its divergent and isolated position as the sister taxon of the remaining members of the tribe Melanthieae. Autapomorphies of this distinctive taxon (discussed in Zomlefer, 1997) include an unusual chromosome number ($n = 26$, tentatively reported by Preece, 1956), a rhizome lacking a bulb, two ovate glands per tepal, and several anatomical features (foliar stomata with two aperture lips, distinct root exodermis, bracteolate pedicels, and dense tannin-like inclusions; Ambrose, 1975).

The original spelling of the genus has priority over the orthographic variant "*Zygadenus*" (from Endlicher, 1836), commonly used in herbaria and some older floras (e.g., Small, 1903, 1933; Gleason, 1952). *Cyanotris* Rafinesque, nom. rej. against *Camassia* Lindley (Agavaceae), is miscited as a synonym of *Zigadenus* in Preece (1956).

Taxa Incertae Sedis

Monadenus R. A. Salisbury, Gen. Pl. 51. 1866.

This taxon is often cited as a synonym of *Zigadenus* s.l. (e.g., Walsh, 1940; Preece, 1956; Cowley et al., 2001), and therefore is presumably a synonym for one of the genera in this paper. Salisbury (1866) did not, however, mention any species or make any species combinations. No specimens are labeled *Monadenus* or *Zigadenus* among Salisbury's few remaining collections at BM (R. Vickery, pers. comm.), the repository of his collections (Stafleu & Cowan, 1985). The description of the plant (from somewhere in America and cultivated at a nursery in England) is ambiguous: the partly inferior ovary may indicate placement in *Anticlea* (rather than other segregates of *Zigadenus*), but each tepal has "one melliferous semi-circular cavity" at the base (Salisbury, 1866: 52) and not the characteristic conspicuous bilobed gland of *Anticlea*. Another possibility is *Stenanthium gramineum*, characterized by a large paniculate inflorescence with "fine slender branches" (as Salisbury mentioned) and a partly inferior ovary—but this species lacks any glandular tissue or cavities on the tepals. Therefore, the description of *Monadenus* cannot be matched with certainty to any species or segregate of the *Zigadenus* assemblage.

Gomphostylis Rafinesque, Fl. Tellur. 2: 30. 1836 [1837].

This taxon has been associated with elements in the *Zigadenus* complex (Walsh, 1940; Zimmerman, 1958; Cowley, 2001), considered here in *Anticlea*, *Toxicoscordion*, and *Zigadenus* s. str. Rafinesque (1836: 30) based *Gomphostylis* on three mixed elements, two of them indicated as ambiguously placed with a "?": *G. bracteata* Rafinesque [= "*Helonias bracteata* Brereton mpt."], "*Gomphostylis? paniculata*" Rafinesque [= *Toxicoscordion paniculatum* (Nuttall) Rydberg], and "*Gomphostylis?* or *Z. fuscatus*" Rafinesque [an unidentified name; see Preece, 1956]. The "?" notation for the two latter species indicates that Rafinesque was unsure of their placement in *Gomphostylis*, and therefore, *G. bracteata* (which lacks a "?") would be the type of the genus (K. Gandhi, pers. comm.). However, the identity of this species is unclear. The short and vague description for this Virginian plant is not sufficient to distinguish the species. Three species of the *Zigadenus* complex occur in Virginia: *Anticlea elegans* (Pursh) Rydberg, *Stenanthium leimanthoides* (A. Gray) Zomlefer & Judd, and *Zigadenus glaberrimus* Michaux; all lack the spicate inflorescence described by Rafinesque (racemose panicles in *Anticlea elegans* and *Stenanthium leimanthoides*, and spreading paniculate inflorescences in *Z. glaberrimus*). *Helonias bracteata* Sims is *Zigadenus glaberrimus* (rhizome with no bulb, two glands per tepal; see Sims, 1815), and Preece (1956) included "*G. bracteata* Raf." [properly *G. bracteata* (Sims) Rafinesque, since cited in synonymy with Sims's name] as a synonym for *Z. glaberrimus*. However, "*Helonias bracteata* Brereton mpt." cited by Rafinesque is a manuscript name with no nomenclatural standing. Therefore, the name *Gomphostylis* cannot be applied with certainty to any known taxon.

The following key utilizes field characters and institutes a new taxonomy of the former *Zigadenus* complex.

Key to Segregate Genera of the Former *Zigadenus* Complex

1a. Plants with rhizome (lacking bulb), 2 conspicuous glands per tepal . . . . . *Zigadenus* Michaux
1b. Plants with bulb, 1 gland per tepal or nectaries obscure or absent.
  2a. Tepal glands obscure to absent.
    3a. Bulb ovoid, ovary superior, seeds with red to purple sarcotesta . . . . . *Amianthium* A. Gray
    3b. Bulb slender (cylindrical), ovary superior to half-inferior, seeds brown and lacking sarcotesta . . . . . *Stenanthium* (A. Gray) Kunth
  2b. Tepal glands conspicuous.
    4a. Tepals conspicuously clawed, tepal glands obovate, ovary superior . . . . . *Toxicoscordion* Rydberg
    4b. Tepals cuneate to gradually narrowed at base (not clawed), tepal glands bilobed, ovary half-inferior . . . . . *Anticlea* Kunth

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