A PHYLOGENETIC AND MONOGRAPHIC STUDY OF *OXYPOLIS*, *PTILIMNIUM*, AND CLOSELY RELATED GENERA (APIACEAE)

BY

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DISSERTATION

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ABSTRACT

A phylogenetic and monographic study of *Oxypolis*, *Ptilimnium,* and closely related genera in the North American endemics clade of tribe Oenantheae (Apiaceae) was carried out. Sequences from the nuclear ribosomal DNA internal transcribed spacer (ITS) region and the chloroplast DNA *trnQ-5'rps16* and *3'rps16-5'trnK* intergeneric spacer regions were used to estimate the phylogenetic relationships of *Oxypolis*, *Ptilimnium*, and closely related genera. The sequence data were analyzed using maximum parsimony, maximum likelihood and Bayesian methods. Results of the phylogenetic analyses showed that neither *Oxypolis* nor *Ptilimnium* was monophyletic. In the analyses, each genus was separated into two strongly supported clades that corresponded to differences in leaf morphology within the groups. While most species of *Oxypolis* and *Ptilimnium* have compound leaves, others share a unique leaf morphology known as rachis leaves. Rachis leaves are linear, terete, hollow, and septate and are equivalent to the rachis of a pinnately compound leaf in which the pinnae are not expressed. Fruit anatomical characters were explored and were also found to support these splits. Based on the analyses of the molecular data (ITS and cpDNA sequences) and the corroboration of morphological and fruit anatomical data, new circumscriptions for the genera *Oxypolis* and *Ptilimnium* were formalized. The two polyphyletic genera (*Oxypolis* and *Ptilimnium*) were split, two genera (*Tiedemannia* and *Harperella*) were resurrected, and new combinations were made. In addition to these generic level questions, the results of the phylogenetic analyses were used to examine a number of interspecific and infraspecific relationships within *Oxypolis* and *Ptilimnium*. As a result, the species *P. texense* was resurrected, *P. ahlesii* was placed in synonymy under *P. capillaceum*, and a case was made for the recognition of *O. filiformis* subsp. *greenmanii*. Also, a nomenclatural issue concerning the correct name for the species *Oxypolis ternata* was resolved. Finally, taxonomic treatments including keys, species and genus descriptions, and brief taxonomic discussions are presented for the following genera: *Ptilimnium, Tiedemannia, Harperella, Limnosciadium, Cynosciadium,* and *Oxypolis*. These treatments adopt the newly reinstated genera *Harperella* and *Tiedemannia* and include the closely related genera *Cynosciadium* and *Limnosciadium.* Treatments are written according to the *Flora of North America Guide for Contributors* for publication in Volume 13 of the *Flora of North America* series.

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CHAPTER 1
INTRODUCTION

The Apiaceae are a large and economically important family of flowering plants comprising approximately 465 genera and 3500 species (Plunkett et al.). Their distribution is worldwide but concentrated in the North Temperate Zone. Many familiar vegetables and herbs belong to this family, including carrot, parsnip, celery, fennel, dill, cilantro, and parsley. Some of the world's most poisonous plants are also a part of this family, such as water hemlock and poison hemlock. Many members of Apiaceae share the characteristic showy umbellate inflorescences with small white flowers and schizocarpic fruits. Due to these shared qualities and their edible and poisonous properties, these plants drew the attention of early taxonomists. The Apiaceae were the first group of flowering plants to be monographed (by Robert Morrison in 1672) and they have been the subjects of many different classification schemes since (e.g., Drude 1898; Koso-Poljansky 1916; Cerceau-Larrival 1962). Despite this attention, there had been little consensus regarding higher-level relationships within the family (i.e., subfamily, tribal, and subtribal) until recently. This change has come about due to the use of molecular data to examine phylogenetic relationships.

Estimations of relationships based on nuclear and chloroplast DNA sequence data have been largely congruent with one another, although quite different from those implied in traditional classifications of the Apiaceae. As a result, new classifications are being made at every level. For example, traditionally three subfamilies were recognized (i.e., Apioideae, Saniculoideae, and Hydrocotyloideae), but now four subfamilies are recognized (i.e., Apioideae, Saniculoideae, Azorelloideae, and Mackinlayoideae) and *Hydrocotyle* and its allies have been realigned across the entire order Apiales (Nicolas and Plunkett 2009). At the tribal level, tribe Oenantheae when first described contained just three genera and was defined based on the presence of radiately ribbed fruit (Hardway et al. 2004; Downie at al. 2008). As currently delimited, based on DNA sequence data, tribe Oenantheae contains 17 genera (Downie et al. 2008). These genera share several ecological and morphological traits such as glabrous leaves and stems, fascicled roots, globose to broadly ovate fruits, and a preference for moist or wet habitats, yet their close affinity was not recognized until molecular phylogenetic studies were conducted (Hardway et al. 2004; Downie et al. 2008). Studies of tribe Oenantheae utilizing

DNA sequence data have revealed that even relationships within genera may not be well understood. For example, as many as five genera within the tribe have been found to be polyphyletic or paraphyletic (Downie et al. 2004; Hardway et al. 2004; Lee & Downie 2006; Feist & Downie 2008; Downie et al. 2008; Spalik et al. 2009). Two such genera are *Oxypolis* and *Ptilimnium* and they are the main focus of the present study.

Oxypolis and *Ptilimnium* are two small genera of tribe Oenantheae. As currently circumscribed, the genus *Oxypolis* is comprised of seven species and the genus *Ptilimnium* six species. Most species of *Oxypolis* and *Ptilimnium* are endemic to North America, but each genus has one species (i.e., *O. filiformis*, *P. capillaceum*) with a range that extends into the West Indies (Brace 1929; Liogier & Martorell 2000). Each genus also has one species (i.e., *Oxypolis canbyi*, *Ptilimnium nodosum*) listed as federally endangered (U. S. Fish and Wildlife Service 1986; 1988). All species of *Oxypolis* and *Ptilimnium* can be considered to be hydrophytic and they grow in a variety of wetland habitats including wet prairies, fens, acid seeps, bogs, freshwater and brackish marshes, and streambanks. Two very different leaf morphologies exist within each genus. While most species of *Oxypolis* and *Ptilimnium* have compound leaves, others share a unique leaf morphology known as rachis leaves. Rachis leaves are linear, terete, hollow, and septate and are equivalent to the rachis of a pinnately compound leaf in which the pinnae are highly reduced and transformed into nodal appendages that function as hydathodes. Rachis leaves are thought to be an adaption to an aquatic or semi-aquatic environment (Kaplan 1970) and species of *Oxypolis* and *Ptilimnium* with rachis leaves (i.e., *O. canbyi*, *O. filiformis*, *O. greenmanii*, and *P. nodosum)* grow in the wettest of habitats including shallow ponds and stream channels. The fruits of *Oxypolis* species are strongly dorsally compressed and have thin, broadly winged lateral ribs, whereas the fruits of *Ptilimnium* species are globose to slightly dorsally compressed and have thick, corky lateral ribs. Despite their radically different leaf morphologies, the rachis-leaved and compound-leaved species of each genus have been grouped together based primarily on their similar fruit morphologies. Some taxonomic authorities, however, have advocated that the rachis-leaved and compound-leaved species be placed into separate genera (e.g., de Candolle 1829; Rose 1905).

Several other genera within tribe Oenantheae possess rachis or rachis-like leaves. All species of *Lilaeopsis* have rachis leaves, although in some species the leaves are flattened distally (Affolter 1985). *Cynosciadium* and *Limnosciadium* have basal leaves that are linear to linear-lanceolate, entire, and septate, however, they are flattened throughout and are not terete or hollow and their cauline leaves are generally palmately and pinnately lobed, respectively. *Cynosciadium* is a monotypic genus and *Limnosciadium* has just two species. Both genera are endemic to the United States and, like *Oxypolis* and *Ptilimnium*, grow in wetland habitats. Hardway et al. (2004) examined the phylogenetic relationships of *Oxypolis* and *Ptilimnium* and these other genera with reduced leaf morphologies. They (Hardway et al. 2004) found that these genera fell within a strongly-supported monophyletic group now recognized as the North American Endemics (NAE) clade (Downie et al. 2008). The NAE clade was found to be evolving at a much faster rate than other lineages within tribe Oenantheae and to include several taxa characterized by severe reduction of leaf morphology. Only compound-leaved species of *Ptilimnium* and *Oxypolis*, however, were included in that study so additional sampling and analyses were needed to assess the monophyly of these genera and the placement of the rachis-leaved *Oxypolis* and *Ptilimnium* species within this clade. For the present study, multiple accessions of all species, infraspecific taxa, and putative hybrids within the genera *Oxypolis* and *Ptilimnium* are included. All genera within the NAE clade (*Cynosciadium*, *Limnosciadium*, *Lilaeopsis*, *Neogoezia*, *Daucosma*, *Atrema*, and *Trepocarpus*) are also represented. The main objectives of the present study are 1) to evaluate the monophyly of the genera *Oxypolis* and *Ptilimnium* and their placement within the NAE clade, 2) to elucidate infrageneric and infraspecific relationships within *Oxypolis* and *Ptilimnium,* and 3) to produce a monograph for the genera *Oxypolis, Ptilimnium, Cynosciadium,* and *Limnosciadium* which has as its basis the phylogenetic history of the group.

In Chapter 2, taxonomic histories of the genera *Oxypolis* and *Ptilimnium* are provided and nuclear rDNA ITS sequences are used to create a phylogenetic hypothesis for these and other closely related genera from the Oenantheae tribe. In Chapter 5, cpDNA *trnQ-5'rps16* and *3'rps16-5'trnK* intergeneric spacer sequences are analyzed alone and in combination with ITS sequences to reinforce the findings from Chapter 2. Fruit anatomical characters are also examined and used to corroborate the results of the phylogenetic analyses. The genera *Oxypolis* and *Ptilimnium* are both found not to be monophyletic. The genera *Tiedemannia* and *Harperella* are reinstated to include the rachis-leaved *Oxypolis* species and rachis-leaved *Ptilimnium* species, respectively. *Cynosciadium* and *Limnosciadium* are found to form a strongly supported clade with all species of *Ptilimnium* and the rachis-leaved *Oxypolis* species. In addition, a number of infrageneric relationships are elucidated.

In Chapter 3, a nomenclatural issue regarding *Oxypolis ternata* is investigated. The combination *O. denticulata* was made by Edmondson and stated to supersede the name *O. ternata* (Edmondson 2004). The resolution of this issue required an investigation into the taxonomic and nomenclatural history of this species as well as *O. rigidior*. A table outlining the major taxonomic differences between these two species and a complete synonymy are provided.

In Chapter 4, the taxonomic status of *Ptilimnium texense* is determined. *Ptilimnium texense* was described as a distinct species by Coulter and Rose (1909), but was later considered a hybrid between *P. capillaceum* and P. *nuttallii* (Mathias and Constance 1945; Easterly 1957), and then finally assumed as a synonym under *P. costatum* (Mathias and Constance 1961). Results from the phylogenetic analyses presented in Chapters 2 and 5, however, indicated that *P. texense* might be a distinct species. This was verified by examining the morphology, ecology, and geographic distribution of the species.

The final chapter, Chapter 6, contains keys, genus and species descriptions, and brief taxonomic discussions for the following genera: *Ptilimnium*, *Tiedemannia, Harperella, Limnosciadium, Cynosciadium,* and *Oxypolis*. These treatments adopt the newly reinstated genera *Harperella* and *Tiedemannia* and also include the closely related genera *Cynosciadium* and *Limnosciadium. Ptilimnium*, *Tiedemannia, Harperella, Limnosciadium, Cynosciadium* all formed a strongly supported clade in the phylogenetic analyses based on cpDNA and ITS sequence data. Treatments are written according to the *Flora of North America Guide for Contributors* (FNAEC 2007) and will be submitted for publication in Volume 13 of this series. As required by Flora of North America Editorial Committee these treatments are synoptic and descriptive, yet succinct with diagnostic characters emphasized.

REFERENCES

Affolter, J.M. 1985. A monograph of the genus *Lilaeopsis* (Umbelliferae). *Systematic Botany Monographs* 6: 1–140.

Brace, L.J.K. 1929. Notes on the occurrence of *Oxypolis filiformis* in the Bahamas. *Torreya* 1: 16–17.

Candolle, A.P. 1829. *Memoire sur la Famille des Ombelliferes*. Paris: Treuttel et Würtz.

Cerceau-Larrival, M.T. 1962. Plantules et pollen d'Ombellifères, leur intérêt systématique et phylogénetique. *Mémoires Muséum National d'Histoire Naturelle Série B* 14: 1-164.

Coulter J.M. and J.N. Rose. 1909. Supplement to the monograph of the North American Umbelliferae. *Contributions from the U.S. National Herbarium* 12: 441–451.

Downie, S.R., F.-J. Sun, D.S. Katz-Downie, and G.J. Colletti. 2004. A phylogenetic study of *Perideridia* (Apiaceae) based on nuclear ribosomal DNA ITS sequences. *Systematic Botany* 29: 737–751.

Downie, S.R., D.S. Katz-Downie, F.-J. Sun, and C.-S. Lee. 2008. Phylogeny and biogeography of Apiaceae tribe Oenantheae inferred from nuclear rDNA ITS and cpDNA *psbI-5'trnK*$^{(UUU)}$ sequences, with emphasis on the North American Endemics clade. *Botany* 86: 1039–1064.

Drude, C.G.O. 1898. Umbelliferae. Pp. 63–250 in *Die natürlichen Pflanzenfamilien*, vol. 3, eds. A. Engler and K. Prantl. Leipzig, Germany: Wilhelm Engelmann.

Easterly, N.W. 1957. A morphological study of *Ptilimnium*. *Brittonia* 9: 136–145.

Edmondson, J.R. 2005. A new combination in *Oxypolis* Raf. (Apiaceae). *Novon* 15: 109.

Feist, M.A. and S.R. Downie. 2008. A phylogenetic study of *Oxypolis* and *Ptilimnium* based on nuclear rDNA ITS sequences. *Systematic Botany* 33: 447–458.

Flora of North America Editorial Committee. 2007. *Flora of North America Guide for Contributors*. (http://fna.huh.harvard.edu/files/FNA%20ContribGuide%202008.pdf).

Hardway, T.M., K. Spalik, M.F. Watson, D.S. Katz-Downie, and S.R. Downie. 2004. Circumscription of Apiaceae tribe Oenantheae. *South African Journal of Botany* 70: 393–406.

Kaplan, D.R. 1970. Comparative development and morphological interpretation of 'rachis-leaves' in Umbelliferae. *Botanical Journal of the Linnean Society* 63 (Supplement 1): 101–126.

Koso-Poljansky, B. 1916. Sciadophytorum systematis lineamenta: mantissa prior. *Bulletin de la Sociêtê Impêriale des Naturalistes* (Moscow) 30: 277-290.

Lee, C.-S. and S.R. Downie. 2006. Phylogenetic relationships within *Cicuta* (Apiaceae tribe Oenantheae) inferred from nuclear rDNA and cpDNA sequence data. *Canadian Journal of Botany* 84: 453–468.

Liogier, H.A. and L.F. Martorell. 2000. *Flora of Puerto Rico and adjacent islands: A systematic synopsis*, 2nd ed. San Juan, Puerto Rico: Editorial de la Universidad de Puerto Rico.

Nicolas, A.N. and G.M. Plunkett. 2009. The demise of subfamily Hydrocotyloideae (Apiaceae) and the re-alignment of its genera across the entire order Apiales. Molecular Phylogenetics and Evolution 53:134-151.

Plunkett, G.M., M.G. Pimenov, J.-P. Reduron, E.V. Kljuykov, B.-Y. Lee, B.-E. van Wyk, P.M. Tilney, M.F. Watson, T.A. Ostroumova, K. Spalik, J.M. Hart, M.J. Henwood, C.J. Webb, F.-D. Pu, A.D.Mitchell, and B. Muckensturm. *Accepted.* Apiaceae. In K. Kubitzki (ed.) *The Families and Genera ofVascular Plants.* Berlin, Germany: Springer-Verlag.

Mathias, M. and L. Constance. 1945. Umbelliferae. *North American Flora* 28B: 43–295.

Mathias, M. and L. Constance. 1961. Umbelliferae. Pp. 263–329 in *Flora of Texas,* vol. 3, ed. C. L. Lundell. Renner: Texas Research Foundation.

Rose, J.N. 1905. Two new umbelliferous plants from the coastal plain of Georgia. *Proceedings of the U.S. National Museum* 29: 441–445.

Spalik, K., S.R. Downie, and M.F. Watson. 2009. Generic delimitation within the *Sium* alliance (Apiaceae tribe Oenantheae) inferred from cpDNA *rps16-5'trnK*$^{(UUU)}$ and nrDNA ITS sequences. *Taxon* 58: 735–748.

U. S. Fish and Wildlife Service. 1986. Determination of *Oxypolis canbyi* (Canby's dropwort) to be an endangered species. *Federal Register* 37: 6690–6693.

U.S. Fish and Wildlife Service. 1988. Endangered and threatened wildlife and plants: determination of *Ptilimnium nodosum* (harperella) to be an endangered species. *Federal Register* 50: 37978–37982.

CHAPTER 2

A PHYLOGENETIC STUDY OF *OXYPOLIS* AND *PTILIMNIUM* (APIACEAE) BASED ON NUCLEAR RDNA ITS SEQUENCES[1]

Abstract: *Oxypolis* and *Ptilimnium* are two endemic genera of North America within tribe Oenantheae (Apiaceae subfamily Apioideae). Both genera are small, with 12 species currently recognized. Some members of each genus share an unusual leaf morphology. Rather than having the pinnately compound leaves that generally characterize apioid umbellifers, they have highly reduced, linear, terete, hollow, septate appendages known as rachis leaves. It has long been questioned whether the species with rachis leaves should be placed in separate genera. In this study, we use data from the internal transcribed spacer region of nuclear ribosomal DNA to explore relationships within and between these genera. A total of 147 internal transcribed spacer sequences were obtained from multiple accessions of all species of *Oxypolis* and *Ptilimnium* and for several other genera from tribe Oenantheae. These included *Lilaeopsis*, which also has rachis leaves, and *Cynosciadium* and *Limnosciadium*, which have rachis-like leaves. These sequence data were analyzed using maximum parsimony, maximum likelihood, and Bayesian methods. The results from each of these analyses were congruent and suggest that neither *Oxypolis* nor *Ptilimnium* as presently defined is monophyletic. *Oxypolis* and *Ptilimnium* are each separated into two clades according to leaf morphology. The rachis-leaved *Oxypolis* species are provisionally recognized as the genus *Tiedemannia* and the rachis-leaved *Ptilimnium* species are provisionally recognized as the genus *Harperella*, pending further investigation. The relationships among these four clades and the genera *Cynosciadium*, *Daucosma,* and *Limnosciadium* are not clear. Nevertheless, it appears that the rachis-leaf habit has evolved multiple times in the tribe. Geographic structure is apparent in the phylogenetic trees and, pending further study, may suggest new taxa; in addition, the presence of *O. occidentalis* on the Queen Charlotte Islands, well-separated from other populations of this species, suggests that it may have survived the last glaciation in a refugium in this area.

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INTRODUCTION

Oxypolis Raf. and *Ptilimnium* Raf. are two closely related genera of tribe Oenantheae (Apiaceae subfamily Apioideae) endemic to North America. Both genera are small, with a total of 12 species currently recognized (Table 2.1). *Oxypolis canbyi* and *Ptilimnium nodosum* are federally endangered. These genera share several traits with other members of tribe Oenantheae, including glabrous leaves and stems, fascicled roots, and a preference for moist or wet habitats. The plants are of particular interest because some members of each genus exhibit a unique morphological trait known as rachis leaves, while others have compound leaves typical of subfamily Apioideae. Rachis leaves are linear, terete, hollow, and septate and are equivalent to the rachis of a pinnately compound leaf in which the pinnae are not fully expressed. Instead, these pinnae are highly reduced and are transformed into nodal appendages that function as hydathodes (Kaplan 1970). Rachis leaves are an adaptation to a semi-aquatic habitat, and species of *Oxypolis* and *Ptilimnium* with rachis leaves (i.e., *O. canbyi*, *O. filiformis*, *O. greenmanii*, and *P. nodosum)* spend much of the growing season at least partially submerged. Compound-leaved species of *Oxypolis* have pinnately or ternately compound leaves with pinnae that are generally somewhat broad (except for *O. ternata* in which they are long and narrow). Compound-leaved *Ptilimnium* species have finely dissected, pinnately decompound leaves with linear or filiform pinnae.

The first *Oxypolis* species with compound leaves to be described was originally placed in the genus *Sium* L. (as *Sium rigidius* L.; Linnaeus 1753). The first described *Oxypolis* species with rachis leaves (now called *Oxypolis filiformis*) was originally placed in the genus *Oenanthe* L. (Walter 1788). Subsequently, the latter was grouped with *Sium rigidius* under the name *Sium teretifolium* Elliot. Although Elliot (1817) stated that "this plant is remarkable for its terete, fistulose leaves," he grouped it with the compound-leaved species based on features of the fruit. Similarly, Rafinesque (1825) included taxa with both leaf types in his new genus *Oxypolis*. In contrast, de Candolle (1829) advocated the separation of the rachis-leaved species (*Tiedemannia* DC.) from the compound-leaved taxa (*Archemora* DC.) based on leaf morphology and anther attachment; this classification, however, was never widely accepted. Coulter and Rose (1887) argued that *Tiedemannia* and *Archemora* should not be considered separate genera because they could find no significant differences in fruit characters between them. They believed that the leaves of *Oxypolis ternata* (which are long, narrow, and ternate) were intermediate between compound and rachis leaves. The fruits of all species of *Oxypolis* are remarkably similar in appearance, being dorsally flattened and winged. However, dorsal flattening and wing formation have evolved in several independent lineages of Apiaceae, most likely as a dispersal mechanism (Theobald 1971; Plunkett et al. 1996; Downie et al. 1998; Lee et al. 2001). In addition, dorsal flattening and wing formation can develop in different ways (Theobald 1971), therefore such similarities in fruit morphology cannot be taken as evidence of close relationship without further study.

The genus *Ptilimnium* was first described by Rafinesque (1819; 1825) based on *Ptilimnium capillaceum*, a compound-leaved species. The genus *Harperella* Rose was described by Rose (1906) to include three rachis-leaved taxa (*H. nodosa, H. fluviatilis,* and *H. vivipara*). In 1936, however, these species were referred to the genus *Ptilimnium* by Mathias (1936) who argued that *Harperella* differed from *Ptilimnium* "only in its striking vegetative character of leaves reduced to fistulous petioles, its less conspicuous involucres and involucel bracts, and its more attenuated petal tips; characters which cannot be considered generic." Easterly (1957a) studied *Ptilimnium* by examining morphology, seedling development, and chromosome number. He agreed with Mathias's assessment and recognized five species and one putative hybrid within the genus: *P. nodosum*, *P. fluviatile* (Rose) Mathias, *P. capillaceum*, *P. nuttallii*, *P. costatum*, and *P.* × *texense* J. M. Coult. & Rose. The latter was considered a hybrid between *P. capillaceum* and *P. nuttallii*. Easterly (1957b) synonymized *P. viviparum* (Rose) Mathias with P. *fluviatile* based on their shared habitat type, phenology, and lack of clear morphological differences. Kral (1981) further grouped the taxa and included *P. fluviatile* and *P. viviparum* within *P. nodosum* sensu lato (s.l.). Later, *P. nodosum* s.l. was recognized as a federally endangered species (US Fish and Wildlife Service 1988). *Ptilimnium ahlesii* was recognized in 2004 (Weakley and Nesom 2004). This entity had generally been assumed under *P. capillaceum,* but Weakley and Nesom believed it was distinctive enough to warrant species status, based primarily on fruit size and flowering phenology.

Several other genera within tribe Oenantheae possess rachis or rachis-like leaves. All species of *Lilaeopsis* Greene have rachis leaves, although in some species the leaves are flattened distally (Affolter 1985). In *Lilaeopsis*, the leaves are linear, septate, terete, and hollow, and similar to those of rachis-leaved *Oxypolis* and *Ptilimnium* species. A study by Kaplan (1970) demonstrated that the leaves of *Lilaeopsis occidentalis* J. M. Coult. & Rose and *Oxypolis* *greenmanii* follow the same developmental pathways and concluded, "morphologically [*Oxypolis greenmanii*] is essentially a gigantic form of *Lilaeopsis.*" *Cynosciadium* DC. and *Limnosciadium* Mathias & Constance have basal leaves that are linear to linear-lanceolate, entire, and septate, however, they are flattened throughout and are not terete or hollow. Moreover, their cauline leaves are generally palmately and pinnately lobed, respectively. We refer to the leaves of *Cynosciadium* and *Limnosciadium* as rachis-like. It is not known whether these leaves are truly rachis leaves because anatomical and developmental studies have yet to be carried out for these taxa.

Hardway et al. (2004) recognized a strongly-supported monophyletic group within tribe Oenantheae as the North American Endemics (NAE) clade. This group comprised single exemplars from the genera *Atrema* DC., *Cynosciadium, Daucosma* Engelm. & A. Gray ex A. Gray*, Lilaeopsis, Limnosciadium, Neogoezia* Hemsl.*, Ptilimnium,* and *Trepocarpus* Nutt. ex DC. The genus *Ptilimnium* was represented by *P. capillaceum*, a compound-leaved species. Hardway et al. (2004) acknowledged, however, that there were taxa outside of this clade that are also endemic to North America, such as *Oxypolis* which was represented by three compound-leaved species (i.e., *O. fendleri, O. occidentalis,* and *O. rigidior*). The relationship between the NAE clade and *Oxypolis* was unclear because of short branches and weak bootstrap support. Additional sampling and analyses are necessary to evaluate the putative close relationship between *Lilaeopsis occidentalis* and *Oxypolis greenmanii,* as suggested by leaf morphology, as well as the relationships among the compound- and rachis-leaved species of *Oxypolis* and *Ptilimnium*.

The major purpose of this study is to produce a phylogenetic hypothesis for *Oxypolis* and *Ptilimnium* to assess their monophyly and to explore infrageneric relationships, especially with regard to the placement of rachis-leaved taxa relative to their compound-leaved congeners. The relationships of rachis-leaved *Oxypolis* and *Ptilimnium* to other genera of tribe Oenantheae exhibiting rachis or rachis-like leaves (i.e., *Cynosciadium, Lilaeopsis,* and *Limnosciadium*) will also be assessed. The phylogenetic hypothesis has been reconstructed using sequences of the nuclear ribosomal DNA (nrDNA) internal transcribed spacer (ITS) region. Although the utilization of ITS data has come under scrutiny of late (Álvarez and Wendel 2003), it is widely employed and the benefits of its use in Apiaceae at low taxonomic levels have recently been elaborated (Spalik and Downie 2006).

MATERIALS AND METHODS

Taxon Sampling and Outgroup Selection. Complete sequences of the nrDNA ITS region were obtained for all seven species of *Oxypolis* (70 accessions), all five species of *Ptilimnium* (64 accessions), and the two purported hybrids, "Oxypolis × intermedia" ined. and *P.* × *texense* (Table 2.1). "Oxypolis × intermedia" ined. is not a validly published name, but represents herbarium specimens collected by Walter Judd (University of Florida, Gainesville) which were recognized as putative hybrids between *O. greenmanii* and *O. filiformis* (Judd 1982) and annotated as "intermediate between *O. greenmanii* and *O. filiformis*." *Ptilimnium texense* was originally described as a species (Coulter and Rose 1909), but Mathias and Constance (1945) and Easterly (1957b) treated it as a hybrid (*P.* × *texense*) between *P. capillaceum* and *P. nuttallii*. *Ptilimnium* × *texense* is used in this study to represent herbarium specimens that were given this designation. All *Oxypolis* and *Ptilimnium* taxa were represented by multiple accessions to assess infraspecific variation. Thirteen accessions from eight other oenanthoid genera were also included, for a total of 147 accessions. Taxa sampled, taxonomic authorities, voucher information, and GenBank accession numbers are given in Appendix A. Nomenclature follows Kartesz (1999), except for *Ptilimnium ahlesii* (Weakley and Nesom 2004), *Atrema americanum* (Hardway et al. 2004), and *Lilaeopsis* (Affolter 1985).

Previous phylogenetic studies of tribe Oenantheae (Plunkett et al. 1996; Downie et al. 1998; Downie et al. 2000a; Downie et al. 2000b) have shown the genus *Perideridia* Rchb. to be a sister group to a clade comprising all other members of the tribe; therefore, all trees were rooted with three species of *Perideridia* [*P. americana* (Nutt. ex DC.) Rchb., *P. gairdneri* (Hook. & Arn.) Mathias subsp. *borealis* T. I. Chuang & Constance, and *P. kelloggii* (A. Gray) Mathias]. In addition, the genera *Atrema*, *Cynosciadium*, *Daucosma*, *Lilaeopsis*, *Limnosciadium*, *Neogoezia*, and *Trepocarpus* allied with compound-leaved *Ptilimnium* within the NAE clade (Hardway et al. 2004). As such, single accessions of these genera were included in the phylogenetic analyses to explore their placements relative to *Oxypolis* and *Ptilimnium*. Some of these genera have rachis leaves (at least basally), permitting an assessment of the relationships among the rachis-leaved species.

DNA Extraction, Purification, and Sequencing. Details of DNA extraction, PCR-amplification, purification, and sequencing of previously published ITS sequences are provided elsewhere (Downie and Katz-Downie 1996; Downie et al. 2000a; Hardway et al. 2004).

Methods for sequences generated specifically for this study are as follows. Leaf material was taken from either herbarium specimens or field-collected, silica-dried samples. DNA was isolated using a DNeasy Plant Mini Kit (Qiagen Inc., Valencia, California) according to the manufacturer's instructions. The entire ITS region (ITS-1, 5.8S rDNA, and ITS-2) was amplified using primers 18S-ITS1-F (Spalik and Downie 2006) and C26A (Wen and Zimmer 1996) or primers 18S-for (5'-GTC CAC TGA ACC TTA TCA TTT AG-3') and C26A. The PCR amplification methods used are described elsewhere (Downie et al. 2000a). PCR products (templates) were purified using either a QIAquick Gel Extraction Kit or a QIAquick PCR Purification Kit (Qiagen Inc.) following manufacturer's instructions. Sequence reactions were carried out using an ABI Prism Big Dye Terminator vers. 3.1 Ready Reaction Cycle Sequencing Kit (Applied Biosystems, Foster City, California). Sequence reaction products were visualized using an ABI 3730XL high-throughput DNA capillary sequencer at the Genetic Engineering Facility at the University of Illinois at Urbana-Champaign's Biotechnology Center.

Sequence Alignment and Phylogenetic Analysis. Sequences were aligned using Clustal X (Thompson et al. 1997) and manually adjusted as necessary using the alignment editor BioEdit (Hall 1999). Gaps were scored as additional binary characters according to the "simple indel coding" method of Simmons and Ochoterena (2000). Therefore, two matrices were constructed, one that included the aligned nucleotide data and binary-coded indels (combined dataset) and one that omitted the indel characters (nucleotide only dataset). To facilitate analysis, identical sequences were represented by single terminals, except where identical sequences were from individuals from geographic areas of interest (Table 2.2). Sequence characteristics were obtained for the entire ITS region, as well as for the separate partitions (ITS-1, 5.8S, and ITS-2). Uncorrected pairwise nucleotide distances were calculated using the distance matrix option of PAUP* version 4.0b10 (Swofford 2003). Only positions that were aligned unambiguously were included in the analyses. The aligned data matrix is available in TreeBASE (study number S1939).

Maximum parsimony (MP) analyses of the two data matrices were implemented in PAUP*. All characters were treated as unordered and all character transformations were weighted equally. Heuristic maximum parsimony searches were replicated 1000 times with random addition of taxa and the following options in effect: MULTREES, TBR branch swapping, gaps treated as missing data. Bootstrap (BS) analyses were done on both data sets to assess clade support. One thousand bootstrap replicates were performed using the heuristic search option, with TBR branch swapping, random stepwise addition of taxa, and MULTREES options in effect. In addition, MP analyses were performed on data sets that both included and excluded the putative hybrids ("Oxypolis × intermedia" ined. and *P.* × *texense*). This was done to assess whether the inclusion of putative hybrids had any effect on the placement of other taxa in the phylogenetic trees. Alternative alignments were also analyzed to assess their effects on the phylogenetic hypothesis. These included alignments created by employing a range of weighting schemes for gap opening and gap extension in Clustal, as well as alignments created by making different manual adjustments to the Clustal-generated alignments. The constraint option of PAUP* was used to determine how many additional steps were needed to force the monophyly of particular groups.

Modeltest version 3.7 (Posada and Crandall 1998) was used to select an appropriate evolutionary model of nucleotide substitution for these ITS sequences. The model that best fit these data, as selected by the Akaike Information Criteria (AIC) estimator, was used. The parameters of this model were input into PAUP* and a maximum likelihood (ML) analysis of the nucleotide only data matrix was implemented. One hundred heuristic searches were performed using random addition sequence and TBR branch swapping. Bootstrap analysis of 1000 replicates was conducted using the NJ method with ML distance estimates using the ML parameters inferred by Modeltest.

MrBayes version 3.1.2 (Huelsenbeck and Ronquist 2001) was used to conduct Bayesian inference of the nucleotide only matrix. The same model of evolution used in the ML analysis was also used in this analysis. Two independent runs were conducted for 2,000,000 generations each with a sample frequency of 100. The log-likelihood scores of the sample points were plotted against generation time in Microsoft Excel. Stationarity was determined to be reached when the log-likelihood values of the sample points achieved a stable equilibrium value. The initial 5,000 trees from each run were discarded as burn in. A majority rule consensus tree was constructed from the remaining 30,000 trees using PAUP*.

RESULTS

Characteristics of ITS Sequences. Sequence characteristics of the ITS region are provided in Table 2.3. The length of the entire ITS region for the 83 terminals (147 accessions) included in the phylogenetic analysis ranged from 580 to 605 bp. Alignment of these sequences resulted in a matrix of 632 positions. Thirty-five positions were removed because of alignment ambiguities. The number of parsimony informative positions was 268 and the number of autapomorphic positions was 47. Alignment of the remaining 597 unambiguous positions required the inclusion of 34 gaps: 30 1-bp gaps, one 2-bp gap, one 3-bp gap, one 6-bp gap, and one 8-bp gap. Fifteen gaps were parsimony informative. The ITS-2 region is generally longer and has more potentially informative sites than the ITS-1 region, even though it has four times as many sites excluded because of ambiguities.

The maximum amount of sequence divergence across the entire ITS region for all 147 terminals was 22.7% (Table 2.3), which was between *Oxypolis canbyi* and one outgroup accession, *Perideridia americana*. Considering only *Oxypolis* and *Ptilimnium*, the maximum amount of sequence divergence was 20.7% between *O. fendleri* (a compound-leaved taxon) and *O. canbyi* (a rachis-leaved taxon). The maximum sequence divergence among compound-leaved *Oxypolis* species was 8.5%, whereas among rachis-leaved *Oxypolis* species it was 9.9%. Maximum sequence divergence among *Ptilimnium* species only was 14.9%; however, it was just 3.5% among compound-leaved *Ptilimnium* and 0.7% among the rachis-leaved *Ptilimnium*. All species of *Ptilimnium* and *Oxypolis* showed infraspecific variation in their ITS sequences, except for *P. ahlesii, P. capillaceum*, and *P. nuttallii,* which showed no variation. All sequences of *P. ahlesii* were identical to all sequences of *P. capillaceum.* Sequence heterogeneity was detected in all accessions of *O. greenmanii* and one of two accessions of “Oxypolis × intermedia” ined. These sequences exhibited a C/T polymorphism at position 156 (ITS-1) and an A/G polymorphism at position 537 (ITS-2) in the aligned matrix. None of the accessions of *O. filiformis,* the other putative parent of “Oxypolis × intermedia” ined., were polymorphic at these loci, but all had either a C or T at position 156 and either an A or G at position 537.

Phylogenetic Analysis. MP analysis of ITS sequence data (nucleotide only dataset) recovered 350 trees of 843 steps each (CI = 0.5475, without uninformative characters; RI = 0.9173). The strict consensus of these trees is presented in Fig. 2.1 with accompanying bootstrap values (MPBS). MP analysis of the combined dataset (aligned nucleotide data plus 15 parsimony informative binary-scored indels) recovered 353 trees of 864 steps each (CI = 0.5519, without uninformative characters; RI = 0.9181). The strict consensus tree resulting from analysis of combined data was almost identical to that from the previous analysis, with the only difference being the union of *P. nodosum* 2789 and *P. nodosum* 2786 in the former. Bootstrap support values were either identical or within a few percentage points in both analyses; therefore, the combined dataset will not be considered further. Changes to the alignment resulting from employing a variety of costs for gap opening and gap extension or by making different manual adjustments to the Clustal-generated alignments resulted in strict consensus trees similar to the one presented in Fig. 2.1, with no differences in the five major clades inferred (discussed below).

The ML analysis was carried out using the SYM+I+G model of nucleotide substitution (Akaike weight = 0.9960). Base frequencies were: A = 0.22790, C = 0.25304, G = 0.28357, T = 0.23549. Substitution rates were: A–C = 0.6534, A–G = 1.9859, A–T = 1.2774, C–G = 0.4769, C–T = 4.5628, G–T= 1.000. The assumed proportion of invariable sites was 0.2743 and the gamma distribution shape parameter was 1.4138. ML analysis resulted in 38 trees, each with a -Ln likelihood score of 4962.61109. The strict consensus of these 38 trees is presented in Fig. 2.2. The majority-rule consensus tree of the 30,000 trees derived from Bayesian analysis is congruent with the ML tree, therefore both bootstrap (MLBS) and posterior probability (PP) values, the latter also expressed as percentages, are given on the ML tree.

The trees resulting from MP, ML and Bayesian analyses are nearly fully congruent except for the placements of the *Limnosciadium pinnatum/Daucosma laciniatum* clade and *Cynosciadium digitatum* (Figs. 2.1–2.2). However, the placements of these taxa are not strongly supported and if these weakly supported branches are collapsed the trees become fully congruent. All trees show four major clades which correspond to compound-leaved *Ptilimnium* species (Clade 1), rachis-leaved *Ptilimnium* species (Clade 2), rachis-leaved *Oxypolis* species (Clade 3), and compound-leaved *Oxypolis* species (Clade 4). Each of these clades is strongly supported by MP and ML BS and Bayesian PP values (97–100%). The compound-leaved and rachis-leaved *Oxypolis* species clearly do not form a monophyletic group. A tree of 36 additional steps (879 steps) is required to force the monophyly of *Oxypolis*. The compound-leaved and rachis-leaved *Ptilimnium* species may also not form a monophyletic group, and constraint analysis showed that a tree of three additional steps is required to force their monophyly (846 steps). Relationships among the compound-leaved *Ptilimnium*, rachis-leaved *Ptilimnium,* and rachis-leaved *Oxypolis* clades are not resolved. These clades, together with *L. pinnatum, D. laciniatum,* and *C. digitatum*, constitute a moderately (77% MPBS) to strongly (97% MLBS, 100% PP) supported group (Clade 5). In none of the analyses do the *Ptilimnium* clades and the rachis-leaved *Oxypolis* clade ever form a monophyletic group without *Limnosciadium* and *Daucosma*.

Daucosma and *Limnosciadium* form a strongly supported monophyletic group in each analysis (100% BS and PP values). *Limnosciadium* and *Cynosciadium* have rachis-like basal leaves and compound cauline leaves and fall alongside the rachis-leaved and compound-leaved species of Clade 5. The four examined accessions of *Lilaeopsis* form a strongly supported monophyletic group that is clearly separate from *Oxypolis greenmanii* and other rachis-leaved species with which it shares the rachis-leaf morphology. *Lilaeopsis* is sister group to Clade 5 (90% MPBS, 94% MLBS, 100% PP), while the clade of *Atrema*, *Neogoezia*, and *Trepocarpus* is sister group to the aforementioned assemblage (97% MPBS, 96% MLBS, 100% PP).

Within the compound-leaved *Ptilimnium* clade (Clade 1), all accessions of *P. nuttallii* form a strongly supported monophyletic group (100% BS and PP values) that is sister group to the other compound-leaved *Ptilimnium* taxa. *Ptilimnium ahlesii* and *P. capillaceum*, which have identical sequences for all 12 accessions examined, form a monophyletic group. *Ptilimnium costatum* and *P.* × *texense* also form a monophyletic group (89% MPBS, 71 MLBS, 99% PP) which is divided into two strongly supported subclades: A, comprising all specimens of *P. costatum* from Arkansas, Georgia, Illinois, Missouri, and Tennessee (82% MPBS, 96% MLBS, 100% PP); and B, comprising *P.* × *texense* and all *P. costatum* specimens from Texas and Louisiana (99% MPBS, 99% MLBS, 100% PP). The removal of the putative hybrid *P.* × *texense* from the MP analyses did not affect the relationships among the remaining taxa.

The rachis-leaved *Ptilimnium* clade (Clade 2) comprises all 19 accessions of *P. nodosum*. Some geographic structure is apparent within this clade. Subclade C is made up of specimens from Maryland, North Carolina, and West Virginia, and subclade D is made up of specimens from South Carolina. Both subclades are moderately to weakly supported in the MP and ML analyses, as is their sister group relationship in all analyses. The remaining *P. nodosum* specimens are from Alabama, Arkansas, and Georgia (group E) and comprise part of a polytomy along with the branch leading to subclades C+D.

Three rachis-leaved species of *Oxypolis* plus the putative hybrid between *O. greenmanii* and *O. filiformis* ("Oxypolis × intermedia" ined.) comprise Clade 3. All seven accessions of *Oxypolis canbyi* form a strongly supported clade (100% BS and PP values) sister group to a clade comprising all accessions of *O. filiformis, O. greenmanii,* and "Oxypolis × intermedia" ined. (100% BS and PP values). There is no resolution among *O. filiformis*, *O. greenmanii*, and

“Oxypolis × intermedia” ined. When “Oxypolis × intermedia” ined. is excluded from subsequent MP analyses, the relationships among the remaining taxa do not change.

Within the compound-leaved *Oxypolis* clade (Clade 4), *O. fendleri* (13 accessions) is a strongly supported sister group (98% MPBS, 97% MLBS, 100% PP) to the other compound-leaved *Oxypolis* species. In addition, *O. rigidior* (10 accessions) and *O. ternata* (10 accessions) form strongly supported monophyletic sister taxa that collectively form a clade that is sister group to *O. occidentalis* (15 accessions). *Oxypolis occidentalis* is further separated into three subclades showing some geographic structure: subclade F is made up of plants from the Queen Charlotte Islands, British Columbia and the Cascade Mountain region of Oregon; subclade G is made up of plants from the Cascade Range Foothills in northern California; and subclade H is made up of specimens from the Sierra Nevada, San Bernardino, White, and Inyo Mountains of California. The maximum pairwise sequence divergence between subclades F and G is 0.51% and between subclades F+G and subclade H it is 4.86%.

DISCUSSION

Generic Level Phylogenetic Relationships. Classifications separating *Ptilimnium* and *Oxypolis* into two genera each (i.e., *Ptilimnium* and *Harperella,* and *Oxypolis* and *Tiedemannia*) based on the presence of compound or rachis leaves have been proposed (de Candolle 1829; Rose 1905, 1906), but this remarkably different leaf morphology has generally not been seen as a worthy character on which to base generic separation. Rather, similarities in fruits and flowers have been emphasized, resulting in the two genera recognized today. The ITS-based phylogenies clearly show that neither *Oxypolis* nor *Ptilimnium* as currently delimited is monophyletic. The four major clades recognized, comprising the compound-leaved *Ptilimnium* species (Clade 1), the rachis-leaved *Ptilimnium* species (Clade 2), the compound-leaved *Oxypolis* species (Clade 4), and the rachis-leaved *Oxypolis* species (Clade 3), coincide precisely with the four aforementioned genera. Each of these groups is strongly supported as monophyletic. The separation of the compound-leaved *Oxypolis* species from its rachis-leaved congeners is most dramatic, with trees of 36 steps longer than those maximally parsimonious required to force monophyly of the genus. Maximum pairwise sequence divergence values between these two *Oxypolis* clades is 20.7%. Differences between the clades are also apparent in chromosome number. The three rachis-leaved *Oxypolis* species are all $n = 14$, whereas the compound-leaved

Oxypolis species are $n = 16$ or $n = 18$ (Bell and Constance 1957; Bell and Constance 1960; Crawford and Hartman 1972; Tucker et al. 1983; Pimenov et al. 2003).

The separation of the rachis-leaved and compound-leaved *Ptilimnium* species is not as dramatic. Trees of three steps longer are required to force monophyly of *Ptilimnium* in the MP analysis, and the rachis-leaved *Oxypolis* clade is sister group to the compound-leaved *Ptilimnium* clade in both ML and Bayesian trees, although this relationship is very weakly supported. Maximum pairwise sequence divergence between *P. nodosum* and the compound-leaved *Ptilimnium* species is 14.9%, whereas it is just 3.5% among all compound-leaved species of *Ptilimnium* and 0.7% among the accessions of *P. nodosum*. The rachis-leaved species *P. fluviatile* and *P. nodosum* each have a chromosome number of n = 6, whereas the compound-leaved species have chromosome numbers of $n = 16$ (*P. costatum*), $n = 7$ (*P. capillaceum* and *P. nuttallii*), and $n = 8$ or $n = 14$ (*P. capillaceum*) (Easterly 1957a; Constance et al. 1976; Weakley and Nesom 2004).

On the basis of these molecular and cytological results and to facilitate communication, we provisionally treat members of the rachis-leaved *Oxypolis* clade as the genus *Tiedemannia*, a name proposed by de Candolle (1829). Members of the rachis-leaved *Ptilimnium* clade are provisionally recognized as the genus *Harperella*, as proposed by Rose (1906). Before nomenclatural changes are effected, however, additional evidence will be obtained from the independently evolving chloroplast genome. It is reassuring that the four major clades recognized herein are similar to those inferred based on preliminary analysis of chloroplast DNA *psbI-5'trnK*$^{\text{(UUU)}}$ sequence data (S.R. Downie, unpubl. data).

The relationships among *Ptilimnium*, *Tiedemannia*, and *Harperella* are confounded by the placements of *Cynosciadium*, *Daucosma,* and *Limnosciadium*. The positions of the latter three genera vary depending upon optimality criteria selected, and other than the strongly-supported sister group relationship between *Daucosma* and *Limnosciadium,* no analysis resolves relationships among these taxa with strong branch support. The monotypic genus *Daucosma* was transferred to *Ptilimnium* as *Ptilimnium laciniatum* Kuntze (Kuntze 1891), but later returned to *Daucosma* based on morphology (Easterly 1957a). The placement of the *Daucosma* + *Limnosciadium* clade as sister group to either *Ptilimnium* (Fig. 2.1) or *Harperella* (Fig. 2.2) suggests an affinity of these taxa with *Ptilimnium*, as traditionally circumscribed. Their differences in morphology, however, suggest that *Daucosma* and *Limnosciadium* be maintained as separate genera, distinct from *Ptilimnium* and *Harperella*.

The polytomy and weak branch support at the base of Clade 5 in all phylogenetic trees preclude an hypothesis on the number of times the rachis-leaved habit evolved in tribe Oenantheae. Rachis leaves (being defined as linear, septate, terete, and hollow) occur in *Lilaeopsis*, *Tiedemannia*, and *Harperella*. They could have evolved just once in Oenantheae in the immediate ancestors of the *Lilaeopsis* clade + Clade 5, but this would require at least one, and possibly as many as three reversals back to the compound-leaved trait depending upon the reconstruction. Alternatively, rachis leaves could have evolved three times independently within the tribe. The latter scenario seems more likely given that rachis-leaves can also be found in the distantly related *Ottoa oenanthoides* Humb., Bonpl. & Kunth. of Apiaceae tribe Selineae (C.A. Danderson & S. R. Downie, unpubl. data), as well as in other genera of Apiaceae (Affolter 1985).

Specific and Infraspecific Level Phylogenetic Relationships. *Ptilimnium nodosum* is a semi-aquatic plant whose disjunct populations are ecologically distinct (Kress et al. 1994). Although presently recognized as one species (Kral 1981), evidence suggests that it may be a species complex (Kress et al. 1994; Bartgis 1997; Kartesz 1999). Prior to 1957, three species were recognized in the group (Easterly 1957a). Populations from Maryland, North Carolina, and West Virginia were given the name *P. viviparum*, while those from Alabama and Arkansas were called *P. fluviatile*. Only populations from South Carolina and Georgia were recognized as *P. nodosum* sensu stricto (s.s.). A study of isozyme variation found that there was substantial genetic differentiation among rather than within these three geographic groups, suggesting they might be separate, genetically-distinct species (Kress et al. 1994). Reveal and Broome (1982), upon examining morphological differences between *P. fluviatile* and *P. viviparum*, advocated that these should be recognized as *P. fluviatile* and *P. fluviatile* var. *viviparum* (Rose) Reveal & Broome. Kral (1981), however, also conducted a morphological study and concluded that *P. fluviatile*, *P. nodosum* s.s., and *P. viviparum* should be treated as one taxon.

In our study, all accessions of *P. nodosum* from Maryland, North Carolina, and West Virginia form a monophyletic group (subclade C). These plants were formally recognized as *P. viviparum.* This relationship is in accordance with the results of Kress et al. (1994) who showed that populations of *P. nodosum* from these three states were genetically more similar to each other than they were to populations from elsewhere. Further resolution within *Harperella* is not obtained, however. Five accessions from South Carolina also comprise a monophyletic group (subclade D), but other specimens previously attributable to *P. nodosum* s.s. occur at the base of *Harperella* alongside accessions referable to *P. fluviatile* from Alabama and Arkansas. *Ptilimnium nodosum* s.l. is listed as endangered by the U.S. Fish and Wildlife Service (1988) and the determination of boundaries among its constituent taxa will have an impact on management strategies implemented for its conservation.

Ptilimnium × *texense* was described as a distinct species (*P. texense* J. M. Coult. & Rose) by Coulter and Rose (1909), but was later considered to be a hybrid between *P. capillaceum* and P. *nuttallii* (Mathias and Constance 1945; Easterly 1957b) and then finally assumed under *P. costatum* (Mathias and Constance 1961). In the present study, the two specimens from Texas identified by Easterly as *P.* × *texense* and all specimens of *P. costatum* from Texas and Louisiana comprise a well-supported monophyletic group (*Ptilimnium*, subclade B). This clade is a sister group to subclade A, which is made up of *P. costatum* from Arkansas, Georgia, Illinois, Missouri, and Tennessee. *Ptilimnium* × *texense* allies with neither of its putative progenitors. Its close association with *P. costatum*, however, supports the work of Mathias and Constance (1961) where these plants were considered within this species. While our study was not set up to confirm the hybrid status of *P.* × *texense* and its parentage, it appears that *P. costatum* should be considered as one of its parents in future studies, if indeed it is a hybrid.

Collectively, subclade A (*P. costatum* from Arkansas, Georgia, Illinois, Missouri, and Tennessee) and subclade B (*P.* × *texense* and *P. costatum* from Texas and Louisiana) comprise a moderately to strongly supported group. Notable morphological differences, however, have been observed between specimens of subclades A and B. Style length and orientation are important characters which have been used to distinguish among species of *Ptilimnium* in numerous keys (Easterly 1957b; Mathias and Constance 1945, 1961). The length and orientation of styles of specimens of subclade A (0.5–1.0 mm in length and strongly recurved) are different from those of subclade B (1.0–3.0 mm long and spreading). *Ptilimnium nuttallii* also has styles that are between 0.5 and 1.0 mm in length and strongly recurved. In addition, plants from subclade B exhibit a unique leaf morphology. They have linear leaflets which are subterete and have no distinct midrib. The leaflets of *P. costatum* from subclade A, *P. nuttallii*, and *P. capillaceum* are all also linear, but they are flattened and have a distinct midrib. Future studies are planned to ascertain if these morphological differences warrant taxonomic recognition.

Ptilimnium capillaceum is the most common and wide-ranging species of *Ptilimnium*. All examined specimens have identical ITS sequences suggesting a recent and rapid radiation throughout its range. Moreover, these sequences are identical to those of *P. ahlesii*, further suggesting a very recent divergence of these species. Despite their identical ITS sequences, we maintain these species as distinct because of their morphological and phenological differences. *Ptilimnium ahlesii* has larger ovaries and fruits, while *P. capillaceum* has more umbellets per umbel and more flowers per umbellet (Weakley and Nesom 2004). In addition, *P. ahlesii* flowers earlier than *P. capillaceum,* although their flowering times do overlap (Weakley and Nesom 2004).

Neither *O. greenmanii* nor *O. filiformis* is monophyletic, but together they form a strongly supported monophyletic group with “Oxypolis × intermedia” ined., a putative hybrid of these two species. Sequence heterogeneity was detected in all accessions of *O. greenmanii* and one of the two accessions of “Oxypolis × intermedia” ined., but not in *O. filiformis*. Both *O. filiformis* and *O. greenmanii* share a chromosome number of $n = 14$, however, the chromosomes of *O. greenmanii* are much larger than those of *O. filiformis* (Bell and Constance 1957; Bell and Constance 1960). The larger chromosomes and ITS sequence polymorphisms of *O. greenmanii* suggest that this species could have been derived from *O. filiformis*. Chromosome number and size are not presently known for “Oxypolis × intermedia” ined. This putative hybrid is found in northwestern Florida where the ranges of *O. greenmanii* and *O. filiformis* overlap. “Oxypolis × intermedia” ined. exhibits intermediate morphological characters of the two species and are highly fertile, leading Judd (1982) to conclude that *O. greenmanii* should be recognized as a subspecies of *O. filiformis*.

All accessions of *O. occidentalis* form a monophyletic group, which is divided into three subclades that correspond to different geographic locations: F, the Cascade Mountains in Oregon and the Queen Charlotte Islands; G, the Cascade Range Foothills in northern California; and H, the Sierra Nevada, San Bernardino, White, and Inyo mountain ranges. The maximum pairwise sequence divergence between subclades F and G is 0.51%, while between subclades F+G and subclade H it is 4.86%. This latter value is greater than the maximum pairwise sequence divergence between *O. rigidior* and *O. ternata* (4.69%), suggesting that the accessions of subclade H may constitute a new species.

The Queen Charlotte Islands, located approximately 80 km off the west coast of British Columbia, are an intriguing geographic area. During the last glacial maximum (ca. 15,000 yrs ago), when glaciers covered much of present-day British Columbia and extended into present-day Washington State, it has been proposed that much of the Queen Charlotte Islands remained ice-free (Heusser 1960; Lacourse et al. 2005) and provided a refugium to plants and animals living there. Studies of the threespine stickleback (O'Reilly et al. 1993), song sparrow (Zink and Dittman 1993), and black bear (Byun et al. 1997) have provided evidence for such a refugium. However, Brunsfeld et al. (2001) reported that "there are no genetic data for plants that clearly support the Queen Charlotte Islands as a glacial refugium." *Oxypolis occidentalis* could potentially be such an example. The glacial refugium hypothesis may explain why *O. occidentalis* occurs on these islands and their highly disjunct geographic distribution. These Queen Charlotte Island populations are approximately 1,100 km north of the nearest known populations in central Oregon. The distribution of this species might have once extended from Oregon to British Columbia with intervening populations being wiped out by glaciers.

Our results suggest that populations of *O. occidentalis* from the Cascade Mountains of Oregon and the Queen Charlotte Islands (subclades F and G) are quite different from those of the Sierra Nevada and other more southern mountain ranges (subclade H). The Californian populations are within a geographic region known as the California Floristic Province which harbors more endemic plant and animal taxa and more identifiable subspecies than any other area of comparable size in North America (Calsbeek et al. 2003). The genetically divergent populations from this area could represent a new taxon and another example of a California Floristic Province endemic. The morphology and phylogeography of *O. occidentalis* is currently being studied to confirm the taxonomic status of these plants.

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REFERENCES

Affolter, J.M. 1985. A monograph of the genus *Lilaeopsis* (Umbelliferae). *Systematic Botany Monographs* 6: 1–140.

Álvarez, I. and J.F. Wendel. 2003. Ribosomal ITS sequences and plant phylogenetic inference. *Molecular Phylogenetics and Evolution* 29: 417–434.

Bartgis, R.L. 1997. The distribution of the endangered plant *Ptilimnium nodosum* (Rose) Mathias (Apiaceae) in the Potomac River drainage. *Castanea* 62: 55–59.

Bell, C.R. and L. Constance. 1957. Chromosome numbers in Umbelliferae. *American Journal of Botany* 44: 565–572.

Bell, C.R. and L. Constance. 1960. Chromosome numbers in Umbelliferae II. *American Journal of Botany* 47: 24–32.

Brunsfeld, S.J., J. Sullivan, D.E. Soltis, and P.S. Soltis. 2001. Comparative phylogeography of northwestern North America: a synthesis. Pp. 319-339 in *Integrating Ecology and Evolution in a Spatial Context,* eds. J. Silvertown and J. Antonovics. Oxford: Blackwell Science.

Byun, S.A., B.F. Koop, and T.E. Reimchen. 1997. North American black bear mtDNA phylogeography: implications for morphology and the Haida Gwaii glacial refugium controversy. *Evolution* 51: 1647–1653.

Calsbeek, R., J.N. Thompson, and J.E. Richardson. 2003. Patterns of molecular evolution and diversification in a biodiversity hotspot: the California Floristic Province. *Molecular Ecology* 12: 1021–1029.

Candolle, A.P. 1829. *Memoire sur la Famille des Ombelliferes*. Paris: Treuttel et Würtz.

Constance, L., T.-I . Chuang, and C.R. Bell. 1976. Chromosome numbers in Umbelliferae V. *American Journal of Botany* 63: 608–625.

Coulter J.M. and J.N. Rose. 1887. Notes on Umbelliferae of the E. United States III. *Botanical Gazette* 12: 73–76

Coulter J.M. and J.N. Rose. 1909. Supplement to the monograph of the North American Umbelliferae. *Contributions from the U.S. National Herbarium* 12: 441–451.

Crawford, D.J. and R.L. Hartman. 1972. Chromosome numbers and taxonomic notes for Rocky Mountain Umbelliferae. *American Journal of Botany* 59: 386–392.

Downie, S.R. and D.S. Katz-Downie. 1996. A molecular phylogeny of Apiaceae subfamily Apioideae: evidence from nuclear ribosomal DNA internal transcribed spacer sequences. *American Journal of Botany* 83: 234–251.

Downie, S.R., D.S. Katz-Downie, and K. Spalik. 2000a. A phylogeny of Apiaceae tribe Scandiceae: evidence from nuclear ribosomal DNA internal transcribed spacer sequences. *American Journal of Botany* 87: 76–95.

Downie, S.R., D.S. Katz-Downie, and M.F. Watson. 2000b. A phylogeny of the flowering plant family Apiaceae based on chloroplast DNA *rpl16* and *rpoC1* intron sequences: towards a suprageneric classification of subfamily Apioideae. *American Journal of Botany* 87: 273–292.

Downie, S.R., S. Ramanath, D.S. Katz-Downie, and E. Llanas. 1998. Molecular systematics of Apiaceae subfamily Apioideae: phylogenetic analyses of nuclear ribosomal DNA internal transcribed spacer and plastid *rpoC1* intron sequences. *American Journal of Botany* 85: 563–591.

Easterly, N.W. 1957a. A morphological study of the genus *Ptilimnium*. Dissertation. Morgantown, WV: University of West Virginia.

Easterly, N.W. 1957b. A morphological study of *Ptilimnium*. *Brittonia* 9: 136–145.

Elliott, S. 1817. *A sketch of the botany of South-Carolina and Georgia.* Charleston: J. R. Schenck.

Hall, T.A. 1999. BioEdit: A user friendly biological sequence alignmant editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95–98.

Hardway, T.M., K. Spalik, M.F. Watson, D.S. Katz-Downie, and S.R. Downie. 2004. Circumscription of Apiaceae tribe Oenantheae. *South African Journal of Botany* 70: 393–406.

Heusser, C.J. 1960. *Late Pleistocene environments of North Pacific North America.* Special Publication, vol. 35. New York: American Geographical Society.

Huelsenbeck, J.P. and F. Ronquist. 2001. MrBayes. Bayesian inference of phylogenetic trees. *Bioinformatics* 17: 754–755.

Judd, W.S. 1982. The taxonomic status of *Oxypolis greenmanii* (Apiaceae). *Rhodora* 84: 265–279.

Kaplan, D.R. 1970. Comparative development and morphological interpretation of 'rachis-leaves' in Umbelliferae. *Botanical Journal of the Linnean Society* 63 (Supplement 1): 101–126.

Kartesz, J.T. 1999. A synonymized checklist and atlas with biological attributes for the vascular flora of the United States, Canada, and Greenland. In Kartesz, J.T. and C.A. Meacham. Synthesis of North American flora, Version 1.0. Chapel Hill: North Carolina Botanical Garden.

Kral, R. 1981. Notes on some "quill-leaved" umbellifers. *SIDA Contributions to Botany* 9: 124–134.

Kress, W.J., G.D. Maddox, and C.S. Roesel. 1994. Genetic variation and protection priorities in *Ptilimnium nodosum* (Apiaceae), an endangered plant of the eastern United States. *Conservation Biology* 8: 271–276.

Kuntze, C.E.O. 1891. Revisio Generum Plantarum. 1: 269.

Lacourse, T., R.W. Mathewes, and D.W. Fedje. 2005. Late-glacial vegetation dynamics of the Queen Charlotte Islands and the adjacent continental shelf, British Columbia, Canada. *Paleogeography, Paleoclimatology, and Paleoecology* 226: 36–57.

Lee, B.Y., G.A. Levin, and S.R. Downie. 2001. Relationships within the spiny-fruited Umbellifers (Scandiceae subtribes Daucinae and Torilidinae) as assessed by phylogenetic analysis of morphological characters. *Systematic Botany* 26: 622–642.

Linnaeus, C. 1753. *Species plantarum: exhibentes plantas rite cognitas, ad genera relatas, cum differentiis specificis, nominbus trivialibus, synonymis selectis, locisnatalibus, secundum systema sexuale digestas.* Stockholm: Impensis Laurentii Salvii.

Mathias, M. 1936. Notes on the genus *Ptilimnium*. *Brittonia* 2: 244.

Mathias, M. and L. Constance. 1945. Umbelliferae. *North American Flora* 28B: 43–295.

Mathias, M. and L. Constance. 1961. Umbelliferae. Pp. 263-329 in *Flora of Texas,* vol. 3, ed. C. L. Lundell. Renner: Texas Research Foundation.

O'Reilly, P., T.E. Reimchen, R. Beech, and C. Strobeck. 1993. Mitochondrial DNA in *Gasterosteus* and Pleistocene glacial refugium on the Queen Charlotte Islands, British Columbia. *Evolution* 47: 678–684.

Pimenov, M.G., M.G. Vasil'eva, M.V. Leonov, and J.V. Daushkevich. 2003. *Karyotaxonomical analysis in the Umbelliferae*. Enfield: Science Publishers, Inc.

Plunkett, G.M., D.E. Soltis, and P.S. Soltis. 1996. Evolutionary patterns in Apiaceae: inferences based on *matK* sequence data. *Systematic Botany* 21: 477–495.

Posada D. and K.A. Crandall. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* 14: 817–818.

Rafinesque, C.S. 1819. The genera of North American plants and a catalogue of the species in the year 1817 by Thomas Nuttall. *American Monthly Magazine and Critical Review* 4: 192.

Rafinesque, C.S. 1825. *Neogenyton*, *or indication of sixty-six new genera of plants of North America.* Lexington: published by the author.

Reveal, J.L. and C.R. Broome. 1982. Comments on the proposed endangered and threatened vascular plants of Maryland: USA. *Castanea* 47: 191–200.

Rose, J.N. 1905. Two new umbelliferous plants from the coastal plain of Georgia. *Proceedings of the U.S. National Museum* 29: 441–445.

Rose, J.N. 1906. New names for two recently described genera of plants. *Proceedings of the Biological Society of Washington* 19: 96–98.

Simmons, M.P. and H. Ochoterena. 2000. Gaps as characters in sequence-based phylogenetic analyses. *Systematic Biology* 49: 369–381.

Spalik, K. and S.R. Downie. 2006. The evolutionary history of *Sium* sensu lato (Apiaceae): dispersal, vicariance, and domestication as inferred from ITS rDNA phylogeny. *American Journal of Botany* 93: 76–95.

Swofford D.L. 2003. PAUP*: Phylogenetic analysis using parsimony (*and other methods), Version 4.0 beta 10. Sunderland: Sinauer Associates.

Theobald, W.L. 1971. Comparative anatomical and developmental studies in the Umbelliferae. In *The biology and chemistry of the Umbelliferae*, ed. V. H. Heywood. *Botanical Journal of the Linnean Society* 64 (Supplement 1): 177–197.

Thompson, J.D., T.J. Gibson, F. Plewniak, F. Jeanmougin, and D.G. Higgins. 1997. The Clustal X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research* 24: 4876–4882.

Tucker, A.O., N.H. Dill, T.D. Pizzolato, and R.D. Kral. 1983. Nomenclature, distribution, chromosome numbers, and fruit morphology of *Oxypolis canbyi* and *O. filiformis* (Apiaceae). *Systematic Botany* 8: 299–304.

U.S. Fish and Wildlife Service. 1988. Endangered and threatened wildlife and plants: determination of *Ptilimnium nodosum* (harperella) to be an endangered species. *Federal Register* 50: 37978–37982.

Walter, T. 1788. *Flora caroliniana, secundum systema vegetabilium perillustris Linnæi digesta; characteres essentiales naturalesve et differentias veras exhibens; cum emendationibus numerosis: descriptionum antea evulgatarum: adumbrationes stirpium plus mille continens: necnon, generibus novis non paucis, speciebus plurimis novisq. ornata.* London: Sumptibus J. Fraser.

Weakley, A.S. and G.L. Nesom. 2004. A new species of *Ptilimnium* (Apiaceae) from the Atlantic coast. *SIDA Contributions to Botany* 21: 743–752.

Wen, J. and E.A. Zimmer. 1996. Phylogeny and biogeography of *Panax* L. (the ginseng genus, Araliaceae): inferences from ITS sequences of nuclear ribosomal DNA. *Molecular Phylogenetics and Evolution* 6: 167–177.

Zink, R.M., and D.L. Dittmann. 1993. Gene flow, refugia, and evolution of geographic variation in the song sparrow (*Melospiza melodia*). *Evolution* 47: 717–729.

TABLES AND FIGURES

Table 2.1. Currently recognized species of *Oxypolis* and *Ptilimnium* and their distributions according to Kartesz (1999). *Ptilimnium ahlesii* was described by Weakley and Nesom (2004). The two putative interspecific hybrids are not listed.

Oxypolis canbyi (J. M. Coult. & Rose) Fernald – DE, MD, GA, NC, SC
Oxypolis fendleri (A. Gray) A. Heller – AZ, CO, NM, UT, WY
Oxypolis filiformis (Walter) Britton – AL, FL, GA, LA, MS, NC, SC, TX
Oxypolis greenmanii Mathias & Constance – FL
Oxypolis occidentalis J. M. Coult. & Rose – CA, OR, BC (Canada)
Oxypolis rigidior (L.) Raf. – AL, AR, DC, DE, FL, GA, IA, IL, IN, KY, LA, MD, MI, MN, MO, MS, NC, NJ, NY, OH, OK, PA, SC, TN, TX, VA, WI, WV, ON (Canada)
Oxypolis ternata (Nutt.) A. Heller – FL, GA, NC, SC, VA
Ptilimnium ahlesii Weakley & G. L. Nesom – GA, NC, SC
Ptilimnium capillaceum (Michx.) Raf. – AL, AR, CT, DC, DE, FL, GA, KS, KY, LA, MA, MO, MS, NC, NJ, NY, PA, PR, RI, SC, SD, TN, TX, VA
Ptilimnium costatum (Elliott) Raf. – AL, AR, GA, IL, KY, LA, MO, NC, OK, TN, TX
Ptilimnium nodosum (Rose) Mathias – AL, AR, GA, MD, NC, SC, VA, WV
Ptilimnium nuttallii (DC.) Britton – AL, AR, IL, KS, KY, LA, MO, MS, OK, TN, TX

Table 2.2. A summary of accessions with identical ITS sequences that were represented by a single terminal accession in the phylogenetic analyses, except when sequences were from individuals from geographic areas of interest. Accession numbers in the second column are those identifying terminals in Figs. 2.1–2.2. Accession numbers in the third column have identical ITS sequences to those presented in the second column. Voucher information for all accessions is provided in Appendix A.

Species	**Accession number presented in Figs. 2.1–2.2**	**Accessions with identical sequences**
Oxypolis canbyi	2745	2744, 2743
	2747	2746
Oxypolis fendleri	2759	2758
	2764	1509, 2350, 2351, 2353, 2369, 2762
Oxypolis filiformis	2356	2357, 2371
	2653	2652
	2783	2713
Oxypolis occidentalis	2753	1435
	2755	2929
	2898	2897
	2972	2359
Oxypolis rigidior	1653	1652, 1806, 1962
	2771	2768
Oxypolis ternata	2738	2736, 2739
	2741	2740
	2939	2735, 2737
	2940	2360
Ptilimnium capillaceum	2619	2618, 2627, 2628, 2704, 2794, 2795
Ptilimnium costatum	1651	1805
	2625	1503, 1504, 1514, 1646, 1648, 1649, 1650, 1801, 1802, 1970, 2402
	2904	2641
	1981	2905, 2906, 2914
Ptilimnium nodosum	2635	2784, 2785
	2786	2970
	2792	2787
	2900	2901
	2930	2791
	2934	2933
	2936	2790
Ptilimnium nuttallii	2623	2165, 2404, 2617, 2637, 2644, 2708

Table 2.3. Sequence characteristics of the entire nuclear rDNA internal transcribed spacer region and partitioned ITS-1, 5.8S rDNA, and ITS-2 regions for 83 terminals (representing 147 accessions) used in the phylogenetic analyses.

Sequence characteristic	**ITS-1**	**5.8S**	**ITS-2**	**Entire ITS region**
Length variation (bp)	201–213	162–165	206–230	580–605
Aligned length (bp)	228	165	239	632
No. of excluded sites	6	2	27	35
No. of sites not variable	81	144	57	282
No. of sites autapomorphic	24	2	21	47
No. of sites parsimony informative	117	17	134	268
No. of unambiguous alignment gaps (indels)	22	1	11	34
No. of unambiguous alignment gaps parsimony informative	7	0	8	15
Maximum pairwise sequence divergence (%):				
All 83 terminals	30.6	5.5	34.4	22.7
Oxypolis and *Ptilimnium*	27.1	5.5	29.1	20.7
Oxypolis only (all, compound-leaved, rachis-leaved)	27.1, 13.0, 10.6	5.5, 2.5, 1.2	29.1, 9.3, 15.9	20.7, 8.5, 9.9
Ptilimnium only (all, compound-leaved, rachis-leaved)	17.0, 4.6, 1.0	3.1, 1.2, 0.0	23.7, 5.3, 1.0	14.9, 3.5, 0.7

Figure 2.1. Strict consensus of 350 minimal length 843-step trees derived from equally weighted maximum parsimony analysis of 147 ITS sequences represented by 83 terminals (CI = 0.5475, without uninformative characters; RI = 0.9173). The numbers in parentheses correspond to the number of identical ITS sequences represented by that terminal (Table 2.2). Numbers on branches represent bootstrap estimates; a value less than 50% is indicated with an asterisk. Five major clades are identified. These include the compound-leaved *Ptilimnium* species (Clade 1, *Ptilimnium*), the rachis-leaved *Ptilimnium* species (Clade 2, *Harperella*), the rachis-leaved *Oxypolis* species (Clade 3, *Tiedemannia*), and the compound-leaved *Oxypolis* species (Clade 4, *Oxypolis*). Clades 1–3 plus representatives from *Cynosciadium, Daucosma, Limnosciadium* comprise Clade 5. Subclades or groups A–H represent plants from the indicated geographic regions.

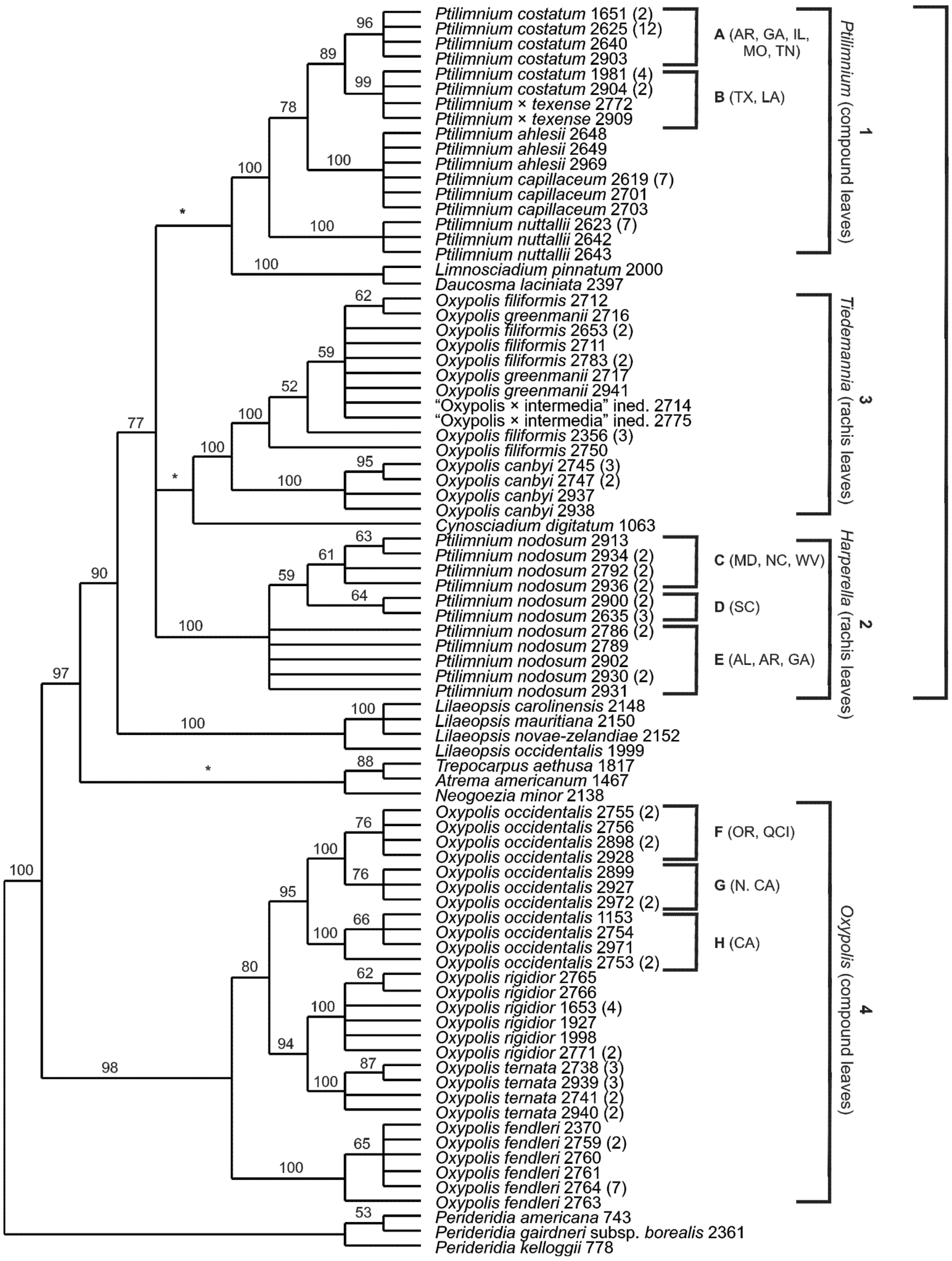
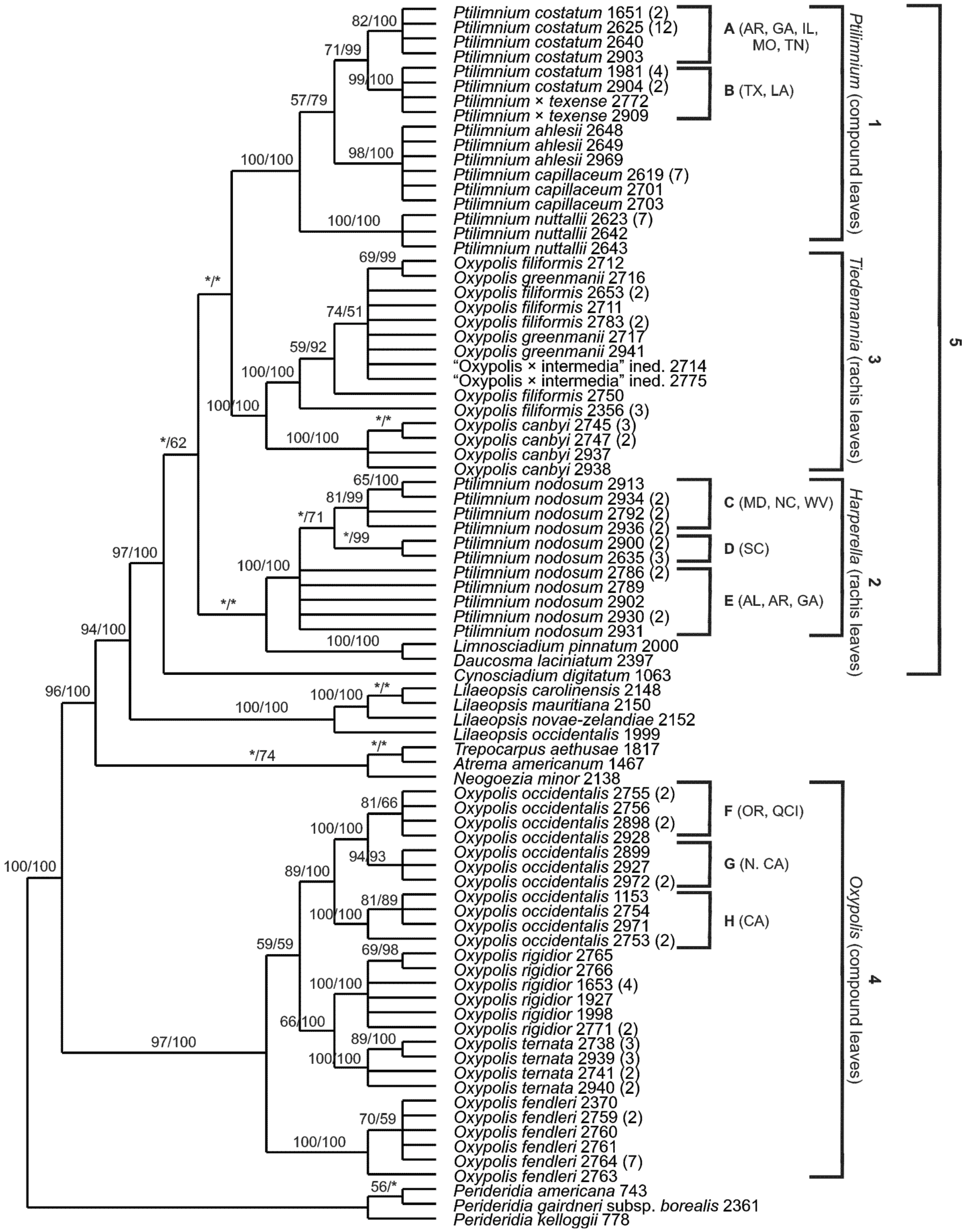


Figure 2.2. Strict consensus of 38 trees resulting from maximum likelihood analysis of 147 ITS sequences represented by 83 terminals (-Ln likelihood score = 4962.61109). This tree was nearly identical to the majority-rule consensus tree of 30,000 trees derived from Bayesian analysis. The numbers in parentheses correspond to the number of identical ITS sequences represented by that terminal (Table 2.2). Numbers on branches represent bootstrap estimates and Bayesian posterior probability values, respectively; a value less than 50% is indicated with an asterisk. Clade and subclade descriptors and all abbreviations are the same as described in Fig. 2.1.



CHAPTER 3

CLARIFICATIONS CONCERNING THE NOMENCLATURE AND TAXONOMY OF *OXYPOLIS TERNATA* (APIACEAE)[2]

Abstract: John R. Edmondson made the combination *Oxypolis denticulata* (Baldwin) J.R. Edm. based on the assumption that *Sium denticulatum* Baldwin was synonymous with *O. ternata* (Nutt.) A. Heller. An in-depth investigation into the taxonomic and nomenclatural history of these species has shown, however, that *S. denticulatum* Baldwin and *O. ternata* (Nutt.) A. Heller are not synonyms. In addition, the name *O. denticulata* (Baldwin) J.R. Edm. is an isonym of *O. denticulata* (Baldwin) Raf.

In 2005, J.R. Edmondson published what he believed to be a new combination, *Oxypolis denticulata* (Baldwin) J.R. Edm., to include the names *Sium denticulatum* Baldwin, *Peucedanum ternatum* Nutt., and *O. ternata* (Nutt.) A. Heller. He argued that the name *O. denticulata* superseded *O. ternata*, the commonly cited modern name for this species. Further investigation into the nomenclatural and taxonomic history of these and related taxa has shown, however, that Edmondson made two important errors in proposing this combination: his name is an isonym, and *S. denticulatum* is not synonymous with *P. ternatum* and *O. ternata*.

In 1898, A. Heller transferred *Peucedanum ternatum* to *Oxypolis* and *O. ternata* became the commonly cited modern name for this species. Edmondson (2005) found an isotype of *Sium denticulatum* in the herbarium of the Linnean Society of London (LINN). He made the assumption that *P. ternatum* was synonymous with *S. denticulatum*. Since Heller's combination was based on Nuttall (1818) epithet published after Baldwin's (Elliott 1817), Edmonson reasoned that the earlier name had priority and a new combination was warranted. Thus Edmondson proposed the combination *O. denticulata* and designated as the lectotype the LINN specimen (LINN-Smith no: 508.5) labeled "*Sium denticulatum* nov. sp." and collected by William Baldwin in 1817.

Edmondson went on to explain that when Rafinesque established the new genus *Oxypolis* (Rafinesque 1825) he included *Sium denticulatum* under *Oxypolis* but failed to make a new

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[2] This chapter has been previously published. From Feist 2009, J. Bot. Res. Inst. Texas 3(2), 2009. Courtesy of Botanical Research Institute of Texas, Fort Worth.

combination for the species. Edmondson was correct that Rafinesque did not make the new combination in 1825, but he overlooked that Rafinesque did make the combination five years later in the first volume of Bulletin Botanique (Bull. Bot. 1:218. 1830). Rafinesque's combination was clearly based on *S. denticulatum*, the same basionym upon which Edmondson based his combination. Consequently, the Edmondson isonym is without nomenclatural status and should be disregarded according to Article 6 Note 2 of the *International Code of Botanical Nomenclature* (McNeill et al. 2006).

The second error in Edmondson's combination was in assuming that *Sium denticulatum* was synonymous with *Peucedanum ternatum*, when in actuality, *S. denticulatum* is a synonym of *Oxypolis rigidior* (L.) Raf. The recognition of this synonymy is not unprecedented for in 1840 Torrey and Gray recognized *S. denticulatum* as a synonym of *S. rigidius* L., the basionym for *O. rigidior*.

The protologues for *Sium denticulatum* and *Peucedanum ternatum* provide the first clue that these species are not synonyms. Baldwin (Elliott 1817) described *S. denticulatum* as having "leaves unequally pinnate; leaflets oval, toothed, acute; … generally with three pairs of leaflets and an odd one." In contrast, Nuttall (1818) characterized *P. ternatum* as having: "leaves all ternate, upon very long common petioles; partial leaves entire, long, linear, acute, and attenuated below… perfectly entire and scarcely three lines wide."

Comparing the lectotype of *Sium denticulatum* (Fig. 3.1) with the lectotype of *S. rigidius* (Fig. 3.2), and comparing these with herbarium specimens and published descriptions of *Oxypolis ternata* and *O. rigidior,* provide further clues and convincing evidence that *S. denticulatum* is a synonym of *O. rigidior* not *O. ternata*. Differences are especially apparent in the leaf morphology (Figs. 3.1–3.3). These and other morphological differences between the species are summarized in Table 3.1. Information in Table 3.1 was compiled from a number of sources (Weakley 2008; Radford & et al. 1968; Rodgers 1950; Mathias & Constance 1945; Torrey & Gray 1840) as well as from personal examination of numerous specimens from the following herbaria: DUKE, F, ILL, ILLS, NCU, UGA, USF, and USCH.

Oxypolis ternata and *O. rigidior* can be distinguished by the following: The leaves of *O. ternata* are either unifoliate or ternate and palmately disposed. The leaflets are petiolulate, parallel-veined, always entire, and filiform to linear, typically being no more than 6 mm wide. The number of rays on the compound umbel is 5–10. In contrast, the leaves of *O. rigidior* are pinnately disposed with 5–13 sessile leaflets, reticulate-veined, remotely dentate or entire (it is rare to find a plant without some leaflets that are dentate in the upper part of the leaf), linear-lanceolate to elliptic-lanceolate, and 5–45 mm wide. The number of rays is 12–45.

No type has been located for *Peucedanum ternatum*. Inquiries or searches were made of all herbaria listed by the Harvard University Herbarium Index of Botanists to have known Nuttall collections. Nuttall gave North and South Carolina as the locality for *P. ternatum*. A specimen collected in South Carolina by A.E. Radford is herein designated as the neotype (Fig. 3.3).

Oxypolis ternata (Nutt.) A. Heller, Cat. N. Amer. Pl. 5. 1898. *Peucedanum ternatum* Nutt., Gen. N. Amer. Pl. 1:182. 1818. *Sataria linearis* Raf., New Fl. 4:21. 1838 (nom. illeg.). *Archemora ternata* (Nutt.) Nutt. in Torr. & A. Gray, Fl. N. Amer. 1:631. 1840. *Tiedemannia ternata* (Nutt.) J.M. Coult. & Rose, Bot. Gaz. 12:74. 1887. Type: U.S.A. South Carolina. Georgetown Co.: ditch, near US 701, 3 mi S–SW of Yauhannah, 20 Oct 1957, *A.L. Radford 31381* (neotype, designated here: NCU!; duplicates of the neotype: UC!, UF!, SMU!).

Sataria linearis Raf., var. *longipes* Raf., New Fl. 4:21. 1838. Rafinesque did not cite a specific collection or give a locality.

Neurophyllum longifolium Torr. & A. Gray, Fl. N. Amer. 1:613. 1840. Types: U.S.A. North Carolina. [Cravern Co.]: “Swamps near Newbern, North Carolina, *Mr. Croom! Dr. Loomis!* Middle Florida, *Mr. Croom!* Sept.” (lectotype, designated here: NY, digital image!). Syntype: NORTH CAROLINA: New Bern, s.d., *H.B. Croom s.n.* (PH!).

Oxypolis rigidior (L.) Raf., Bull. Bot. 1:218. 1830. *Sium rigidius* L., Sp. Pl. 1:251. 1753. *Oenanthe rigidius* (L.) Crantz, Cl. Umbell. Emend. 85. 1767, ‘*rigida*’. *Pastinaca rigidior* (L.) Spreng. in Roemer & Schultes, Syst. Veg. 6:586. 1820, ‘*rigida*’. *Archemora rigidior* (L.) DC., Prodr. 4:188. 1830, ‘*rigida*’. *Peucedanum rigidius* A.W. Wood, Amer. Bot. Fl. 136. 1870, *nom. illeg*., non Bunge (1833), ‘*rigidum*’. *Tiedemannia rigidior* (L.) J.M. Coult. & Rose, Bot. Gaz. 12:74. 1887, ‘*rigida*’. Type: U.S.A. Virginia: *J. Clayton 279* (lectotype, designated by J.L. Reveal in C.E. Jarvis et al., Taxon 55:215. 2006: BM, digital image!).

Archemora serrata Raf., Herb. Raf. 78. 1833. Type: U.S.A. Kentucky & Tennessee: specimen not located.

Archemora trifoliata Raf., Herb. Raf. 78. 1833. Type: U.S.A. Missouri: specimen not located.

Oenanthe ambigua Nutt., Gen. N. Amer. Pl. 1:189. 1818. *Pastinaca ambigua* (Nutt.) Torr., Fl. N. Middle United States 315. 1824. *Archemora ambigua* (Nutt.) DC., Prodr. 4:188.1830. *Archemora rigidior* (L.) DC. var. *ambigua* A. Gray, Manual 158. 1848, '*rigida*'. *Peucedanum rigidius* A.W. Wood var. *ambiguum* A.W. Wood, Amer. Bot. Fl. 136. 1870, '*rigidum*'. *Tiedemannia rigidior* (L.) J.M. Coult. & Rose var. *ambigua* (Nutt.) J.M. Coult. & Rose, Rev. N. Amer. Umbell. 47. 1888, '*rigida*'. *Oxypolis rigidior* (L.) Raf., var. *ambigua* (Nutt.) B.L. Rob., Rhodora 10:35. 1908. Type: U.S.A. Pennsylvania. Philadelphia Co.: banks of the Delaware River near Philadelphia, s.d., *T.Nuttall s.n.* (PH, digital image!).

Oxypolis turgida Small, Man. S.E. Fl. 986. 1933. Type: U.S.A. Virginia. Staunton Co.: Staunton, 2 Oct 1895, *W.A. Murrill s.n.* (lectotype, designated here: NY, digital image!).

Sium denticulatum Baldwin in S. Elliott, Sketch Bot. S. Carolina 1:354. 1817. *Archemora denticulata* (Baldwin) DC., Prodr. 4:188. 1830. *Oxypolis denticulata* (Baldwin) Raf., Bull. Bot. 1:218. 1830. *Pastinaca denticulata* (Baldwin) D. Dietr., Syn. Pl. 2:971. 1840. Type: U.S.A. Georgia: 1817, *W. Baldwin s.n.* (lectotype, designated by Edmondson 2005: LINN-Smith, digital image!).

Sium longifolium Pursh, Fl. Amer. Sept. 194. 1813. *Oxypolis rigidior* (L.) Raf., var. *longifolia* (Pursh) Britton, Mem. Torrey Bot. Club 5:239. 1894, '*rigidus* var. *longifolius*'. *Oxypolis longifolia* (Pursh) Small, Fl. S.E. U.S. 875, 1336. 1903. *Oxypolis rigidior* (L.) Raf. subsp. *Longifolia* (Pursh) W. Stone, Pl. S. New Jersey 2:600. 1911. Type: U.S.A. New Jersey: (lectotype, designated with reservations by Ewan 1979: PH, digital image!).

Sium tricuspidatum Elliott, Sketch Bot. S. Carolina 1:354. 1817. *Archemora tricuspidata* (Elliott) DC., Prodr. 4:188. 1830. *Oxypolis tricuspidata* (Elliott) Raf., Bull. Bot. 1:218. 1830. *Pastinaca tricuspidata* (Elliott) D. Dietr., Syn. Pl. 2:971. 1840. Type: U.S.A. South Carolina: (holotype: CHARL!).

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REFERENCES

Edmondson, J.R. 2005. A new combination in *Oxypolis* Raf. (Apiaceae). *Novon* 15: 109.

Elliott, S. 1817. *A sketch of the botany of South-Carolina and Georgia.* Charleston: J.R. Schenck.

Ewan, J. 1979. Introduction to the facsimile reprint of Frederick Pursh, *Flora Americae Septentrionalis* (1814). In: F.T. Pursh, *Flora Americae Septentrionalis*. Facsimile reprint. Braunschweig, Germany: J. Cramer.

Mathias, M. and L. Constance. 1945. Umbelliferae. *North American Flora* 28B: 43–295.

McNeill J., F.R. Barrie, H.M. Burdet, V. Demouli n, D.L. Hawksworth, K. Marhold, D.H. Nicolson, J. Prado, P.C. Silva, J.E. Skog, J.H. Wiersema, and N.J. Turland. 2006. International code of botanical nomenclature (Vienna Code). *Regnum Vegetable* 146.

Nuttall, T. 1818. *The genera of North American plants, and a catalogue of species to the year 1817*. 2 vols. Philadelphia, Pennsylvania: D. Heartt.

Radford, A.E., H.E. Ahles, and C.R. Bell. 1968. *Manual of the vascular flora of the Carolinas*. Chapel Hill: University of North Carolina Press.

Rafinesque, C.S. 1825. *Neogenyton, or indication of sixty-six new genera of plants of North America.* Lexington: published by the author.

Rafinesque, C.S. 1830. Extract d'une lettre de M.S.C. Rafinesque, professeur à Philadelphie, addressée à M. le professeur De Candolle. *Bulletin Botanique (Seringe)* 1: 214–221.

Rodgers C.L. 1950. The Umbelliferae of North Carolina and their distribution in the southeast. *Journal of the Elisha Mitchell Scientific Society* 66: 195–266.

Torrey, J. and A. Gray. 1840. *A flora of North America.* New York: Wiley & Putnam.

Weakley, A.S. 2010. *Flora of the Southern and Mid-Atlantic States: working draft of 8 March 2010.* University of North Carolina Herbarium, University of North Carolina at Chapel Hill. (http://www.herbarium.unc.edu/WeakleyFlora2010Mar.pdf).

TABLES AND FIGURES

Table 3.1. Morphological characters distinguishing *Oxypolis ternata* (Nutt.) A. Heller and *Oxypolis rigidior* (L.) Raf.

Characters	***Oxypolis ternata***	***Oxypolis rigidior***
Petiole length	10–30 (35) cm	5–10 cm
Leaf disposition	palmate	pinnate
Leaflet number	(1) 3	(5) 7–11 (13)
Leaflet venation	parallel	reticulate
Leaflet margin	entire	(entire) remotely dentate
Leaflet shape	linear to filiform	linear-lanceolate to elliptic-lanceolate
Leaflet length	7–22	7–15 cm
Leaflet width	1–6 mm	5–45 mm
Leaflets	petiolulate	sessile
Ray number	5–10	12–45

Figure 3.1. *Sium denticulatum* lectotype (LINN-Smith no.: 508.5) collected by William Baldwin in 1817. Image used with kind permission of the Linnean Society of London.

Figure 3.2. *Sium rigidius* L./*Oxypolis rigidior* (L.) Raf. lectotype (BM-000042233) collected by Clayton (no date given). Image used with kind permission of the Museum of Natural History, London.

Figure 3.3. *Oxypolis ternata* neotype duplicate (FLAS-78405) collected by Radford in 1957.

CHAPTER 4

THE REINSTATEMENT OF *PTILIMNIUM TEXENSE* (APIACEAE) AND A NEW KEY TO THE GENUS.[3]

Abstract: *Ptilimnium texense* J.M. Coult. & Rose is currently treated as either a synonym of *P. costatum* (Elliott) Raf. or a hybrid of *P. capillaceum* (Michx.) Raf. and *P. nuttallii* (DC.) Britton. A study utilizing molecular, morphological, and ecological data was undertaken to determine its taxonomic status. Evidence is presented for the recognition of *P. texense* as a distinct species. *Ptilimnium texense* is endemic to the West Gulf Coastal Plain where it occurs in bogs, acid seeps, and wet pine savannas in east central Texas, west central Louisiana, and southern Arkansas. A key to the genus *Ptilimnium* Raf. is provided.

INTRODUCTION

Ptilimnium texense J.M. Coult. & Rose is currently most commonly treated as a synonym of *P. costatum* (Elliott) Raf., but some authors continue to recognize it as the hybrid *P.* × *texense,* with the putative parents *P. capillaceum* (Michx.) Raf. and *P. nuttallii* (DC.) Britton. A recent study utilizing nrDNA ITS sequences indicated that *Ptilimnium texense* was more closely related to *P. costatum* than to *P. capillaceum* or *P. nuttallii* (Feist & Downie 2008), but also brought into question the synonymy of *P. texense* and *P. costatum*. This was followed by extensive herbarium and field studies to examine the taxonomic status of *P. texense*. Combined evidence from morphology, ecology, and DNA sequences indicates that *P. texense* should be reinstated. *Ptilimnium texense* occurs in acidic habitats in the West Gulf Coastal Plain Region of east central Texas, west central Louisiana, and southern Arkansas (Fig. 4.1).

Taxonomic History. In 1909 J.M. Coulter and J.N. Rose described *Ptilimnium texense* based on a specimen from Hockley, Texas, collected by F.W. Thurow. They noted that it combined “the cleft involucral bracts, characteristic fruit ribs, and shorter styles of *P. capillaceum* with the stouter habit, smaller fruit, and larger calyx teeth of *P. nuttallii*.” In 1945, Mathias and Constance speculated that plants described as *P. texense* “seemed to be of hybrid origin,” and listed the putative parents as *P. capillaceum* and *P. nuttallii*. Easterly (1957) was unable to find distinctive characters for *P. texense* and so accepted this assessment, stating that

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[3] This chapter has been previously published. From Feist 2009, J. Bot. Res. Inst. Texas 3(2), 2009. Courtesy of Botanical Research Institute of Texas, Fort Worth.

"this plant combines the fruit characteristics of *P. nuttallii* with the vegetative characteristics of *P. capillaceum*." None of these authors, however, presented evidence beyond these statements to support the hybrid status of *P. texense* and later Mathias and Constance relegated it to synonymy under *P. costatum* with no explanation (Lundell 1961). Some authors, however, have continued to recognize *P.* × *texense* (Correll & Johnston 1970; Correll & Correll 1972; Diggs et al. 1999) and have given its distribution as eastern Texas in acid bogs and marshlands. These same authors have also continued to recognize *P. costatum* as occurring in Texas.

Molecular Studies. In a study utilizing nrDNA ITS sequence data (Feist & Downie 2008), specimens from Texas identified by Easterly as *Ptilimnium* × *texense* did not ally with either of their putative parents (*P. capillaceum* and *P. nuttallii*), but rather showed a close association with *P. costatum*. These specimens formed a strongly supported clade with all specimens identified as *P. costatum* from Texas and Louisiana (hereafter the *P. texense* clade). The *P. texense* clade was sister to another strongly supported clade made up of *P. costatum* from Georgia, Illinois, Missouri, and Tennessee (hereafter the *P. costatum* clade). These results indicated that *P.* × *texense* was allied with *P. costatum*, but that populations of each from Louisiana or Texas (the *P. texense* clade) were molecularly distinct (Feist & Downie 2008). Average ITS sequence divergence between the *P. texense* and *P. costatum* clades was 2.6%, which is just slightly less than that between *P. costatum* and *P. capillaceum* (2.9%). Results from a recent analysis of cpDNA sequence data (*trnQ-rps16* 5'exon, *rps16* intron, *rps16* 3'exon-*trnK*) were congruent with the ITS findings (Feist & Downie unpublished data). At first glance, these results seemed to support Mathias and Constance's conclusion (1961) that *P. texense* should be synonymized under *P. costatum*, but morphological differences between specimens making up the *P. texense* clade and the *P. costatum* clade were also observed. Taken together with the geographical and molecular differences, this suggested that members of the *P. texense* clade might represent a taxon distinct from *P. costatum*. Additional herbarium and field studies were undertaken to investigate the taxonomic status of these populations. Morphology, habit, phenology, habitat requirements, and distribution were all considered. The results of these studies are presented below.

METHODS

Field Visits and Morphological Studies. Six populations of *Ptilimnium,* three in Louisiana and three in Texas, all previously identified as *P. costatum* but determined to be *P.*

texense during the course of this study, were visited during Sep 15–21, 2009 (Feist & Molano-Flores specimens listed in Appendix B). Habitat and associate species were recorded and voucher specimens were collected for additional morphological study. In addition, a total of five plants were collected live and placed in a greenhouse at the Illinois Natural History Survey.

A large number of specimens from the genus *Ptilimnium* were examined during the course of this study. Specimens were either collected by the author or borrowed from the following herbaria: ANHC, AUA, BAYLU, BRIT, DOV, DUKE, EKY, F, FLAS, FSU, GA, ILL, ILLS, JEPS, LAF, LL, LSU, LSUS, MO, NCSC, NCU, NO, NY, OKL, OKLA, OS, OSC, PH, RM, RSA-POM, SMU, TAMU, TENN, TEX, UARK, UC, UNA, UNC, US, USCH, USF, USFS, and WVA. A total of 144 specimens were determined to be *Ptilimnium texense*. These included 4 from Arkansas, 54 from Louisiana, and 86 from Texas (Appendix B). The majority of these specimens were not identified as *P. texense* prior to this study, but were annotated to *P. texense* by the author.

Morphological data were collected from herbarium specimens. These are summarized in the taxonomic description below, and the characters critical for species identification are highlighted in the key to *Ptilimnium*. Phenology, habitat, and distribution were determined from the herbarium specimens and the accompanying label data and through field visits. Observations of root-budding (cormlet development) were made in the field and in the greenhouse.

HABITAT AND DISTRIBUTION

According to the USDA Plants Database, which treats *Ptilimnium texense* as a synonym of *P. costatum*, *P. costatum* occurs in 25 parishes in Louisiana and 13 counties in Texas (USDA, NRCS 2010). All specimens labeled as *P. costatum* examined by the author from these states are *P. texense* (10 parishes in Louisiana and 19 counties in Texas) or were misidentified collections of *P. capillaceum* or *P. nuttallii*. No specimens of *P. costatum* from Texas or Louisiana were found. Accessions of *P. costatum* cited from Dallas and Grayson counties (Mathias & Constance 1961; Diggs et al. 2006) could not be located. Both species grow in Arkansas but are allopatric, with *P. texense* occurring in two southern counties and *P. costatum* in three counties farther north (Fig. 4.1).

Ptilimnium texense is endemic to the West Gulf Coastal Plain (WGCP). This physiographic region encompasses much of eastern Texas, western Louisiana, southeastern Oklahoma, and southern Arkansas (Fig. 4.1). Approximately 3900 species occur in the WGCP, which has been divided into four ecoregions: Oak-Pine-Hickory Forest, Longleaf-Pine Forest, Post Oak Savanna, and Prairie (MacRoberts & MacRoberts 2003). *Ptilimnium texense* occurs primarily in the Oak-Pine-Hickory Forest and Longleaf-Pine Forest ecoregions. The primary habitats of *P. texense* are bogs, acid seeps, and wet pine savannas. Common associates include *Pinus palustris*, *Liquidambar styraciflua*, *Acer rubrum*, *Nyssa sylvatica*, *Magnolia virginiana*, *Sphagnum* spp., *Sarracenia alata*, *Oxypolis rigidior*, *Eryngium integrifolium*, *Eriocaulon* spp., *Osmunda regalis* and *O. cinnamomea*. *Ptilimnium texense* can be added to the list of 96 species endemic to the WGCP (MacRoberts et al. 2002). About 9% of WGCP endemics are found in bogs/wet pine savannas, which occupy 10% of the total area of the WGCP (MacRoberts et al. 2002).

DISCUSSION

Ptilimnium texense was proposed as a hybrid of *P. capillaceum* and *P. nuttallii* because earlier authors felt that *P. texense* combined characteristics of these species and possessed no stable characters of its own (Mathias & Constance 1945; Easterly 1957). Upon closer inspection of additional specimens, unique characters that distinguish *P. texense* were found. Contrary to Easterly's assessment, the fruits of *P. texense* and *P. nuttallii* are easily differentiated. The fruits of *P. texense* are longer than those of *P. nuttallii* (2.2–3.5 mm versus 1–1.9 mm) and the dorsal ribs are narrow and blunt versus thick and rounded. Vegetatively, *P. texense* differs from *P. capillaceum* in that its leaf segments are always 3–4-angled to subterete and the midveins are not visible, whereas the leaf segments of *P. capillaceum* are often flattened with the midveins apparent. Unique characters of *P. texense* not found in *P. capillaceum* or *P. nuttallii* include root system and habit. Both *P. capillaceum* and *P. nuttallii* have fibrous roots and are annuals, whereas *P. texense* has a distinctive rounded corm at the base of the stem and is a perennial. *Ptilimnium texense* has a more limited geographic range than either *P. capillaceum* or *P. nuttallii*, and more restrictive habitat requirements, as it requires acidic environments such as bogs, acid seeps, and wet pine savannas. Where the ranges of the three species overlap, *P. capillaceum* and *P. nuttallii* flower and fruit much earlier than *P. texense*. By the time *P. texense* begins to flower in August, the fruit of *P. capillaceum* and *P. nuttallii* have already matured and fallen from the plant. The fruit of *P. texense* matures between mid-October and late November.

Molecular data provided no evidence that *Ptilimnium texense* might be a hybrid. The results of studies utilizing nuclear and chloroplast DNA sequences were congruent (Feist &

Downie 2008; Feist & Downie unpublished data) and there were no site polymorphisms visible on the chromatograms of accessions identified as *P*. *texense*. Incongruence and site polymorphisms may both be signs of hybridization (Baldwin et al. 1995; Alvarez & Wendel 2003). Taken together with the lack of morphological evidence provided by earlier authors and the distinctive characters of *P. texense* presented in this study, the hybrid status of *P. texense* is not supported.

Ptilimnium texense was synonymized under *P. costatum* (Mathias & Constance 1961) and it is most closely related to this species (Feist & Downie 2008). These species share some morphological traits, such as root morphology and perennial habit, but are also distinct in a number of ways (Figs. 4.2–4.3). These differences are highlighted in the last two couplets of the key. A major difference distinguishing the species is their leaf morphology. As with *P. capillaceum*, leaf segments of *P. costatum* differ from those of *P. texense* by being flat with the midvein apparent. Other differences in leaf morphology include geometry and overall shape. The leaves of *P. costatum* are distinctive in that the primary leaf segments become progressively shorter from the leaf base to the apex and the blade apex is acute. In *P. texense,* the primary segments remain about the same length along the rachis and the blade apex is blunt or rounded. The leaves of *P. texense* are also stiffer and more three-dimensional than the leaves of *P. costatum* and the other *Ptilimnium* species. Style length also distinguishes *P. texense* and *P. costatum*. Although there can be some overlap, the styles of *P. costatum* are typically longer [(0.8–)1–2 mm] than those of *P. texense* [(0.3–)0.5–0.8(–1) mm]. There is no overlap, however, in the geographic range of these species and their habitats are different as well, with *P. texense* again requiring a more acidic environment. As mentioned above, both *P. costatum* and *P. texense* are perennials with corms. This structure is usually more elongate in *P. costatum* than in *P. texense* and may be slightly L-shaped. These characters have not been noted in previous studies of *Ptilimnium.* All species of *Ptilimnium* had been thought to be annuals with fibrous roots. *P. costatum* and *P. texense* do develop numerous adventitious roots which may obscure the corm, but both species develop buds from the corm (cormlets) that grow into new stems (Fig. 4.4).

As *Ptilimnium texense* has been purported to be a hybrid or not differentiated from *P. costatum*, it has not been included in keys to the genus. It clearly does not fit the description of any of the other species and this has lead to confusion when attempting to identify it. Of the 138 specimens identified as *P. texense* in the course of this study (not including the author's own collections), 22 were not initially identified to species or not identified as *Ptilimnium*, 34 were identified as *P. capillaceum*, 44 as *P. costatum*, 36 as *P. nuttallii*, and just two as *P. texense*. About one-third of these were annotated to *P.* × *texense*, *P. capillaceum* × *P. nuttallii,* or *P. costatum* by subsequent workers. This poor record of identification clearly demonstrates the need for a more inclusive and refined key. Previous keys to the genus have emphasized style length, number of segments of the involucral bracts, and whether the primary leaf segments are alternate or opposite on the rachis. Although these characters can be useful, there is variability and overlap among them and relying exclusively on these characters can lead to confusion. For this reason, additional characters have been utilized in the key below.

KEY TO PTILIMNIUM

1. Middle and upper petiole bases papillate on the abaxial surface; styles 0.1–0.2 mm long (on fruit), erect-ascending to spreading; calyx teeth < 0.2 mm, deltoid………***P. capillaceum*** (including ***P. ahlesii***[4])

1. Middle and upper petiole bases not papillate on the abaxial surface; styles (0.3–)0.4–2 mm long (on fruit), spreading to strongly recurved; calyx teeth > 0.2 mm, narrowly triangular.

  2. Mid-stem leaves with 2–4(–5) nodes along the rachis, primary leaf segments usually alternate or opposite at the nodes (not including at the apex of the petiole); individual leaf segments often much longer than the rachis; involucral bract segments 1(–3); roots fibrous, stem sometimes slightly thickened at the base but never forming a corm; styles (0.3–)0.4–0.6 mm long; fruit 1–1.9 mm long, dorsal ribs thick, rounded; flowering Apr–Jul, fruiting late May–early Aug…………………***P. nuttallii***

  2. Mid-stem leaves with (6–)7–16 nodes along the rachis, primary leaf segments whorled or verticillate at the major nodes; individual leaf segments shorter than the rachis (rarely as long as in *P. texense*); involucral bract segments (1–)3(–7); stem thickened and rounded at the base forming a globose or slightly elongate corm; styles (0.3–)0.5–2 mm long; fruit 2.2–4 mm long, dorsal ribs narrow, sharp-edged to blunt; flowering Jul–Oct, fruiting mid-Jul–Nov.

    3. Leaf segments flat (at least near the nodes but usually throughout), midvein visible; mid-stem leaves with (8–)10–16 nodes per rachis, longest primary segments with 9–22 secondary segments; leaf shape in outline deltoid or trullate (trowel-shaped), leaf segments getting progressively and noticeably shorter towards apex, apex acute; styles (0.8–)1–2 mm long, slightly spreading to

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[4] *Ptilimnium ahlesii* Weakley & Nesom (2004) is included under *P. capillaceum* in this key. Studies utilizing nrITS and cpDNA sequences found no molecular difference between these two taxa (Feist & Downie 2008; M.A. Feist et al., unpublished data). The morphological distinctiveness of *P. ahlesii* is also questioned by the author and is currently under review.

spreading; flowering Jul–Oct, fruiting mid-Jul–Oct; bottomland forest, swamps, streambanks, and pond margins……………………………………………………………………..……***P. costatum***

3. Leaf segments 3–4-angled to subterete, midvein not visible; mid-stem leaves with (6–)7–10 nodes per rachis, longest primary segments with 3–7(–8) secondary segments; leaf shape in outline oblong or oval, leaf segments not getting progressively and noticeably shorter towards apex, apex blunt; styles (0.3–)0.5–0.8(–1) mm long, spreading to strongly recurved; flowering Aug–Oct, fruiting Sep–Nov; seeps,bogs, and wet pine savannas………………………………………………...***P. texense***

TAXONOMIC DESCRIPTION

Ptilimnium texense J.M. Coult. & Rose, Contr. U.S. Natl. Herb. 12:445. 1909. Type: U.S.A. Texas. Harris Co.: near Hockley, Sep 1890, *F.W. Thurow s.n*. (holotype: US).

Plants perennial, 5–12 dm, roots from a small rounded corm at base of stem. **Leaves**: blades 3–12 cm, stiff, 3-dimensional, oblong to oval in outline, apex blunt, mid-stem leaves with (6–)7–10 nodes along the rachis, 3–5 primary leaf segments at the major nodes; leaf segments dissected, filiform to linear, 3–4-angled to subterete, midvein not visible, individual leaf segments shorter than (–as long as) the rachis, primary leaf segments not getting progressively and noticeably shorter towards apex, longest primary segments with 3–7(–8) secondary segments; petioles 0.5–3 cm, hyaline borders narrow, often inconspicuous and only visible at the distal and proximal ends, abaxial surface not papillate at the base. **Peduncle** 2–12 cm. **Umbels** 3–8(–10), rays 8–20(–25), 1–3.5(–4.5) cm, subequal to of varying lengths; involucral bracts linear, entire or 3-parted, rarely further divided. **Pedicels** 2–12 mm. **Flowers** 12–24 per umbellet; calyx teeth conspicuous, 0.2–0.4 mm, narrowly triangular; petals (0.6–)0.7–1.3 mm; styles (0.3–)0.5–0.8 (–1) mm, spreading to strongly recurved. **Schizocarps** 2.2–3.5 × 1.5–2.2 mm, ovate to orbicular, slightly compressed laterally, often maroon- or purple-tinged, dorsal ribs narrow, blunt, corky-thickened extension of the lateral ribs conspicuous; oil tubes dark brown. Flowering/fruiting Aug–Oct/Sep–Nov.

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REFERENCES

Álvarez, I. and J.F. Wendel. 2003. Ribosomal ITS sequences and plant phylogenetic inference. *Molecular Phylogenetics and Evolution* 29: 417–434.

Baldwin, B.G., M.J. Sanderson, J.M. Porter, M.F. Wojciechowski, C.S. Campbell, and M.J. Donoghue. 1995. The ITS region of nuclear ribosomal DNA: a valuable source of evidence on angiosperm phylogeny. *Annals of the Missouri Botanical Garden* 82: 247–277.

Correll, D.S. and M.C. Johnston. 1970. *Manual of the vascular flora of Texas*. Renner: Texas Research Foundation.

Correll, D.S. and H.B. Correll. 1972. *Aquatic and wetland plants of the southwestern United States*. Washington D.C.: Environmental Protection Agency.

Diggs, G.M., B.L. Lipscomb, and R.J. O'Kennon. 1999. Illustrated flora of north central Texas. *SIDA Botanical Miscellany* 16: 1–1626.

Diggs, G.M., B.L. Lipscomb, M.D. Reed, and R.J. O'Kennon. 2006. Illustrated flora of east Texas. *SIDA Botanical Miscellany* 26: 1–1594.

Coulter J.M. and J.N. Rose. 1909. Supplement to the monograph of the North American Umbelliferae. *Contributions from the U.S. National Herbarium* 12: 441–451.

Easterly, N.W. 1957. A morphological study of *Ptilimnium*. *Brittonia* 9: 136–145.

Feist, M.A. and S.R. Downie. 2008. A phylogenetic study of *Oxypolis* and *Ptilimnium* based on nuclear rDNA ITS sequences. *Systematic Botany* 33: 447–458.

Lundell, C.L. 1961. *Flora of Texas*. Renner: Texas Research Foundation.

MacRoberts, M.H. and B.R. MacRoberts. 2003. West Gulf Coastal Plain ecoregions. *SIDA Contributions to Botany* 20: 1247–1276.

MacRoberts, M.H., B.R. MacRoberts, B.A. Sorrie, and R.E. Evans. 2002. Endemism in the West Gulf Coastal Plain: importance of xeric habitats. *SIDA Contributions to Botany* 20: 767–280.

Mathias, M.E. and L. Constance. 1945. Umbelliferae. *North American Flora* 28B: 43–295.

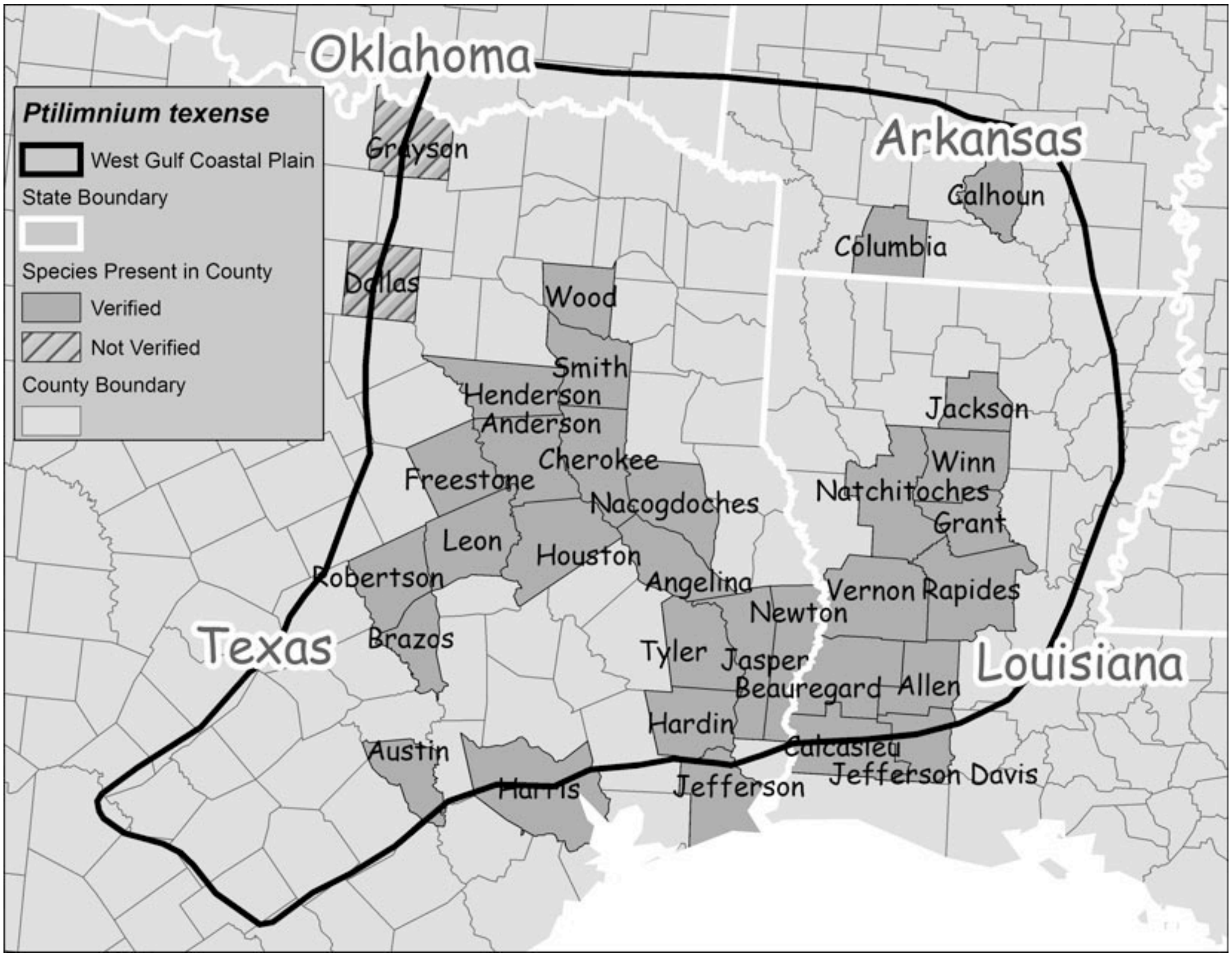
Mathias, M.E. and L. Constance. 1961. Umbelliferae. Pp. 263-329 in *Flora of Texas,* vol. 3, ed. C. L. Lundell. Renner: Texas Research Foundation.

USDA, NRCS. 2010. The PLANTS Database (http://plants.usda.gov, 1 April 2010). National Plant Data Center, Baton Rouge, LA 70874-4490, USA.

Weakley, A.S. and G.L. Nesom. 2004. A new species of *Ptilimnium* (Apiaceae) from the Atlantic coast. *SIDA Contributions to Botany* 21: 743–752.

FIGURES

Figure 4.1.[5] Distribution of *Ptilimnium texense* in Arkansas, Louisiana, and Texas.



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[5] Figure 4.1 was created by Diane Szafoni of the Illinois Natural History Survey.

Figure 4.2. Scanned image of *Ptilimnium texense* (LAF-46206) collected by D.S. Correll in 1969.

Figure 4.3. Scanned image of *Ptilimnium costatum* (ILLS-183385) collected by L.R. Phillippe in 1993.

Plants of Illinois

228 Apiaceae

Ptilmnium costatum (Ell.) Raf.

Illinois: Jackson County
T. 10S, R. 3W, N part NE1/4 NW1/4 NE1/4 Sect. 4
Shawnee National Forest, Oakwood Bottoms, Murphysboro Ranger District, Compartment 16. Gorham 7.5 minute topographic map.

Bottomland woods. White flowered herb.

Loy R. Phillippe 22870
20 August 1993

Illinois Natural History Survey (ILLS)

Figure 4.4. Corms with root-budding of *Ptilimnium costatum* (top) and *Ptilimnium texense* (bottom).

CHAPTER 5

REVISED GENERIC DELIMITATIONS FOR *OXYPOLIS* AND *PTILIMNIUM* (APIACEAE TRIBE OENANTHEAE) BASED ON COMPARATIVE FRUIT ANATOMY AND PHYLOGENETIC ANALYSIS OF NUCLEAR RDNA ITS AND CPDNA *TRNQ* AND *TRNK* SEQUENCE DATA[6]

Abstract: A phylogenetic study of *Oxypolis* and *Ptilimnium*, two small genera of tribe Oenantheae (Apiaceae, subfamily Apioideae), was carried out. Generic circumscriptions and infrageneric and infraspecific relationships were investigated through parsimony and Bayesian inference analyses of nuclear rDNA ITS and cpDNA *trnQ-5'rps16* and *3'rps16-5'trnK* intergenic spacer sequences. Fruit anatomical characters were examined and used in conjunction with leaf morphology to corroborate the results of the phylogenetic analyses. Each genus as currently delimited has both compound-leaved and rachis-leaved species. Results of the phylogenetic analyses show that neither *Oxypolis* nor *Ptilimnium* is monophyletic; each genus is split into two strongly supported clades that correspond to differences in leaf morphology within the groups. Fruit anatomical characters support these splits. The fruits of compound-leaved and rachis-leaved *Oxypolis* species differ in the number of commissural vittae per mericarp, the branching of the vittae, and the lignification of mericarp around the seed. The fruits of compound-leaved and rachis-leaved *Ptilimnium* species differ in the compression of the mericarps and the length of the wings relative to the vascular bundles. Based on the analyses of the molecular data and the corroboration of morphological and fruit anatomical data, new circumscriptions for the genera *Oxypolis* and *Ptilimnium* are formalized. The two polyphyletic genera (*Oxypolis* and *Ptilimnium*) are split, two genera (*Tiedemannia* and *Harperella*) are resurrected, and new combinations are made.

INTRODUCTION

Oxypolis Raf. and *Ptilimnium* Raf. are two small genera of tribe Oenantheae (Apiaceae, subfamily Apioideae). As currently circumscribed, the genus *Oxypolis* is comprised of seven species and the genus *Ptilimnium* six species. These names with taxonomic authorities are presented in Table 5.1. Most species of *Oxypolis* and *Ptilimnium* are endemic to North America,

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[6] This chapter is to be submitted to the journal *Taxon* and has the following co-authors: S.R. Downie, A.R. Magee, and Mei (Rebecca) Liu.

but each genus has one species (i.e., *O. filiformis*, *P. capillaceum*) with a range that extends into the West Indies (Brace 1929; Liogier & Martorell 2000). Each genus also has one species (i.e., *Oxypolis canbyi*, *Ptilimnium nodosum*) listed as federally endangered in the United States (U. S. Fish and Wildlife Service 1986, 1988). The genera *Oxypolis* and *Ptilimnium* share several ecological and morphological traits including glabrous leaves and stems, fascicled roots, globose to broadly ovate fruits, and a preference for wet habitats. In addition, two very different leaf morphologies are found within each genus. While most species of *Oxypolis* and *Ptilimnium* have compound leaves, as is typical in subfamily Apioideae, others share a unique leaf morphology known as rachis leaves. Rachis leaves are linear, terete, hollow, and septate and are equivalent to the rachis of a pinnately compound leaf in which the pinnae are not fully expressed. Instead, the pinnae are highly reduced and transformed into nodal appendages that function as hydathodes (Kaplan 1970). One other genus within tribe Oenantheae, *Lilaeopsis* Greene, has species with rachis leaves, but this genus has no compound-leaved species. *Cynosciadium* DC. and *Limnosciadium* Mathias & Constance, also of tribe Oenantheae, have rachis-like basal leaves (linear and septate, but flattened not hollow), but their cauline leaves are palmately and pinnately lobed, respectively. Rachis leaves are thought to be an adaptation to an aquatic or semi-aquatic habitat, and species of *Oxypolis* and *Ptilimnium* with rachis leaves (i.e., *O. canbyi*, *O. filiformis*, *O. greenmanii*, and *P. nodosum)* spend much of the growing season at least partially submerged.

The compound-leaved species of *Oxypolis* have pinnately or ternately compound leaves with pinnae that are generally somewhat broad (except for *O. ternata* in which they are long and narrow). Compound-leaved *Ptilimnium* species have finely dissected, pinnately decompound leaves with linear or filiform pinnae. Despite having radically different leaf morphologies from their compound-leaved congeners, the rachis-leaved *Oxypolis* and *Ptilimnium* species were placed in their respective genera based primarily on fruit morphology (Elliott 1817; Mathias 1936). Elliott (1817) placed the compound-leaved *Sium rigidius* L. (now *O. rigidior*) and the rachis-leaved *S. teretifolium* Elliott (now *O. filiformis*) in the same genus based on their shared features of the fruit, including their strong dorsal compression, number of dorsal ribs, and broad lateral wings. De Candolle (1829) created separate genera for the rachis-leaved and compound-leaved *Oxypolis* species (*Tiedemannia* and *Archemora*, respectively), but Coulter and Rose (1887; 1888) united them once again arguing that “no fruit character can be made to separate them, and the only distinction would have to be drawn from the leaves.” The rachis-leaved

Ptilimnium (then divided into three taxa) were originally placed in their own genus, *Harperella* Rose, but Mathias (1936) moved them into the genus *Ptilimnium* based on morphological similarities of the fruit, including the corky-thickened lateral ribs. Easterly (1957a), in his monograph of the genus *Ptilimnium*, agreed with Mathias stating that "the strikingly different vegetative character" of the leaves was not sufficient to warrant generic recognition for *Harperella*.

Traditional higher-level classifications within Apiaceae have relied heavily on fruit characters. In recent years, these classifications have not always held up to molecular systematic studies (Plunkett et al. 1996; Downie & Katz-Downie 1996; Downie et al. 1996; Downie et al. 1998; Downie et al. 2001). This is the result of a complex pattern of parallelisms and convergences of the fruit characters within the family (Plunkett et al. 1996; Downie et al. 1998; Lee et al. 2001; Liu et al. 2009). For example, characters such as dorsal flattening and wing formation have evolved in several independent lineages of Apiaceae, most likely as a dispersal mechanism (Theobald 1971; Downie et al. 2000c; Spalik & Downie 2001), and therefore cannot necessarily be taken as evidence of close relationship. This has brought the taxonomic value of fruit characters into question (Downie et al. 2001; Spalik & Downie 2001; Liu et al. 2006). Liu et al. (2006), however, are against abandoning the use of these characters altogether. They argue that "fruit anatomy, if studied carefully, can provide an excellent source of characters to test, support, and supplement findings based on molecular evidence."

In the past decade, tribe Oenantheae has been the subject of several studies utilizing DNA sequence data to examine phylogenetic relationships (Downie et al. 2004; Hardway et al. 2004; Lee & Downie 2006; Spalik et al. 2006; Downie et al. 2008; Feist & Downie 2008; Spalik et al. 2009). Results of these studies have shown that as many as five genera within the tribe are not monophyletic. Two of these studies examined the relationship of the rachis-leaved *Ptilimnium* and *Oxypolis* species to their compound-leaved congeners (Downie et al. 2008; Feist & Downie 2008). The first study was based solely on nrDNA ITS (ITS) sequences; the second incorporated both ITS and cpDNA *psbI*-5'*trnK* sequences but took a broader look at relationships within the whole tribe Oenantheae and did not thoroughly sample *Oxypolis* and *Ptilimnium*. The results of both studies agreed that *Oxypolis* and *Ptilimnium* as currently delimited are not monophyletic and should each be split into two genera. For each genus, the suggested split corresponds to the split between rachis-leaved and compound-leaved taxa.

Although these two previous studies suggested that neither *Oxypolis* nor *Ptilimnium* is monophyletic, nomenclatural changes were postponed until confirmation from additional data could be obtained. In this paper we present additional sequences from the chloroplast genome and combine these with ITS and cpDNA sequences from these earlier studies. We also examine an independent source of evidence, fruit anatomical data, to determine if it corroborates the molecular results. We then provide new circumscriptions for the genera *Oxypolis* and *Ptilimnium* based on the molecular (cpDNA and ITS sequences) and fruit anatomical data. The two polyphyletic genera (*Oxypolis* and *Ptilimnium*) are split, two genera (*Tiedemannia* and *Harperella*) are resurrected, and new combinations are made. Infrageneric and infraspecific relationships are also examined and our results are compared to former taxonomic treatments.

MATERIALS AND METHODS

Taxon Sampling and Outgroup Selection. In a study of tribe Oenantheae which included several species of *Oxypolis* and *Ptilimnium*, Downie et al. (2008) found that among the five noncoding loci they examined, the *trnQ*-5'*rps16* and 3'*rps16*-5'*trnK* intragenic spacers (hereafter, *trnQ* and *trnK*) were the most variable. Therefore these regions were used for this study. Complete sequences of the *trnQ* and *trnK* regions were obtained for 76 accessions; complete sequences of the nrDNA ITS region were obtained for 66 accessions (Appendix C). Sequences were obtained for all seven species of *Oxypolis* and six species of *Ptilimnium* (Table 5.1). Sequence data for one accession of the purported hybrid, *Oxypolis filiformis* × *greenmanii* were also included. All *Oxypolis* and *Ptilimnium* taxa were represented by multiple accessions to assess infraspecific variation. Two species of *Perideridia* Rchb. were chosen as outgroups (Appendix C). Previous phylogenetic studies which have included the *Oenanthe* clade or tribe Oenantheae (Plunkett et al. 1996; Downie et al. 1996; Downie et al. 1998; Downie et al. 2000b) have shown the genus *Perideridia* to be sister group to a clade comprising all other members of the tribe. The genera *Atrema* DC., *Cynosciadium*, *Daucosma* Engelm. & A. Gray ex A. Gray, *Lilaeopsis*, *Limnosciadium*, *Neogoezia* Hemsl., and *Trepocarpus* Nutt. ex DC. have allied with *Ptilimnium* and *Oxypolis* in previous studies and together make up what has become known as the North American Endemics (NAE) clade (Hardway et al. 2004; Downie et al. 2008). Accessions of these genera were included in the phylogenetic analyses to show their placements relative to *Oxypolis* and *Ptilimnium* (Appendix C). Nomenclature follows Kartesz (2010), except *Oxypolis ternata* which follows Feist (2009), *Atrema americanum* DC. (=*Bifora americana*

Benth. & Hook. f. ex S. Watson) which follows Hardway et al. (2004), and *Lilaeopsis* which follows Affolter (1985).

DNA Extraction, Purification, and Sequencing. For this study, *trnQ*, *trnK*, and ITS sequences were obtained for 55, 44, and 17 accessions, respectively. The remaining sequences used had already been published (Downie & Katz-Downie 1996; Downie et al. 2000a; Hardway et al. 2004; Downie et al. 2008; Feist & Downie 2008). The new sequences were generated according to the following methods. Leaf material was taken from either herbarium specimens or field-collected and silica-dried samples. DNA was isolated using a DNeasy Plant Mini Kit (Qiagen Inc., Valencia, California) according to the manufacturer's instructions. The entire nrDNA ITS region (ITS-1, 5.8S rDNA, and ITS-2) was amplified using primers 18S-ITS1-F (Spalik & Downie 2006) and C26A (Wen & Zimmer 1996) or primers 18S-for (Feist & Downie 2008) and C26A. The PCR amplification methods used are described elsewhere (Downie et al. 2000a). PCR products (templates) were purified using either a QIAquick Gel Extraction Kit or a QIAquick PCR Purification Kit (Qiagen Inc.) following manufacturer's instructions. For cpDNA, sequences were obtained for the *trnQ*$^{\text{(UUG)}}$-*rps16* 5' exon and *rps16* 3' exon-*trnK*$^{\text{(UUU)}}$ intergenic spacers using the primers trnQ, rps16-1R, rps16-2, and trnK (Downie & Katz-Downie 1996; Lee & Downie 2006; Downie et al. 2008). The ''rpl16'' program of Shaw et al. (2005) was used for the cpDNA regions because it is effective across a wide range of taxa and genomic regions (Shaw et al. 2007). PCR products were checked on 1% agarose gels and then purified according to the ExoSAP protocol of Werle et al. (1994) using 5 U of Exonuclease I (New England Biolabs, Ipswich, MA, USA) and 0.5 U of Shrimp Alkaline Phosphatase (Promega, Madison, WI, USA). Sequence reactions for all sequences were carried out using an ABI Prism Big Dye Terminator vers. 3.1 Ready Reaction Cycle Sequencing Kit (Applied Biosystems, Foster City, California). Sequence reaction products were visualized using an ABI 3730XL high-throughput DNA capillary sequencer at the Genetic Engineering Facility at the University of Illinois at Urbana-Champaign's Biotechnology Center. All newly acquired sequences used in this study have been deposited in GenBank (www.ncbi.nlm.nih.gov/genbank/).

Sequence Alignment and Phylogenetic Analysis. Sequences were aligned using Clustal X (Thompson et al. 1997) and manually adjusted as necessary using the alignment editor Bioedit (Hall 1999). For the *trnQ* and *trnK* datasets only, informative gaps were scored as additional binary characters according to the "simple indel coding" method of Simmons and Ochoterena

(2000). Indels were not scored for the ITS dataset, as they had been used in a previous study of the group (Feist & Downie 2008) and had not been useful. Three matrices of sequence data were constructed. The first included the aligned nucleotide data from the *trnQ* and *trnK* regions (cpDNA), the second included these data and the binary-coded indels (cpDNA/indels), and the third included the aligned nucleotide data from the *trnQ*, t*rnK*, and ITS regions (cpDNA/ITS). To facilitate analysis, identical sequences were represented by single terminals, except where identical sequences were from individuals from distinct geographic areas of interest (Table 5.2). The cpDNA and cpDNA/indels datasets included sequences of 74 accessions (65 terminals). The cpDNA/ITS data set included sequences of 66 accessions (63 terminals). Most of the ITS sequences used represented a subset of a larger ITS matrix of 147 accessions used in Feist & Downie (2008). Sequence characteristics were obtained for the ITS and cpDNA (*trnQ*/*trnK*) regions. Uncorrected pairwise nucleotide distances were calculated using the distance matrix option of PAUP* version 4.0b10 (Swofford 2003). Before combining the ITS and cpDNA datasets, the incongruence length difference test of Farris et al. (1995) was performed using the partition-homogeneity test in PAUP* to evaluate the extent of conflict between them. This test was executed with 100 replicate analyses, using the heuristic search option, simple stepwise addition of taxa, and TBR branch swapping; MaxTrees was set to 20,000. The aligned data matrices are available in TreeBASE (www.treebase.org/treebase-web/home.html).

Maximum parsimony (MP) analyses of the three data matrices were implemented in PAUP*. All characters were treated as unordered and all character transformations were weighted equally. Heuristic MP searches were replicated 10,000 times with random addition of taxa and the following options in effect: MULTREES, TBR branch swapping, gaps treated as missing data. Bootstrap (BS) analyses were done on all datasets to assess clade support. For the cpDNA and cpDNA/indels datasets, 100 bootstrap replicates were performed with 10 random sequence addition replicates; for the cpDNA/ITS dataset 1,000 bootstrap replicates were performed with 100 random sequence addition replicates. All BS analyses were performed with the heuristic search option, TBR branch swapping, and MULTREES options in effect; MaxTrees was set to 20,000 per replicate.

MrBayes version 3.1.2 (Huelsenbeck & Ronquist 2001) was used to conduct Bayesian inference (BI) analyses of the three datasets (cpDNA, cpDNA/indels, and cpDNA/ITS). Modeltest version 3.7 (Posada & Crandall 1998) was used to select the appropriate evolutionary models of nucleotide substitution for these three regions independently: *trnQ*, *trnK*, and ITS. The models that best fit the data, as selected by the Akaike Information Criteria (AIC) estimator, were used. For each dataset, two independent runs were conducted for 2,000,000 generations each with a sample frequency of 100. The log-likelihood scores of the sample points were plotted against generation time. Stationarity was determined to be reached when the log-likelihood values of the sample points achieved a stable equilibrium value. Convergence of the MCMC chains was also explored graphically using the online program AWTY (Wilgenbusch et al. 2004). For each dataset, trees sampled prior to stationarity were discarded as "burn-in" and a majority-rule consensus tree was constructed from the remaining trees to show the posterior probability values of all observed bipartitions.

Fruit Anatomy. Fruits from herbarium specimens were used in an anatomical study (Appendix D). Each of the seven *Oxypolis* and six *Ptilimnium* species were represented. In addition, accessions of the closely related *Cynosciadium digitatum*, *Limnosciadium pinnatum*, and *L. pumilum* were included. Fruits from one accession of each species were examined, except for *Oxypolis rigidior*, *O. occidentalis*, and *P. nodosum* where two, two, and three accessions were examined, respectively. The fruits were first rehydrated and then placed in FAA for a minimum of 24 h. These samples were subsequently treated according to a modification of the method of Feder & O'Brien (1968) for embedding in glycol methacrylate (GMA). Transverse sections of about 3 μm thick were made using a Porter-Blüm ultramicrotome and stained using the periodic acid Schiff/toluidine blue (PAS/TB) method of Feder & O'Brien (1968). To study the three-dimensional structure of the vittae, fruits from the same accessions used in the anatomical study, plus one or two additional accessions per species (Appendix D), were placed in boiling water and left to cool and soak for at least 24 h. Thereafter, the exocarp was removed while keeping the fruit submerged in water to prevent desiccation.

RESULTS

ITS Dataset. The ITS matrix had an aligned sequence length of 639 positions. One hundred and four positions were excluded from further analyses due to alignment ambiguities. The number of parsimony informative positions was 242 and the number of autapomorphic positions was 30. Uncorrected pairwise sequence divergence values for the ITS region across all 63 terminals was 24.23%. Considering just *Oxypolis* s.l. and *Ptilimnium* s.l., the maximum sequence divergence was 21.86% between *O. canbyi* (a rachis-leaved species) and *O. ternata* (a compound-leaved species). Phylogenetic analyses were not carried out on this dataset alone since these analyses had been performed on a larger ITS dataset previously (Feist & Downie 2008). Modeltest 3.7 selected the SYM+I+G model of evolution to be used in the BI anaysis of combined data.

cpDNA Datasets. The cpDNA dataset had an aligned sequence length of 2,813 positions. Four hundred and nine positions were excluded from further analyses due to alignment ambiguities. Of the remaining 2,404 aligned positions, 280 were parsimony informative and 88 were autapomorphic. MP analysis resulted in 23,229 trees of 473 steps each (CI = 0.854 and 0.824, with and without uninformative characters, respectively; RI = 0.964) (Fig. 5.1). The cpDNA/indel dataset with 63 binary-scored alignment gaps had a total of 343 parsimony informative characters. MP analysis resulted in 4,698 trees of 554 steps each (CI = 0.843 and 0.811, with and without uninformative characters, respectively; RI = 0.963) (Fig. 5.2). Modeltest 3.7 selected the GTR+G and GTR+I+G models for the *trnQ* and *trnK* regions, respectively, for use in the BI analysis.

The MP strict consensus tree and BI majority rule consensus tree (not shown) for the analyses of the cpDNA data matrix (without binary-scored indels) were congruent except that in the BI tree, all accessions of *Ptilimnium costatum* and all accessions of *Oxypolis rigidior* each formed weakly supported monophyletic groups (PP = 0.51 and PP = 0.54, respectively), whereas in the MP strict consensus tree, they did not. The addition of the binary-scored indels into the cpDNA matrix had only a minimal effect on the resulting tree topologies and support values. The only significant change was that all accessions of *P. costatum* were resolved as monophyletic in the cpDNA/indels MP and BI trees (BS = 81, PP = 0.89). Other species not resolved as monophyletic in the cpDNA and cpDNA/indels MP and BI trees were *P. ahlesii*, *P. capillaceum*, *O. filiformis*, *O. rigidior*, and *O. ternata*. *Ptilimnium ahlesii* formed a monophyletic group with *P. capillaceum* in both cpDNA analyses (BS = 99, PP = 1.00; BS = 100, PP = 1.00, without and with binary-coded indels, respectively), as did *O. ternata* with *O. rigidior* (BS = 78, PP = 1.00; BS = 92, PP = 1.00, without and with binary-coded indels, respectively).

The taxon *Oxypolis occidentalis* is divided into two strongly to moderately supported clades (Figs. 5.1–5.2). The two major clades of *O. occidentalis* consist of populations that are separated geographically and can be referred to as the North and South clades. The North Clade (BS = 92, PP = 1.00; BS = 88, PP = 1.00, without and with binary-coded indels, respectively) consists of individuals from populations from the Queen Charlotte Islands in British Columbia, the Cascade Mountains in Oregon, and the Cascade Range Foothills in northern California. The South Clade (BS = 68, PP = 0.96; BS = 70, PP = 0.98, without and with binary-coded indels, respectively) consists of individuals from populations in the Sierra Nevada, San Bernardino, White, and Inyo mountain ranges in California.

At the generic level, the MP and BI trees of the cpDNA and cpDNA/indels data matrices were wholly congruent. The genera *Ptilimnium* s.l. and *Oxypolis* s.l. were each not monophyletic. The genus *Ptilimnium* s.l. was split between two clades, Clade 1 (*Ptilimnium*) containing the compound-leaved species (i.e., *P. ahlesii, P. capillaceum*, *P. costatum*, *P. nuttallii*, and *P. texense*) and Clade 2 (*Harperella*) containing the single rachis-leaved species (i.e., *P. nodosum*). The genus *Oxypolis* s.l. was also split between two clades. Clade 3 (*Tiedemannia*), which is sister to the compound-leaved *Ptilimnium*, was comprised of the rachis-leaved species (i.e., *O. canbyi*, *O. filiformis*, and *O. greenmanii*). Clade 4 (*Oxypolis*), which is quite distant in the tree, was comprised of the compound-leaved species (i.e., *O. fendleri*, *O. occidentalis*, *O. rigidior*, and *O. ternata*). Clades 1, 2, and 3 were strongly supported, whereas Clade 4, the compound-leaved *Oxypolis*, had weak support (BS = 62, PP = 0.95); this support was higher when the binary-coded indels were added (BS = 83, PP = 0.99).

In previous analyses based on ITS sequences (Feist & Downie 2008), the evolutionary relationships among the following groups were not resolved: Clade 1 (*Ptilimnium*), Clade 2 (*Harperella*), Clade 3 (*Tiedemannia*), *Limnosciadium*, and *Cynosciadium*. These groups formed what was essentially a polytomy (Fig. 1 in Feist & Downie 2008). The results of the cpDNA analyses presented herein, however, strongly support the sister relationship of Clade 1 (*Ptilimnium*) and Clade 3 (*Tiedemannia*) (BS = 99, PP = 1.00, for both data matrices). Together these two groups form a strongly supported sister relationship with Clade 2 (*Harperella*) (BS = 98, PP = 1.00; BS = 90, PP = 0.99, without and with binary-coded indels, respectively), followed by the successively basal sister groups *Limnosciadium* (BS = 72, PP = 0.88; BS = 67, PP = 0.85, without and with binary-coded indels, respectively) and *Cynosciadium* (BS = 100, PP = 1.00, for both data matrices).

Uncorrected pairwise sequence divergence values for the cpDNA region across all 65 terminals was 5.56%. Considering only *Oxypolis* s.l. and *Ptilimnium* s.l., the maximum sequence divergence was 3.82% between *P. nodosum* (rachis leaves) and *O. ternata* (compound leaves).

Two new accessions of *Daucosma laciniata* Engelm. & A. Gray were used in this study. As a result, the placement of *Daucosma* differs from that found in previous studies where the accession *D. laciniata* 2397, a misidentified specimen of *Limnosciadium pinnatum* (DC.) Mathias & Constance, was used (Hardway et al. 2004, Downie et al. 2008, Feist & Downie 2008). In this study, the two accessions of *D. laciniata* are monophyletic and are sister to a clade formed by *Atrema americana* and *Trepocarpus aethusae* Nutt. (BS = 99, PP = 1.00, BS = 87, PP = 1.00, without and with binary-coded indels, respectively).

Combined Dataset (cpDNA/ITS). The results of the partition homogeneity test for 63 terminals common to both the cpDNA and ITS datasets revealed that these loci do not yield significantly different phylogenetic estimates (ILD probability value = 0.21). Therefore, these datasets were combined for simultaneous analysis. The combined cpDNA (without binary-scored indels) and ITS data matrix (cpDNA/ITS) had an aligned sequence length of 3,452 positions. Five hundred and thirteen positions were excluded from further analyses due to alignment ambiguities. Of the remaining 2,939 aligned positions, 522 were parsimony informative and 118 were autapomorphic. Adding the cpDNA *trnQ* and *trnK* sequences to the ITS matrix more than doubled the number of parsimony informative characters from the previous study by Feist & Downie (2008). MP analysis resulted in 32 trees of 1,184 steps each (CI = 0.689 and 0.634, with and without uninformative characters, respectively; RI = 0.919).

The BI majority rule consensus tree is presented in Fig. 5.3 with branch lengths. The BI tree is consistent with the MP strict consensus tree (not shown) except at the nodes where an * is given to indicate that the BS value was < 50%. As in the cpDNA analyses, *Ptilimnium ahlesii* and *P. capillaceum* are each not resolved as monophyletic, but together they form a strongly supported monophyletic group (BS = 100, PP = 1.00). *Oxypolis filiformis* is not monophyletic, but it forms a monophyletic group with *O. greenmanii* and their purported hybrid (BS = 100, PP = 1.00). The North and South clades of *O. occidentalis* are again apparent and strongly supported (BS=100, PP=1.00, for both clades). *Ptilimnium costatum* is resolved as monophyletic as it was in the cpDNA/indel strict consensus tree (BS = 94, PP = 1.00). In contrast to the cpDNA analyses, *O. ternata* and *O. rigidior* are each resolved as monophyletic with strong support (BS = 100, PP = 1.00; BS = 99, PP = 1.00, respectively).

At the generic level, *Oxypolis* s.l. and *Ptilimnium* s.l. again are shown not to be monophyletic. The sister relationship of Clade 1 (*Ptilimnium*) and Clade 3 (*Tiedemannia*) continues to be strongly supported (BS = 96, PP = 1.00), while the relationships of Clade 2 (*Harperella*), *Limnosciadium* and *Cynosciadium* to these groups and to each other are less well-supported. Clade 4 (*Oxypolis*) is strongly supported (BS = 99; PP = 1.00). As in the cpDNA trees (Figs. 5.1–5.2), *Daucosma laciniata* is monophyletic and is sister to a clade formed by *Atrema americana* and *Trepocarpus aethusae* (BS = 96, PP = 1.00).

Uncorrected pairwise sequence divergence values for the combined cpDNA/ITS dataset across all 63 terminals was 9.74% between *Oxypolis canbyi* and *Daucosma laciniata*. Considering just *Oxypolis* s.l. and *Ptilimnium* s.l., maximum sequence divergence was 7.62%, between *O. canbyi* (a rachis-leaved species) and *O. ternata* (a compound-leaved species). Maximum sequence divergence among compound-leaved *Oxypolis* species was 2.40%, whereas among rachis-leaved *Oxypolis* it was 2.99%. Maximum sequence divergence among *Ptilimnium* s.l. species was 6.22%; however, it was just 1.43% among compound-leaved *Ptilimnium* species and just 0.19% among the rachis-leaved *Ptilimnium*. All species of *Ptilimnium* s.l. and *Oxypolis* s.l. showed intraspecific variation, except for *P. ahlesii* and *P. capillaceum* which had sequences that were identical to one another.

Fruit Anatomy. Based on fruit anatomy, the species previously recognized within *Oxypolis* s.l. and *Ptilimnium* s.l. can be separated into four groups corresponding to Clades 1–4 recovered in the molecular analyses. All the species have homomericarpic fruits with a very broad commissure that extends over the full width of the mericarp. The mericarps are generally dorsally compressed with narrow to broadly winged marginal ribs, except those of *P. nodosum* which are prominently isodiametric and distinctly ribbed (Fig. 5.4A). The compound-leaved species of *Ptilimnium* (i.e., *P. ahlesii*, *P. capillaceum*, *P. costatum*, *P. nuttallii*, and *P. texense)* have fruit with dorsally compressed mericarps and narrow, thick narrowly winged marginal ribs that extend only slightly beyond the marginal vascular bundles (Fig. 5.4B–F). The fruit from the species of *Ptilimnium* s.l. (Fig. 5.4A–F) are distinguished from those of *Oxypolis* s.l. (Fig. 5.4G–L; *O. ternata*, not shown), as well as *Cynosciadium* (Fig. 5.4M) and *Limnosciadium* (Fig. 5.4N–

O), by the presence of prominent square or somewhat elongated cells external to the vittae (not shown); a character also reported in the genus *Dasispermum* Raf. (Magee et al. 2009, 2010). The fruit of the species of *Oxypolis* s.l. are distinguished from the others by the very broad, thin marginal wings and usually smaller, less lignified vascular bundles. While most of the species studied have a lignified layer of mesocarp cells surrounding the endocarp, this character is conspicuously absent in the compound-leaved species of *Oxypolis* (i.e., *O. fendleri*, *O. occidentalis*, *O. rigidior*, and *O. ternata*; Fig. 5.4J–L). This latter group is easily distinguished from all the species studied by the presence of four to eight, often branching commissural vittae (Fig. 5.5A–D). They are distinguished furthermore from the rachis-leaved species of *Oxypolis* (i.e., O. *canbyi*, O. *filiformis*, and *O. greenmanii*) in that the vittae are smaller than or equal in size to the vascular bundles. In the rachis-leaved *Oxypolis* species the vittae are distinctly larger than the vascular bundles. The fruit of the closely related genera *Limnosciadium* (Fig. 5.4N–O) and *Cynosciadium* (Fig. 5.4M) can be distinguished from both *Oxypolis* s.l. and *Ptilimnium* s.l. by the presence of a lignified commissural keel, and in *Limnosciadium* by the sclerification of the mesocarp between the vascular bundles so that they appear continuous.

*O*xypolis *canbyi* (a rachis-leaved species) has a unique wing type not found in any of the other species examined. In *O. canbyi*, the marginal wing is formed through the expansion of the mesocarp between the vascular bundle and the endocarp so that the vascular bundle is located near the wing tip to form a pseudo-marginal wing (Fig. 5.4I). Also, as mentioned by Tucker et al. (1983), a sclerified band of mesocarp cells is formed between the vascular bundle and the endocarp (Fig. 5.4I). In the other species examined, the wing is formed through the expansion of the mesocarp beyond the vascular bundle so that the vascular bundle is located at the base of the wing (Fig. 5.4A–F, J–O) and a sclerified band of mesocarp cells is not present between the vascular bundle and the endocarp. In *Ptilimnium* s.l., *Cynosciadium*, and *Limnosciadium*, the true marginal wing remains narrow and extends slightly beyond the marginal vascular bundle (Fig. 5.4A–F, M–O). In the compound-leaved *Oxypolis*, *O. filiformis*, and *O. greenmanii*, the true marginal wing extends significantly beyond the vascular bundle (Fig. 5.4G–H, J–M).

DISCUSSION

***Ptilimnium*/*Harperella*.** Morphological and molecular results from this study confirm what was proposed in previous studies (Feist & Downie 2008; Downie et al. 2008) that the genus *Ptilimnium* is not monophyletic. Differences in leaf morphology, fruit anatomy, and DNA sequence data, as well as reproductive strategy and chromosome number, support removing *P. nodosum* from the genus. *Ptilimnium nodosum* has rachis-leaves whereas the other members of the genus have pinnately decompound leaves that are finely dissected. The fruits of *P. nodosum* are isodiametric and prominently five ribbed (Fig. 5.4A), whereas the fruits of the compound-leaved-*Ptilimnium* species are dorsally compressed and have thick, narrowly winged marginal ribs that extend slightly beyond the vascular bundles (Fig. 5.4B–F). *Ptilimnium nodosum* can proliferate extensively through vegetative reproduction. Vegetative shoots are produced at the nodes of decumbent flowering stems and develop into individual plantlets when the flowering stalks die back in winter (Marcinko & Randall 2008). This method of reproduction has not been observed in the compound-leaved *Ptilimnium*. Furthermore, the chromosome number for *P. nodosum* is n = 6, whereas chromosome numbers for the compound-leaved species are n = 16 (*P. costatum*), n = 7 (*P. capillaceum* and *P. nuttallii*), and n = 8 or n = 14 (*P. capillaceum*) (Easterly 1957a, Constance et al. 1976, Weakley & Nesom 2004). Maximum pairwise sequence divergence (from the combined cpDNA/ITS dataset) between *P. nodosum* and the compound-leaved *Ptilimnium* species is 6.22%, whereas it is just 1.43% among all compound-leaved species of *Ptilimnium* and 0.19% among the accessions of *P. nodosum*. In addition, the compound-leaved *Ptilimnium* are more closely related to the rachis-leaved *Oxypolis*, with which they form a strongly supported sister group, then they are to *P. nodosum*.

The type for the genus *Ptilimnium* is *P. capillaceum*. The taxa *P. ahlesii*, *P. costatum*, *P. nuttallii*, and *P. texense* form a monophyletic group with *P. capillaceum* in the phylogenetic analyses and share a common fruit and leaf structure. These taxa should therefore remain together in the genus *Ptilimnium*. Prior to 1936 (Mathias 1936), *P. nodosum* was recognized as belonging to the genus *Harperella* Rose. Three species of *Harperella* were recognized (*H. nodosa* Rose, *H. fluviatilis* Rose, and *H. vivipara* Rose). Easterly (1957b) synonymized *P. viviparum* (Rose) Mathias with P. *fluviatile* (Rose) Mathias based on their shared habitat type, phenology, and lack of clear morphological differences. Kral (1981) further grouped the taxa and included *P. fluviatile* and *P. viviparum* within *P. nodosum* s.l. Although results from the ITS analyses (Feist & Downie 2008) showed some geographic separation of populations that conformed to these previous delimitations, the addition of the *trnQ* and *trnK* data did not support these relationships. The ability of *P. nodosum* s.l. to root at the nodes and produce individual plantlets (as described above) had been used as a character to distinguish *P. fluviatile* from *P.*

nodosum s.s. This ability, however, has been observed in populations previously attributed to *P. nodosum* s.s. and in populations previously attributed to *P. fluviatile* and, therefore, cannot be used as a character to separate these taxa. As we have found no consistent molecular or morphological evidence to suggest otherwise, the authors agree with the assessment of Kral (1981) that these three taxa should be recognized as one species. We propose the reinstatement of the genus *Harperella* Rose with the single species *H. nodosa* Rose, including *H. fluviatilis* and *H. vivipara* as taxonomic synonyms.

The results of this study support the recent reinstatement of the taxon *Ptilimnium texense* (Feist 2010). In the combined cpDNA/ITS analyses, *P. texense* and *P. costatum* are sister to one another but form separate strongly supported clades. The separation of *P. ahlesii* from *P. capillaceum* (Weakley & Nesom 2004), however, is not supported. In this study and in all previous analyses where these two taxa have been included (Downie at al. 2008; Feist & Downie 2008), *P. ahlesii* and *P. capillaceum* always form a strongly supported monophyletic group, but the two taxa are never separated. DNA sequences for both accessions of *P. ahlesii* used in this study were identical to sequences of accessions of *P. capillaceum*. In addition, in a study conducted during the writing of the treatment of the genus for the *Flora of North America* (Feist, unpublished data), the morphological characters used to separate the two taxa were found to be inconsistent when specimens from across the range of *P. capillaceum* were examined. There was much overlap found with the characters that were used to separate *P. ahlesii* and *P. capillaceum*, such as flowering and fruiting times, fruits size, and number of flowers per umbellet. Therefore, the authors treat *P. ahlesii* herein as a synonym of *P. capillaceum*.

***Oxypolis*/*Tiedemannia*.** Morphological and molecular results from this study confirm what was proposed in previous studies (Downie et al. 2008; Feist & Downie 2008) that the genus *Oxypolis* is not monophyletic. As with *Ptilimnium*, differences in leaf morphology, fruit anatomy, and DNA sequence data support splitting the genus *Oxypolis* into two genera. *Oxypolis canbyi, O. filiformis,* and *O. greenmanii* have rachis-leaves whereas the other members of the genus have pinnately or palmately compound leaves. Although the fruits of the compound-leaved and rachis-leaved *Oxypolis* species are superficially similar in that they are all prominently dorsally compressed and have broadly winged marginal ribs, they can readily be distinguished anatomically. The mesocarp is lignified around the seed of the rachis-leaved *Oxypolis* species*,* but not of the compound-leaved species. The vittae are larger than the vascular bundles in the rachis-leaved taxa, but smaller than or equal to the vascular bundles in the compound-leaved species. The rachis-leaved *Oxypolis* taxa have four vallecular vittae and two commissural vittae, whereas the compound-leaved species have four vallecular vittae and four to eight commissural vittae, the latter often branching. Maximum pairwise sequence divergence (from the combined cpDNA/ITS dataset) between the rachis-leaved and compound-leaved *Oxypolis* species is 7.62%, whereas it is just 2.40% among all compound-leaved species of *Oxypolis* and 2.99% among the rachis-leaved *Oxypolis*. The clade formed by the rachis-leaved *Oxypolis* (Clade 3) is quite distant from the compound-leaved *Oxypolis* clade (Clade 4). In fact, the rachis-leaved *Oxypolis* taxa (Clade 3) are more closely related to all of the other genera within the NAE clade (i.e., *Ptilimnium*, *Limnosciadium*, *Cynosciadium*, *Lilaeopsis*, *Atrema*, *Trepocarpus*, *Daucosma*, and *Neogoezia*) than they are to the compound-leaved *Oxypolis* species (Clade 4). The chromosome numbers for the rachis-leaved *Oxypolis* taxa are all n = 14, whereas the chromosome numbers for the compound-leaved species are n = 16 or n = 18 (Bell & Constance 1957; Bell & Constance 1960; Crawford & Hartmen 1972; Tucker et al. 1983; Pimenov et al. 2003).

The type of the genus *Oxypolis* is *O. rigidior*. *Oxypolis rigidior* forms a monophyletic group with the other compound-leaved *Oxypolis* (i.e., *O. fendleri*, *O. occidentalis*, and *O. ternata*). We propose to split the genus *Oxypolis* into two genera conforming to the compound-leaved and rachis-leaved clades. In 1829 de Candolle created the genus *Tiedemannia* (de Candolle 1829). He believed that the taxon *Oenanthe teretifolia* Muhl. (a synonym of *Oxypolis filiformis*) was different enough from the compound-leaved members of *Oxypolis* to place it in its own genus. We agree with this assessment and propose the reinstatement of the genus *Tiedemannia* to accommodate the three rachis-leaved taxa, *O. canbyi, O. filiformis,* and *O. greenmanii*.

Furthermore, we accept the conclusion of Judd (1982) that the taxon *Oxypolis greenmanii* is a subspecies of *O. filiformis* (i.e., *O. filiformis* subsp. *greenmanii* (Mathias & Constance) Judd). Although at first glance, *O. greenmanii* appears to be strikingly different from *O. filiformis*, with its larger stature and maroon-colored flowers and fruits, many intermediate populations exist which completely bridge the morphological gap between the two taxa (Judd 1982). In addition, *O. filiformis* and *O. greenmanii* share the same chromosome number and flowering phenology, and when populations of the two do come into contact, they produce highly fertile offspring

(Judd 1982). Furthermore, DNA sequence data provide no support for recognizing the two as distinct species. Maximum pairwise sequence divergence between *O. filiformis* and *O. canbyi* is 2.99%, whereas maximum pairwise sequence divergence between *O. filiformis* and *O. greenmanii* is just 0.11%.

Finally, the two major clades of *Oxypolis occidentalis* that were seen in previous analyses based on ITS sequence data (Feist & Downie 2008) are again recovered in all analyses in this study. The cpDNA sequence data presented herein support the findings of the ITS data alone. A North Clade and a South Clade of *O. occidentalis* are recovered and strongly supported. Our results suggest that populations of *O. occidentalis* from the Queen Charlotte Islands, the Cascade Mountains of Oregon, and the Cascade Range Foothills in northern California are quite different from those of the Sierra Nevada and the other more southern mountain ranges of California (South Clade). The maximum sequence divergence among the North Clade is 0.24% and among the South Clade 0.32%, whereas the maximum sequence divergence between the North and South Clades is 1.49%. This is greater than the maximum pairwise sequence divergence between *O. rigidior* and *O. ternata* (1.31%). The populations represented by the South Clade are within a geographic region known as the California Floristic Province, which harbors more endemic plant and animal taxa and more identifiable subspecies than any other area of comparable size in North America (Calsbeek et al. 2003). Populations from this area could represent a new taxon and another example of a California Floristic Province endemic.

There is a major disjunction between the populations of *Oxypolis occidentalis* that are represented in the North Clade. The northernmost populations of *O. occidentalis* in Oregon are approximately 1400 km from the populations on the Queen Charlotte Islands (Cheney & Marr 2007). The Queen Charlotte Islands, located approximately 80 km off the west coast of British Columbia, are an intriguing geographic area. It has been proposed that during the last glacial maximum (ca. 15,000 yrs ago), when glaciers covered much of present-day British Columbia and extended into present-day Washington State, much of the Queen Charlotte Islands remained ice-free (Heusser 1960; Lacourse et al. 2005) and provided a refugium to plants and animals living there. The glacial refugium hypothesis may explain why *O. occidentalis* occurs on these islands and their highly disjunct geographic distribution. The distribution of this species might have once extended from Oregon to British Columbia with intervening populations being wiped out by glaciers. The morphology and phylogeography of *O. occidentalis* is currently being studied to confirm the taxonomic status of these plants.

TAXONOMIC TREATMENT

I. ***Harperella*** Rose, Proc. Biol. Soc. Wash. 19: 96. 1906 – Type: *Harperia nodosa* Rose

1.1. ***Harperella nodosa*** Rose. Biol. Soc. Wash. 19: 96. 1906 ≡ *Harperia nodosa* Rose, Proc. U.S. Nat. Mus. 29: 441. 1905, nom. illeg. ≡ *Carum nodosum* (Rose) K.-Pol., Bull. Soc. Nat. Mosc. II. 29: 199. 1916. ≡ *Ptilimnium nodosum* (Rose) Mathias, Brittonia 2: 244. 1936 – Type: U.S.A., Georgia, Schley County, *R.M. Harper 1411* (holotype: US 514914!).

= *Harperella fluviatilis* Rose, Contr. U.S. Na t. Herb. 13: 290. 1911. ≡ *Ptilimnium fluviatilis* (Rose) Mathias, Brittonia 2: 244. 1936. – Type: U.S.A., Alabama, Dekalb County, *R.M. Harper 8* (holotype: US 51421!).

= *Harperella vivipara* Rose, Contr. U.S. Nat. Herb. 13: 290. 1911. ≡ *Carum viviparum* (Rose) K.-Pol., Bull. Soc. Nat. Mosc. II. 29: 199. 1916. ≡ *Ptilimnium viviparum* (Rose) Mathias, Brittonia 2: 244. 1936. – Type: U.S.A., Maryland, *J. N. Rose s.n.* (holotype: US 640627!).

II. ***Tiedemannia*** DC., Coll. Mem. 5: 51. 1829 – Type: *T. teretifolia* DC.

2.1. ***Tiedemannia canbyi*** (J.M. Coult. & Rose) Feist & S.R. Downie **comb. nov.** ≡ *Oxypolis filiformis* var. *canbyi* J.M. Coult. & Rose, Contr. U.S. Nat. Herb. 7:193. 1900. ≡ *Oxypolis canbyi* (J.M. Coult. & Rose) Fernald, Rhodora 41:139. 1939. – Type: U.S.A., Delaware, *Canby s.n.* (holotype: US 280510!).

2.2. ***Tiedemannia filiformis*** (Walter) Feist & S.R. Downie **comb. nov.** ≡ *Oenanthe filiformis* Walter, Fl. Car. 113. 1788. ≡ *Oxypolis filiformis* (Walter) Britton, Mem. Torrey Club 5: 239. 1894 ≡ – Type: U.S.A., South Carolina, Berkeley County, *Porcher s.n.* (neotype, designated by A.O. Tucker et al., Syst. Bot. 8: 300. 1983: BM; isoneotypes: CITA, DOV).

= *Oenanthe carolinensis* Pers., Syn. Pl. 1:318. 1805, nom. illeg. ≡ *Oxypolis caroliniana* Raf., Bull. Bot. Seringe 218. 1830, nom. illeg.

= *Oenanthe teretifolia* Muhl., Cat. 32. 1813. nom. illeg. ≡ *Sium teretifolium* Elliott, Sketch Bot. S. Carolina 1: 354. 1817, nom. illeg. ≡ *Tiedemannia teretifolia* DC., Coll. Mem. 5: 81. 1829, nom. illeg. ≡ *Peucedanum teretifolium* Wood, Bot. & Fl. 136. 1870, nom. illeg.

= *Tiedemannia bakeri* H. Wolff ex Urb., Symb. Ant. 5: 452. 1908. ≡ *Oxypolis bakeri* (H. Wolff ex Urb.) Britton & P. Wilson ex Bracelin, Torreya 29: 16. 1929 – Type: Cuba, Havana, *Baker & Wilson 2215* (holotype: location unknown).

2.2.1. *Tiedemannia filiformis* (Walter) Feist & S.R. Downie subsp. ***filiformis***

2.2.2. *Tiedemannia filiformis* subsp**. *greenmannii*** (Mathias & Constance) Feist & S.R. Downie **comb. nov.** ≡ *Oxypolis greenmanii* Mathias & Constance, Bull. Torrey Club 69: 152. 1942. ≡ *Oxypolis filiformis* ssp. *greenmanii* (Mathias & Constance) Judd, Rhodora 84: 277. 1982 – Type: U.S.A., Florida, Gulf County, *A.W. Chapman s.n.* (holotype: MO 787696!).

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REFERENCES

Affolter, J.M. 1985. A monograph of the genus *Lilaeopsis* (Umbelliferae). *Systematic Botany Monographs* 6: 1–140.

Bell, C.R. and L. Constance. 1957. Chromosome numbers in Umbelliferae. *American Journal of Botany* 44: 565–572.

Bell, C.R. and L. Constance. 1960. Chromosome numbers in Umbelliferae II. *American Journal of Botany* 47: 24–32.

Brace, L.J.K. 1929. Notes on the occurrence of *Oxypolis filiformis* in the Bahamas. *Torreya* 1: 16–17.

Calsbeek, R., J.N. Thompson, and J.E. Richardson. 2003. Patterns of molecular evolution and diversification in a biodiversity hotspot: the California Floristic Province. *Molecular Ecology* 12: 1021–1029.

Candolle, A.P. 1829. *Memoire sur la Famille des Ombelliferes*. Paris: Treuttel et Würtz.

Cheney, M. and K.L. Marr. 2007. Cowbane, *Oxypolis occidentalis*, a new native vascular plant species for the Queen Charlotte Islands, British Columbia. *Canadian Field-Naturalist* 121:421–422.

Constance, L., T.-I . Chuang, and C.R. Bell. 1976. Chromosome numbers in Umbelliferae V. *American Journal of Botany* 63: 608–625.

Coulter J.M. and J.N. Rose. 1887. Notes on Umbelliferae of the E. United States III. *Botanical Gazette* 12: 73–76

Coulter, J.M. and J.N. Rose. 1888. *Revision of North American Umbelliferae.* Crawfordsville, Indiana: Wabash College.

Crawford, D.J. and R.L. Hartman. 1972. Chromosome numbers and taxonomic notes for Rocky Mountain Umbelliferae. *American Journal of Botany* 59: 386–392.

Downie, S.R. and D.S. Katz-Downie. 1996. A molecular phylogeny of Apiaceae subfamily Apioideae: evidence from nuclear ribosomal DNA internal transcribed spacer sequences. *American Journal of Botany* 83: 234–251.

Downie, S.R., D.S. Katz-Downie, and K.-J. Cho. 1996. Phylogentic analysis of Apiaceae subfamily Apioideae using using nucleotide sequences from the chloroplast *rpoC1* intron. *Molecular Phylogenetics and Evolution* 6: 1–18.

Downie, S.R., S. Ramanath, D.S. Katz-Downie, and E. Llanas. 1998. Molecular systematics of Apiaceae subfamily Apioideae: phylogenetic analyses of nuclear ribosomal DNA internal transcribed spacer and plastid *rpoC1* intron sequences. *American Journal of Botany* 85: 563–591.

Downie, S.R., D.S. Katz-Downie, and K. Spalik. 2000a. A phylogeny of Apiaceae tribe Scandiceae: evidence from nuclear ribosomal DNA internal transcribed spacer sequences. *American Journal of Botany* 87: 76–95.

Downie, S.R., D.S. Katz-Downie, and M.F. Watson. 2000b. A phylogeny of the flowering plant family Apiaceae based on chloroplast DNA *rpl16* and *rpoC1* intron sequences: towards a suprageneric classification of subfamily Apioideae. *American Journal of Botany* 87: 273–292.

Downie, S.R., M.F. Watson, K. Spalik, and D.S. Katz-Downie. 2000c. Molecular systematics of Old World Apioideae (Apiaceae): relationships among some members of tribe *Peucedaneae* sensu lato, the placement of several island-endemic species, and resolution within the apioid superclade. *Canadian Journal of Botany* 78: 506–528.

Downie, S.R., G.M. Plunkett, M.F. Watson, K. Spalik, D.S. Katz-Downie, C.M. Valiejo-Roman, E.I. Terentieva, A.V. Troitsky, B.-Y. Lee, J. Lahham, and A. El-Oqlah. 2001. Tribes and clades within Apiaceae subfamily Apioideae: the contribution of molecular data. *Edinburgh Journal of Botany* 58: 301–330.

Downie, S.R., F.-J. Sun, D.S. Katz-Downie, and G.J. Colletti. 2004. A phylogenetic study of *Perideridia* (Apiaceae) based on nuclear ribosomal DNA ITS sequences. *Systematic Botany* 29: 737–751.

Downie, S.R., D.S. Katz-Downie, F.-J. Sun, and C.-S. Lee. 2008. Phylogeny and biogeography of Apiaceae tribe Oenantheae inferred from nuclear rDNA ITS and cpDNA *psbI-5'trnK*$^{(UUU)}$ sequences, with emphasis on the North American Endemics clade. *Botany* 86: 1039–1064.

Easterly, N.W. 1957a. A morphological study of the genus *Ptilimnium*. Dissertation. Morgantown, West Virginia: University of West Virginia.

Easterly, N.W. 1957b. A morphological study of *Ptilimnium*. *Brittonia* 9: 136–145.

Elliott, S. 1817. *A sketch of the botany of South-Carolina and Georgia.* Charleston: J.R. Schenck.

Farris, J.S., M. Källersjö, A.G. Kluge, and C. Bult. 1995. Constructing a significance test for incongruence. *Systematic Biology* 44: 570–572.

Feder, N. and T.P. O'Brien. 1968. Plant microtechnique: Some principles and new methods. *American Journal of Botany* 55: 123–42.

Feist, M.A. and S.R. Downie. 2008. A phylogenetic study of *Oxypolis* and *Ptilimnium* based on nuclear rDNA ITS sequences. *Systematic Botany* 33: 447–458.

Feist, M.A. 2009. Clarifications concerning the nomenclature and taxonomy of *Oxypolis ternata* (Apiaceae). *Journal of the Botanical Research Institute of Texas* 3: 661–666.

Feist, M.A. 2010. The reinstatement of *Ptilimnium texense* (Apiaceae) and a new key to the genus. *Journal of the Botanical Research Institute of Texas* 4: 641–651.

Hall, T.A. 1999. BioEdit: A user friendly biological sequence alignmant editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95–98.

Hardway, T.M., K. Spalik, M.F. Watson, D.S. Katz-Downie, and S.R. Downie. 2004. Circumscription of Apiaceae tribe Oenantheae. *South African Journal of Botany* 70: 393–406.

Huelsenbeck, J.P. and F. Ronquist. 2001. MrBayes. Bayesian inference of phylogenetic trees. *Bioinformatics* 17: 754–755.

Heusser, C.J. 1960. *Late Pleistocene environments of North Pacific North America.* Special Publication, vol. 35. New York: American Geographical Society.

Judd, W. S. 1982. The taxonomic status of *Oxypolis greenmanii* (Apiaceae). *Rhodora* 84: 265-279.

Kaplan, D.R. 1970. Comparative development and morphological interpretation of 'rachis-leaves' in Umbelliferae. *Botanical Journal of the Linnean Society* 63 (Supplement 1): 101–126.

Kartesz, J.T. 2010. A synonymized checklist and atlas with biological attributes for the vascular flora of the United States, Canada, and Greenland. In Kartesz, J.T. and C.A. Meacham. Synthesis of North American flora, Version 1.0. Chapel Hill: North Carolina Botanical Garden.

Kral, R. 1981. Notes on some "quill-leaved" umbellifers. *SIDA Contributions to Botany* 9: 124–134.

Lacourse, T., R.W. Mathewes, and D.W. Fedje. 2005. Late-glacial vegetation dynamics of the Queen Charlotte Islands and the adjacent continental shelf, British Columbia, Canada. *Paleogeography, Paleoclimatology, and Paleoecology* 226: 36–57.

Lee, B.Y., G.A. Levin, and S.R. Downie. 2001. Relationships within the spiny-fruited Umbellifers (Scandiceae subtribes Daucinae and Torilidinae) as assessed by phylogenetic analysis of morphological characters. *Systematic Botany* 26: 622–642.

Lee, C.-S. and S.R. Downie. 2006. Phylogenetic relationships within *Cicuta* (Apiaceae tribe Oenantheae) inferred from nuclear rDNA and cpDNA sequence data. *Canadian Journal of Botany* 84: 453–468.

Liogier, H.A. and L.F. Martorell. 2000. *Flora of Puerto Rico and adjacent islands: A systematic synopsis*, 2nd ed. San Juan, Puerto Rico: Editorial de la Universidad de Puerto Rico.

Liu, M., G.M. Plunkett, P.P. Lowry, B.-E. Van Wyk, and P.M. Tilney. 2006. The taxonomic value of fruit wing types in the order Apiales. *American Journal of Botany* 93: 1357–1368.

Liu, M., B.-E. Van Wyk**,** P.M. Tilney**,** G.M. Plunkett, and P.P. Lowry. 2009. Evidence from fruit structure supports in general the circumscription of Apiaceae subfamily Azorelloideae. *Plant Systematics and Evolution* 280: 1–13.

Magee, A.R., B.-E. Van Wyk, P.M. Tilney, and S.R. Downie. 2009. Generic delimitations and relationships of the Cape genera *Capnophyllum*, *Dasispermum* and *Sonderina*, the North African genera *Krubera* and *Stoibrax*, and a new monotypic genus of the subfamily Apioideae (Apiaceae). *Systematic Botany* 34: 580–594.

Magee, A.R., B.-E. Van Wyk, P.M. Tilney, and S.R. Downie. 2010. A taxonomic revision of the South African endemic genus *Dasispermum* (Apiaceae, Apioideae) *South African Journal of Botany* 76: 308–323

Marcinko S.E. and J.L. Randall. 2008. Protandry, mating systems, and sex expression in the federally endangered *Ptilimnium nodosum* (Apiaceae). *Journal of the Torrey Botanical Society* 135: 178–188.

Mathias, M. 1936. Notes on the genus *Ptilimnium*. *Brittonia* 2: 244.

Pimenov, M.G., M.G. Vasil'eva, M.V. Leonov, and J.V. Daushkevich. 2003. *Karyotaxonomical analysis in the Umbelliferae*. Enfield: Science Publishers, Inc.

Plunkett, G.M., D.E. Soltis, and P.S. Soltis. 1996. Evolutionary patterns in Apiaceae: inferences based on *matK* sequence data. *Systematic Botany* 21: 477–495.

Posada D. and K.A. Crandall. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* 14: 817–818.

Shaw, J., E.B. Lickey, J.T. Beck, S.B. Farmer, W. Liu, J. Miller, K.C. Siripun, C.T. Winder, E.E. Schilling, and R.L. Small. 2005. The tortoise and the hare II: Relative utility of 21 noncoding chloroplast DNA sequences for phylogenetic analysis. *American Journal of Botany* 92: 142–166.

Shaw, J., E.B. Lickey, E.E. Schilling, and R.L. Small. 2007. Comparison of whole chloroplast genome sequences to choose noncoding regions for phylogenetic studies in angiosperms: The tortoise and the hare III. *American Journal of Botany* 94: 275–288

Simmons, M.P. and H. Ochoterena. 2000. Gaps as characters in sequence-based phylogenetic analyses. *Systematic Biology* 49: 369–381.

Spalik, K. and S.R. Downie. 2001. The utility of morphological characters for inferring phylogeny in Scandiceae subtribe Scandicinae (Apiaceae). *Annals of the Missouri Botanical Garden* 88: 270–301

Spalik, K. and S.R. Downie. 2006. The evolutionary history of *Sium* sensu lato (Apiaceae): dispersal, vicariance, and domestication as inferred from ITS rDNA phylogeny. *American Journal of Botany* 93: 76–95.

Spalik, K., S.R. Downie, and M.F. Watson. 2009. Generic delimitation within the *Sium* alliance (Apiaceae tribe Oenantheae) inferred from cpDNA *rps16-5'trnK*$^{(\mathrm{UUU})}$ and nrDNA ITS sequences. *Taxon* 58: 735–748.

Swofford D.L. 2003. PAUP*: Phylogenetic analysis using parsimony (*and other methods), Version 4.0 beta 10. Sunderland: Sinauer Associates.

Theobald, W.L. 1971. Comparative anatomical and developmental studies in the Umbelliferae. In *The biology and chemistry of the Umbelliferae*, ed. V. H. Heywood. *Botanical Journal of the Linnean Society* 64 (Supplement 1): 177–197.

Thompson, J.D., T.J. Gibson, F. Plewniak, F. Jeanmougin, and D.G. Higgins. 1997. The Clustal X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research* 24: 4876–4882.

Tucker, A.O., N.H. Dill, T.D. Pizzolato, and R.D. Kral. 1983. Nomenclature, distribution, chromosome numbers, and fruit morphology of *Oxypolis canbyi* and *O. filiformis* (Apiaceae). *Systematic Botany* 8: 299–304.

U. S. Fish and Wildlife Service. 1986. Determination of *Oxypolis canbyi* (Canby's dropwort) to be an endangered species. *Federal Register* 37: 6690–6693.

U.S. Fish and Wildlife Service. 1988. Endangered and threatened wildlife and plants: determination of *Ptilimnium nodosum* (harperella) to be an endangered species. *Federal Register* 50: 37978–37982.

Weakley, A.S. and G.L. Nesom. 2004. A new species of *Ptilimnium* (Apiaceae) from the Atlantic coast. *SIDA Contributions to Botany* 21: 743–752.

Wen, J. and E.A. Zimmer. 1996. Phylogeny and biogeography of *Panax* L. (the ginseng genus, Araliaceae): inferences from ITS sequences of nuclear ribosomal DNA. *Molecular Phylogenetics and Evolution* 6: 167–177.

Werle, E., C. Schneider, M. Renner, M. Volker, and W. Fiehnet. 1994. Convenient single-step, one tube purification of PCR products for direct sequencing. *Nucleic Acids Research* 22: 4354–4355

Wilgenbusch, J.C., D.L., Warren, and D.L., Swofford. 2004. AWTY: A system for graphical exploration of MCMC convergence in Bayesian phylogenetic inference. (http://ceb.csit.fsu.edu/awty).

TABLES AND FIGURES

Table 5.1. Current circumscription of *Oxypolis* and *Ptilimnium* and proposed new combinations for taxa assessed in this study.

Current classification	**New Combination**
Oxypolis canbyi (J.M. Coult. & Rose) Fernald	*Tiedemannia canbyi* (J.M. Coult. & Rose) Feist & S.R. Downie
Oxypolis filiformis (Walter) Britton	*Tiedemannia filiformis* (Walter) Feist & S.R. Downie subsp. *filiformis*
Oxypolis greenmanii Mathias & Constance	*Tiedemannia filiformis* subsp. *greenmanii* (Mathias & Constance) Feist & S.R. Downie
Oxypolis fendleri (A. Gray) A. Heller	
Oxypolis filiformis (Walter) Britton	
Oxypolis rigidior (L.) Raf	
Oxypolis ternata (Nutt.) A. Heller	
Ptilimnium ahlesii Weakley & G. L. Nesom	
Ptilimnium capillaceum (Michx.) Raf.	
Ptilimnium costatum (Elliott) Raf.	
Ptilimnium nodosum (Rose) Mathias	*Harperella nodosa* Rose
Ptilimnium nuttallii (DC.) Britton	
Ptilimnium texense J.M. Coult. & Rose	

Table 5.2. A summary of identical sequences that were represented by a single terminal accession in the phylogenetic analyses, except when these sequences were from individuals from geographic areas of interest. Accession numbers in the second column are those identifying terminals in Figs. 5.1, 5.2, or 5.3. Accession numbers in the third column have identical ITS sequences to those presented in the second column. Voucher information for all accessions is provided in Appendix C.

Species	**Accession number (figure it appears in as a terminal)**	**Accessions with identical sequences (regions for which it is identical)**
Daucosma laciniata	3411 (Figs. 5.1–5.2)	3412 (*trnQ*/*trnK*)
Oxypolis canbyi	2937 (Figs. 5.1–5.2)	2938 (*trnQ*/*trnK*)
Oxypolis fendleri	2350 (Figs. 5.1–5.2)	2351, 2369 (*trnQ*/*trnK*)
Oxypolis greenmanii	2941 (Figs. 5.1–5.3)	2717 (*trnQ*/*trnK*/ITS)
Oxypolis occidentalis	3464 (Figs. 5.1–5.2)	3465, 3466 (*trnQ*/*trnK*)
	2929 (Fig. 5.3)	2937 (*trnQ*/*trnK*/ITS)
	2928 (Figs. 5.1–5.2)	2927 (*trnQ*/*trnK*)
	2755 (Figs. 5.1–5.2)	3442 (*trnQ*/*trnK*)
Ptilimnium nodosum	2784 (Fig. 5.3)	2635 (*trnQ*/*trnK*/ITS)

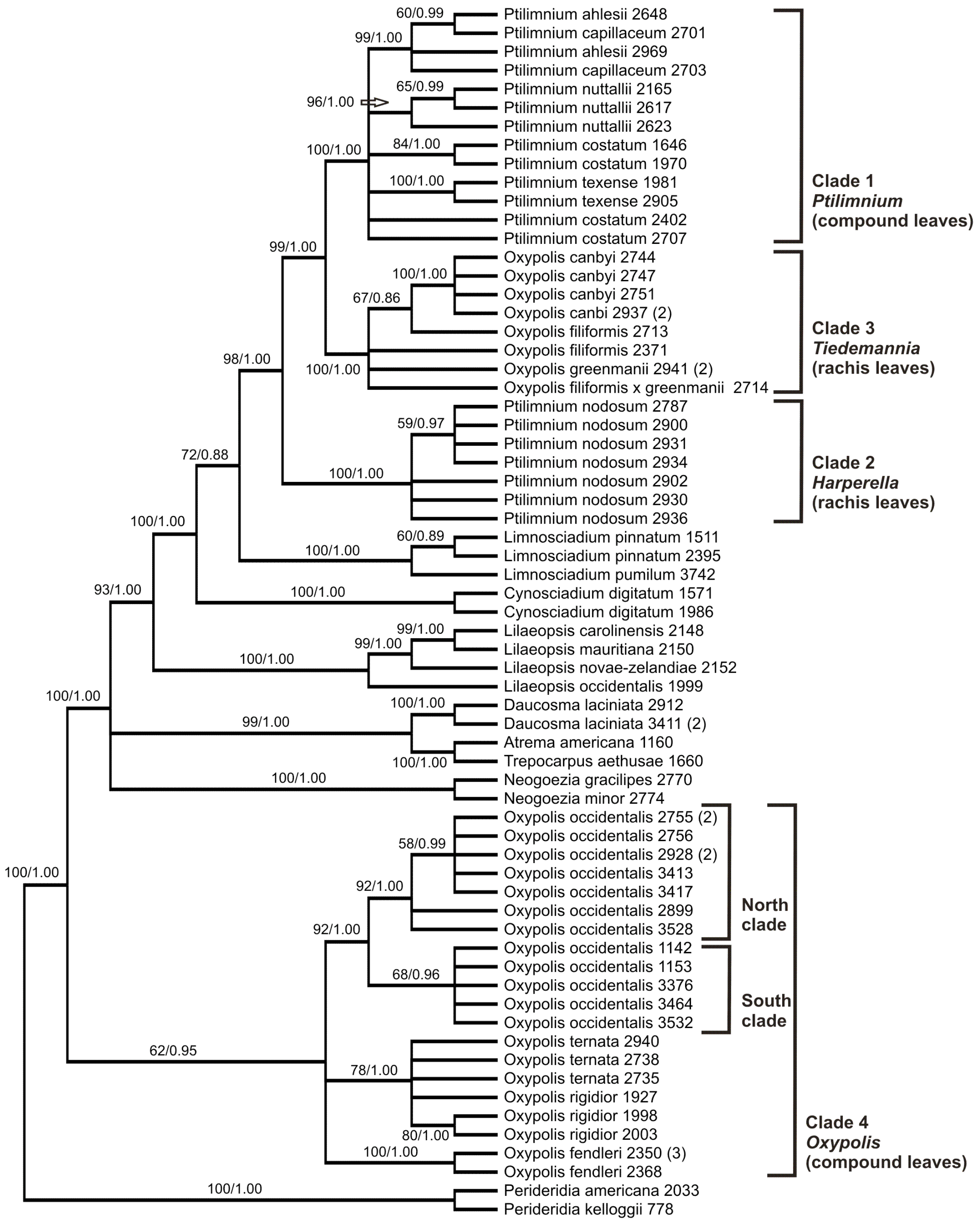

Fig. 5.1. Strict consensus tree of 23,229 minimal length 473-step trees obtained from the MP analysis of the cpDNA dataset (CI = 0.854 and 0.824, with and without uninformative characters, respectively; RI = 0.964). Numbers on branches represent bootstrap estimates and Bayesian posterior probability values, respectively. Numbers in parentheses following the name of a taxon indicate the number of accessions of that taxon having identical DNA sequences (Table 5.2).

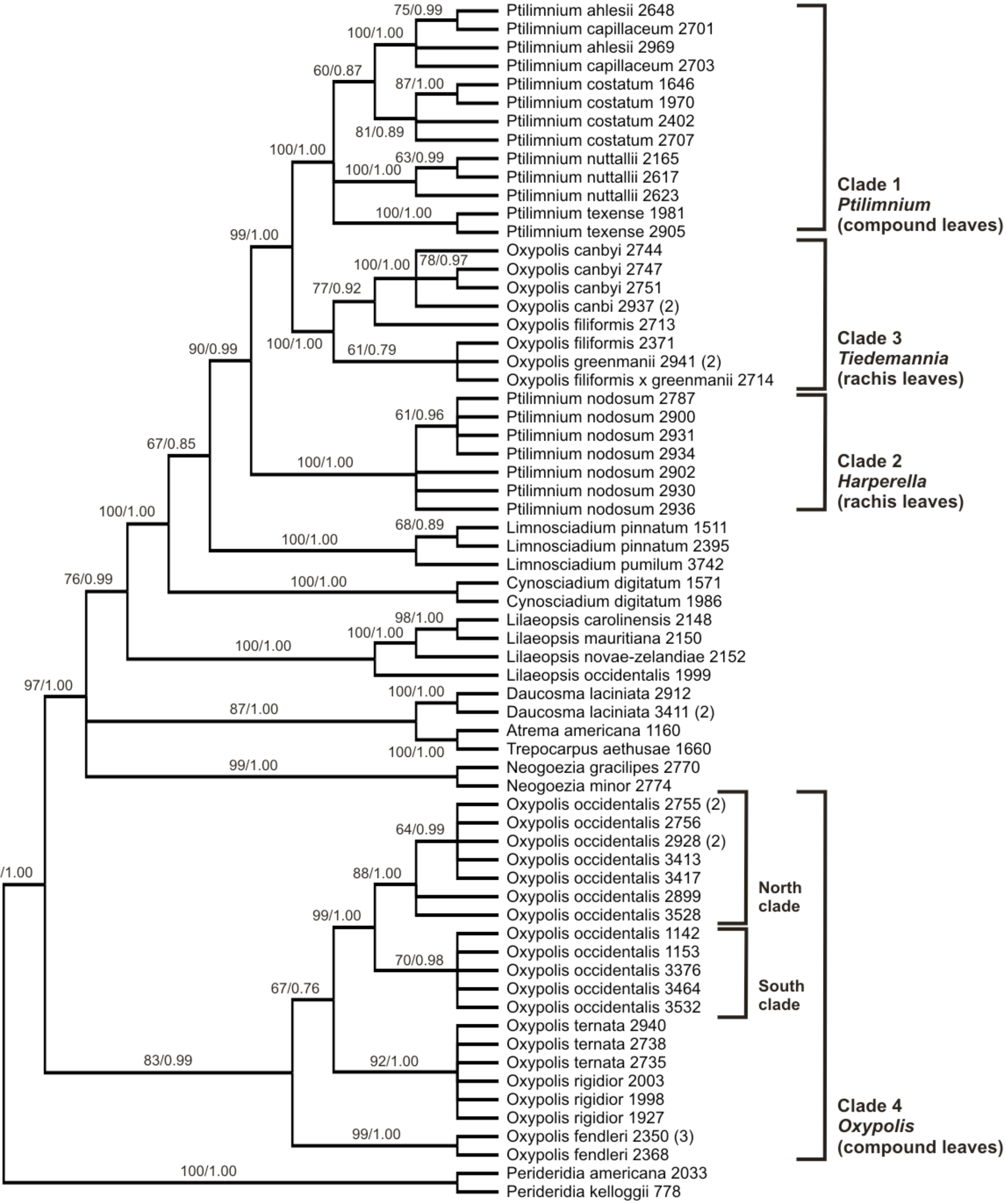

Fig. 5.2. Strict consensus tree of 4,698 minimal length 554-step trees obtained from the MP analysis of the cpDNA/indels dataset (CI = 0.843 and 0.811, with and without uninformative characters, respectively; RI = 0.963). Numbers on branches represent bootstrap estimates and Bayesian posterior probability values, respectively. Numbers in parentheses following the name of a taxon indicate the number of accessions of that taxon having identical DNA sequences (Table 5.2).

Fig. 5.3. Majority rule consensus tree obtained from the BI analysis of the cpDNA/ITS dataset. Numbers on branches represent bootstrap estimates and Bayesian posterior probability values, respectively; a bootstrap estimate of less than 50% is indicated with an asterisk. Numbers in parentheses following the name of a taxon indicate the number of accessions of that taxon having identical DNA sequences (Table 5.2).

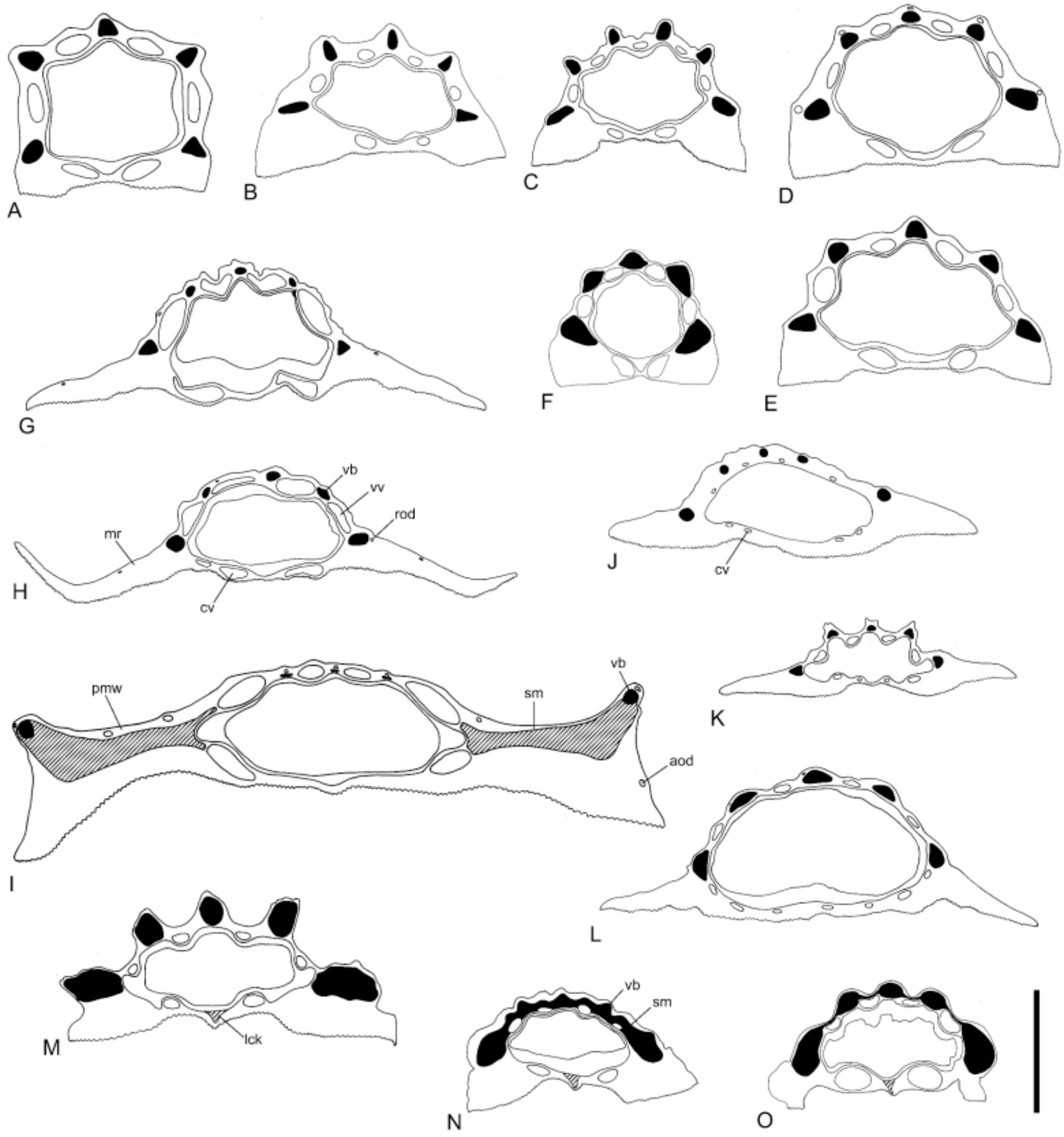

Fig. 5.4.[7] Transverse sections through the fruits of *Ptilimnium* s.l. (**A–F**), *Oxypolis* s.l. (**G–L**), *Cynosciadium* (**M**), and *Limnosciadium* (**N–O**). **A.** *Ptilimnium nodosum* (*Feist & Molano-Flores 2967.1*, ILLS); **B.** *Ptilimnium ahlesii* (*Bozeman 6100*, NCU); **C.** *Ptilimnium capillaceum* (*Valentine s.n.,* BRIT-SMU); **D.** *Ptilimnium costatum* (*Feist s.n.*, ILLS); **E.** *Ptilimnium texense* (*Shinners 11830*, BRIT-SMU); **F.** *Ptilimnium nuttallii* (*Cory 53275*, BRIT-SMU); **G.** *Oxypolis filiformis* (*Feist & Molano-Flores 3197*, ILLS); **H.** *Oxypolis greenmanii* (*Godfrey 53756,* NCSC); **I.** *Oxypolis canbyi* (*Nelson 4269*, USCH); **J.** *Oxypolis fendleri* (*Sturges 205*, RM); **K.** *Oxypolis occidentalis* (*Feist & Molano-Flores 4106*, ILLS); **L.** *Oxypolis rigidior* (*Webster & Webster 7206*, DUKE); **M.** *Cynosciadium digitatum* (*Sundell 15406*, BRIT); **N.** *Limnosciadium pumilum* (*Gentry 1996*, BRIT); **O.** *Limnosciadium pinnatum* (*Lundell 14012*, LL). **aod** additional oil duct; **cv** commissural vitta; **lck** lignified commissural keel; **mr** marginal rib; **pmw** pseudo-marginal wing; **rod** rib oil duct; **sm** sclerified mesocarp; **vb** vascular bundle; **vv** vallecular vitta. Scale: A = 500 μM; B–O = 2 mm. Additional voucher information is provided in Appendix D.

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[7] Figure 5.4 created by Anthony R. Magee of the South African National Biodiversity Institute.

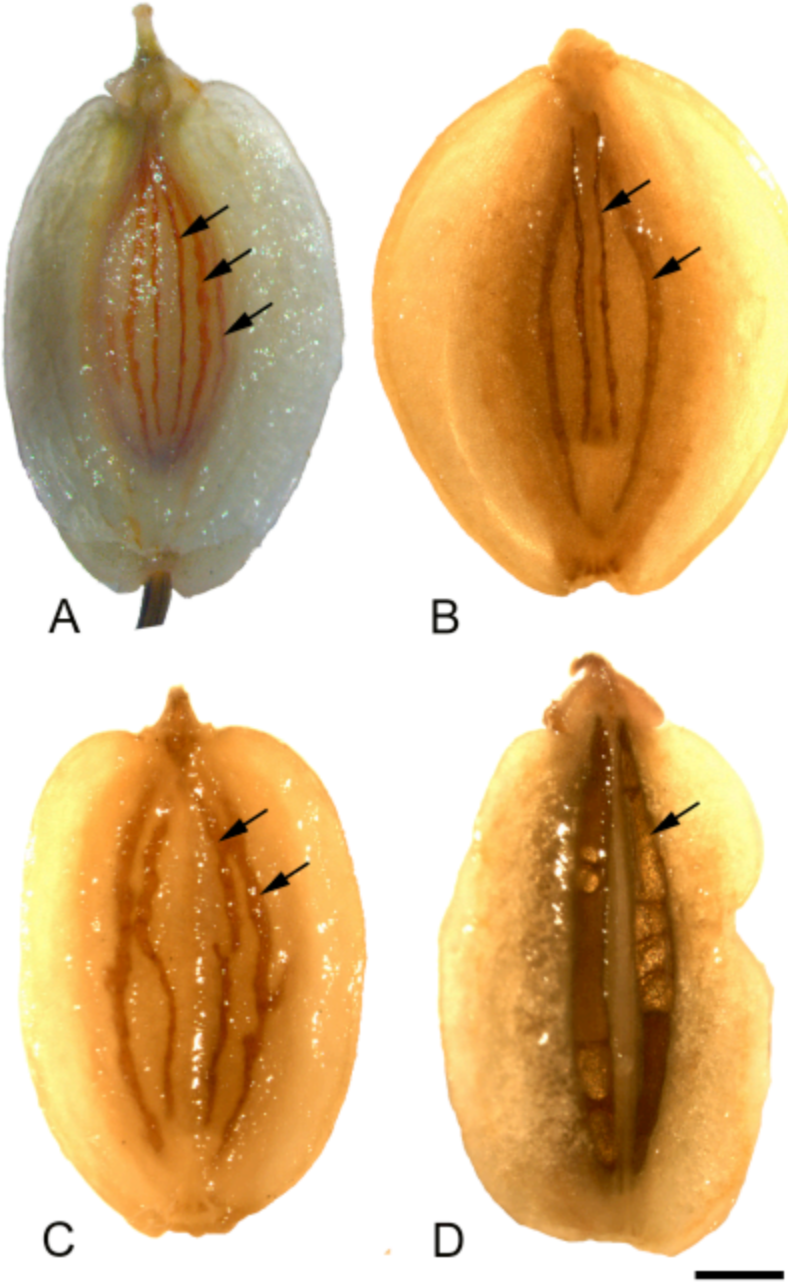

Fig. 5.5.[8] Three-dimensional structure of the commissural vittae in the fruit of *Oxypolis* s.l.. **A.** *Oxypolis rigidior* (dorsal view; *Oldham 6994*, CAN); **B.** *Oxypolis occidentalis* (commissural view; *Feist & Molano-Flores 4106*, ILLS); **C.** *Oxypolis fendleri* (commissural view; *Sturges 205*, RM); **D.** *Oxypolis filiformis* (commissural view; *Feist & Molano-Flores 3197*, ILLS); arrows indicate commissural vitta. Scale: A–D = 1.4 mm.

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[8] Figure 5.5 created by Anthony R. Magee of the South African National Biodiversity Institute. Photographs provided by Mei (Rebecca) Liu of Harbin Normal University.

CHAPTER 6

TAXONOMIC TREATMENTS FOR *PTILIMNIUM, TIEDEMANNIA, HARPERELLA, LIMNOSCIADIUM*, *CYNOSCIADIUM,* AND *OXYPOLIS*

INTRODUCTION

The publication of the *Flora of North America,* in 30 volumes, is currently underway. As part of the contributing efforts for Apiaceae, taxonomic treatments for the following genera are provided: *Ptilimnium*, *Tiedemannia, Harperella, Limnosciadium, Cynosciadium,* and *Oxypolis*. These treatments adopt the newly reinstated genera *Harperella* and *Tiedemannia* and also include the closely related genera *Cynosciadium* and *Limnosciadium. Harperella* and *Tiedemannia* have been reinstated based on the results of molecular phylogenetic studies and corroborating evidence from morphology and fruit anatomy (Downie et al 2008; Feist & Downie 2008, M.A. Feist et al., unpublished data). *Cynosciadium* and *Limnosciadium* are included because, in these same molecular phylogenetic studies, they were found to form a strongly supported clade with the other genera mentioned above (Downie et al. 2008; Feist & Downie 2008; M.A. Feist et al., unpublished data). A Key to the Genera is provided, as well as keys for the non-monotypic genera *Ptilimnium*, *Tiedemannia, Limnosciadium,* and *Oxypolis.* Taxonomic descriptions are included for all genera, species, and subspecies. Brief taxonomic discussions are provided as needed. These discussions are not comprehensive but rather highlight noteworthy features such as protected status, interesting distribution patterns, relationships and taxonomic problems, and excluded taxa and names. Treatments are written according to the *Flora of North America Guide for Contributors* (FNAEC 2007) and will be submitted for publication in Volume 13 of this series. As required by Flora of North America Editorial Committee these treatments are synoptic and descriptive, yet succinct with diagnostic characters emphasized.

KEY TO THE GENERA

1. Leaves simple, blades reduced to rachis (thus appearing linear, terete, hollow, and septate).
    2. Mericarps not compressed; marginal wings thick and corky, very narrow; carpophore 2-fid at apex; plants without rhizomes or caudices ………………………..….3. ***Harperella***
    2. Mericarps strongly dorsally compressed; marginal wings thin, broad; carpophore 2-cleft nearly to the base; plants with a rhizome or short caudex………………...2. ***Tiedemannia***
1. Leaves 1-pinnate, 1-ternate, palmate, or pinnately decompound, or some leaves simple, blades with well-developed lamina.
    3. Leaves pinnately decompound, ultimate blade divisions filiform …………1. ***Ptilimnium***
    3. Leaves 1-pinnate, 1-ternate, or palmate, or some leaves simple, ultimate blade divisions linear to broadly ovate.
        4. Mericarps slightly dorsally compressed; marginal wings thick and corky, narrow, extending only slightly beyond the lateral ribs; carpophore merely notched or 2-fid at the apex; roots fibrous.
            5. Fruits without a beak; carpophore 2-fid; main stem leaves 1-pinnate ….4. ***Limnosciadium***
            5. Fruits with a small beak; carpophore subentire (merely notched at apex); main stem leaves palmate ....……………………………………..5. ***Cynosciadium***
        4. Mericarps strongly dorsally compressed; marginal wings thin and papery, broad, extending well beyond the lateral ribs; carpophore 2-cleft nearly to the base; roots tuberous-thickened ………………………………………………..…....6. ***Oxypolis***

1. *Ptilimnium* Rafinesque, Neog. 1: 2. 1825 * Bishopweed, mock bishopweed [Greek *ptilon*, soft feather or down, alluding to the highly divided leaves]

Herbs, annual or perennial, 1–15 dm, glabrous. **Roots** fibrous. **Stems:** above ground erect; below-ground a corm, short rhizome, or absent. **Leaves:** basal/proximal cauline mostly withered by anthesis, phyllodial to 1-pinnate to pinnately decompound, mid/distal cauline pinnately decompound; petiole present; blade oblong to deltate in outline, not septate; dissected, filiform, margins entire. **Umbels** compound, terminal and axillary; rays spreading, subequal; involucre bracts simple or with 3(–7) linear segments; involucel bracts simple, linear. **Pedicels** present.

Flowers bisexual; calyx teeth persistent, distinct, deltate, narrowly triangular, or lanceolate; petals white, apex narrowed and inflexed; styles erect to strongly recurved; stylopodium conic. **Schizocarps** of mericarps splitting, elliptic to orbicular, mericarps somewhat dorsally compressed, dorsal ribs 3, lateral ribs 2; marginal wings thick, corky, narrow, extending only slightly beyond the lateral ribs; oil tubes 1 in the intervals, 2 on the commissure, not branching; carpophore 2-fid at apex. **x** = 7, 8, 11.

Species 4: United States; West Indies.

The circumscription of the genus *Ptilimnium* has undergone several changes in recent years. Molecular systematic studies showed that the genus is not monophyletic (Downie et al. 2008; Feist & Downie 2008; M.A. Feist et al., unpublished data). As a result, the sole rachis-leaved species within the genus, *P. nodosum*, was removed and placed in the newly resurrected genus *Harperella* (M.A. Feist et al., unpublished data). In addition to leaf morphology (compound leaves vs. rachis leaves), fruit morphology also supports this split (M.A. Feist et al., unpublished data). The fruits of the compound-leaved-*Ptilimnium* species are dorsally compressed and have thick, narrowly winged marginal ribs that extend slightly beyond the vascular bundles. The fruits of *P. nodosum* are isodiametric and the marginal ribs may be somewhat corky-thickened, but are not winged beyond the vascular bundles.

1. Middle and distal petiole bases papillate on the abaxial surface; styles 0.1–0.2 mm (on fruit), erect-ascending to spreading; calyx teeth < 0.2 mm, deltate.. 1. *Ptilimnium capillaceum*

1. Middle and distal petiole bases not papillate on the abaxial surface; styles (0.3–)0.4–2 mm (on fruit), spreading to strongly recurved; calyx teeth ≥ 0.2 mm, narrowly triangular.

2. Mid-stem leaves with 2–4(–5) nodes along the rachis, 1–2(–3) primary leaf segments at the major nodes (not including at the apex of the petiole); individual leaf segments often much longer than the rachis;

involucre bract segments 1(–3); stem sometimes slightly thickened at the base but never forming a corm; styles (0.3–)0.4–0.6 mm; fruit 1–1.9 mm, dorsal ribs thick, rounded ....4. *Ptilimnium nuttallii*

2. Mid-stem leaves with (6–)7–16 nodes along the rachis, 3–5(–7) primary leaf segments at the major nodes; individual leaf segments shorter than the rachis (rarely as long as in P. texense); involucre bract segments (1–)3(–7); stem thickened and rounded at the base forming a globose or slightly elongate corm; styles (0.3–)0.5–2 mm; fruit 2.2–4 mm, dorsal ribs narrow, sharp-edged to blunt.

3. Leaf segments flat (at least near the nodes but usually throughout), midvein visible; mid-stem leaves with (8–)10–16 nodes per rachis, longest primary segments with 9–22 secondary segments; leaf shape in outline deltate or trullate, leaf segments getting progressively and noticeably shorter towards apex, apex acute; styles (0.8–)1–2 mm, slightly spreading to spreading; bottomland forest, swamps, streambanks, and pond margins... 2. *Ptilimnium costatum*

3. Leaf segments 3–4-angled to subterete, midvein not visible; mid-stem leaves with (6–)7–10 nodes per rachis, longest primary segments with 3–7(–8) secondary segments; leaf shape in outline oblong or oval, leaf segments not getting progressively and noticeably shorter towards apex, apex blunt; styles (0.3–)0.5–0.8(–1) mm long, spreading to strongly recurved; seeps, bogs, and wet pine savannas ....3. *Ptilimnium texense*

1 ***Ptilimnium capillaceum*** (Micheaux) Rafinesque, Bull. Bot. (Seringe) 1: 217. 1830 *
Atlantic bishopweed, eastern bishopweed, herbwilliam, thread-leaf mock bishopweed

Ammi capillaceum Micheaux, Fl. Bor.-Amer. 1: 164. 1803; *Ptilimnium ahlesii* Weakley & G.L. Nesom.

Plants annual, 2–8.5(–13) dm; below ground stem absent. **Leaves:** petiole 0.2–1.5(–2.5) cm, winged by a hyaline border along the entire length, abaxial surface papillate at the base; blade oblong to oval to ovate in outline, 4–13(–21) cm, apex blunt, mid-stem leaves with 4–9 nodes along the rachis, 2–3 primary leaf segments at the major nodes; leaf segments capillary to filiform, 0.1–0.4(–1.9) mm wide, 3-angled to distinctly flattened, midvein often visible, especially on flattened segments, individual leaf segments shorter than the rachis, primary leaf segments not getting progressively and noticeably shorter towards apex, longest primary segments with (1–)3–6(–8) secondary segments. **Peduncle** 2–10.5(–14) cm. **Umbels:** rays 5–22, 0.5–2.5(–3.5) cm; involucre bracts simple or with 3(–5) linear segments; umbellets with 4--20 flowers. **Pedicels** 3–12 mm. **Flowers:** calyx teeth, deltate, < 0.2 mm; petals 0.3–0.6(–0.8) mm; styles erect-ascending to spreading, 0.1–0.2 mm. **Schizocarps** ovate to orbicular, 1.4–2.5(–4.2) × 0.8–1.6(–2.2) mm; dorsal ribs narrow, sharp-edged to blunt; marginal wings corky-thickened, conspicuous (prominent). **2n** = 14, 16, 28.

Flowering/fruiting (Apr)May–Sep. Moist depressions in openings of mesic to dry forests or pine savannas and flatwoods, open bottomland, swamps, seeps, brackish and freshwater marshes, shores of ponds and lakes, ditches, low pastures, fencerows and other wet places; 0–200 m; Ala., Ark., Conn., Del., Fla., Ga., Kans., Ky., La., Md., Mass., Miss., Mo., N.C., N.J., N.Y., Okla., Pa., R.I., S.C., S.Dak., Tenn., Tex., Va.; Bahamas, Cuba, Puerto Rico.

A new species, *P. ahlesii*, was added to the genus *Ptilimnium* in 2004 (Weakley & Nesom 2004). This species, however, is herein treated as a synonym of *P. capillaceum.* This treatment is based both on the results of molecular systematic studies and the lack of consistent morphological characters to separate *P. ahlesii* and *P. capillaceum* (M.A. Feist et al., unpublished data).

2 **Ptilimnium costatum** (Elliott) Rafinesque, Bull. Bot. (Seringe) 1: 217. 1830 * Big bishopweed, big mock bishopweed, ribbed mock bishopweed E[9]

Ammi costatum Elliott, Bot. S. C. & Ga. 1: 350. 1817.

Plants perennial, 6–15 dm; below ground stem a corm or short rhizome. **Leaves:** petiole 1–5.5 cm, hyaline borders very narrow, inconspicuous, usually only visible at the distal and proximal ends, abaxial surface not papillate at the base; blade deltate or trullate in outline, 5–15 cm, apex acute, mid-stem leaves with (8–)10–16 nodes along the rachis, 3–5(–7) primary leaf segments at the major nodes; leaf segments dissected, linear, flat (at least near the nodes but usually throughout), midvein visible, individual leaf segments much shorter than the rachis, primary leaf segments getting progressively and noticeably shorter towards apex, longest primary segments with 9–22 secondary segments. **Peduncle** 7–14 cm. **Umbels:** rays 12–30, 1.5–5 cm; involucre bracts simple or with 3(–7) linear segments; umbellets with (5--)15--20 flowers. **Pedicels** 2–12 mm. **Flowers:** calyx teeth narrowly triangular, 0.2–0.3 mm; petals (0.6)0.8–1.3 mm; styles loosely ascending to spreading, (0.8–)1–2 mm. **Schizocarps** oval to suborbiculate, 2.2–4 × 1.8–3 mm, dorsal ribs narrow, sharp-edged to blunt; marginal wings corky-thickened, conspicuous. **2n** = 22, 32

Flowering/fruiting Jul–Oct. Swamps, bottomland forests, pine savannas, edges of moist woods, banks of streams, sloughs, acid seeps, fens, boggy areas, pond margins, ditches, and other wet places; 0–300 m; Ala. Ark., Ga., Ill., Ky., Mo., N.C., Okla., Tenn.

See the discussion under *P. texense*.

3 **Ptilimnium texense** J. M. Coult. & Rose, Contr. U.S. Nat. Herb. 12: 445. 1909. * Texas bishopweed, Texas mock bishopweed; E

Plants perennial, 5–12 dm; below ground stem a small rounded corm. **Leaves:** petiole 0.5–3 cm, hyaline borders narrow, often inconspicuous and only visible at the distal and proximal ends, abaxial surface not papillate at the base; blade oblong to oval in outline, 3–12 × 3–8 cm, apex blunt, mid-stem leaves with (6–)7–10 nodes along the rachis, 3–5 primary leaf segments at the major nodes; leaf segments dissected, filiform to linear, 3–4-angled to subterete, midvein not visible, individual leaf segments shorter than (to as long as) the rachis, primary leaf segments not

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[9] E = endemic to North America

getting progressively and noticeably shorter towards apex, longest primary segments with 3–7(–8) secondary segments. **Peduncle** 2–12 cm. **Umbels:** rays 8–20(–25), 1–3.5(–4.5) cm; involucre bracts simple or with 3(–5) linear segments; umbellets with 12--24 flowers. **Pedicels** 2–12 mm. **Flowers:** calyx teeth narrowly triangular, 0.2–0.4 mm; petals (0.6–)0.7–1.3 mm; styles spreading to strongly recurved, (0.3–)0.5–0.8(–1) mm. **Schizocarps** (often maroon- or purple-tinged) ovate to orbicular, 2.2–3.5 × 1.5–2.2 mm, dorsal ribs narrow, blunt; marginal wings corky-thickened, conspicuous. **2n** = 14.

Flowering/fruiting Aug–Nov. Hillside seepage bogs, muck bogs, forested acid seeps, wet pine savannahs; 0–200 m; Ark., La., Tex.

Ptilimnium texense has been treated as a hybrid of *Ptilimnium capillaceum* and *P. nuttallii* and as a synonym of *P. costatum*. The results of molecular systematic studies combined with *P. texense's* unique morphological features and distinct habitat requirements support its recognition as a species (Feist 2010). Although distinct, *P. texense* and *P. costatum* are closely related and share an attribute not seen elsewhere in the genus, a perennial habit. This conclusion is based on recent observation of corms and cormlet development on living specimens of both species, and the observation of rhizomes in *P. costatum* (Feist 2010).

4 ***Ptilimnium nuttallii*** (A. P. de Candolle) Britton, Mem. Torrey Bot. Club 5(16): 244. 1894 * Nuttall's bishopweed, Nuttall's mock bishopweed, Ozark bishopweed, Ozark mock bishopweed, Midwestern bishopweed, laceflower E

Discopleura nuttallii A. P. de Candolle, Coll. Mém. 5: 39. 1829.

Plants annual, 3–7 dm; below ground stem absent. **Leaves:** petiole 0.2–1(–1.4) cm, winged by a narrow hyaline border, usually along the entire length, abaxial surface not papillate at the base; blade oval to orbiculate to reniform or flabellate in outline, 3–10 cm, apex broad, mid-stem leaves with 2–4(–5) nodes along the rachis, 1–2(–3) primary segments at the major nodes (not including the apex of the petiole); leaf segments dissected, filiform to linear, 3-angled, midvein not visible, individual leaf segments often longer than rachis, primary leaf segments not getting progressively and noticeably shorter towards apex, longest primary segments with 1–4(–5) secondary segments;. **Peduncle** 4–12 cm. **Umbels:** rays (15–)25–30, 1.5–2.5(–3.5) cm; involucre bracts simple (–3) linear segments; umbellets with 25--30 flowers. **Pedicels** 3–8 mm. **Flowers:** calyx teeth narrowly triangular to lanceolate, 0.2–0.4 mm; petals (0.6–)0.7–1.3 mm;

styles spreading to strongly recurved, (0.3–)0.4–0.6 mm. **Schizocarps** broadly ovate to orbiculate, 1.0–1.9 × 1.0–2.0 mm (often wider than long), dorsal ribs thick, rounded; marginal wings corky-thickened, conspicuous or inconspicuous, not always well-developed. **2n** = 14.

Flowering/fruiting (Apr–)May–Aug. Low moist or wet prairies, moist depressions of upland prairies and glades, low sandy fields, abandoned rice fields, fens, wet woodlands, swamps, banks of streams, ditches; 0–400 m; Ala. Ark., Ill., Kans., Ky., La., Mo., Miss., Okla., Tenn., Tex.

2. *Tiedemannia* A. P. de Candolle, Coll. Mem. 5: 51. 1829 * Cowbane, dropwort, water-dropwort [For Friedrich Tiedemann (1781–1861), a celebrated German physiologist].

Herbs, perennial, 6–25 dm, glabrous. **Roots** fibrous. **Stems:** above ground erect or assurgent; below ground a caudex and/or rhizome. **Leaves** rachis leaves; blade terete, hollow, septate, linear. **Umbels** compound, terminal and axillary; rays slightly spreading to ascending, subequal to unequal; involucre bracts simple, filiform, linear, or lanceolate; involucel bracts simple, filiform, linear, or lanceolate. **Pedicels** present. **Flowers** bisexual, or some peripheral pistillate and/or some inner staminate; calyx teeth persistent or deciduous, distinct, narrowly-triangular, subulate, or deltate-attenuate; petals white or maroon, apex narrowed and inflexed; stylopodium conic. **Schizocarps** of mericarps splitting, oval, elliptic, or obovate, mericarps strongly dorsally compressed, dorsal ribs 3, lateral ribs 2; marginal wings thin, not corky, broad, extending beyond lateral ribs; oil tubes 1 in the intervals, 2 on the commissure, not branching (additional oil tubes often present in the wings); carpophore 2-cleft nearly to the base. **x** = 14.

Species 2: United States; West Indies.

The genus *Oxypolis* previously consisted of seven species, four with pinnately compound leaves and three with rachis leaves. In 1829 de Candolle created the genus *Tiedemannia* (de Candolle 1829) in order to separate the rachis-leaved species from the compound-leaved species, which he placed in the genus *Archemora.* His classification was never widely accepted and other taxonomists grouped the rachis-leaved and compound-leaved species in the genus *Oxypolis* based primarily on their strongly dorsally flattened and broadly winged fruit. Molecular systematic studies showed, however, that the genus *Oxypolis* is not monophyletic (Feist & Downie 2008; Downie et al. 2008; M.A. Feist et al., unpublished data). In addition to leaf morphology (compound leaves vs. rachis leaves), fruit anatomy and chromosome number support splitting the genus *Oxypolis* (M.A. Feist et al., unpublished data). The following differences were noted between the fruits of the rachis-leaved and compound-leaved *Oxypolis* species. The mesocarp is lignified around the seed of the rachis-leaved *Oxypolis* species*,* but not of the compound-leaved species. The vittae are larger than the vascular bundles in the rachis-leaved taxa, but smaller than or equal to the vascular bundles in the compound-leaved species. The rachis-leaved *Oxypolis* species have four vallecular vittae and two commissural vittae, whereas the compound-leaved species have four vallecular vittae and four to eight commissural vittae, the latter often branching. The genus *Tiedemannia* was reinstated in order to hold the rachis-leaved *Oxypolis* species (M.A. Feist et al., unpublished data).

1. Lateral wings of the fruit as thick as the body; rays mostly 5–9; below ground stems long, slender rhizomes...1. *Tiedemannia. canbyi*

1. Lateral wings of the fruit thinner than the body; rays mostly 10–30; rootstock caudex and/or short, stout rhizomes.............................2. *Tiedemannia filiformis*

1 ***Tiedemannia canbyi*** (J.M. Coult. & Rose) Feist & S.R. Downie. 2011. * Canby's cowbane, Canby's dropwort, Canby's water-dropwort C[10] E

Oxypolis filiformis var. *canbyi* J.M. Coult. & Rose, Contr. U.S. Nat. Herb. 7: 193. 1900; *Oxypolis canbyi* (J.M. Coult. & Rose) Fernald

Plants 6–25 dm **Stems:** caudex absent, rhizomes long, slender. **Leaves:** blade slightly keeled to elliptic in cross section; septa inconspicuous, not brittle, not easily disarticulated. **Peduncles** 2–10 cm. **Umbels:** rays (3–)5–9(–12), spreading-ascending, subequal, 1–3 cm; involucre bracts 3–7, filiform to linear, 5–25 mm; involucel bracts 5–9, filiform to linear, 3–10 mm; umbellets with 6--15 flowers. **Pedicels** 2–7 mm. **Flowers:** petals white, 1–1.2 mm. **Schizocarps** 4–7 × 4–6 mm, elliptic, broadly obovate to nearly orbiculate, 4–7 × 4–6 mm; marginal wings as thick as the body, 0.8–2 mm. **2n** = 28

Flowering/fruiting Jun–Oct. Borders and shallows of cypress-pine ponds, sloughs, wet meadows, shallow pools, and ditches; 0–200 m; Del., Ga., Md., N.C., S.C.

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[10] C = of conservation concern; applies to taxa that are globally rare or threatened based on NatureServe's G1 or G2 designation (http://natureserve.org).

Tiedemannia canbyi is a federally endangered species. Its Global Conservation Status is G2, imperiled, and it is listed as SX (presumed extirpated) in Delaware, S1 (critically imperiled) in Maryland and North Carolina, and S2 (imperiled) in South Carolina and Georgia. Less than 30 known populations of high or moderate quality remain. *Tiedemannia canbyi* requires relatively open wetland habitat which is inundated for much of the growing season. Many of the known sites are under the threat of being drained or altered by woody encroachment (USFWS 2010). *Tiedemannia canbyi* can be mistaken for *T. filiformis* in a vegetative state but is readily distinguished by its fruit. In *T. canbyi* the lateral wings are as thick as the body of the fruit, whereas in *T. filiformis* the wings are thinner than the body. The thickness of the wings is caused by a layer of sclerified mesophyll cells found only in the wings of *T. canbyi* (Tucker et al. 1983).

2 ***Tiedmannia filiformis*** (Walter) Feist & S.R. Downie. 2011. * Water cowbane, water-dropwort

Oenanthe filiformis Walter, Fl. Car. 113. 1788; *Oxypolis filiformis* (Walter) Britton

Plants 6–25(–30) dm. **Stems:** caudex and/or stout rhizomes. **Leaves** flat and strongly keeled to elliptic or round in cross section; septa inconspicuous, not brittle, not easily disarticulated or septa conspicuous, brittle, and easily disarticulated. **Peduncle** 3–18 cm. **Umbels:** rays (5–)10–30, slightly spreading, unequal or subequal, 1–5 cm; involucre bracts 4–11, linear to lanceolate, 5–25 mm; involucel bracts 2–10, linear to lanceolate, 2–10 mm; umbellets with 10–25 flowers. **Pedicels** 2–15 mm. **Flowers:** petals white or maroon, 0.8–1.2 mm. **Schizocarps** oval, elliptic, obovate, 3–9 × 1–5.5 mm, marginal wings thinner than the body, 0.2 mm thick. **2n**=28.

Flowering Jul–Sep(–Feb in subtropics). Borders and shallows of cypress-pine ponds, sloughs, wet meadows, shallow pools, and ditches; 0–200 m; Ala., Fla., Ga., La., Miss., N.C., S.C., Tex.; Bahamas, Cuba.

Subspecies 2: se United States, West Indies

1. Petals white; septa of the rachis leaves inconspicuous, not brittle (blade
   not easily disarticulated) .... 2a. *Tiedemannia filiformis* subsp. *filiformis*

1. Petals maroon; septa of the rachis leaves conspicuous, brittle (blade
   easily disarticulated) ....2b. *Tiedemannia filiformis* subsp. *greenmanii*

2a ***Tiedemannia filiformis*** (Walter) Feist & S.R. Downie subsp. ***filiformis*** * Water cowbane, water-dropwort

Plants 6–15(–25) dm. **Leaves** flat and strongly keeled to elliptic and only slightly keeled in cross section; septa inconspicuous, not brittle, not easily disarticulated. **Peduncle** 3–15 cm. **Umbels:** rays (5–)10–25, slightly spreading, unequal, 1–4.5 cm; involucre bracts 4–11, linear to lanceolate, 5–25 mm; involucel bracts 2–4, linear to lanceolate, 3–10 mm; umbellets with 10–22 flowers. **Pedicels** 2–10 mm. **Flowers:** petals white, 0.8–1.2 mm. **Schizocarps** oval, elliptic, obovate, 3–8 × 1–5 mm.

Flowering Jul–Sep(–Feb in subtropics). Borders and shallows of cypress-pine ponds, sloughs, wet meadows, shallow pools, and ditches; 0–200 m; Ala., Fla., Ga., La., Miss., N.C., S.C., Tex.; Bahamas, Cuba.

2b ***Tiedemannia filiformis*** (Walter) Feist & S.R. Downie subsp. ***greenmannii*** (Mathias & Constance) Feist & S.R. Downie. 2011 * Giant cowbane, giant dropwort, giant water-dropwort

Oxypolis greenmanii Mathias & Constance, Bull. Torrey Club 69: 152. 1942; *Oxypolis filiformis* subsp. *greenmanii* (Mathias & Constance) Judd.

Plants 6–25(–30) dm. **Leaves** round or elliptic in cross-section, not keeled, articulations conspicuous; septa conspicuous, brittle, easily disarticulated. **Peduncle** 3–18 cm. **Umbels:** rays (7–)10–30, 2.5–5 cm, spreading, subequal; involucre bracts 6–10, 10–20 mm, lanceolate; involucel bracts 6–10, 2–8 mm, linear to lanceolate. **Pedicels** 3–15 mm. **Flowers** 16–25 per umbellet; petals 1–1.2 mm, maroon. **Schizocarps** 6–9 × 3.5–5.5 mm, oval, elliptic, narrowly obovate, oval.

Flowering/fruiting Jul–Sep. *Hypericum* bogs, acid swamps, cypress ponds, pine flatwoods depressions, drainage canals, ditches; 0–200 m; Fla.

*S*ubspecies *greenmanii* is known from just five counties in Florida. Its Global Conservation Status is G3 and its State Conservation Status in Florida is S3; it is considered to be vulnerable to extinction due to its limited range and developmental pressures from the conversion of its natural habitat to pine plantations. Morphologically subsp. *greenmanii* can appear to be quite different from subsp. *filiformis*. The flowers and fruit of subsp. *greenmanii* are a deep maroon color and it has larger leaves with very conspicuous septations that can be easily disarticulated. When populations of subsp. *greenmanii* and subsp. *filiformis* come in to contact, however, they readily interbreed and produce highly fertile offspring that exhibit a range of intermediate morphological characters (Judd 1982). This led Judd (1982) to conclude that *Oxypolis greenmanii* should be recognized as a subspecies of *O. filiformis*. Molecular systematic studies utilizing nuclear rDNA ITS and cpDNA sequences provided no support for the recognition of *T. greenmanii* as a distinct species (Feist & Downie 2008, M.A. Feist et al., unpublished data). In agreement with Judd (1982), *T. greenmanii* is treated as a subspecies of *T. filiformis*.

3. *Harperella* Rose, Proc. Biol. Soc. Wash. 19: 96. 1906. [For Dr. Roland M. Harper (1878-1966), noted Alabama botanist]

Herbs, perennial, 1.5–10.5 dm, glabrous. **Roots** fibrous roots. **Stems:** above ground erect, or forced into an inclinate or horizontal position (then rooting at nodes producing independent ramets); below ground absent. **Leaves** rachis leaves; blade terete, hollow, septate, linear. **Umbels** compound, terminal and axillary; rays spreading, subequal; involucre bracts simple, lanceolate, or absent; involucel bracts simple, lanceolate, or absent. **Pedicels** present. **Flowers** bisexual and staminate; calyx teeth persistent, distinct, lanceolate or deltate; petals white, apex narrowed and inflexed; styles spreading; stylopodium conic. **Schizocarps** of mericarps splitting, suborbiculate, mericarps not compressed, dorsal ribs 3, lateral ribs 2, marginal wings thick, corky, very narrow, not extending beyond the lateral ribs; oil tubes 1 in the intervals, 2 on the commissure, not branching; carpophore 2-fid at apex. **x** = 6.

Species 1: United States.

See *Ptilimnium* for a discussion of the genus *Harperella*.

1 ***Harperella nodosa*** Rose, Proc. Biol. Soc. Wash. 19: 96. 1906 * Harperella C E

Harperella fluviatilis Rose; *Harperella vivpara* Rose; *Ptilimnium nodosum* (Rose) Mathias; *Ptilimnium fluviatile.* (Rose) Mathias; *Ptilimnium viviparum* (Rose) Mathias.

Leaves 4–30(–38) × 0.1–0.5 cm. **Peduncle** 1–6.5 cm. **Umbels:** rays 2–15, 0.1–2.5 cm; involucre bracts 1–5 mm; umbellets with (2--)6--15 flowers. **Pedicels** 2–15, 1–6 mm. **Flowers:**

calyx teeth 1–2 mm; petals 0.6–0.8 mm; styles 0.4–0.8 mm. **Schizocarps** 1–2 × 1–2 mm. **2n** = 12

Flowering/fruiting May–Oct. Shallow ponds, rocky shoals, sand bars, banks of rocky streams and rivers; 0–400 m; Ala., Ark., Ga., Md., N.C., S.C., Va., W. Va.

Harperella nodosa is a federally endangered species. Its Global Conservation Status is G2, imperiled, but it is listed as S1 (critically imperiled) in all of the states in which it occurs except Arkansas (S2, imperiled). Approximately 45 occurrences from 24 drainages or watersheds have been recorded. The largest population concentrations occur along the West Virginia/Maryland border and in the Ouachita Mountains of Arkansas, where it had not been discovered until 1991. *Harperella nodosa* is dependent on narrow hydrologic conditions and is vulnerable to alterations to the natural hydrologic regime, siltation and erosion, water quality reductions, disturbance and trampling, and, possibly, competition from invasive plants; land-use conversion is also a threat at some sites. *Harperella nodosa* was separated into three different species (i.e., *H. nodosa*, *H. fluviatilis*, and *H. vivpara*), but molecular systematic studies (Feist & Downie 2008; M.A. Feist et al., unpublished data) and morphology (Easterly 1957; Kral 1981) support the recognition of *H. nodosa* as a single species.

4. *Limnosciadium* Mathias & Constance, Amer. J. Bot. 28: 162. 1941. * Dogshade
[Greek *limne*, marsh and *sciados*, canopy, umbel, alluding to the habitat and family]

Herbs, annual, 0.5–8 dm, glabrous. **Roots** fibrous. **Stems:** above ground erect, ascending, assurgent, or spreading; below ground absent. **Leaves:** basal simple or 1-pinnate; cauline 1-pinnate, or basal and terminal simple; petiole present; blade lanceolate to elliptic-ovate in outline; leaf segments 3–9, simple, terminal segment broader and more elongate, segments and simple leaves filiform to linear-lanceolate, base attenuate or cuneate, margins entire, apex acute, venation parallel, septate. **Umbels** compound, terminal or axillary; rays spreading-ascending, unequal (some umbellets sessile); involucre bracts simple, linear to linear-lanceolate or narrowly triangular; involucel bracts simple, linear to linear-lanceolate or narrowly triangular. **Pedicels** present. **Flowers** bisexual; calyx teeth persistent, distinct, ovate-lanceolate; petals white, apex not narrowed and inflexed; stylopodium conic. **Schizocarps** of mericarps splitting, oblong-oval to orbiculate base rounded, apex rounded, mericarps slightly flattened dorsally; dorsal ribs 3, filiform, lateral ribs 2; marginal wings thick, corky, narrow, extending only slightly beyond the lateral ribs; oil tubes 1 in intervals, 2 on the commissure, not branching; carpophore 2-fid at apex. **x** = 6.

Species 2: United States.

The two species of *Limnosciadium* were once attributed to the genus *Cynosciadium* but were segregated into *Limnosciadium* by Mathias and Constance (1941). Recent analysis of DNA sequence data (nuclear rDNA ITS and cpDNA *trnQ* and 5'*trnK* intergenic spacers) supports this split (Feist & Downie 2008; M.A. Feist et al., unpublished data).

1. Stems erect or ascending; calyx teeth 0.1–0.5 mm or less, attached well below and shorter than the stylopodium; fruit 2–4 × 1–2 mm..1. *Limnosciadium pinnatum*

1. Stems spreading or assurgent; calyx teeth 0.4–1.5 mm, attached shortly below and equaling the stylopodium; fruit 2–3 × 1.5–2.5 mm..2. *Limnosciadium pumilum*

1 ***Limnosciadium pinnatum*** (A. P. de Candolle) Mathias & Constance, Amer. J. Bot. 28: 162. 1941 * Tansy dogshade E

Cynosciadium pinnatum A. P. de Candolle, Coll. Mem. 5: 45. 1829

Plants 0.6–5(–8) dm. **Stems** erect or ascending. **Leaves:** petiole 1.5–10 cm; blade 2–20 cm; leaf segments 3–9(–11), linear to linear-lanceolate, (0.6–)3–10 × 0.1–0.6 cm. **Peduncle** 1–8 cm, some umbellets sessile. **Umbels:** rays 3–12, 0.5–3.5 cm; involucre bracts 2–8, linear to linear-lanceolate or narrowly triangular, 2–6 mm; involucel bracts 3–7, linear or narrowly triangular, 1–5 mm; umbellets with 4--20 flowers. **Pedicels** 2–8 mm. **Flowers:** calyx teeth 0.1–0.5 mm, attached well below and shorter than the stylopodium; petals 1.1–2 mm. **Schizocarps** elliptic to oblong to oval, 2–4 × 1–2 mm.

Flowering/fruiting Apr–Jul. Banks of ponds and lakes, moist depressions of glades and prairies, roadside ditches; 0–300 m; Ala., Ark., Ill., Kans., La., Miss., Mo., Okla., Tex.

2 ***Limnosciadium pumilum*** (Engelmann & A. Gray) Mathias & Constance, Amer. J. Bot. 28: 162. 1941 * Prairie dogshade E

Cynosciadium pinnatum var. *pumilum* Engelmann & A. Gray, Bost. Jour. Nat. Hist. 5:218. 1845; *Cynosciadium pumilum* (Engelmann & A. Gray) J.M. Coulter & Rose.

Plants 0.5–4 dm. **Stems** spreading or assurgent. **Leaves:** petiole 2–7 cm; blade 3–8 cm; leaf segments 3–7, filiform to lanceolate, 3–8 × 0.1–0.8 cm. **Peduncle** 0.5–7.5 cm, some umbellets frequently sessile. **Umbels:** rays 3–8, 1–5 cm; involucre bracts absent or 3–5, linear to linear-lanceolate, 2–6 mm; involucel bracts 3–6, linear to linear-lanceolate, 2–4 mm; umbellets with 4–12 flowers. **Pedicels** 2–4 mm. **Flowers:** calyx teeth 0.4–1.5 mm, attached shortly below and about equaling the stylopodium; petal 0.8–1.6 mm. **Schizocarps** oval to orbiculate, 2–3 × 1.5–2.5 mm. **2n** = 12

Flowering/fruiting Mar–Jun. Wet meadows and bogs; 0–200 m; Ark., La., Tex.

5. *Cynosciadium* A. P. deCandolle, Coll. Mém. 5: 44. 1829. * Dogshade [Greek *cyno*, dog; *sciados*, canopy, umbel, alluding to the inflorescence]

Herbs, annual, (1.5–)3–8(–12) dm, erect, glabrous. **Roots** fibrous. **Stems:** above ground erect; below ground absent. **Leaves**: basal simple, proximal cauline simple or palmate, distal cauline palmate; petiole present; blade broadly flabellate in outline; leaf segments 3–5, simple, of similar lengths and widths, petiolulate, segments and simple leaves linear to linear-lanceolate, base attenuate or cuneate, margins entire, apex apex, venation parallel, septate. **Umbels** compound, terminal and axillary; rays spreading-ascending, unequal, some umbellets sessile; involucre bracts simple, linear, or absent; involucel bracts simple, linear, or absent. **Pedicels** present. **Flowers** bisexual; calyx teeth persistent, distinct, ovate-deltate; petals white, apex narrowed and inflexed; stylopodium conic. **Schizocarps** of mericarps splitting, ovate-elliptic, base rounded, apex tapering abruptly to a prominent beak, mericarps slightly flattened dorsally; dorsal ribs 3, lateral ribs 2; marginal wings thick, corky, narrow, extending only slightly beyond the lateral ribs; oil tubes 1 in intervals, 2 on the commissure, not branching; carpophore subentire (merely notched at apex). **x** = 6.

Species 1: United States.

1 ***Cynosciadium digitatum*** A. P. de Candolle, Coll. Mém. 5: 44. 1829. * Finger dogshade C E

Leaves: petiole 0.2–2 cm; blade 2–15 cm; leaf segments 2–15 × 0.1–0.6(–0.9) cm. **Peduncle** (1.5–)2–8 cm. **Umbels:** rays 2–10, (0–)1–4 cm; involucre bracts 0 or 3–5, 2–10 mm; involucel bracts 0 or 2–5, 1-6 mm; umbellets with 2--20 flowers. **Pedicels** (1–)3–12 mm. **Flowers:** calyx teeth 0.1–0.2 mm; petals 0.4–0.6. **Schizocarps** 2–3.2 × 1.5–2.5 mm (including the stout 0.5–1 mm beak). **2n** = 12

Flowering/fruiting May–Jul. Low woods, wet prairies and fields, roadside ditches; 0–900 m; Ala., Ark., Ill., La., Miss., Mo., Okla., Tenn., Tex.

6. *Oxypolis* Rafinesque, Neog. 1: 2. 1825. * Cowbane, hog-fennel, dropwort, water-dropwort [Greek, *oxys*, sharp, and *polios*, white, alluding to the bright white petals]

Archemora de Candolle; *Neurophyllum* Torrey & A. Gray

Herbs, perennial, 3–15 dm, erect, glabrous. **Roots** tuberous-thickened. **Stems:** above ground erect; below ground absent (rhizomes occasionally present in *O. occidentalis*). **Leaves** 1-pinnate, 1-ternate, or simple; petiole present; blade oblong, oval, ovate, to deltate in outline; leaf segments (1–)3–13, sessile, subsessile, or petiolulate, simple (lobed), filiform, linear, lanceolate, or broadly ovate, , margins crenate, dentate, serrate, incised, or entire, venation parallel or netted, not septate. **Umbels** compound, terminal and axillary; rays spreading to ascending, equal to very unequal; involucre bracts simple, filiform to linear, or absent; involucel bracts simple, filiform to linear, or absent. **Pedicels** present. **Flowers** bisexual; calyx teeth persistent, distinct, deltate to deltate-acuminate; petals white, apex narrowed and inflexed; stylopodium conic. **Schizocarps** of mericarps splitting, elliptic to oblong to oval, mericarps strongly dorsally compressed, dorsal ribs 3, lateral ribs 2; marginal wings thin, not corky, broad, extending beyond lateral ribs; oil tubes 1 in the intervals, 4–8 on the commissure, often branching (additional oil tubes occasionally present in the wings); carpophore 2-cleft to base. **x** = 16, 18.

Species 5: North America.

See the discussion under *Tiedemannia*.

1. Leaves 1-ternate or occasionally simple; leaflets parallel-veined; petioles very slender; bractlets of involucel filiform; calyx teeth 0.2–0.4 mm ....2. *Oxypolis ternata*

1. Leaves 1-pinnate; leaflets net-veined; petioles stout; bractlets of involucel linear or absent; calyx teeth ≤ 0.1 mm.

2. Leaflets remotely salient-dentate or entire; roots distally tuberous-thickened...1. *Oxypolis rigidior*

2. Leaflets crenate-dentate, serrate or incised; roots tuberous-thickened throughout.

3. Involucel present; umbel rays 12-24, spreading-ascending...........3. *Oxypolis occidentalis*

3. Involucel absent; umbel rays 5-14, strictly ascending ....4. *Oxypolis fendleri*

1 ***Oxypolis rigidior*** (Linnaeus) Rafinesque, Bul. Bot. Seringe 218. 1830 * Cowbane, stiff cowbane, water-dropwort, common water-dropwort E

Sium rigidius Linnaeus, Sp. Pl. 251. 1753.

Plants (3–)6–15 dm. **Roots** tuberous-thickened distally. **Stems:** rhizomes absent. **Leaves:** basal/proximal cauline 1-pinnate, mid/distal cauline 1-pinnate or reduced to nearly bladeless sheaths; petiole 5–10 cm, stout; blade ovate to broadly triangular in outline, (4–)10–30 × (4–)10–25 cm; leaflets (3–)5–11(–15), sessile, simple, linear or lanceolate to oblong or narrowly obovate, (2.5–)3.5–15 × (0.2–)0.5–4.5 cm, margins remotely salient-dentate (entire), venation netted. **Peduncles** 6–30 cm. **Umbels:** rays (10–)15–45, spreading, subequal, 2–12 cm; involucre bracts 0–4, linear, 2–20 mm; involucel bracts 0–9, linear, 2–5 mm; umbellets with 10–45 flowers. **Pedicels** 4–20 mm. **Flowers:** calyx teeth deltate, ≤ 0.1 mm; petals 1–1.2 mm. **Schizocarps** elliptic, oblong, or oval, 4–7 × 2.5–4 mm. **2n** = 32

Flowering/fruiting Aug–Nov. Streambanks, wet prairies, bogs, fens, marshes, swamps, wet woods, ditches, and low pastures; 0–400 m; Ont.; Ala., Ark., D.C., Del., Fla., Ga., Ill., Ind., Iowa, Ky., La., Md., Mich., Minn., Miss., Mo., N.J., N.Y., N.C., Ohio, Okla., Pa., S.C., Tenn., Tex., Va., W.Va., Wis.

2 ***Oxypolis ternata*** (Nuttall) A. Heller, Bull. Torrey Club 24: 478. 1897 * Piedmont cowbane, savanna cowbane, three-leaved water-dropwort E

Peucedanum ternatum Nuttall, Gen. N. Amer. Pl. 1: 182. 1818.

Plants 4–9 dm. **Roots** tuberous-thickened distally. **Stems:** rhizomes absent. **Leaves:** basal/proximal cauline 1-ternate, mid/distal cauline 1-ternate or simple; petiole 10–35 cm, very slender; blade cuneate to obdeltate in outline, 7–22 × 3–8 cm; leaflets (1–)3(–5), petiolulate, simple, filiform to linear, 7–22 × 0.1–0.6 cm, margins entire, venation parallel. **Peduncles** 2–15 cm. **Umbels:** rays 4–11, spreading-ascending, subequal, 2–8 cm; involucre bracts 0–5, filiform to linear, 5–10 mm; involucel bracts 0–4, filiform, 2–4 mm; umbellets with 8--12 flowers. **Pedicels** 4–15 mm. **Flowers:** calyx teeth persistent, distinct, deltate-acuminate, 0.2–0.4 mm; petals 1–1.2 mm. **Schizocarps** elliptic, oblong, oval, or orbiculate, 3–5 × 3–3.5 mm.

Flowering/fruiting Sep–Nov. Wet pine savannas, hillside seepage bogs, margins of bushy swamps in pine forests, open margins of bogs and pocosins; 0–200 m; Fla., Ga., N.C., S.C., Va.

In 2005, J.R. Edmondson published what he believed to be a new combination, *Oxypolis denticulata* (Baldwin) J.R. Edmondson, to include the names *Sium denticulatum* Baldwin, *Peucedanum ternatum* Nuttall, and *O. ternata* (Nuttall) A. Heller. He stated that these later three names were synonyms and that the name *O. denticulata* superseded *O. ternata*, the commonly cited modern name for this species (Edmondson 2005). *Sium denticulatum* is not synonymous with *P. ternatum* and *O. ternata*, however, and Edmondson's combination is an isonym (Feist 2009). Therefore the name *O. ternata* is the correct name for this species.

3 ***Oxypolis occidentalis*** J. M. Coulter & Rose, Contr. U.S. Nat. Herb. 7: 196. 1900 * Western cowbane E

Plants 6–15 dm. **Roots** tuberous-thickened throughout. **Stems:** rhizomes occasionally present. **Leaves**: basal/proximal cauline 1-pinnate, mid/distal cauline 1-pinnate or reduced to dilated sheaths with a few narrow leaflets; petiole 1–5 cm, stout; blade oblong in outline, 12–30 × 6–20 cm; leaflets 5–13, sessile to subsessile, simple (lobed), lanceolate to broadly ovate, 3.5–9.5 × 1–3 cm, margins crenate, dentate, serrate, or incised, venation netted. **Peduncles** 6–30 cm. **Umbels:** rays 12–24, spreading-ascending, equal, 2–8.5 cm; involucre bracts 0–1(–8), linear, 5–25 mm; involucel bracts 0-4, linear, 5–10(–15) mm; umbellets with 14--24 flowers. **Pedicels** 3–15 mm. **Flowers:** calyx teeth deltate, ≤ 0.1 mm; petals 1.1–1.5 mm. **Schizocarps** oblong or oval, 5–6 × 3–4 mm. **2n** = 36

Flowering/fruiting Jul–Oct. Bogs, wet meadows, streambanks, often in coniferous forests; 10—2600 m; B.C.; Calif., Ore.

Previously known from just California and Oregon, the known range of *Oxypolis occidentalis* was expanded when it was discovered on the Queen Charlotte Islands, B.C., Canada in 2001 (Cheney & Marr 2007). Since its initial discovery, over 15 populations have been found on the Queen Charlotte Islands. These populations represent a significant disjunct from the closest known populations over 1400 km to the south in west central Oregon. This species grows at elevations of 10--370 m in the Queen Charlotte Islands and at 1200--2600 m in the United States. [It would be good to include some discussion about the two genetic groups here.]

4 ***Oxypolis fendleri*** (A. Gray) A. Heller, Bull. Torrey Club 24: 478. 1897 * Fendler's cowbane E

Archemora fendleri A. Gray, Mem. Am. Acad. II. 4: 56. 1849; *Tiedemannia fendleri* (A. Gray) J. M. Coulter & Rose.

Plants (3–)6–10 dm. **Roots** tuberous-thickened throughout. **Stems:** rhizomes absent. **Leaves**: basal/proximal cauline 1-pinnate, mid/distal cauline 1-pinnate or reduced to dilated sheaths with a few narrow leaflets; petiole (3–)5–15 cm, slender; blade oblong in outline, 7–17 × 4–9 cm, ; leaflets 5–9(–13), sessile to subsessile, simple, narrowly lanceolate to broadly ovate, (1.5–)3–5(–6) × (0.2–)1–4 cm, margins crenate-dentate, serrate, (incised), or on distal leaflets sometimes entire, venation netted. **Peduncles** (1–)4–20 cm. **Umbels:** rays 5–14(–20), strictly ascending, very unequal, 1–6 cm; involucre bracts 0; involucel bracts 0. **Pedicels** 3–10 mm. **Flowers** 8–18 per umbellet; calyx teeth deltate, ≤ 0.1 mm; petals 1–1.2 mm. **Schizocarps** elliptic, oblong, oval, or orbiculate 3–5 × 2–3 mm. **2n** = 36

Flowering/fruiting Jun–Aug. Streambanks, seeps, marshy ground near streams; 2100–3400 m; Ariz., Colo., N.M., Utah, Wyo.

REFERENCES

Abrams, L. 1951. *Illustrated Flora of the Pacific States: Washington, Oregon, and California,* vol.3. Stanford, California: Stanford University Press.

Candolle, A. P. 1829. *Memoire sur la Famille des Ombelliferes*. Paris: Treuttel et Würtz.

Chafin, L.G. 2007. *Field Guide to the Rare Plants of Georgia.* Athens: State Botanical Garden of Georgia.

Cheney, M. and K. L., Marr. 2007. Cowbane, *Oxypolis occidentalis*, a new native vascular plant species for the Queen Charlotte Islands, British Columbia. *Canadian Field-Naturalist* 121: 421–422.

Correll, D.S. and M.C. Johnston. 1970. *Manual of the vascular flora of Texas*. Renner: Texas Research Foundation.

Correll, D.S. and H.B. Correll. 1972. *Aquatic and wetland plants of the southwestern United States*. Washington D.C.: Environmental Protection Agency.

Coulter J.M. and J.N. Rose. 1887. Notes on Umbelliferae of the E. United States III. *Botanical Gazette* 12: 73–76

Coulter J.M. and J.N. Rose. 1909. Supplement to the monograph of the North American Umbelliferae. *Contributions from the U.S. National Herbarium* 12: 441–451.

Cronquist, A., N. H. Holmgren and P. K. Holmgren. 1997. *Vascular Plants of the Intermountain West, U.S.A: Subclass Rosidae (except Fabales),* vol. 3A. Bronx: The New York Botanical Garden.

Diggs, G.M., B.L. Lipscomb, and R.J. O'Kennon. 1999. Illustrated flora of north central Texas. *SIDA Botanical Miscellany* 16: 1–1626.

Diggs, G.M., B.L. Lipscomb, M.D. Reed, and R.J. O'Kennon. 2006. Illustrated flora of east Texas. *SIDA Botanical Miscellany* 26: 1–1594.

Downie, S. R.**,** D. S., Katz-Downie, F.-J., Sun, and C.-S., Lee. 2008. Phylogeny and biogeography of Apiaceae tribe Oenantheae inferred from nuclear rDNA ITS and cpDNA *psbI-5'trnK(UUU)* sequences, with emphasis on the North American Endemics clade. *Botany* 86: 1039–1064.

Easterly, N.W. 1957a. A morphological study of the genus *Ptilimnium*. Dissertation. Morgantown: University of West Virginia Press.

Easterly, N.W. 1957b. A morphological study of *Ptilimnium*. *Brittonia* 9: 136–145.

Edmondson, J. R. 2005. A new combination in *Oxypolis* Raf. (Apiaceae). *Novon* 15: 109–110.

Feist, M.A. and S.R. Downie. 2008. A phylogenetic study of *Oxypolis* and *Ptilimnium* based on nuclear rDNA ITS sequences. *Systematic Botany* 33: 447–458.

Feist, M.A. 2009. Clarifications concerning the nomenclature and taxonomy of *Oxypolis ternata* (Apiaceae). *Journal of the Botanical Research Institute of Texas* 3: 661–666.

Feist, M.A. 2010. The reinstatement of *Ptilimnium texense* (Apiaceae) and a new key to the genus. *Journal of the Botanical Research Institute of Texas* 4: 641–651.

Gleason, H.A. and A. Cronquist. 1991. *Manual of the Vascular Plants of Northeastern United States and Adjacent Canada,* 2nd ed. Bronx: New York Botanical Garden.

Godfrey, R.K. and J.W. Wooten. 1981. *Aquatic and Wetland Plants of Southeastern United States: Dicotyledons*. Athens: University of Georgia Press.

Hickman, J.C. 1993. *The Jepson Manual: Higher Plants of California*. Berkeley: University of California Press.

Judd, W.S. 1982. The taxonomic status of *Oxypolis greenmanii* (Apiaceae). *Rhodora* 84: 265–279.

Kearney, T.H. and R.H. Peebles. 1951. *Arizona Flora.* Berkeley: University of California Press.

Kral, R. 1981. Notes on some "quill-leaved" umbellifers. *SIDA Contributions to Botany* 9: 124–134.

Long, R. W. & O. Lakela. 1971. *A Flora of Tropical Florida: A Manual of the Seed Plants and Ferns of Southern Peninsular Florida*. Miami: Banyan Books.

Marcinko S.E. and J.L. Randall. 2008. Protandry, mating systems, and sex expression in the federally endangered *Ptilimnium nodosum* (Apiaceae). *Journal of the Torrey Botanical Society* 135: 178–188.

Martin, W.C. and C.R. Hutchins. 1981. A Flora of New Mexico, vol. 2. Germany: Strauss & Cramer.

Mathias, M.E. and L. Constance. 1941. *Limnosciadium*, a new genus of Umbelliferae. *American Journal of Botany* 28(2): 162–163.

Mathias, M.E. and L. Constance. 1945. Umbelliferae. *North American Flora* 28B: 43–295.

McDougall, W.B. 1973. *Seed Plants of Arizonia*. Flagstaff: The Museum of Northern Arizona.

Munz, P.A. 1970. *A California Flora*. Berkeley: University of California Press.

Peck M.E. 1961. *A Manual of the Higher Plants of Oregon*, 2nd ed. Portland, Oregon: Binfords & Mort, Publishers.

Radford, A.E., H.E. Ahles, and C.R. Bell. 1968. *Manual of the vascular flora of the Carolinas*. Chapel Hill: University of North Carolina Press.

Rydberg, P.A. 1954. *Flora of the Rocky Mountains and the Adjacent Plains*. New York: Hafner Publishing Company.

Smith, E.B. 1994. *Keys to the Flora of Arkansas*. Fayetteville: The University of Arkansas Press.

Tucker, A.O., N.H. Dill, T.D. Pizzolato, and R.D. Kral. 1983. Nomenclature, distribution, chromosome numbers, and fruit morphology of *Oxypolis canbyi* and *O. filiformis* (Apiaceae). *Systematic Botany* 8: 299–304.

U.S. Fish and Wildlife Service. 2010. *Canby's Dropwort (Oxypolis canbyi) 5-Year Review.* Charleston: Southeast Region South Carolina Ecological Services Field Office.

Weakley, A.S. and G.L. Nesom. 2004. A new species of *Ptilimnium* (Apiaceae) from the Atlantic coast. *SIDA Contributions to Botany* 21: 743–752.

Weakley, A.S. 2010. *Flora of the Southern and Mid-Atlantic States: working draft of 8 March 2010.* University of North Carolina Herbarium, University of North Carolina at Chapel Hill. (http://www.herbarium.unc.edu/WeakleyFlora2010Mar.pdf).

Welsh, S.L., N.D. Atwood, L.C. Higgins, and S. Goodrich. 1987. A Utah Flora. *Great Basin Naturalist Memoirs* 9: 1–894.

Wunderlin, R.P. 1998. *Guide to the Vascular Plants of Florida.* Gainesville: University Press of Florida.

Yatskievych, G. 2006. *Steyermark's Flora of Missouri*, vol. 2 (revised edition). St. Louis: Missouri Botanical Garden Press.

APPENDIX A

SPECIMENS EXAMINED IN CHAPTER 2 FOR NRDNA ITS SEQUENCE VARIATION WITH VOUCHER OR SOURCE INFORMATION AND DNA AND GENBANK ACCESSION NUMBERS.

Oxypolis canbyi, U.S.A. North Carolina: Scotland Co., McIntosh Bay complex, W side of US 401 just N of jct. SR 1421, ca. 3.5 mi S of Wagram, 3 September 1984, *Boyer 930* (NCU 550796), 2746, EF647758. North Carolina: Scotland Co., McIntosh Carolina Bay, US 401 NE of Laurinburg, 13 September 1992, *Sorrie 6946* (NCU 562048), 2747, EF647757. South Carolina: Orangeburg Co., E side of US 21, ca. 2 mi N of Branchville, 13 September 1985, *Nelson 4301* (NCU 538037), 2743, EF177733. South Carolina: Richland Co., Carolina Bay on N side of Vero Road and ca. 0.3 mi E of Sec. Hwy 2206, ca. 2 air mi NW of downtown Gadsden, 7 September 1984, *Nelson 3687* (NCU 537890), 2744, EF647756. South Carolina: Barnwell Co., S side of Hwy 169 ca. 1 mi W of jct. with SC 3, between Blackville and Barnwell, 17 August 1984, *Nelson 3620* (NCU 538042), 2745, EF647755. South Carolina: Bamberg Co., Bamberg Bay Preserve, 28 August 2005, *Feist, Molano-Flores, and Glitzenstein 3193* (ILLS), 2937, EF647759. South Carolina: Bamberg Co., Oxypolis Bay Preserve, 28 August 2005, *Feist, Molano-Flores, and Glitzenstein 3194* (ILLS), 2938, EF647760. ***O. fendleri***, U.S.A. Colorado: Rio Blanco Co., Flat Tops/White River Plateau, Rough Creek, ca. 17 air mi WSW of Oak Creek, 4 August 1991, *Vanderhorst 3759* (RM 616920), 1509, AY360253. Colorado: Boulder Co., Forth of July Canyon, 10 July 1962, *Jones 34084* (ILL), 2350, EF647767. Colorado: Boulder Co., along Boulder Creek, 24 June 1962, *Jones 34450* (ILL), 2351, EF647768. Colorado: Gunnison Co., 0.8 mi W of Kebler Pass near the Crested Butte-Paonia Rd., 27 July 1984, *Barrie 849* (MO 3751099), 2353, EF647769. Colorado: Chafee Co., CO 306, 14 mi W of Buena Vista, 2 August 1973, *Haber and Given 2049* (CAN 370800), 2369, EF177734. Colorado: Conejos Co., 5 mi N of Sheep Creek, 4 mi SE of McIntyre Peak, 3 mi W of Aspen Glade Campground, 17 June 1986, *Douglas 974* (RM 394593), 2762, EF647770. Colorado: Dolores Co., Lone Cone State Wildlife Area, ca 26 air mi NNE of Dolores, E of FR 526, 9 July 1995, *Moore 6628* (RM 706723), 2763, EF647765. Colorado: Summit Co., Boreas Pass Road, 6.5 mi E of CO 9, 21 July 1972, *Nelson 771* (RM 345087), 2764, EF647766. New Mexico: Colfax Co., Porcupine Camp, 24 June 1968, *Hartman 2087* (RM 296467), 2760, EF647763. New Mexico: Miguel Co., Windsor Cr., Pecos Rd., 9 July 1976, *Pase 2090* (RM 406192), 2761, EF647764. Wyoming: Carbon Co., W slope of Sierra Madre, W of Encampment, Battle Creek, 15 July 1966, *Porter and Porter 10218* (DAO 456446), 2370, EF177735. Wyoming: Carbon Co., Sierra Madre, Continental Divide Trail, ca. 10.5-11 air mi SW of Encampment, 1 August 1987, *Williams 588* (RM 396608), 2758, EF647762. Wyoming: Carbon Co., Sierra Madre, ca 13 mi SE of encampment, along a trib. of Big Creek at SE base of Bear Mountain, 30 June 1988, *Nelson 16083* (RM 570852), 2759, EF647761. ***O. filiformis,*** U.S.A. Florida: Bay Co., Callaway Bayou, 2 mi E of junction of Rt. 22 and US 98 on FL Rt. 22, 15 September 1979, *Judd and Perkins 2428* (FLAS 174230), 2711, EF647775. Florida: Bay Co., N side of narrow river at end of road, SW of US 98, ca. 9.5 mi E of the East Bay Bridge on Tyndall Air Force Base, 12 August 1977, *Perkins 469* (FLAS 131850), 2712, EF647776. Florida: Alachua Co., Gainesville, N side of NE 39th Ave. N. just E of Main St., 9 September 1987, *Alcorn 155* (FLAS 166610), 2713, EF177737. Florida: Echols Co., along both sides of GA 94, 20.4 mi W of jct. with Clinch Co. Line in roadside ditch, 27 July 1998, *Horn 1305* (UGA 229714), 2783, EF647778. Georgia: Lanier Co., alongside US 85 2.5 mi E of Stockton, Coastal Plain Province, 11 August 1965, *Faircloth 2730* (NCU 396688), 2652, EF647774. Georgia: Echols Co., 2.7 mi N of Tarver, Coastal Plain Province, 11 August 1965, *Faircloth 2728* (NCU 396687), 2653, EF647773. Louisiana: Vernon Parish, along RR and US 171 N of Pinewood, 22 August 1971, *Thomas 24700* (ILL), 2356, EF647771. Louisiana: Newton Parish, 0.3 mi W of Bon Wier, Texas, 7 September 1987, *Thomas and Allen 101876* (MO 3671227), 2357, EF647772. Louisiana: Vernon Parish, E of Drake's Creek, ca. 2 mi E of Johnsville Church and LA 10, ca. 7 mi E of Pickering, Kisatchie National Forest, 7 September 1987, *Thomas 101486* (DAO 574521), 2371, EF177736. South Carolina: Lee Co., Mount Pleasant Church Bay, 2.5 mi SE of Elliott, 21 August 1994, *Nifong 513* (NCU 565136), 2750, EF647777. ***O. greenmanii,*** U.S.A. Florida: Bay Co., along FL Rt. 22, 5.2 mi E of junction with FL Rt. 167, 30 August 1980, *Judd and Perkins 2741* (FLAS 172279), 2716, EF647779. Florida: Bay Co., ca. 1 mi E of road to Baker Pt. and 1 mi N of US 98 on Tyndall Air Force Base, 15 September 1979, *Judd and Perkins 2439* (FLAS 174274), 2717, EF177738. Florida: Gulf Co., just E of Wetappo Creek and 3.6 mi S of FL 22, 2 September 2005, *Feist and Molano-Flores 3244* (ILLS), 2941, EF647780. **"Oxypolis × intermedia" ined.,** U.S.A. Florida: Bay Co., along US 231, 1.8 mi N of the junction with FL Rt. 388, N of Youngstown, 29 August 1980, *Judd and Perkins 2714* (FLAS 174297), 2714, EF177739. Florida: Bay Co., along FL Rt. 22, 5.2 mi E of junction with FL Rt. 167, 30 August 1980, *Judd and Perkins 2741b* (FLAS 174318), 2775, EF647781. ***O. occidentalis,*** U.S.A. California: Fresno Co., Wishon Reservoir Dam, *Call 2455* (UC 282880), 1153, EF177740. California: El Dorado Co., Osgood Swamp, Foot of Meyers Grade, 3 August 1982, *Follette s.n.* (JEPS 82187), 1435, AY360254. California: Butte Co., N side of Coon Hollow Rd., 1.2 mi E of junction with Humbug Rd., ca. 12 mi NE of Stirling City, 15 August 1981, *Taylor and Hart 4193* (MO 3835050), 2359, EF647794. California: El Dorado Co., Sierra Nevada, Osgood Swamp N of highway 50, ca. 1.5 mi SW of Meyers, 7 August 1982, *Tiehm and Follette 7524* (RM 341173), 2753, EF647782. California: Tulare Co., Sequoia National Forest, on trail between Mineral King P.O. and Cold Spring Public Camp, 22, August 1946, *Ferris and Lorraine 11205* (RM 210334), 2754, EF647783. California: Tehama Co., Forest Rd. 26N09 at Cascade Creek, NW of Chico Meadows, 1.1 mi SE of Hwy 32, 9 September 1997, *Oswald and Ahart 8863* (JEPS 94369), 2899, EF647789. California: Sierra Co., ca. 1.25 mi N of Scales, ca. 2 mi (air) SE of Poverty Hill, 28 September 2001, *Ahart 9295* (JEPS 102455), 2927, EF647790. California: Tulare Co., Southern High Sierra Nevada, middle of headwaters meadow that eventually feeds into Deep Meadow and Boulder Creek, along road 20S79 (road to Lewis Camp Trailhead), 30 July 2004, *Janeway 8214* (CSUC 89572), 2971, EF647792. California: Butte Co., exactly 6.9 mi from the junction of Humboldt Rd. and Hwy 32 (towards Butte Meadows), 11 September 1977, *Hayes and Warner 74* (CSUC 25438), 2972, EF647793. Oregon: Douglas and Jackson Co., Abbott Creek Research Natural Area, ca. 20 mi W of Crater Lake near Abbott Butte, 29 July 1972, *Mitchell 348* (USFS 406185), 2755, EF647784. Oregon: Lane Co., Quaking Aspen Swamp, 6 mi W of S end of Cougar Reservoir, 28 July 1979, *Wagner 2318* (ORE 103195), 2928, EF647791. Oregon: Klamath Co., near W boundary of Crater Lake Park, 24-29 August ?, *Wynd 1745* (ORE 64782), 2929, EF647785. Canada. British Columbia: Queen Charlotte Islands, Graham Island, 2003, *Cheney s.n.* (ILLS), 2756, EF647786. British Columbia: Queen Charlotte Islands, Graham Island, 08 U 0677503 5915030, June, 2004, *Cheney s.n.* (ILLS), 2897, EF647788. British Columbia: Queen Charlotte Islands, Graham Island, 08 U 0685969 5912636, June, 2004, *Cheney s.n.* (ILLS), 2898, EF647787. ***O. rigidior,*** U.S.A. Alabama: Covington Co., ca. 4 mi E of Florala, roadside of Co. Hwy 4 at 1 mi E of junction w/ Hwy 54, 4 October 1999, *MacDonald 13559* (DUKE 382196), 2768, EF647802. Georgia: Rabun Co., Patterson Gap Road, ca 2 mi E of Tumbling Waters Camp, 17 September 1999, *Stiles 1349* (UGA 226955), 2771, EF647801. Illinois: Cook Co., Paintbrush Prairie, Markham, Millard Ave. off Frontage Rd. of I-294, 12 August 1996, *Masi and Epting 553* (ILLS 195720), 1652, EF647796. Illinois: Lawrence Co., Chauncey Marsh, ca. 0.5 mi SW of Embarras River and ca. 4.6 mi E of Chauncey, 4 August 1995, *Phillippe, Tate, and Ebinger 26766* (ILLS 195822), 1653, EF647795. Illinois: Vermilion Co., 3.5 mi SE of Collison, 23 August 1973, *Evers 111785* (ILLS 152167), 1806, EF647797. Illinois: Vermilion Co., Windfall Hill Prairie Nature Preserve, Windfall Prairie Seep, 17 July 1991, *Phillippe, Morris, and Simon 19411* (ILLS 177487), 1927, AY360255. Illinois: Livingston Co., Pontiac, 27 July 1978, *Cull s.n.* (ILLS 188204), 1962, EF647798. Louisiana: Winn Parish., along LA 126, 1.2 mi E of Jct. LA 1233, Kisatchie National Forest, 20 September 1981, *Kessler 1877* (ILL), 1998, EF177743. North Carolina: Polk Co., along C.R.1154 in a small segment of NCWRC Game Lands improvement, 5 October 1973, *DuMond 1871* (NCSC 57816), 2765, EF647799. North Carolina: Pender Co., just W of the Lanier Marl Quarry, ca 2.5 mi SE of Maple Hill on CR 1532, 2 October 1990, *Wilbur 57659* (DUKE 331952), 2766, EF647800. ***O. ternata,*** U.S.A. Florida: Franklin Co., N side of Ridge Rd., ca 1.0 air mi NE of Eastpoint, 21 October 1987, *Anderson*

11051 (MO 3681641), 2360, EF647810. Florida: Wakulla Co., Saint Mark's National Wildlife Refuge, Panacea Unit Longterm Burn Plot (P13), ca. 2 km SE of Sopchoppy, 1 September 2005, *Feist, Molano-Flores, and Glitzenstein 3222* (ILLS), 2940, EF647809. Georgia: Turner Co., N side of CR 249 (S1531) connecting US 41 and GA 33 at head of trib. to West Fork Deep Creek, 10 October 1998, *Horn 1590* (DUKE 363352), 2740, EF647806. Georgia: Coffee Co., along a small stream at "the Rocks," 7.2 mi E of Pridgen, 17 October 1970, *Faircloth 6924* (UGA 114062), 2741, EF647805. North Carolina: Harnett Co., Pine View, 27 September 1966, *Dumond 399* (NCSC 70046) 2736, EF647803. North Carolina: Pender Co., Holly Shelter Game Land, 3 October 1997, *Horn and Dirig 362* (DUKE 363865), 2738, EF177746. North Carolina: Scotland Co., at the head of a trib. leading to Kinney Cameron Lake, Scotland Lane Annual Burn Site, Sandhills Game Land, 30 September 2000, *Horn 3416* (DUKE 379607), 2739, EF647804. South Carolina: Horry Co., 3.8 mi S. of Socastee and ca. 1 mi W. on dirt road, 25 October 1970, *Massey and Thomas 3480* (NCU 422851), 2735, EF177745. South Carolina: Horry Co., Cartwheel Bay Heritage Preserve, between Cartwheel Bay and Mossy Bay, 7 October 1998, *Pittmann and Darr 10079813* (DUKE 362749), 2737, EF647808. South Carolina: Georgetown Friendfield Plantation, Georgetown Property, 29 August 2005, *Feist, Molano-Flores, and Glitzenstein 3203* (ILLS), 2939, EF647807.

Ptilimnium ahlesii, U.S.A. North Carolina: Brunswick Co., just E of Brunswick River and just N of the 74-76 causeway, ca. 2 mi W of Wilmington, 10 June 2004, *Weakley and LeBlond 7317* (sheet 2 of 2) (NCU), 2969, EF647814. South Carolina: Berkeley Co., Cooper River at the mouth of Durham Creek, 7 June 1990, *McAninch 23* (NCU 557199), 2648, EF177747. South Carolina: Colleton Co., 1.4 mi NE of Ashepoo on US 17, 26 June 1956, *Bell 3703* (NCU 97912), 2649, EF647813. ***P. capillaceum,*** U.S.A. Arkansas: *Maddox VB-Cap-12,* 2795, EF647821. Georgia: Elbert Co., SE of Elberton on dirt lane to Anthony Shoals on Broad River, 23 June 1977, *Craft Coile 1000* (GA 140247), 2627, EF647817. Florida: Wakulla Co., Appalachia National Forest, FSR 369, 2 mi from junction with FL 267, SW from Helen Work Center and Springhill, 14 June 1990, *Godfrey 83887* (GA 185564), 2628, EF647818. Florida: Nassau Co., White Oak Plantation in the wedge formed by the junction of the Little St. Mary's River and St. Mary's River about 8-10 mi NW of Yulee, 19 June 1997, *Wilbur 67597* (BRIT), 2703, EF647822. Louisiana: LaSalle Parish, N edge of Saline Wildlife Area, off LA 28 ca. 9 mi SW of Archie, 2 June 1979, *Allen and Vincent 8765 and 2029* (WVA 114846), 2619, EF647815. North Carolina: Jones Co., Croatan National Forest, N floodplain of Hunter Creek, E side of NC Rt. 58, 17 April 1999, *Hill 31281A* (ILLS 200452), 2704, EF647819. North Carolina: Tyrrell Co., SR 1307 at Frying Pan Lake boating access area, 8 August 1980, *McDonald and Nash 1802* (WVA 114842), 2618, EF647816. North Carolina: *Maddox NC-Cap-15,* 2794, EF647820. Virginia: Lancaster Co., Bellwood Marsh, S of Rt. 3 bridge, W of Lancaster, 22 July 1994, *Weldy 849* (BRIT), 2701, EF177748. ***P. costatum,*** U.S.A. Arkansas: Bradley Co., near Lanark Branch along a dirt road, 3.1 mi S of Arkansas 4, SW of Banks, 17 June 1986, *Dale and Leslie 96999 and 2145* (USF 200503), 2640, EF647837. Georgia: Chattooga Co., Mosely Spring, Lyerly Quadrangle, S of Lyerly, ca. 0.5 mi N of AL state line, 28 June 1970, *Foote 6043A* (UGA 100623), 2903, EF647838. Illinois: Jackson Co., Shawnee National Forest, Oakwood Bottoms, Murphysboro Ranger District, Compartment 15, 14 July 1993, *Phillippe 22406* (ILLS 181777), 1503, EF647829. Illinois: Jackson Co., Shawnee National Forest, Oakwood Bottoms, Murphysboro Ranger District, Compartment 16, 20 August 1993, *Phillippe 22870* (ILLS 18338), 1504, EF647830. Illinois: Jackson Co., Shawnee National Forest, 20 September 1989, *Stritch 2159* (ILLS 172136), 1646, EF177749. Illinois: Jackson Co., 11 September 1989, *Stritch 2125* (ILLS 172159), 1648, EF647832. Illinois: Johnson Co., in a swamp forest at Grantsburg Swamp (Bell Pond) off of IL Rt. 146 at Grantsburg, 2 July 1992, *Basinger 4638* (ILLS 179577), 1649, EF647833. Illinois: Jackson Co., 20 September 1989, *Stritch 2163* (ILLS 172191), 1650, EF647834. Illinois: Johnson Co., N of Karnak, 12 September 1989, *Smith 1427* (ILLS 172057), 1651, EF647823. Illinois: Jackson Co., 12 September 1989, *Stritch 2139* (ILLS 172154), 1801, EF647835. Illinois: Alexander Co., Horseshoe Lake Conservation Area, 3 July 1993, *Basinger 6009* (ILLS 181612), 1802, EF647836. Illinois: Johnson Co., N of Karnak, 12 September 1989, *Smith 1425* (ILLS 172055), 1805, EF647824. Illinois: Jackson Co., Shawnee National Forest, 11 September 1989, *Stritch 2124* (ILLS

172160), 1970, EF177750. Illinois: Jackson Co., near Howardton, 16 July 2003, *Feist 2508,* 2625, EF647828. Louisiana: Natchitoches Parish, moist seepage area beside LA 479 at Strange Rd., W of Goldonna in Kisatchie National Forest, 14 August 1989, *Thomas and Bell 112081* (ILL), 1981, EF177751. Louisiana: Natchitoches Parish, near bridge on Longleaf Vista (FSR 337), ca. 9 mi NW of Gorum, 28 August 1976, *Karl Vincent 561* (GA 127326), 2641, EF647840. Louisiana: Jefferson Parish., Davis, roadside ditch and RR ROW beside US 165, N of Fenton, 18 October 1975, *Thomas 47944* (FLAS 168822), 2904, EF647839. Missouri: Wayne Co., Hattie's Ford Fen Area, 12 October 2001, *Brant 4857* (MO 5573699), 2402, EF177752. Tennessee: Coffee Co., E of I-24 on US 41, ca. 3 mi SE Manchester, 20 August 1971, *Kral 43657* (MO 3671221), 1514, EF647831. Texas: Anderson Co., Gus Engeling Wildlife Management Area, NW of Palestine, Lake 2 bog area, pasture 2, 16 October 1993, *Dubrule Reed 1354* (TAMU 24011), 2905, EF647825. Texas: Anderson Co., Chester's Pitcher Plant Bog, N end of Gus Engeling Wildlife Management Area, on Gibson Branch, S of FM 2961 just down stream from lake, August 1997, *MacRoberts and MacRoberts 3412* (BRIT), 2906, EF647826. Texas: Hardin, along roadside of Hwy 327 between Silsbee and Kountze, 30 September 1971, *Amerson 834* (BRIT/SMU), 2914, EF647827. ***P. nodosum****,* U.S.A. Alabama: Little River, *Maddox LR-35-15,* 2786, EF647845. Alabama: DeKalb Co., Little River near AL Hwy. 35 bridge, DeSoto State Park, 15 July 1987, *Freeman s.n.* (AUA 46749), 2931, EF647853. Alabama: Cherokee Co., on E side of Little River S of AL Hwy 35 SE of Fort Payne, 16 July 1987, *Thomas 100873* (USCH 42952), 2970, EF647846. Arkansas: *Maddox ARK-7,* 2791, EF647852. Arkansas: Yell Co., Ouachita Mountains, below the Hwy 27 bridge over Irons Fork, 16 October 1990, *Bates 10558* (UARK), 2930, EF647851. Georgia: *Maddox GA-5,* 2789, EF647847. Georgia: Greene Co., Siloam Outcrop, 12 May 2005, *Feist and Molano-Flores 2976,* EF647849. 2787, Maryland: *Maddox MG-4,* 2902, EF177754. Maryland: Sideling Creek, *Maddox MD-94-6,* 2792, EF647848. North Carolina: *Maddox NC-T-8,* 2790, EF647857. North Carolina: Granville County, Tar River, 26 August 2005, *Feist 3286* (ILLS)*,* 2936, EF647856. South Carolina: Aiken Co., Monetta, Windmill High Pond, Carolina Bay Road, 20 July 1992, *Hill 23921* (USF 206922), 2635, EF647843. South Carolina: Aiken Co., *Maddox SC-7-4,* 2784, EF177753. South Carolina: Saluda Co., *Maddox SC-7-3,* 2785, EF647844. South Carolina: Saluda Co., near Hibernia, Saluda Highpond, 11 May 2005, *Feist and Molano-Flores 3287* (ILLS)*,* 2900, EF647841. South Carolina: Aiken Co., Janet Harrison Highpond Heritage Preserve, 11 May 2005, *Feist and Molano-Flores 2967* (ILLS), 2901, EF647842. West Virginia: Morgan Co., along Sleepy Creek, 24 August 2005, *Feist, Harmon, and O'Malley 3181* (ILLS)*,* 2913, EF647850. West Virginia: Morgan Co., along the Cacapon River, 25 August 2005, *Feist, Harmon, and O'Malley 3284* (ILLS), 2933, EF647855. West Virginia: Berkeley Co., along Back Creek, 25 August 2005, *Feist, Harmon, and O'Malley 3285* (ILLS)*,* 2934, EF647854. ***P. nuttallii,*** U.S.A. Arkansas: Union Co., N of Calion and Chapelle Slough, 8 July 1993, *Thomas and Amason 134699* (MO 4995947), 2404, EF647858. Arkansas: Ashley Co., SE of Hamburg and NE of Ark. 52, 20 June 1986, *Thomas 97154* (WVA 114836), 2617, EF177758. Arkansas: Randolph Co., Water Valley, 1 July 1951, *Demaree 30962* (DUKE 139050), 2644, EF647860. Illinois: Randolph Co., W of Sparta, 16 July 2003, *Feist 2510* (ILLS), 2623, EF177759. Kansas: Labette Co., Mound Valley, 5 mi W, 2.5 mi S., 19 July 1995, *Freeman 7322* (WVA 114956), 2637, EF647859. Louisiana: Union Parish, ROW of LA 143 and power line in pine woods, 0.7 mi W of Haile, 10 June 1986, *Thomas 96932* (USF 200202), 2708, EF647861. Oklahoma: LeFlore Co., 1 mi S of Heavener along Kansas City and South RR, 21 May 1944, *Hopkins, Nelson, and Nelson 525* (RM 200002), 2643, EF647863. Mississippi: Monroe Co., ca. 3 mi W of Aberdeen, roadside of Hwy 8, 4.7 mi E of junction with Hwy 45 alternate, 6 June 1996, *MacDonald 9514* (DUKE 375296), 2642, EF647862. Oklahoma: Rogers Co., Claremore, along railroad in moist ground, 12 June 1974, *Jones 3030* (ILL), 2165, AY360256. ***P. × texense,*** U.S.A. Texas: Robertson Co., Mill Creek Bog, 4 October 1987, *Starbuck 1097* (TAMU 15147), 2772, EF647864. Texas: Smith Co., Swan, 17 September 1902, *Reverchon s.n.* (US 415665), 2909, EF647865.

Outgroup taxa. ***Atrema americanum*** DC., U.S.A. Texas: Williamson Co., S. of Jarrell, *Nesom and Grimes 6415* (MO 3691937), 1467, AY360232. ***Cynosciadium digitatum*** DC., U.S.A. Illinois: Jackson Co., Shawnee National Forest, *Phillippe 21886* (ILLS 183947), 1063, AY360237. ***Daucosma***

laciniatum Engelm. & A. Gray, U.S.A. Texas: Kerr Co., 26-30 June 1894, *Heller 1943* (MO 2535181), 2397, AY360238. ***Lilaeopsis carolinensis*** J. M. Coult. & Rose, U.S.A. cultivated, origin unknown, 1985, *Bogner s.n.*, material sent from *Petersen GPL4-1* (C), 2148, AF466276. ***L. mauritiana*** G. Petersen & Affolter, Republic of Mauritius. Le Val Nature Park, 3 May 1992, *Windelov s.n.*, material sent from *Petersen GPL8-1* (C), 2150, AF466277. ***L. novae-zelandiae*** (Gand.) A. W. Hill, New Zealand. cultivated, origin unknown, material sent from *Petersen GPL-9* (C), 2152, AF466278. ***Lilaeopsis occidentalis*** J. M. Coult. & Rose, U.S.A. Oregon: Douglas Co., East Gardiner, *Hill and Dutton 32982* (ILLS 203634), 1999, AY360242. ***Limnosciadium pinnatum*** (DC.) Mathias & Constance, U.S.A. Illinois: Champaign Co., *Hill 30580* (ILLS 198706), 2000, AY360243. ***Neogoezia minor*** Hemsl., Mexico. Oaxaca: Sierra de San Felipe, 1 August 1963, *Molseed 278* (ISU 1060), 2138, AY360244. ***Perideridia americana*** (Nutt. ex DC.) Rchb., U.S.A. Illinois: Champaign Co., Urbana, Hart Woods, 14 June 1994, *Downie 743* (ILL), 743, AY246908. ***P. gairdneri*** (Hook. & Arn.) Mathias subsp. ***borealis*** T. I. Chuang & Constance, U.S.A. Wyoming: Yellowstone National Park, 13 July 1961, *Comte 4300* (MO 3179847), 2361, EF647811. ***P. kelloggii*** (A. Gray) Mathias, U.S.A. California: Sonoma Co., King Ridge Rd., 5 mi N. of Cazadero, 6 August 1993, *Ornduff et al., s.n.* (UC), 778, U78373. ***Trepocarpus aethusae*** Nutt., U.S.A. Illinois: Alexander County, Horseshoe Lake Conservation Area, 8 July 1996, *Basinger 10891* (ILLS 19458), 1817, AY360264.

APPENDIX B

SPECIMENS EXAMINED FOR CHAPTER 4 WITH VOUCHER INFORMATION

ARKANSAS. Calhoun Co.: 2 mi S of Harrel, clearcut sweetbay Magnolia woods, 17 Sep 1987, *Sundell & Etheridge 7922* (BRIT, NO). Columbia Co.: Emerson, 8 Sep 1948, *D.M. Moore 480649* (SMU, UARK).

LOUISIANA. Allen Pa.: off LA 112 ca. 4 mi W of Elizabeth, infrequent in pine forest, 5 Sep 1981, *C.M. Allen 11315* (LSU). Beauregard Pa.: beside LA 110 6.5 mi SE of Merryville near Bearhead Creek, wet area, 3 Aug 1974, *R.D. Thomas 40979* (TENN). Calcasieu Pa.: Lake Charles, prairies, 14 Sep 1906, *R.S. Cocks s.n.* (NO); 4 mi S of Holmwood, grassy roadside, 23 Sep 1967, *J.W. Thieret 27955* (LAF); S of Lake Charles, on Hwy. 27, prairie, 19 Sep 1969, *C.A. Brown 20872* (LSU). Grant Pa.: Breezy Hill vicinity, ca. 1 mi N, Kisatchie N.F., longleaf pine woods on silty soil in a hillside seepage bog, 18 Aug 1997, *P.E. Hyatt & A. Martin 7691* (USCH). Jackson Pa.: beside LA 147 2 mi NW of LA 34 at Winn Parish Line S of Chatham, swampy area, 7 Sep 1987, *R.D. Thomas 101940* (TENN). Jefferson Davis Pa.: roadside ditch and RR ROW beside US 165 N of Fenton, 18 Oct 1975, *R.D. Thomas 47944* (FLAS, USCH). Natchitoches Pa.: ca. 7.5 mi NE of Kisatchie, in seepage area with pitcher plants, 28 Sep 1974, *C.M. Allen 5961* (LAF); near bridge on Longleaf Vista (FSR 337), ca. 9 mi NW of Gorum, abundant in bog, 28 Aug 1976, K. *Vincent 561* (DUKE, GA, LAF); Red Dirt Game Management Area, Kisatchie N.F., near Montrose Rd., stream near bog, 16 Sep 1976, *W.C. Holmes 2820* (UNA); on Strange Rd. in Kisatchie N.F., N of LA 479 and W of Goldonna near Ragan, bog, 17 Oct 1986, *R.D. Thomas & N. Gilmore 98858* (MO); Strange Road Bog, 0.8–0.9 mi N on FR 570, off Hwy. 479 near Goldonna, Kisatchie N.F., pitcher plant bog, 22 Aug 1987, *B.R. & M.H. MacRoberts 545* (LSUS); Strange Road Bog, 0.8–0.9 mi N on FR 570, off Hwy. 479 near Goldonna, Kisatchie N.F., pitcher plant bog, 20 June 1987, *B.R. & M.H. MacRoberts 432* (LSU); beside USFS 380 (Middle Branch Rd.) S of Longleaf Vista Rd. in Kisatchie N.F., E of LA 117, 17 Sep 1988, *R.D. Thomas 107272* (TENN); beside LA 479 at Strange Rd. W of Goldonna in Kisatchie N.F., moist seepage area, 14 Aug 1989, *R.D. Thomas & D. Bell 112081* (ILL); Kisatchie N.F., Winn Dist., Compt. 18, along Strange Rd. (USFS 570) N of Pitcher Plant Bog and S of Luster Creek, N of LA 479 W of Goldonna, pitcher plant bog, 29 Aug 1997, *R.D. Thomas 155187* (GA); Strange Road Bog, N of LA 479 and FSR 570 NW of Goldonna, pitcher plant bog area in pine forest, 26 Sep 2001, *D.M. Ferguson 366* (LSU); ca. 0.1 mi N of SR 126 and 0.7 mi E of SR 1233 (Pine Ridge) and 0.1 mi N of SR 126, Kisatchie N.F., in bog opening with longleaf pine and pitcher plant, 24 Sep 2009, *M.A. Feist & B. Molano-Flores 4426* (ILLS).Rapides Pa.: IPCO slash plantation (thinning study) near Hineston, longleaf pine, 20 Aug 1963, *H.E. Grelan 340* (USFS); next to Pecan Rd., just N of Arrowhead Rd., weedy clearcut longleaf pine forest, 20 Aug 1993, *C. Slaughter & J. Thompson 4115* (LSU); Hwy. 488 to FS 240, left at FS 2402, along dirt track, Kisatchie N.F., Evangeline District, bog with *Rhexia petiolata*, 15 Sep 1993, *J. Bruser 229* (LSU); W of Brushy Creek Rd., 4.85 km SW of S end of West Twin Lake, ca. 7.1 km W of Flagon Bayou, wooded seep, 16 Oct 2003, *P. Douglas, M. Arnett, & N. Hastings 1125* (LSU). Vernon Pa.: near Pickering, boggy branch long leaf pine hills with *Magnolia glauca*, black gum, poison sumac, pitcher plant, 3 Oct 1936, *C.A. Brown 6878* (LSU); 2 mi S of Evans along highway to Merryville, roadside near creek, 14 Aug 1967, *A. Lasseigne 730* (LAF); ca. 1.5 mi E of Pickering, roadside ditch, 4 Sep 1967, *J.W. Thieret 27754* (LAF); 2 mi W of LA 464 and Caney, swampy area in pine barrens, 3 Oct 1967, *R.D. Thomas 5515* (FLAS); Hwy. 312 near Toledo Bend Dam on Sabine River, long leaf pine woods, 4 Oct 1969, *C.A. Brown 21067* (LSU); ca. 3.5 mi E of Rosepine, abundant in bog near pond, 25 Sep 1976, *K. Vincent & C.M. Allen 655* (LAF, USF); along Pearl Creek ca. 3/4 mi NE of Burr Ferry on LA 111, infrequent in pine woods along Pearl Creek, 4 Nov 1979, *K. Vincent & C.M. Allen 3220* (LAF); on LA 28 ca. 1.2 mi W of Rapides-Vernon Parish line, pitcher plant bog, 11 Sep 1981, *F.M. Givens 2217* (LSU); W of Plainview Community Rd., 2.6 mi N of LA 392 and Hornsbeck, pitcher plant bog on gentle slope in pine woods, 13 Oct 1985, *R.D. Thomas 94549* (MO, TENN); E of Drake's Creek, ca. 2 mi E of Johnsonville Church and LA 10, ca. 7 mi E of Pickering, Kisatchie N.F., 7 Sep 1987, *R.D. Thomas 101487* (USCH); ca. 0.5 mi N of Big Branch Creek along Plainview Community Rd. 1.5 mi N from LA 392, 0.4 mi E of jct. LA 392 and US 171 in Hornbeck, sandy pasture and roadside with hillside seeps, 23 Aug 1989, *L.E. Urbatsch 5977* (LSU); S of 421 near Yoke Creek, Kisatchie N.F., bog in clay-soiled seepage savanna, 14 Sep 1990, *M.S. Olson 355* (LSU); Fort Polk Army Post, S of Range 8 and 8A, disturbed area in rolling upland, fine sandy loam, 27 Jul 1991, *C.M. Allen & A. Allen PLK0541* (OKL); Cooter's Bog, Kisatchie N.F., longleaf pine savannah with pitcher plant bog, 25 Sep 2009, *M.A. Feist & B. Molano-Flores 4447* (ILLS). Winn Pa.: 4 mi W of Winnfield, vicinity of limestone quarry, boggy open soil at edge of pocosin, 3 Aug 1938, *D.S Correll & H.B. Correll 10042* (DUKE); ca. 2.5 mi N of Verda, locally abundant in bog in pine forest, 11 Aug 1976, *K. Vincent & C.M. Allen 7152* (LAF, OS); ca. 1.1. mi E of SR 1233 (at Pine Ridge), just S of SR 126, Kisatchie N.F., roadside with *Cephalanthus occidentalis, Oxypolis rigidior, Eryngium integrifolium*, etc., 24 Sep 2009, *M.A. Feist & B. Molano-Flores 4442* (ILLS).

TEXAS. Anderson Co.: Gus Engeling W.M.A., NW of Palestine, boggy area around Lake 2, 28 Sep 1980, *C. Crozier s.n.* (BAYLU); Gus Engeling W.M.A., NW of Palestine, Lake 2 bog area, pasture 2, boggy area, with *Eupatorium, Helianthus, Eryngium*, 16 Oct 1993, *M. Dubrule Reed 1353* (TAMU); Gus Engeling W.M.A., NW of Palestine, Lake 2 bog area, pasture 2, sandy soil, with *Eupatorium, Helianthus, Eryngium*, 16 Oct 1993, *M. Dubrule Reed 1354* (TAMU); Chester's Pitcher Plant Bog, N end of Gus Engeling W.M.A., on Gibson Branch, S of FM 2961 just downstream from lake, pitcher plant bog, 9 Aug 1997, *B.R. & M.H. MacRoberts 3412* (BRIT, TEX). Angelina Co.: Angelina near Boykin Springs, Angelina N.F., seepage slope along stream in longleaf pine area, 30 Nov 1962, *D.S. Correll 26860* (LL); 2 mi NW of Bouton Lake along road on way to Rte. 69, Angelina N.F., on open-wooded seepage slope, 30 Nov 1962, *D.S. Correll 26883* (LL); about lake at Boykin Springs, Angelina N.F., wet soil, 7 Sep 1967, *D.S. Correll 34925* (LL); SW of FSR 313 and FSR 313A, N of Boykin Spring Recreation Area, Angelina N.F., acid seep in old-growth, burned, dry upland longleaf pine savannah, 14 Aug 1989, *S.L. Orzell & E.L. Bridges 11438* (TEX). Austin Co.: Austin Co., 15 Oct 1939, *B.C. Tharp s.n.* (MO, TEX). Brazos Co.: at College Station, road ditch, 25 Aug1948, *N.L. Byrd 230* (OSC). Cherokee Co.: Jacksonville, 8 Oct. 1884, *J.F. Joor s.n.* (MO). Freestone Co.: ca. 14.5 mi S of Fairfield, in bog, sandy valley bottom, 2 Oct 1949, *L.H. Shinners 11830* (SMU); ca. 15 mi S of Fairfield on US 75, 20 Sep 1958, *H. Gentry 2897* (BRIT, UNC); Womach Ranch, 7 mi NE of Buffalo, deep muck quaking bogs, upland basin (bowl), 17 Sep 2003, *J. Singhurst & E. Bridges 12343* (BAYLU). Hardin Co.: Nona, damp flat pinebarrens, 15 Nov 1893, *C. Mohr s.n.* (US); cut over longleaf pine, 5 Sep 1924, *B.C. Tharp 3158* (TEX); near Kountze, in sour flat in longleaf pine, 25 Aug 1945, *S.R. Warner 47-12* (TEX); 4 mi W of Silsbee, savannah, 10 Oct 1965, *D.S. Correll 31994* (LL, MO); along roadside of Hwy. 327 between Silsbee and Kountz, along pipeline crossing, 30 Sep 1971, *P.A. Amerson 834* (SMU); Roy E. Larson Sandylands Preserve, Tract 4, ca. 3.3 mi E of jct. of Hwy. 69 and Hwy. 418 on 418, S side of 418 and W side of Village Creek, 12 Aug 1994, *J. Singhurst 2270* (BAYLU); Roy E. Larson Sandylands Preserve, Tract 4, ca. 3.3 mi E of jct. of Hwy. 69 and Hwy. 418 on 418, S side of 418 and W side of Village Creek, 15 Oct 1994, *J. Singhurst 2019* (BAYLU); Roy E. Larson Sandylands Preserve, Tract 4, ca. 3.3 mi E of jct. of Hwy. 69 and Hwy. 418 on 418, S side of 418 and W side of Village Creek, 15 Oct 1994, *J. Singhurst 2050* (BAYLU); roadside ditch just outside of Roy E. Larson Sandylands Preserve, within the Hyatt Lake Estates, roadside ditch near longleaf pine savannah, 25 Sep 2009, *M.A. Feist & B. Molano-Flores 4464* (ILLS). Harris Co.: near Hockley, Sep 1890, *F.W. Thurow s.n.* (US). Henderson Co.: 8 mi from Athens, seepage slope along stream, 28 Aug 1946, *V.L. Cory 14188* (LL). Houston Co.: Grapeland, open sandy bogs, 16 Sep 1918, *E.J. Palmer 14423* (MO). Jasper Co.: off TX 63 NW of Beans Place, in pineland, 10 Sep 1942, *C.L. & A.A. Lundell 11903* (LL); in longleaf pine region in rolling country, 6 mi N of Kirbyville, evergreen shrub bog, 10 Nov 1962, *D.S. Correll 26755* (LL); 2 mi W of McGee Bend Dam, seepage slope among *Magnolia virginiana* and *Sarracenia*, 13 Nov 1963, *D.S. Correll 28638* (LL); Boykin Bog, bog, 23 Aug 1964, *R.P. Turner 144* (TEX); N side of Little Rocky Creek NE of Grubbs House, Little Rocky Preserve, ca. 3.4 mi E of jct. US 96 and FM 1007 near Browndell, locally frequent in wet sandy soil in forested seep in loblolly pine-hardwoods forest below open hillside seepage bog, 24 Sep 1997, *W.R. Carr 17060* (TEX); E of CR 348A, along small roadside stream in cutover longleaf pine savannah, 25 Sep 2009, *M.A. Feist & B. Molano-Flores 4458* (ILLS); E of CR 348A, along small stream in cutover longleaf pine savannah, 25 Sep 2009, *M.A. Feist & B. Molano-Flores 4463* (ILLS). Jefferson Co.: Beaumont, 15 Sep 1936, *J.L. Hooks s.n.* (TEX). Leon Co.: ca. 8.5 mi NE of Buffalo on US 79, seepage *Sarracenia* bog, 16 Sep 1994, *W.C. Holmes 7466* (BAYLU); Cripple Fawn Ranch, NE of Flynn, *Sarracenia* bog with *Pluchea, Myrica, Lobelia*, and *Solidago*, 10 Nov 1995, *M. Dubrule Reed 1738* (TAMU). Nacogdoches Co.: near Nacogdoches, 24 Sep 1938, *E. Whitehouse 11376* (SMU). Newton Co.: SF 1, 5 mi E of Kirbyville, moist sandy woods, 30 Sep 1945, *V.L. Cory 49817* (SMU, US); 1.5 mi E of county line along Farm Rd. 363 to Bon Wier, savannah between road and railroad, 30 Oct 1968, *D.S Correll & H.B. Correll 36692* (LL); 5 mi due W of Deweyville, edge of moist woods, 14 Sep 1968, *D.S. Correll 36530* (LL); Scrappin Valley Distinctive Site, Temple Inland Corp Land, 5.1 mi N of jct. of R 255 and Hwy. 87 at Mayflower Community on Hwy. 87, E side of Hwy. 87, *Sphagnum*-beakrush community, hill-side seepage slope bogs, acid seep spring bogs, 15 Oct 2002, *J. Singhurst 11262* (BAYLU). Robertson Co.: near Newbaden, widespread on bog, 30 Oct 1943, *J.J. Brady, B.C. Tharp, & F.A. Barkley 13750* (DUKE, MO NO, OKL, OKLA, RM, TEX, UARK, UNC, US); 15 mi SE of New Baden, moist area of bog, 11 Oct 1948, *E.M. Trew, Jr. 96* (TEX); 4 mi E of New Baden, bog, 21 Aug 1948, *G.L. Webster & C.M. Rowell 1904* (TEX); 5 mi E of New Baden, peat bog, 24 Oct 1948, *G.L. Webster & C.M. Rowell 1953* (TEX, UARK); Southworth bog, ca. 15 mi SE of New Baden, moist portion of bog, 11 Oct 1948, *J.J. Sperry 2157* (TAMU); Southworth Peat Bog, 12 mi E of New Baden, bog in Carrizo sands with cattails, pitcher plants, and panic grass, 20 Aug 1954, *E.L. Rabb 108* (TAMU); S.W. 1/4 Camp Creek Lake Quad., Mill Creek Bog, bog, 4 Oct 1981, *T. Starbuck 1097* (BRIT, TAMU). Smith Co.: Swan, swamps, 17 Sep 1902, *J. Reverehon 3193* (MO, US); Swan, swamps, 17 Sep 1902, *J. Reverchon s.n.* (MO, US); western Tyler, on ROW of Cotton Belt Railway, frequent in muddy ground along a small drainageway, 5 Sep 1949, *V.L. Cory 56892* (US). TylerCo.: Kirby Forest, near Warren and Kountze, 25 Aug 1945, *S.R. Warner 475* (TEX); ca. 2 mi NE of Warren, in a draw near a creek, 1 Oct 1945, *V.L. Cory 49869* (OKLA, SMU, US); 2.5 mi S of Warren, frequent in pitcher plant bog, 28 Sep 1948, *V.L. Cory 54898* (LL, SMU); ca. 10 mi E of Hillister on road to Spurger, evergreen shrub bog, pinelands, 15 Nov 1963, *D.S. Correll 28680* (LL); ca. 2 mi S of Warren on Rte. 69, boggy area, 15 Oct 1969, *D.S. Correll 38163* (LAF, LL, MO, UNC); Turkey Creek Unit, Big Thicket National Preserve, longleaf pine-black gum savannah, 10 Sep 1981, *A. Pecotte 32* (TAMU); NW corner of Big Thicket Bogs & Pineylands Preserve (TNC), 100 ft S of CR 4770, ca. 0.4–0.5 mi E of its jct. with US 69/287 near Lake Hyatt, frequent in moist to wet sandy loam in portion of boggy wetland with *Sphagnum* and *Sarracenia*, 25 Sep 1997, *W.R. Carr 17084* (TEX). Wood Co.: in a bog below dam of a small lake, ca. 2 mi N of Mineola, Rte. 37, bog, 29 Sep 1967, *D.S. Correll 35023* (LL). County unknown: damp flat pinebarrens, 15 Nov 1893, *C.N. Sabain s.n.* (US).

APPENDIX C

SPECIMENS FROM WHICH NUCLEAR RDNA ITS AND CPDNA SEQUENCE DATA WERE OBTAINED FOR CHAPTER 5, WITH VOUCHER OR SOURCE INFORMATION AND DNA AND GENBANK ACCESSION NUMBERS (WHEN AVAILABLE)

Taxon name — **DNA accession number**; voucher information; cpDNA GenBank no(s)., ITS GenBank no. Sequences newly generated for this study are marked with an asterisk (*). # -- indicates the *trnQ* and *trnK* sequences used were part of a longer sequence of the entire *psbI-trnK* region deposited to GenBank; ¥ -- indicates the *trnK* sequence used was part of a longer sequence of the *rps16* intron-*trnK* region deposited to GenBank.

Atrema americana Benth. & Hook. f. ex S. Watson — **1160;** U.S.A., Texas, Williamson Co., jnt. Hwys. 183 and 29, *Barclay & Perdue 785* (UC 184750); EF185206#, EF177699. ***Cynosciadium digitatum*** DC. — **1571;** U.S.A., Louisiana, Madison Parish, 1 mi E of Indian Lake, 28 May 1973, *Jones 215* (ILL); EF185219#, EF177704. **1986;** U.S.A., Arkansas, Lafayette Co., 4 mi E of Red River, Hwy. 82, 24 May 1993, *Sundell et al. 10,500* (ILL); EF185221#, EF177706. ***Daucosma laciniata*** Engelm. & A. Gray — **2912**; U.S.A., Texas, Uvalde Co., Garner State Park, 21 June 1958, *Sullivan & Turner 33* (GA 114044); TRNQ*, TRNK*, ITS*. **3411**; U.S.A., Texas, Bexar Co., San Antonio, 31 July 1921, *Schulz 594* (US 1087113); TRNQ*, TRNK*, ITS*. **3412**; U.S.A., Texas, Hays Co., Wimberly, 5 July 1942, *Fisher s.n.* (F 1501788); TRNQ*, TRNK*, ITS*. ***Lilaeopsis carolinensis*** J. M. Coult. & Rose — **2148**; U.S.A., cultivated, origin unknown, 1985, *Bogner s.n.*, material sent from *Petersen GPL4-1* (C); EF185225#, AF466276. ***Lilaeopsis mauritiana*** G. Petersen & Affolter — **2150**; Republic of Mauritius, Le Val Nature Park, 3 May 1992, *Windelov s.n.*, material sent from *Petersen GPL8-1* (C); EF185226, AF466277. ***Lilaeopsis novae-zelandiae*** (Gand.) A. W. Hill — **2152**; New Zealand. cultivated, origin unknown, material sent from *Petersen GPL-9* (C); EF185227#, AF466278. ***Lilaeopsis occidentalis*** J. M. Coulter & Rose — **1999**; U.S.A., Oregon, Douglas Co., East Gardiner, *Hill & Dutton 32982* (ILLS 203634); EF185228#, AY360242. ***Limnosciadium pinnatum*** (DC.) Mathias & Constance — **1511;** U.S.A., Louisiana, Ouachita Parish, Ouachita W.M.A., 20 May 1987, *Thomas et al. 99586I* (MO 3680921); EF185229#, EF177717. **2395;** U.S.A., Missouri, Stoddard Co., Otter Slough Conservation Area, 31 May 2000, *Brant et al. 4380* (MO 5186226); EF185230#, EF177720. ***Limnosciadium pumilum*** (Engelm. & A. Gray) Mathias & Constance — **3742;** U.S.A., Texas, San Patricio Co., US 181 NW of Sinton, 5 April 1984, *Ertter 5263* (NY); TRNQ*, TRNK*, ITS*. ***Neogoezia gracilipes*** (Hemsl.) Hemsl. — **2270;** Mexico, Oaxaca, Nochixtlan, N of La Joya, 2 October 1993, *Panero 3614* (UC 1611523); EF185232#, EF177726. ***Neogoezia minor*** Hemsl. — **2274;** Mexico, Oaxaca, Cerro San Felipe summit, *Breedlove & Almeda 59951* (UC 1518420); EF185236#, EF177730. ***Oxypolis canbyi*** (J.M. Coult. & Rose) Fern. — **2744**; U.S.A., South Carolina, Richland Co., Carolina Bay on N side of Vero Road and ca. 0.3 mi E of Sec. Hwy 2206, ca. 2 air mi NW of downtown Gadsden, 7 September 1984, *Nelson 3687* (NCU 537890); TRNQ*, TRNK*, EF647756. **2747**; U.S.A., North Carolina, Scotland Co., McIntosh Carolina Bay, US 401 NE of Laurinburg, 13 September 1992, *Sorrie 6946* (NCU 562048); TRNQ*, TRNK*, EF647757. **2751**; U.S.A., South Carolina, Lee Co., just NE of Mt Pleasant Church, W of Lynchburg, 10 September 1985, *Nelson 4271* (NCU 537512); TRNQ*, TRNK*, ITS*. **2937**; U.S.A., South Carolina, Bamberg Co., Bamberg Bay Preserve, 28 August 2005, *Feist, Molano-Flores & Glitzenstein 3193* (ILLS); TRNQ*, TRNK*, EF647759. **2938**; U.S.A., South Carolina, Bamberg Co., Oxypolis Bay Preserve, 28 August 2005, *Feist, Molano-Flores & Glitzenstein 3194* (ILLS); TRNQ*, TRNK*, EF647760. ***Oxypolis fendleri*** (A. Gray) A. Heller — **2350**; U.S.A., Colorado, Boulder Co., Forth of July Canyon, 10 July 1962, *Jones 34084* (ILL); TRNQ*, TRNK*, EF647767. **2351**; U.S.A., Colorado, Boulder Co., along Boulder Creek, 24 June 1962, *Jones 34450* (ILL); TRNQ*, TRNK*, EF647768. **2368**; U.S.A., New Mexico, Rio Arriba

Co., Ortega Mountains, 17 August 1984, *Hill 15181* (UC 1508862); TRNQ*, TRNK*, ITS*. **2369**; U.S.A., Colorado, Chafee Co., CO 306, 14 mi W of Buena Vista, 2 August 1973, *Haber & Given 2049* (CAN 370800); TRNQ*, EF185239¥, EF177734. ***Oxypolis filiformis*** (Walter) Britton — **2371**; U.S.A., Louisiana, Vernon Parish, E of Drake's Creek, ca. 2 mi E of Johnsville Church and LA 10, ca. 7 mi E of Pickering, Kisatchie National Forest, 7 September 1987, *Thomas 101486* (DAO 574521); TRNQ*, EF185240¥, EF177736. **2713**; U.S.A., Florida, Alachua Co., Gainesville, N side of NE 39th Ave. N. just E of Main St., 9 September 1987, *Alcorn 155* (FLAS 166610); TRNQ*, TRNK*, EF177737. ***Oxypolis filiformis*** × ***greenmanii*** — **2714**; U.S.A., Florida, Bay Co., along US 231, 1.8 mi N of the junction with FL Rt. 388, N of Youngstown, 29 August 1980, *Judd & Perkins 2714* (FLAS 174297); TRNQ*, EF185242¥, EF177739. ***Oxypolis greenmanii*** Mathias & Constance — **2717**; U.S.A., Florida, Bay Co., Tyndall Airforce Base, 15 September 1979, *Judd & Perkins 2439* (FLAS 174274); TRNQ*, TRNK*, EF177738. **2941**; U.S.A., Florida, Gulf Co., just E of Wetappo Creek and 3.6 mi S of FL 22, 2 September 2005, *Feist & Molano-Flores 3244* (ILLS); TRNQ*, TRNK*, EF647780. ***Oxypolis occidentalis*** J.M. Coult. & Rose — **1142**; U.S.A., California, El Dorado County, Osgood Swamp, *Follette s.n.* (JEPS 82187); EF185243#, AY360254. **1153**; U.S.A., California: Fresno Co., Wishon Reservoir Dam, *Call 2455* (UC 282880); EF185244#, EF177740. **2755**; U.S.A., Oregon, Douglas and Jackson Co., Abbott Creek Research Natural Area, ca. 20 mi W of Crater Lake near Abbott Butte, 29 July 1972, *Mitchell 348* (USFS 406185); TRNQ*, TRNK*, EF647784. **2756**; Canada. British Columbia: Queen Charlotte Islands, Graham Island, 2003, *Cheney s.n.* (ILLS); TRNQ*, TRNK*, EF647786. **2899**; U.S.A., California: Tehama Co., Forest Rd. 26N09 at Cascade Creek, NW of Chico Meadows, 1.1 mi SE of Hwy 32, 9 September 1997, *Oswald & Ahart 8863* (JEPS 94369); TRNQ*, TRNK*, EF647789. **2927**; U.S.A., California: Sierra Co., ca. 1.25 mi N of Scales, ca. 2 mi (air) SE of Poverty Hill, 28 September 2001, *Ahart 9295* (JEPS 102455); TRNQ*, TRNK*, EF647790. **2928**; U.S.A., Oregon, Lane Co., Quaking Aspen Swamp, 6 mi W of S end of Cougar Reservoir, 28 July 1979, *Wagner 2318* (ORE 103195); TRNQ*, TRNK*, EF647791. **2929**; U.S.A., Oregon, Klamath Co., near W boundary of Crater Lake Park, 24-29 August, *Wynd 1745* (ORE 64782); TRNQ*, TRNK*, EF647785. **3376**; U.S.A., California, Kern Co., French Meadow, 3 September 2007, *Feist & Molano-Flores FM-11*; TRNQ*, TRNK*, ITS*. **3413**; Canada, Queen Charlotte Islands, British Columbia, *Feist & Molano-Flores Site 4-2*; TRNQ*, TRNK*, ITS*. **3417**; U.S.A., California, Butte Co., 9 September 2007, *Feist & Molano-Flores BTC-13*; TRNQ*, TRNK*, ITS*. **3442**; U.S.A., Oregon, Lane Co., Quaking Aspen Swamp, 13 September 2007, *Feist & Molano-Flores QAS-25*; TRNQ*, TRNK*, ITS*. **3464**; U.S.A., California, San Bernardino Co., Lemon Lily Springs, 2 September 2007, *Feist & Molano-Flores LLS-24*; TRNQ*, TRNK*, ITS*. **3465**; U.S.A., California, San Bernardino Co., Lemon Lily Springs, 2 September 2007, *Feist & Molano-Flores LLS-16*; TRNQ*, TRNK*, ITS*. **3466**; U.S.A., California, San Bernardino Co., Lemon Lily Springs, 2 September 2007, *Feist & Molano-Flores LLS-10*; TRNQ*, TRNK*, ITS*. **3528**; U.S.A., California, Sierra Co., Scales, 25 October 2007, *Feist & Molano-Flores S-11*; TRNQ*, TRNK*, ITS*. **3532**; U.S.A., California, Tulare Co., Nelson Trail, 4 September 2007, *Feist & Molano-Flores NT-16*; TRNQ*, TRNK*, ITS*. ***Oxypolis rigidior*** (L.) Raf. — **1927**; U.S.A., Illinois, Vermilion Co., Windfall Hill Prairie Nature Preserve, Windfall Prairie Seep, 17 July 1991, *Phillippe, Morris & Simon 19411* (ILLS 177487); TRNQ*, EF185245¥, AY360255. **1998**; U.S.A., Louisiana, Winn Parish, along LA 126, 1.2 mi E of Jct. LA 1233, Kisatchie National Forest, 20 September 1981, *Kessler 1877* (ILL); EF185246#, EF177743. **2003**; U.S.A., Illinois, Lake Co., SE corner of Tri-state Tollway and Buckley Rd. by RR, 13 August 1981, *Robertson 2640* (ILLS 166045); EF185247#, EF177744. ***Oxypolis ternata*** (Nutt.) A. Heller —**2735**; U.S.A., South Carolina, Horry Co., 3.8 mi S. of Socastee and ca. 1 mi W. on dirt road, 25 October 1970, *Massey & Thomas 3480* (NCU 422851); TRNQ*, EF185248¥, EF177745. **2738**; U.S.A., North Carolina, Pender Co., Holly Shelter Game Land, 3 October 1997, *Horn & Dirig 362* (DUKE 363865); TRNQ*, EF185249¥, EF177746. **2940**; U.S.A., Florida, Wakulla Co., Saint Mark's National Wildlife Refuge, Panacea Unit Longterm Burn Plot (P13), ca. 2 km SE of Sopchoppy, 1 September 2005, *Feist, Molano-Flores & Glitzenstein 3222* (ILLS); TRNQ*, TRNK*, EF647809. ***Perideridia americana*** (Nutt. ex DC.) Reichenb. — **2033;** U.S.A., Illinois, Shelby Co., NE of Assumption, 2 June 1981, *Shildneck 12868* (ILL); TRNQ*, TRNK*, ITS*. ***Perideridia kelloggii*** (Gray) Mathias — **778**; U.S.A., California, Sonoma Co., King

Ridge Rd., 5 mi N. of Cazadero, 6 August 1993, *Ornduff et al. s.n.* (UC), cult. University of California Botanical Garden, Berkeley (no. 81.0521); EF185251#, U78373. ***Ptilimnium ahlesii*** Weakley & G.L. Nesom — **2648**; U.S.A., South Carolina, Berkeley Co., Cooper River at the mouth of Durham Creek, 7 June 1990, *McAninch 23* (NCU 557199); TRNQ*, EF185252¥, EF177747. **2969**; U.S.A., North Carolina, Brunswick Co., just E of Brunswick River and just N of the 74-76 causeway, ca. 2 mi W of Wilmington, 10 June 2004, *Weakley & LeBlond 7317* (sheet 2 of 2) (NCU); TRNQ*, TRNK*, EF647814. ***Ptilimnium capillaceum*** (Michx.) Raf. — **2701**; U.S.A., Virginia, Lancaster Co., Bellwood Marsh, S of Rt. 3 bridge, W of Lancaster, 22 July 1994, *Weldy 849* (BRIT); TRNQ*, TRNK*, EF177748. **2703**; U.S.A., Florida, Nassau Co., White Oak Plantation in the wedge formed by the junction of the Little St. Mary's River and St. Mary's River about 8-10 mi NW of Yulee, 19 June 1997, *Wilbur 67597* (BRIT); TRNQ*, TRNK*, EF647822. ***Ptilimnium costatum*** (Elliott) Raf. — **1646**; U.S.A., Illinois, Jackson Co., Shawnee National Forest, 20 September 1989, *Stritch 2159* (ILLS 172136); EF185253#, EF177749. **1970**; U.S.A., Illinois: Jackson Co., Shawnee National Forest, 11 September 1989, *Stritch 2124* (ILLS 172160); EF185254#, EF177750. **2402**; U.S.A., Missouri, Wayne Co., Hattie's Ford Fen Area, 12 October 2001, *Brant 4857* (MO 5573699); EF185256#, EF177752. **2707**; U.S.A., Kentucky, Calloway Co., right 0.7 miles on KY 121S from KY 614, 9 October 1972, *Athey 2197* (NCU 473641); TRNQ*, TRNK*, ITS*. ***Ptilimnium nodosum*** (Rose) Mathias — **2635**; U.S.A., South Carolina; Aiken Co., Monetta, Windmill High Pond, Carolina Bay Road, 20 July 1992, *Hill 23921* (USF 206922); TRNQ*, TRNK*, EF647843. **2784**; U.S.A., South Carolina, Aiken Co., *Maddox SC-7-4;* TRNQ*, EF185257¥, EF177753. **2787**; U.S.A., Maryland, *Maddox MG-4;* TRNQ*, EF185258¥, EF177754. **2900**; U.S.A., South Carolina, Saluda Co., near Hibernia, Saluda Highpond, 11 May 2005, *Feist & Molano-Flores 3287* (ILLS); TRNQ*, TRNK*, EF647841. **2902**; U.S.A., Georgia, Greene Co., Siloam Outcrop, 12 May 2005, *Feist & Molano-Flores Siloam*-5; TRNQ*, TRNK*, EF177754. **2930**; U.S.A., Arkansas, Yell Co., Ouachita Mountains, below the Hwy 27 bridge over Irons Fork, 16 October 1990, *Bates 10558* (UARK); TRNQ*, TRNK*, EF647851. **2931**; U.S.A., Alabama, DeKalb Co., Little River near AL Hwy. 35 bridge, DeSoto State Park, 15 July 1987, *Freeman s.n.* (AUA 46749); TRNQ*, TRNK*, EF647853. **2934**; U.S.A., West Virginia, Berkeley Co., along Back Creek, 25 August 2005, *Feist, Harmon & O'Malley 3285* (ILLS); TRNQ*, TRNK*, EF647854. **2936**; U.S.A., North Carolina, Granville County, Tar River, 26 August 2005, *Feist 3286* (ILLS); TRNQ*, TRNK*, EF647856. ***Ptilimnium nuttallii*** (DC.) Britton — **2165**; U.S.A. Oklahoma, Rogers Co., Claremore, along railroad in moist ground, 12 June 1974, *Jones 3030* (ILL); EF185259#, AY360256. **2617**; U.S.A. Arkansas, Ashley Co., SE of Hamburg and NE of Ark. 52, 20 June 1986, *Thomas 97154* (WVA 114836); TRNQ*, EF185260¥, EF177758. **2623**; U.S.A., Illinois, Randolph Co., W of Sparta, 16 July 2003, *Feist 2510* (ILLS); TRNQ*, EF185261¥, EF177759. ***Ptilimnium texense*** J.M. Coult. & Rose — **1981**; U.S.A., Louisiana, Natchitoches Parish, moist seepage area beside LA 479 at Strange Rd., W of Goldonna in Kisatchie National Forest, 14 August 1989, *Thomas & Bell 112081* (ILL); EF185255#, EF177751. **2905**; U.S.A., Texas, Anderson Co., Gus Engeling Wildlife Management Area, NW of Palestine, Lake 2 bog area, pasture 2, 16 October 1993, *Dubrule-Reed 1354* (TAMU 24011); TRNQ*, TRNK*, EF647825. ***Trepocarpus aethusae*** Nutt. — **1660;** U.S.A., Illinois, Saline Co., US Rt. 45, E of Harrisburg levee, 7 July 1999, *Hill 31876* (ILLS 201642); EF185279#, EF177761.

APPENDIX D

SPECIMENS FROM WHICH FRUIT ANATOMICAL OBSERVATIONS WERE MADE IN CHAPTER 5 WITH VOUCHER INFORMATION

Taxon name — voucher information.

Cynosciadium digitatum DC.— U.S.A., Arkansas, Monroe Co., Ark. Hwy. 1, ca. 2 mi NE of Cross Roads at Branch Missionary Baptist Church, *Sundell 15406* (BRIT). — U.S.A., Louisiana, Morehouse Pa., ½ mi E of Jones, 2 July 1968, *Thieret s.n.* (SMU 37382). ***Limnosciadium pinnatum*** (DC.) Mathias & Constance — U.S.A., Texas, Red River Co., N of Clarksville, 28 June 1945, *Lundell 14012* (LL). — U.S.A., Missouri, Stoddard Co., Otter Slough Conservation Area, 31 May 2000, *Brant et al. 4380* (MO 5186226). ***Limnosciadium pumilum*** (Engelm. & A. Gray) Mathias & Constance — U.S.A., Texas, Calhoun Co., vacant lot in Port O'Connel, 13 April 1952, *Gentry 1996* (BRIT). — U.S.A., Texas, San Patricio Co., US 181 NW of Sinton, 5 April 1984, *Ertter 5263* (NY). ***Oxypolis canbyi*** (J.M. Coult. & Rose) Fern. — U.S.A., South Carolina, Lee Co., W of Lynchburg, 10 September 1985, *Nelson 4269* (USCH 032054). — U.S.A., Georgia, Lee Co., NE Leesberg, 22 August 1948, *Muenscher s.n.* (NCU 65120). ***Oxypolis fendleri*** (A. Gray) A. Heller — U.S.A., Wyoming, Albany, Medicine Bow Forest, Elk Creek Study Bog, *Sturges 205* (RM 272453). — U.S.A., Wyoming, La Plata Mines, *E. Nelson s.n.* (RM 12350). — U.S.A., Colorado, Boulder Co., Eldora, 22 July 1953, *Jones 20071* (ILL). ***Oxypolis filiformis*** (Walter) Britton — U.S.A., South Carolina, Charleston Co., Francis Marion N.F., 29 August 2009, *Feist & Molano-Flores 3197* (ILLS). — U.S.A., Florida, Calhoun Co., 29 August 1980, *Judd & Perkins 2729* (FLAS 174320). ***Oxypolis greenmanii*** Mathias & Constance — U.S.A., Florida, Gulf Co., 17 mi N of Port St. Joe, 7 September 1955, *Godfrey 53756* (NCSC 52879). — U.S.A., Florida, Bay Co., Tyndall Airforce Base, 15 September 1979, *Judd & Perkins 2439* (FLAS 174274). ***Oxypolis occidentalis*** J.M. Coult. & Rose — U.S.A., California, Lemon Lily Springs, 2 September 2007, *Feist & Molano-Flores 4106* (ILLS). — U.S.A., Oregon, Lane Co., Quaking Aspen Swamp, 17 September 2007, *Feist & Molano-Flores 4131* (ILLS). — U.S.A., California, Kern Co. Portuguese Meadow, 27 September 1936, *L. Benson 8007* (POM 287809). ***Oxypolis rigidior*** (L.) Raf. — Canada, Ontario, Essex Co., 5.3 km E & 5.7 km N of Leamington, s.d., *Oldham 6994* (CAN 522163). — U.S.A., Indiana, Tippecanoe Co., Ross Biological Reserve, 2 October 1958, *Webster & Webster 7206* (DUKE 147518). — U.S.A., Tennessee, Munroe Co., Cherokee N.F., 21 September 1938, *M. Shaver s.n.* (UGA 79326). ***Oxypolis ternata*** (Nutt.) A. Heller — U.S.A., Florida, Franklin Co., near Wright Lake, Apalachicola N.F., 12 November 1969, *Godfrey 69254* (USF 88592). — U.S.A., North Carolina, Lee Co., 0.3 mi E of jct. of 1176 and 1179 on 1176, 17 October 1967, *Bozeman 11639* (NCU 303709). ***Ptilimnium ahlesii*** Weakley & G.L. Nesom — U.S.A., Georgia, Chatham Co., Savannah National Wildlife Refuge, along Hwy 17, 14 July 1966, *Bozeman 6100* (NCU 339364). — U.S.A., South Carolina, Beaufort Co., Trichinham Plantation, 27 June 1956, *Bell 3767* (NCU 97910). ***Ptilimnium capillaceum*** (Michx.) Raf. — U.S.A., Louisiana, Vermillion Pa., Pecan Island, 28 June 1963, *Valentine s.n.* (SMU). — U.S.A., South Carolina, Clarendon Co., at St. Paul, *Nelson 13280* (USCH 58378). ***Ptilimnium costatum*** (Elliott) Raf. — U.S.A., Illinois, Washington Co., 25 September 2001, *Feist s.n.* (ILLS). U.S.A., Oklahoma, Pushtamaha Co., Antlers, 23 Oct. 1915, *Palmer 8989* (MO 793414). ***Ptilimnium nodosum*** (Rose) Mathias — U.S.A., South Carolina, Aiken Co., Janet Harrison High Pond, 11 May 2005, *Feist & Molano-Flores 2967.1* (ILLS). — U.S.A., West Virginia, Morgan Co., along Sleepy Creek, 23 August 2005, *Feist 3188* (ILLS). — U.S.A., Alabama, Tuscaloosa Co., North River, 15 mi N of Tuscaloosa, *Easterly Ala. 146* (WVA 114892). ***Ptilimnium nuttallii*** (DC.) Britton — U.S.A., Texas, Kaufman Co., 1.75 mi E of Terrell, 14 June 1946, *Cory 53275* (SMU). — U.S.A., Kansas, Labette Co., Mound Valley, 19 July 1995, *Freeman 7322* (WVU 114956). ***Ptilimnium texense*** J.M. Coult. & Rose — U.S.A., Texas, Freestone Co., 14.5 mi S. of Fairfield, 2 October 1949, *Shinners 11830* (SMU). — U.S.A., Texas, Tyler Co., ca. 2 mi E of Warren, 5 October 1969, *Correll 3813* (LAF 46206).