Revised generic delimitations for *Oxypolis* and *Ptilimnium* (Apiaceae) based on leaf morphology, comparative fruit anatomy, and phylogenetic analysis of nuclear rDNA ITS and cpDNA *trnQ-trnK* intergenic spacer sequence data

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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 also 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 development of the marginal ribs. The fruits of rachis-leaved *Oxypolis* and rachis-leaved *Ptilimnium* species also differ in the compression of the mericarps and the development of the marginal ribs. Based on analyses of molecular data and corroboration with morphological and fruit anatomical data, new circumscriptions for the genera *Oxypolis* and *Ptilimnium* are formalized. Each of the two polyphyletic genera (*Oxypolis* and *Ptilimnium*) is split, two genera (*Tiedemannia* and *Harperella*) are resurrected, and three new combinations are made.

Keywords *Harperella*; new combinations; Oenantheae; *Oxypolis*; *Ptilimnium*; rachis leaves, *Tiedemannia*

◼ 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* of six species. These names with taxonomic authorities are presented in Table 1. 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., *O. canbyi*, *P. nodosum*) listed as federally endangered in the U.S.A. (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 an unusual 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, also 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 and 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 the shared features of their fruit, including their strong dorsal compression and broad marginal wings. Candolle (1829) created separate genera for the rachis-leaved and compound-leaved *Oxypolis* species (*Tiedemannia* and *Archemora*, respectively), but Coulter & 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 species) 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 marginal 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. These classifications, however, have not always held up to molecular systematic studies (Downie & Katz-Downie, 1996; Downie & al., 1996, 1998, 2001; Plunkett & al., 1996; Calviño & Downie, 2007; Magee & al., 2010a). This is the result of a complex pattern of parallelisms and convergences of fruit characters within the family (Plunkett & al., 1996; Downie & al., 1998; Lee & al., 2001; Liu & al., 2009, Magee & al., 2009b). For example, characters such as dorsal flattening and wing formation have evolved in several independent lineages of Apioideae, most likely as a

dispersal mechanism (Theobald, 1971; Downie & al., 2000c; Spalik & Downie, 2001; Winter & al., 2008), and therefore cannot necessarily be taken as evidence of close relationship. This has brought the taxonomic value of fruit characters into question (Downie & al., 2001; Spalik & Downie, 2001; Calviño & al., 2006; Liu & al., 2006). Liu & 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 & al., 2004, 2008; Hardway & al., 2004; Lee & Downie, 2006; Spalik & Downie, 2006; Feist & Downie, 2008; Spalik & 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 & al., 2008; Feist & Downie, 2008). The Feist & Downie (2008) study was based solely on nrDNA internal transcribed spacer (ITS) sequences. The Downie & al. (2008) study 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 the polyphyly of both *Oxypolis* and *Ptilimnium*, 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 leaf morphology and an additional independent source of

Table 1. Current circumscription of *Oxypolis* and *Ptilimnium* and proposed new combinations for taxa included in this study.

Current classification	New combinations and reinstatements
Oxypolis canbyi (J.M. Coult. & Rose) Fernald	*Tiedemannia canbyi* (J.M. Coult. & Rose) Feist & S.R. Downie
Oxypolis fendleri (A. Gray) A. Heller	
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 occidentalis J.M. Coult. & Rose	
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	

evidence, fruit anatomical data, to determine if they corroborate the molecular results. We then provide new circumscriptions for the genera *Oxypolis* and *Ptilimnium* based on these multiple lines of evidence. Each of the two polyphyletic genera (*Oxypolis* and *Ptilimnium*) is split, two genera (*Tiedemannia* and *Harperella*) are resurrected, and three new combinations are made. A key to these four genera is included in the Taxonomic Treatment section below. 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 & al. (2008) found that among the five noncoding plastid DNA loci they examined, the *trnQ-5'rps16* and *3'rps16-5'trnK* intergenic 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 from 76 accessions and complete sequences of the nrDNA ITS region from 66 accessions were used in this study (Appendix 1). Sequences were obtained for all seven species of *Oxypolis* and six species of *Ptilimnium*. Sequence data for one accession of the purported hybrid *Oxypolis filiformis × O. 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 1). Previous phylogenetic studies which have included the *Oenanthe* clade or tribe Oenantheae (Plunkett & al., 1996; Downie & al., 1996, 1998, 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 Clade (Hardway & al., 2004; Downie & al., 2008). Accessions of these genera were included in the phylogenetic analyses to show their placements relative to *Oxypolis* and *Ptilimnium* (Appendix 1). 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 & al. (2004), and *Lilaeopsis* which follows Affolter (1985).

DNA extraction, purification, and sequencing. — For this study, *trnQ*, *trnK*, and ITS sequences were newly generated for 55, 44, and 9 accessions, respectively. The remaining sequences used had already been published (Downie & Katz-Downie, 1996; Downie & al., 2000a, 2008; Hardway & al., 2004; 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, Valencia, California, U.S.A.) according to the manufacturer's instructions. The entire ITS region (ITS-1,

5.8S rDNA, 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 & al., 2000a). PCR products (templates) were purified using either a QIAquick Gel Extraction Kit or a QIAquick PCR Purification Kit (Qiagen) following manufacturer's instructions. For cpDNA, sequences were obtained for the $trnQ^{(UUG)}$-*rps16* 5′ exon and *rps16* 3′ exon-$trnK^{(UUU)}$ intergenic spacers using the primers trnQ, rps16-1R, rps16-2, and trnK (Downie & Katz-Downie, 1996; Lee & Downie, 2006; Downie & al., 2008). The "rpl16" program of Shaw & al. (2005) was used for the cpDNA regions because it is effective across a wide range of taxa and genomic regions (Shaw & al., 2007). PCR products were checked on 1% agarose gels and then purified according to the ExoSAP protocol of Werle & al. (1994) using 5 U of Exonuclease I (New England Biolabs, Ipswich, Massachusetts, U.S.A.) and 0.5 U of Shrimp Alkaline Phosphatase (Promega, Madison, Wisconsin, U.S.A.). Sequence reactions for all sequences were carried out using an ABI Prism Big Dye Terminator v.3.1 Ready Reaction Cycle Sequencing Kit (Applied Biosystems, Foster City, California, U.S.A.). Sequence reaction products were visualized using an ABI 3730XL high-throughput DNA capillary sequencer. All newly acquired sequences used in this study have been deposited in GenBank (www.ncbi.nlm.nih.gov/genbank/). See Appendix 1 for GenBank accession numbers.

Sequence alignment and phylogenetic analysis. — Sequences were aligned using Clustal X v.1.83 (Thompson & al., 1997) and manually adjusted as necessary using the alignment editor Bioedit v.7.0.9.0 (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 & 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*, *trnK*, 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 2). The cpDNA and cpDNA/indels datasets included sequences of 76 accessions (65 terminals). The cpDNA/ITS dataset 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* v.4.0b10 (Swofford, 2003). Before combining the ITS and cpDNA datasets, the incongruence length difference test of Farris & 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

Table 2. 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 Fig. 1 and/or Fig. 2. Accession numbers in the third column have identical sequences to those presented in the second column for the regions indicated. Voucher information for all accessions is provided in Appendix 1.

Taxon	Accession number	Accessions with identical sequences (regions for which it is identical)
Daucosma laciniata	3411	3412 (*trnQ*/*trnK*)
Oxypolis canbyi	2937	2938 (*trnQ*/*trnK*)
Oxypolis fendleri	2350	2351, 2369 (*trnQ*/*trnK*)
Oxypolis greenmanii	2941	2717 (*trnQ*/*trnK*/ITS)
Oxypolis occidentalis	3464	3465, 3466 (*trnQ*/*trnK*)
	2929	2937 (*trnQ*/*trnK*/ITS)
	2928	2927 (*trnQ*/*trnK*)
	2755	3442 (*trnQ*/*trnK*)
Ptilimnium nodosum	2784	2635 (*trnQ*/*trnK*/ITS)

branch swapping; MaxTrees was set to 20,000. The aligned data matrices are available in TreeBASE (http://purl.org/phylo/treebase/phylows/study/TB2:S12295).

Maximum parsimony (MP) analyses of each 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, and gaps treated as missing data. Bootstrap (BS) analyses were done on all datasets to assess clade support. For all datasets 1000 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. For the cpDNA and cpDNA/indels datasets MaxTrees was set to 5000 trees per replicate; for the cpDNA/ITS dataset it was set to 20,000 trees per replicate.

MrBayes v.3.1.2 (Huelsenbeck & Ronquist, 2001) was used to conduct Bayesian inference (BI) analyses of the three datasets (cpDNA, cpDNA/indels, cpDNA/ITS). Modeltest v.3.7 (Posada & Crandall, 1998) was used to select the appropriate evolutionary models of nucleotide substitution for each of the three DNA regions. The models that best fit these data, as selected by the Akaike information criteria (AIC) estimator, were used in the BI analyses. A restriction site (binary) model was implemented for the indels partition in the cpDNA/indels dataset. For each dataset, two independent runs of four chains each were conducted for 2,000,000 generations with a sample frequency of 100. Plots of generation number vs. likelihood value were inspected and stationarity was determined to have been reached after 4000 trees were sampled. For each dataset, the 4000 trees sampled prior to stationarity (the burn-in) were discarded and a majority-rule consensus tree was constructed from the remaining trees to show the posterior probability values of all observed bipartitions.

The MP and BI analyses were performed on cpDNA, cpDNA/indel, and combined cpDNA/ITS datasets that both included and excluded the single accession of the hybrid *Oxypolis filiformis* × *O. greenmanii*. This was done to assess whether the inclusion of this hybrid had any effect on the placement of other taxa in the phylogenetic trees.

Fruit anatomy. — Fruits from herbarium specimens were used in an anatomical study (Appendix 2). 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. For each species, fruits from between one and three accessions were examined. To make transverse sections, 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 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. The maximum pairwise sequence divergence value 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 selected the SYM+I+G model of evolution to be used for the ITS region in the BI analysis of combined data.

cpDNA datasets. — The cpDNA dataset had an aligned sequence length of 2813 positions. Due to alignment ambiguities 409 positions were excluded from further analyses. Of the remaining 2404 aligned positions, 280 were parsimony-informative and 88 were autapomorphic. The cpDNA/indel dataset with 63 binary-scored alignment gaps had a total of 343 parsimony-informative characters. The maximum pairwise sequence divergence value 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). Modeltest selected the GTR+G and GTR+I+G models for the *trnQ* and *trnK* regions, respectively, for use in the BI analyses.

MP analysis of the cpDNA dataset resulted in 23,229 trees of 473 steps each (consistency index CI = 0.854 and 0.824, with and without uninformative characters, respectively; retention index RI = 0.964).

MP analysis of the cpDNA/indel dataset resulted in 4698 trees of 554 steps each (CI = 0.843 and 0.811, with and without uninformative characters, respectively; RI = 0.963). 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 (BS = 79) in the cpDNA/indels MP strict consensus tree (Fig. 1) but not in the cpDNA MP strict consensus tree (not shown), and support for this group was increased from PP = 0.51 in the cpDNA BI majority-rule consensus tree (not shown) to PP = 0.89 in the cpDNA/indels BI majority-rule consensus tree (not shown). For this reason, only the results of cpDNA/indels analyses are discussed hereafter.

The cpDNA/indels MP tree and cpDNA/indels BI tree were congruent except that in the BI tree, all accessions of *Oxypolis rigidior* formed a weakly supported monophyletic group (PP = 0.54), whereas in the cpDNA/indels MP tree, they did not. Other species not resolved as monophyletic in the cpDNA/indels MP and BI trees were *P. ahlesii*, *P. capillaceum*, *O. filiformis*, *O. rigidior*, and *O. ternata*. *Ptilimnium ahlesii* formed a strongly supported monophyletic group with *P. capillaceum* in the cpDNA/indels analyses (BS = 100, PP = 1.00), as did *O. ternata* with *O. rigidior* (BS = 96, PP = 1.00). One accession of *O. filiformis* came out as sister group to the clade which includes all accessions of *O. canbyi* (BS = 69, PP = 0.92), while the other accession of *O. filiformis* formed a weakly supported clade with *O. greenmanii* and their purported hybrid *O. filiformis × O. greenmanii* (BS = 64, PP = 0.79). These relationships did not change when *O. filiformis × O. greenmanii* was excluded from the MP and BI analyses.

Oxypolis occidentalis is divided into two strongly to moderately supported clades (Fig. 1). The two major clades of *O. occidentalis* consist of populations that are separated geographically and can be referred to as the North clade and the South clade. The North clade (BS = 89, PP = 1.00) consists

of individuals from populations from Haida Gwaii (formerly the Queen Charlotte Islands) in British Columbia, the Cascade Mountains in Oregon, and the Cascade Range Foothills in northern California. The South clade (BS = 71, PP = 0.98) 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/ indels data matrix were completely congruent. *Ptilimnium* s.l. and *Oxypolis* s.l. were each not monophyletic. *Ptilimnium* s.l. was split between two clades: Clade 1 (*Ptilimnium*) comprised of the compound-leaved species of *Ptilimnium* (i.e., *P. ahlesii*, *P. capillaceum*, *P. costatum*, *P. nuttallii*, and *P. texense*) and Clade 2 (*Harperella*) containing the single rachis-leaved species of *Ptilimnium* (i.e., *P. nodosum*). *Oxypolis* s.l. was also split between two clades: Clade 3 (*Tiedemannia*) comprised of the rachis-leaved species of *Oxypolis* (i.e., *O. canbyi*, *O. filiformis*, and *O. greenmanii*) and Clade 4 (*Oxypolis*) containing the compound-leaved species of *Oxypolis* (i.e., *O. fendleri*, *O. occidentalis*, *O. rigidior*, and *O. ternata*). Clade 3 (*Tiedemannia*) is sister to Clade 1 (*Ptilimnium*) and quite distant in the tree from Clade 4 (*Oxypolis*). Clades 1, 2, and 3 were each strongly supported, whereas Clade 4 (*Oxypolis*) had moderate support (BS = 83, PP = 0.99).

In previous analyses based on ITS sequences (Feist & Downie, 2008), the evolutionary relationships among the following five groups were not resolved: Clade 1 (*Ptilimnium*), Clade 2 (*Harperella*), Clade 3 (*Tiedemannia*), *Limnosciadium*, and *Cynosciadium*. These five groups formed what was essentially a polytomy (fig. 1 in Feist & Downie, 2008). The results of the cpDNA/indels analyses presented herein, however, strongly support the sister relationship between Clade 1 (*Ptilimnium*) and Clade 3 (*Tiedemannia*) (BS = 98, PP = 1.00). Together, these two groups form a strongly supported sister relationship with Clade 2 (*Harperella*) (BS = 86, PP = 0.99), followed by the successively basal sister groups *Limnosciadium* (BS = 66, PP = 0.85) and *Cynosciadium* (BS = 100, PP = 1.00).

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 & al., 2004; Downie & 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 americanum* and *Trepocarpus aethusae* Nutt. (BS = 87, PP = 1.00).

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 3452 positions. Due to alignment ambiguities 513 positions were excluded from further analyses. Of the remaining 2939 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).

The maximum pairwise sequence divergence value 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* species 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
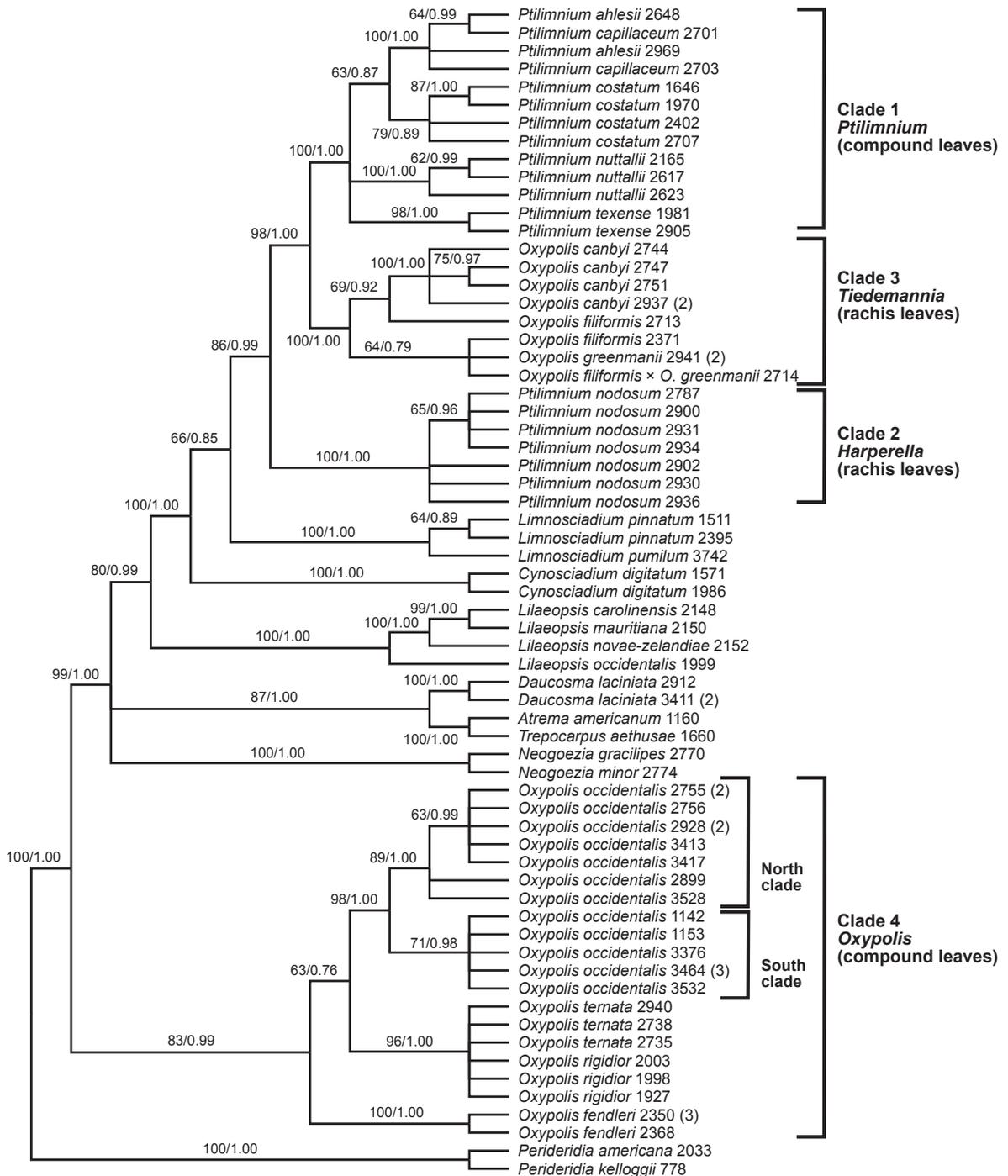

Fig. 1. Strict consensus tree of 4698 minimal-length 554-step trees obtained from the MP analysis of the cpDNA/indels dataset (CI = 0.843 and 0.811, with and without uninformative characters, respectively; RI = 0.963). Numbers on branches represent bootstrap estimates and Bayesian posterior probability values, respectively. Numbers in parentheses following the name of a taxon indicate the number of accessions of that taxon having identical DNA sequences (Table 2).

intraspecific variation, except for *P. ahlesii* and *P. capillaceum* which had sequences that were identical to one another.

MP analysis resulted in 32 trees of 1184 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. 2 with branch lengths. The topology of the BI tree is consistent with that of the MP strict consensus tree

(not shown) except at the nodes where an asterisk (*) is given to indicate that the BS value was less than 50%.

As in the cpDNA/indels analyses, *Ptilimnium ahlesii* and *P. capillaceum* are each not monophyletic, but together they form a strongly supported monophyletic group (BS = 100, PP = 1.00). *Oxypolis filiformis* is also not monophyletic, but it forms a monophyletic group with *O. greenmanii* and their
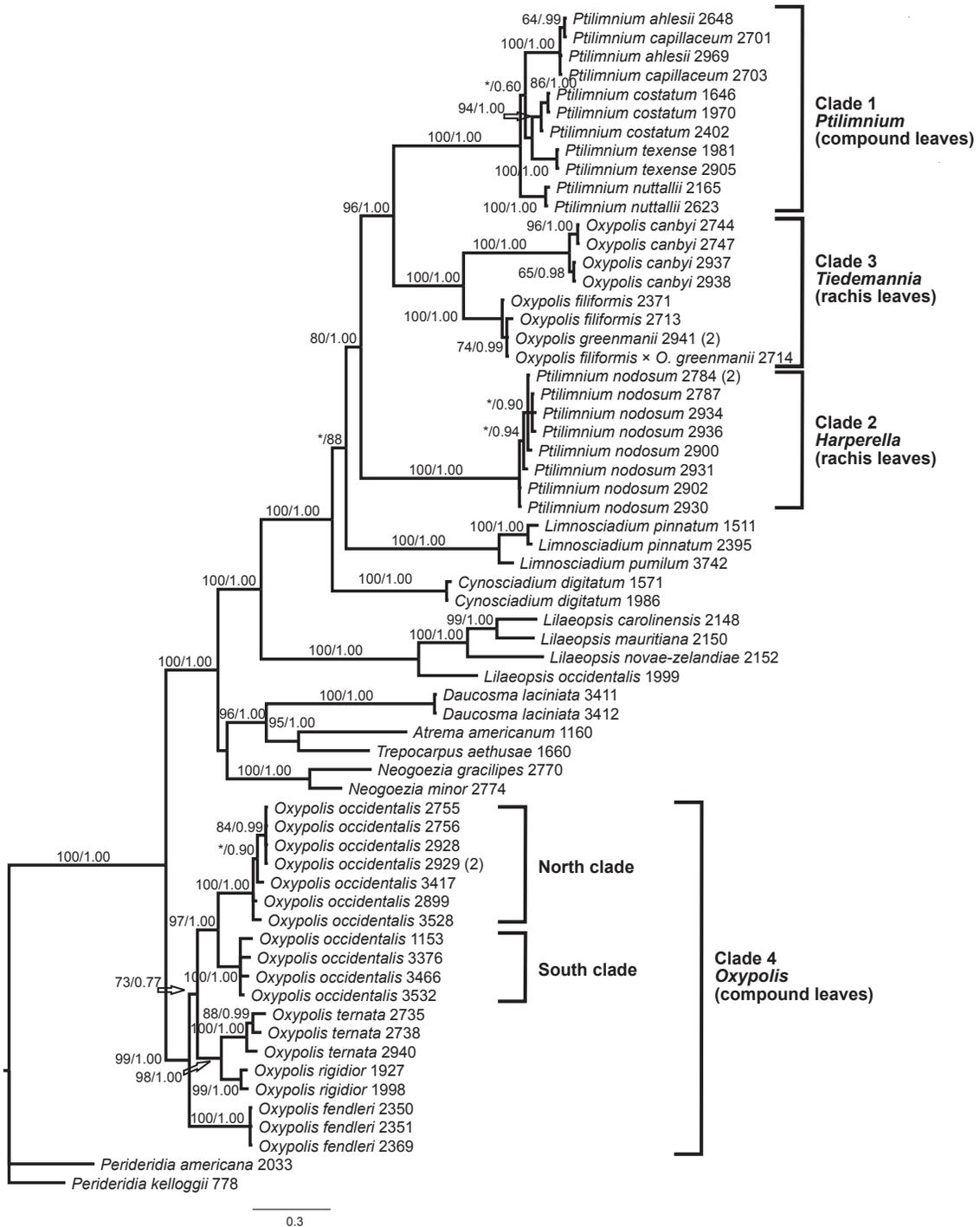
Fig. 2. Majority-rule consensus tree obtained from the BI analysis of the cpDNA/ITS dataset. Numbers on branches represent bootstrap estimates and Bayesian posterior probability values, respectively; a bootstrap estimate of less than 50% is indicated with an asterisk (*). Numbers in parentheses following the name of a taxon indicate the number of accessions of that taxon having identical DNA sequences (Table 2).

hybrid, *O. filiformis* × *O. greenmanii* (BS = 100, PP = 1.00). When *O. filiformis* × *O. greenmanii* is excluded from the MP and BI analyses, the relationships among the remaining taxa do not change.

Both 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 (BS = 94, PP = 1.00) as it was in the cpDNA/indel strict consensus tree. In contrast to the results of the cpDNA/indel 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. are again each 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/indels tree (Fig. 1), *Daucosma laciniata* is monophyletic and is sister to a clade formed by *Atrema americanum* and *Trepocarpus aethusae* (BS = 96, PP = 1.00).

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 species have homomericarpic fruits with a very broad commissure that extends over the full width of the mericarp. The mericarps are slightly to prominently dorsally compressed with narrow to broadly winged marginal ribs, except those of *P. nodosum* which are prominently isodiametric and with the marginal ribs not winged (Fig. 3A). The compound-leaved species of *Ptilimnium* (i.e., *P. ahlesii*, *P. capillaceum*, *P. costatum*, *P. nuttallii*, and *P. texense)* have fruits with slightly dorsally compressed mericarps and thick, narrowly winged marginal ribs that extend only slightly beyond the marginal vascular bundles (Fig. 3B–F). The fruits of the species of *Ptilimnium* s.l. (Fig. 3A–F) are distinguished from those of *Oxypolis* s.l. (Fig. 3G–L; *O. ternata* not shown), as well as *Cynosciadium* (Fig. 3M) and *Limnosciadium* (Fig. 3N–O), by the presence of prominent square or somewhat elongated cells external to the vittae (not shown), a character also reported for *Dasispermum* Raf. (Magee & al., 2009a, 2010b). The fruits of the species of *Oxypolis* s.l. are distinguished from the fruits of the species of *Ptilimnium* s.l., *Cynosciadium*, and *Limnosciadium* by their 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. 3J–L; *O. ternata* not shown). This latter group is distinguished furthermore from all other species studied by the presence of four to eight, often branching commissural vittae (Figs. 3J–L, 4A–C). The other species studied all have two commissural vittae which are never branching (Fig. 3A–I, M–O, 4D). The compound-leaved *Oxypolis* species are distinguished additionally 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 (Fig. 3G–I). In the rachis-leaved *Oxypolis* species the vittae are distinctly larger than the vascular bundles (Fig. 3J–L). The fruits of the closely related genera *Limnosciadium* (Fig. 3N–O) and *Cynosciadium* (Fig. 3M) can be distinguished from both *Oxypolis* s.l. and *Ptilimnium* s.l. by the presence of a lignified commissural keel, and furthermore in *Limnosciadium* by the sclerification of the mesocarp between the vascular bundles so that they appear continuous.

Oxypolis canbyi (a rachis-leaved species) has a unique wing type not found in any of the other winged species examined in this study. 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. 3I). Also, as mentioned by Tucker & al. (1983), a sclerified band of mesocarp cells is formed between the vascular bundle and the endocarp. In the other winged 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. 3B–H, J–O) and a sclerified band of mesocarp cells is not present between the vascular bundle and the endocarp. In the compound-leaved *Ptilimnium*, *Cynosciadium*, and *Limnosciadium* species, the true marginal wing remains narrow and extends slightly beyond the marginal vascular bundle (Fig. 3B–F, M–O). In the compound-leaved *Oxypolis*, *O. filiformis*, and *O. greenmanii*, the true marginal wing extends significantly beyond the vascular bundle (Fig. 3G, H, J–M).

■ DISCUSSION

***Ptilimnium/Harperella.* —** Morphological and molecular results from this study confirm what was proposed in previous studies (Downie & al., 2008; Feist & Downie, 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 but not winged, whereas the fruits of the compound-leaved *Ptilimnium* species are slightly dorsally compressed and have thick, narrowly winged marginal ribs that extend beyond the vascular bundles. In addition, *P. 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 any of the compound-leaved *Ptilimnium* species. 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*, *P. nuttallii*), and $n = 8$ or 14 (*P. capillaceum*) (Easterly, 1957a; Constance & al., 1976; Weakley & Nesom,
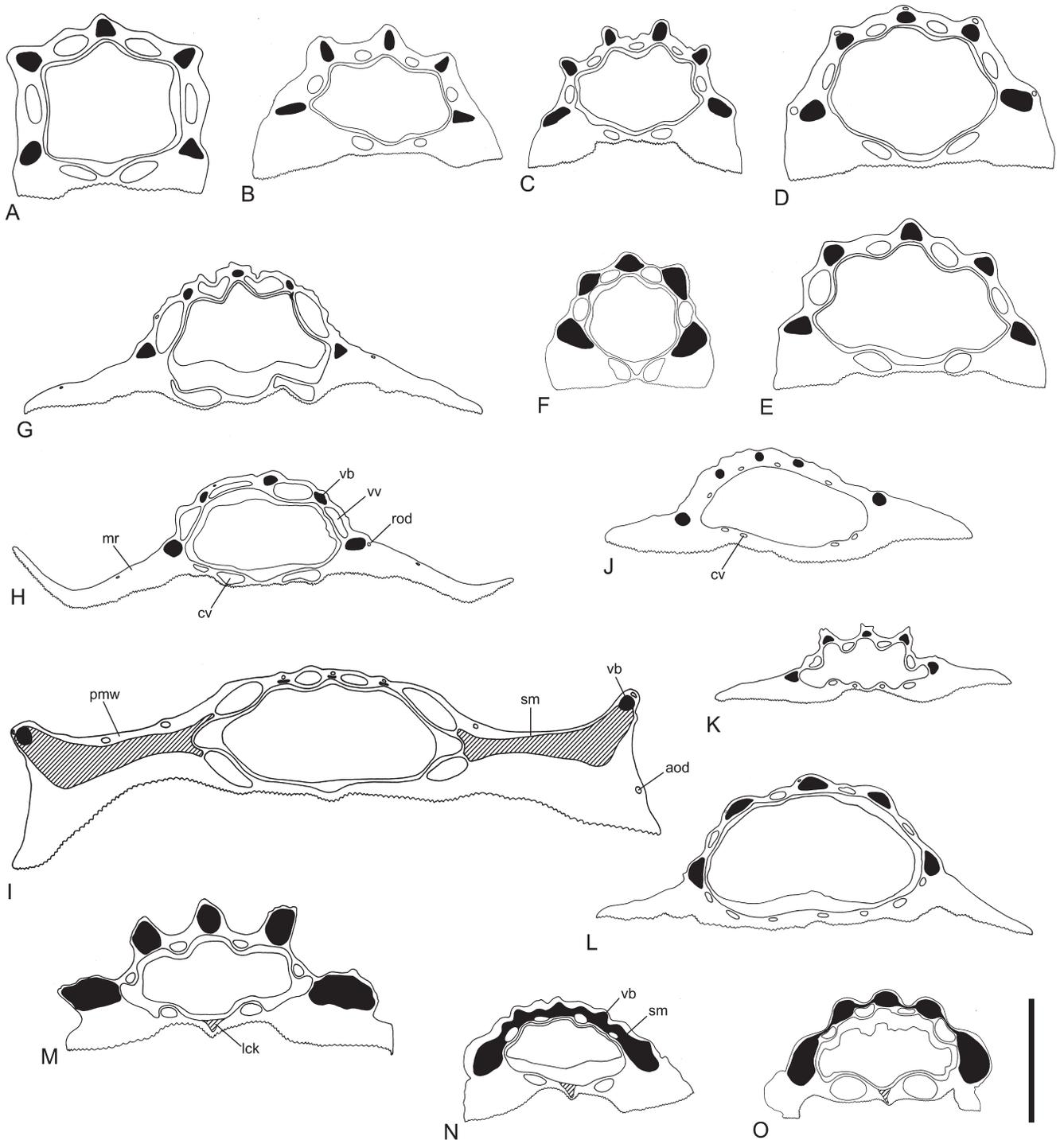
Fig. 3. Transverse sections of fruits of *Ptilimnium* s.l. **(A–F),** *Oxypolis* s.l. **(G–L),** *Cynosciadium* **(M),** and *Limnosciadium* **(N–O). A,** *Ptilimnium nodosum* (*Feist & Molano-Flores 2967.1*, ILLS); **B,** *Ptilimnium ahlesii* (*Bozeman 6100*, NCU); **C,** *Ptilimnium capillaceum* (*Valentine 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). — Abbreviations: 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 2.

2004). Maximum pairwise sequence divergence is much greater between *P. nodosum* and the compound-leaved *Ptilimnium* species (6.22%) than it is among all compound-leaved species of *Ptilimnium* (1.43%), or among the nine accessions of *P. nodosum* (0.19%) included in the study. In addition, the compound-leaved *Ptilimnium* are more closely related to the rachis-leaved *Oxypolis*, with which they form a strongly supported sister group, than they are to *P. nodosum*.

The type of the genus *Ptilimnium* is *P. capillaceum*. *Ptilimnium 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* s.str. was recognized as belonging to the genus *Harperella* Rose. Three species of *Harperella* were recognized (*H. nodosa* Rose, *H. fluviatilis* Rose, *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. *Ptilimnium nodosum* s.str. was still recognized as a separate species due to its unique habitat, phenology, and perceived larger size. Also, it was not thought to be able to proliferate through asexual reproduction, rooting at the nodes and producing individual plantlets, as *P. fluviatile* was known to do. Kral (1981) conducted a morphological study comparing *P. fluviatile* and *P. nodosum* s.str. Finding no consistent morphological differences he further grouped the taxa and included *P. fluviatile* within *P. nodosum* s.l. Furthermore, the ability to reproduce asexually, as described above, has been observed in populations of *P. nodosum* s.str. (Feist, pers. obs.) and so cannot be used to differentiate these taxa. Results from the ITS analyses of Feist & Downie (2008) showed some geographic separation of populations that conformed to the previous delimitations of *P. nodosum* as three species, however, the current analyses based on *trnQ* and *trnK* data and combined cpDNA and ITS data do not support these relationships. 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 species *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 the two previous studies where these two taxa have been included (Downie & 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*. This alone, however, is insufficient evidence for not recognizing *P. ahlesii* as a distinct species. While writing the treatment of the genus for the *Flora of North America* (Feist, unpub. data),

the morphological characters used to separate the two taxa were found to be inconsistent when specimens from across the geographic range of *P. capillaceum* were examined. Therefore, a morphological study is being conducted by the first author to determine the true status of *P. ahlesii*.

Oxypolis/Tiedemannia. — Morphological and molecular results from this study confirm what was proposed in previous studies (Downie & 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
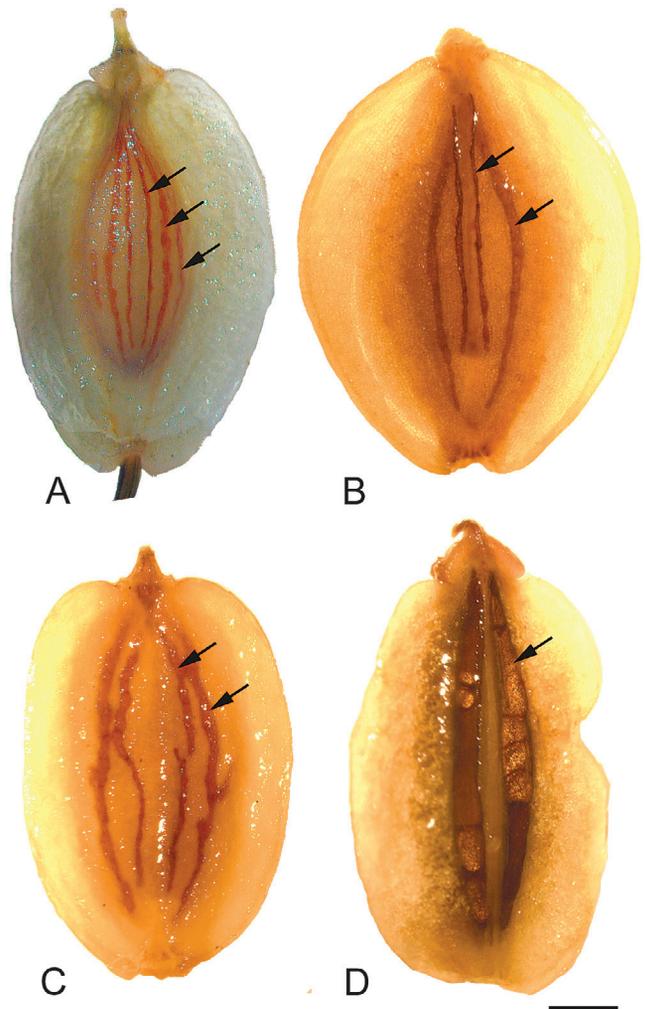
Fig. 4. Three-dimensional structure of the commissural vittae in the fruit of *Oxypolis* s.l. **A,** *Oxypolis rigidior* (*Oldham 6994*, CAN); **B,** *Oxypolis occidentalis* (*Feist & Molano-Flores 4106*, ILLS); **C,** *Oxypolis fendleri* (*Sturges 205*, RM); **D,** *Oxypolis filiformis* (*Feist & Molano-Flores 3197*, ILLS). — Arrows indicate commissural vittae. Scale: A–D = 1.4 mm.

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 is much greater between the rachis-leaved and compound-leaved *Oxypolis* species (7.62%) than it is among all compound-leaved species of *Oxypolis* (2.40%), or among all rachis-leaved species of *Oxypolis* (2.99%). The clade formed by the rachis-leaved *Oxypolis* is quite distant from the compound-leaved *Oxypolis* clade. In fact, the rachis-leaved *Oxypolis* species are more closely related to all the other genera within the North American Endemics Clade (i.e., *Ptilimnium*, *Limnosciadium*, *Cynosciadium*, *Lilaeopsis*, *Atrema*, *Trepocarpus*, *Daucosma*, and *Neogoezia*) than they are to the compound-leaved *Oxypolis* species. 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, 1960; Crawford & Hartman, 1972; Tucker & al., 1983; Pimenov & al., 2003).

The type of *Oxypolis* is *O. rigidior. Oxypolis rigidior* forms a monophyletic group with the other compound-leaved *Oxypolis*. We propose to split the genus *Oxypolis* into two genera conforming to the compound-leaved and rachis-leaved clades. In 1829 Candolle created the genus *Tiedemannia* (Candolle, 1829). He believed that the plant placed in the genus *Oenanthe* by Walter and Persoon (i.e., *Oenanthe filiformis* Walter, 1788; *Oenanthe carolinensis* Persoon, 1805) and *Sium* by Elliott (i.e., *Sium teretifolium* Elliott, 1817), all homotypic synonyms of *O. filiformis*, belonged in its own genus (i.e., *Tiedemannia*) based on the uniqueness of its fruit and its reduced leaf morphology. 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*.

Oxypolis filiformis is a widespread species, abundant in Florida and common in the Southeastern U.S.A. and occurs in a variety of different wetland habitats. *Oxypolis greenmanii* has a more restricted range, occurring in just a few counties in Florida, and seems to have a preference for *Hypericum* bogs, although it can be found in flatwoods, swamps, marshes, and roadside ditches as well. Although at first glance *O. greenmanii* appears to be strikingly different from *O. filiformis*, with its larger stature and maroon-colored flowers and fruits, Judd (1982) found that standard populations of *O. greenmanii* and *O. filiformis* are connected by an extensive series of intermediate populations that completely bridge the morphological gap between the two taxa. Judd (1982) hypothesized that these populations resulted from gradual geographic intergradation. In addition to these intermediate populations, populations that appear to be the result of recent hybridization also exist. These populations are not uniformly intermediate but are rather highly variable being composed of standard *O. greenmanii* and *O. filiformis* individuals, as well as a complete range of intermediate plants. Most plants within both the intermediate and highly variable populations were found to be highly fertile (ca. 90% to nearly all pollen grains stained with cotton-blue in lacto-phenol; Judd, 1982). *Oxypolis filiformis* and *O. greenmanii* also share the same chromosome number and flowering phenology (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%. Therefore, we accept the conclusion of Judd (1982) that *Oxypolis greenmanii* is a subspecies of *O. filiformis* (i.e., *O. filiformis* subsp. *greenmanii* (Mathias & Constance) Judd).

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 Haida Gwaii, 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 clade and the South clade 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 & 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 Haida Gwaii (Cheney & Marr, 2007). Haida Gwaii, located approximately 80 km off the west coast of British Columbia, is an intriguing geographic area. It has been proposed that during the last glacial maximum (ca. 15,000 years ago), when glaciers covered much of present-day British Columbia and extended into present-day Washington State, much of Haida Gwaii remained ice-free (Heusser, 1960; Lacourse & 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

Key to the genera

1. Leaves simple; blades reduced to the rachis (thus appearing linear, terete, hollow, and septate) 2
1. Leaves 1-pinnate, 1-ternate, or pinnately decompound; blades with well-developed lamina 3
2. Mericarps isodiametric, 1–2 × 1–2 mm; marginal ribs not winged; carpophore 2-fid at apex; plants without a rhizome or caudex .... 1. *Harperella*
2. Mericarps strongly dorsally compressed, 4–9 × 3–5.5 mm; marginal ribs broadly winged; carpophore 2-cleft nearly to the base; plants with a rhizome or short caudex .... 2. *Tiedemannia*
3. Mericarps strongly dorsally compressed; marginal ribs broadly winged, thin, not corky; carpophore 2-cleft nearly to the base; leaves 1-pinnate or 1-ternate; ultimate leaf segments linear, lanceolate, ovate, or orbiculate; roots tuberous-thickened .... 3. *Oxypolis*
3. Mericarps slightly dorsally compressed; marginal ribs narrowly winged, thick, corky; carpophore 2-fid at the apex; leaves pinnately decompound; ultimate leaf segments filiform; roots fibrous........................... 4. *Ptilimnium*

1. *Harperella* Rose in Proc. Biol. Soc. Washington 19: 96. 1906 ≡ *Harperia* Rose in Proc. U.S. Natl. Mus. 29: 441. 1905, nom. illeg. non Fitzg. (1904) – Type: *Harperella nodosa* Rose.

1.1 *Harperella nodosa* Rose in Proc. Biol. Soc. Washington 19: 96. 1906 ≡ *Harperia nodosa* Rose in Proc. U.S. Natl. Mus. 29: 441. 1905, nom. illeg. ≡ *Carum nodosum* (Rose) Koso-Pol. in Bull. Soc. Imp. Naturalistes Moscou, n.s., 29: 199. 1916 ≡ *Ptilimnium nodosum* (Rose) Mathias in Brittonia 2: 244. 1936 – Type: U.S.A., Georgia, Schley County, 10 July 1902, *Harper 1411* (US!, holotype; BM!, E!, MO, 2 sheets!, NY, 2 sheets!, US!, isotypes).
= *Harperella fluviatilis* Rose in Contr. U.S. Natl. Herb. 13: 290. 1911 ≡ *Ptilimnium fluviatile* (Rose) Mathias in Brittonia 2: 244. 1936 – Type: U.S.A., Alabama, Dekalb County, 24 Nov. 1905, *Harper 8* (US!, holotype; MO!, isotype).
= *Harperella vivipara* Rose in Contr. U.S. Natl. Herb. 13: 290. 1911 ≡ *Carum viviparum* (Rose) Koso-Pol. in Bull. Soc. Imp. Naturalistes Moscou, n.s., 29: 199. 1916 ≡ *Ptilimnium viviparum* (Rose) Mathias in Brittonia 2: 244. 1936 ≡ *Ptilimnium fluviatile* var. *viviparum* (Rose) Reveal & C.R. Broome in Castanea 46(1): 67. 1981 – Type: U.S.A., Maryland, on the banks of the Potomac River near Hancock, 5 Oct. 1910, *Rose s.n.* (US!, holotype; NY, 2 sheets!, isotypes).

The genus name *Harperia* Rose was found to be a later homonym for *Harperia* Fitzg. (1904) and, therefore, Rose replaced it with the name *Harperella*. Rose designated *Harperella nodosa* Rose as the type for this genus. *Harperella nodosa*, *H. fluviatilis*, and *H. vivipara* were transferred to the genus *Ptilimnium* by Mathias (1936). Easterly (1957a) synonymized *P. viviparum* under *P. fluviatile* and Kral (1981) later synonymized *P. fluviatile* under *P. nodosum*. Morphological

and molecular evidence shows that *P. nodosum* (Rose) Mathias does not belong in the genus *Ptilimnium* but rather should be placed in its own genus. Therefore the genus *Harperella* and the species name *H. nodosa* are reinstated and *P. nodosum* is synonymized under *H. nodosa*.

2. *Tiedemannia* DC., Coll. Mém. 5: 51. 1829 – Type: *T. filiformis* (Walter) Feist & S.R. Downie

Candolle (1829) created the genus *Tiedemannia* because he felt that the plant placed in *Oenanthe* by Walter and Persoon (i.e., *Oenanthe filiformis* Walter, 1788; *Oenanthe carolinensis* Persoon, 1805) and in *Sium* by Elliott (i.e., *Sium teretifolium* Elliott, 1817) did not belong in either of these genera based on the uniqueness of its fruit and reduced leaf morphology. The names *Oenanthe carolinensis* and *Sium teretifolium* are both homotypic synonyms of *Oenanthe filiformis*, and due to the rules of priority (Art. 11.2 of the *International Code of Botanical Nomenclature*, McNeill & al., 2006) are illegitimate names. Candolle made the new combination *Tiedemannia teretifolia* based on an illegitimate name and, therefore, his name is also illegitimate. The correct combination is *Tiedemannia filiformis*. Because Candolle indicated that the name *Tiedemannia teretifolia* is a synonym of *Oenanthe filiformis*, this latter name represents the type species of *Tiedemannia*. This is according to Art. 7.5 of the *ICBN* (McNeill & al., 2006) which states "a name that is illegitimate under Art. 52 is typified either by the type of the name that ought to have been adopted under the rules (automatic typification), or by a different type designated or definitely indicated by the author of the illegitimate name".

2.1 *Tiedemannia canbyi* (J.M. Coult. & Rose) Feist & S.R. Downie, **comb. nov.** ≡ *Oxypolis filiformis* var. *canbyi* J.M. Coult. & Rose in Contr. U.S. Natl. Herb. 7: 193. 1900 ≡ *Oxypolis canbyi* (J.M. Coult. & Rose) Fernald in Rhodora 41: 139. 1939 – Type: U.S.A., Delaware, Ellendale, Aug. 1867, *Canby s.n.* (US!, holotype; E!, PH!, isotypes).

2.2 *Tiedemannia filiformis* (Walter) Feist & S.R. Downie, **comb. nov.** ≡ *Oenanthe filiformis* Walter, Fl. Carol.: 113. 1788 ≡ *Oxypolis filiformis* (Walter) Britton in Mem. Torrey Bot. Club 5: 239. 1894 ≡ *Oenanthe carolinensis* Pers., Syn. Pl. 1: 318. 1805, nom. illeg. ≡ *Oxypolis caroliniana* (Pers.) Raf. in Bull. Bot. (Geneva) 1: 218. 1830, nom. illeg. ≡ *Oenanthe teretifolia* Muhl., Cat. Pl. Amer. Sept.: 32. 1813, nom. illeg. ≡ *Sium teretifolium* (Muhl.) Elliott, Sketch Bot. S. Carolina 1: 354. 1817, nom. illeg. ≡ *Tiedemannia teretifolia* (Muhl.) DC., Coll. Mem. 5: 81. 1829, nom. illeg. ≡ *Peucedanum teretifolium* (Muhl.) Wood, Amer. Bot. Fl.: 136. 1870, nom. illeg. – Type: U.S.A., South Carolina, Berkeley County, 17 Sept. 1981, *Porcher 1977a* (BM!, neotype, designated by A.O. Tucker & al. in Syst. Bot. 8: 300. 1983; CITA, DOV, isoneotypes).
= *Tiedemannia bakeri* H. Wolff ex Urb., Symb. Antill. 5: 452. 1908 ≡ *Oxypolis bakeri* (H. Wolff ex Urb.) Britton & P. Wilson ex Bracelin in Torreya 29: 16. 1929 – Type: Cuba, in Havana Province near Batabano, Oct. 1904, *Baker & Wilson 2215* (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 in Bull. Torrey Bot. Club 69: 152. 1942 ≡ *Oxypolis filiformis* subsp. *greenmannii* (Mathias & Constance) Judd in Rhodora 84: 277. 1982 – Type: U.S.A., Florida, Gulf County, Wewahitchka, Aug. 1896, *Chapman s.n.* (MO!, holotype).

3. *Oxypolis* Raf., Neogenyton: 2. 1825 – Type: *Oxypolis rigidior* (L.) Raf.

3.1 *Oxypolis rigidior* (L.) Raf. in Bull. Bot. (Geneva) 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* (L.) Wood, Amer. Bot. Fl.: 136. 1870, nom. illeg., non Bunge (1833), 'rigidum' ≡ *Tiedemannia rigidior* (L.) J.M. Coult. & Rose in Bot. Gaz. 12: 74. 1887, 'rigida' – Type: U.S.A. Virginia, *Clayton 279* (BM!, lectotype, designated by J.L. Reveal in Taxon 55: 215. 2006).
= *Archemora serrata* Raf., Herb. Raf.: 78. 1833 – Type: U.S.A., Kentucky & Tennessee (location unknown).
= *Archemora trifoliata* Raf., Herb. Raf.: 78. 1833 – Type: U.S.A., Missouri (location unknown).
= *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* (Nutt.) A. Gray, Manual: 158. 1848, 'rigida' ≡ *Peucedanum rigidius* (L.) Wood var. *ambiguum* (Nutt.) 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. in Rhodora 10: 35. 1908 – Type: U.S.A., banks of the Delaware near Philadelphia (PH!).
= *Oxypolis turgida* Small, Man. S.E. Fl.: 986. 1933 – Type: U.S.A., Virginia, Staunton Co., Staunton, 2 Oct. 1895, *Murrill s.n.* (lectotype, designated by M.A. Feist in J. Bot. Res. Inst. Texas 6: 662. 2009: NY!).
= *Sium denticulatum* Baldwin in Elliott, Sketch Bot. S. Carolina 1: 354. 1817 ≡ *Archemora denticulata* (Baldwin) DC., Prodr. 4: 188. 1830 ≡ *Oxypolis denticulata* (Baldwin) Raf. in Bull. Bot. (Geneva) 1: 218. 1830 ≡ *Pastinaca denticulata* (Baldwin) D. Dietr., Syn. Pl. 2: 971. 1840 – Type: U.S.A., Georgia, 1817, *Baldwin s.n.* (lectotype, designated by Edmondson in Novon 15: 109. 2005: LINN-Smith, digital image!).
= *Sium longifolium* Pursh, Fl. Amer. Sept.: 194. 1813 ≡ *Oxypolis rigidior* (L.) Raf. var. *longifolia* (Pursh) Britton in 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) Stone, Pl. S. New Jersey 2: 600. 1911 – Type: U.S.A., New Jersey (lectotype, designated with reservations by J. Ewan in the introduction to the facsimile reprint of F.T. Pursh's *Flora Americae Septentrionalis*, 1979: PH!).
= *Sium tricuspidatum* Elliott, Sketch Bot. S. Carolina 1: 354. 1817 ≡ *Archemora tricuspidata* (Elliott) DC., Prodr. 4: 188. 1830 ≡ *Oxypolis tricuspidata* (Elliott) Raf. in Bull. Bot. (Geneva) 1: 218. 1830 ≡ *Pastinaca tricuspidata* (Elliott) D. Dietr., Syn. Pl. 2: 971. 1840 – Type: U.S.A., South Carolina (CHARL!, holotype).

3.2 *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 in Bot. Gaz. 12: 74. 1887 – Type: U.S.A., North and South Carolina, *Nuttall s.n.* (BM! lectotype, designated herein). This taxon was neotypified by M.A. Feist in J. Bot. Res. Inst. Texas 3: 662. 2009. At that time a type could not be located. This type specimen has since been located, therefore the neotypification is revoked and this specimen is designated as the lectotype.
= *Sataria linearis* Raf. var. *longipes* Raf., New Fl. 4: 21. 1838. Rafinesque did not cite a specific collection or give a locality (location unknown).
= *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." (NY!, lectotype, designated by M.A. Feist in J. Bot. Res. Inst. Texas 3: 662. 2009).

3.3 *Oxypolis fendleri* (A. Gray) A. Heller in Bull. Torrey Bot. Club 24: 478. 1897 ≡ *Archemora fendleri* A. Gray in Mem. Amer. Acad. Arts, n.s., 4: 56. 1849 ≡ *Tiedemannia fendleri* (A. Gray) J.M. Coult. & Rose, Rev. N. Amer. Umbell.: 48. 1888 – Type: U.S.A., New Mexico, Santa Fe Creek, *Fendler 272* (GH!, holotype; GH!, BM!, isotypes).

3.4 *Oxypolis occidentalis* J.M. Coult. & Rose in Contr. U.S. Natl. Herb. 7: 196. 1900 – Type: U.S.A., Oregon, west of Crater Lake, *Leiberg 4413* (US!, holotype; ORE!, isotype).

4. *Ptilimnium* Raf. in Amer. Month. Mag. & Crit. Rev. 4: 192. 1819 (nom. nud.). Neogenyton: 2. 1825 – Type: *Ptilimnium capillaceum* (Michx.) Raf.

4.1 *Ptilimnium capillaceum* (Michx.) Raf. in Bull. Bot. (Geneva) 1: 217. 1830 ≡ *Ammi capillaceum* Michx., Fl. Bor.-Amer. 1: 164. 1803 ≡ *Sison capillaceum* (Michx.) Spreng., Syst. Veg. 1: 897. 1825 ≡ *Discopleura capillacea* (Michx.) DC., Coll. Mém. 5: 38. 1829 – Type: U.S.A., South Carolina (P-MICH).
= *Ammi junceum* Raf., Neogenyton: 2. 1825 (nom. nud.) ≡ *Ptilimnium junceum* (Raf.) Raf. in Bull. Bot. (Geneva) 1: 217. 1830

≡ *Discopleura juncea* (Raf.) Steud., Nomcl. Bot., ed. 2., 1: 520. 1840 – Type: U.S.A., Kentucky (location unknown).

= *Ammi majus* Walter, Fl. Carol.: 113. 1788 non *A. majus* L. (1753) ≡ *Discopleura major* (Walter) Britton & al., Prelim. Cat.: 22. 1888 – Type: U.S.A., South Carolina (location unknown).

= *Ammi rubricaule* Hornem., Hort. Bot. Hafn.: 272. 1813 ≡ *Sison rubricaule* (Hornem.) Eaton & Wright, Man. Bot., ed. 8 [= N. Amer. Bot]: 429. 1840 – Type: U.S.A., Maryland, Baltimore Co., near Baltimore (location unknown).

4.2 ***Ptilimnium ahlesii*** Weakley & G.L. Nesom in Sida 21: 744. 2004 – Type: U.S.A., North Carolina, Brunswick Co., tidal freshwater marsh of the Brunswick River, *Weakley & LeBlond 7317* (NCU!, holotype; MO!, NY!, isotypes)

4.3 ***Ptilimnium costatum*** (Elliott) Raf. in Bull. Bot. (Geneva) 1: 217. 1830 ≡ *Ammi costatum* Elliott, Sketch Bot. S. Carolina 1: 350. 1817 ≡ *Discopleura capillacea* var. *costata* DC., Coll. Mem. 5: 39. 1829 ≡ *Discopleura costata* (Elliott) Steud., Nomencl. Bot., ed. 2, 1: 77, 520. 1840 – Type: U.S.A., Georgia, "In inundatis, Ogeechee" (GH, photo of type!).

= *Ptilimnium missouriense* J.M. Coult. & Rose in Contr. U.S. Natl. Herb. 12: 444. 1909 – Type: U.S.A., Missouri, Allenton, 27 Aug. 1878, *Letterman s.n.* (US!, holotype).

4.4 ***Ptilimnium texense*** J.M. Coult. & Rose in Contr. U.S. Natl. Herb. 12: 445. 1909 – Type: U.S.A., Texas, Near Hockley, Sept. 1890, *Thurow s.n.* (US!, holotype).

4.5 ***Ptilimnium nuttallii*** (DC.) Britton in Mem. Torrey Bot. Club 5: 244. 1894 ≡ *Discopleura nuttallii* DC., Coll. Mem. 5: 39. 1829 ≡ *Discopleura capillacea* var. *nuttallii* (DC.) J.M. Coult. & Rose in Bot. Gaz. 12: 292. 1887 – Type: U.S.A., Red River, *Nuttall s.n.* (G-DC!, holotype; BM! p.p. the type is the specimen on the left side of the sheet, K! p.p. the type is the specimen on the right side of the sheet, PH!, NY!, isotypes).

Peucedanum verticillatum Raf., Fl. Ludov.: 81. 1817, nom. dub. – Type: U.S.A., Louisiana (location unknown).

This name has been listed as a possible synonym of *Ptilimnium nuttallii* (DC.) Britton. However, Rafinesque's description associated with this name is vague and could be applied to a number of different species. It is unknown whether Rafinesque based his description on an actual specimen and no type could be located. Therefore, there is no way to determine for certain that this name is a synonym of *P. nuttallii* and the designation nomen dubium is applied.

■ ACKNOWLEDGEMENTS

■ LITERATURE CITED

Affolter, J.M. 1985. A monograph of the genus *Lilaeopsis* (Umbelliferae). *Syst. Bot. Monogr.* 6: 1–140.

Bell, C.R. & Constance, L. 1957. Chromosome numbers in Umbelliferae. *Amer. J. Bot.* 44: 565–572.

Bell, C.R. & Constance, L. 1960. Chromosome numbers in Umbelliferae II. *Amer. J. Bot.* 47: 24–32.

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

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

Calviño, C.I. & Downie, S.R. 2007. Circumscription and phylogeny of Apiaceae subfamily Saniculoideae based on chloroplast DNA sequences. *Molec. Phylogenet. Evol.* 44: 175–191.

Calviño, C.I., Tilney, P.M., Van Wyk, B.E. & Downie, S.R. 2006. A molecular phylogenetic study of southern African Apiaceae. *Amer. J. Bot.* 93: 1828–1847.

Candolle, A.P. de 1829. *Memoire sur la famille des Ombelliferes.* Paris: Treuttel & Würtz.

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

Constance, L., Chuang, T.-I. & Bell, C.R. 1976. Chromosome numbers in Umbelliferae V. *Amer. J. Bot.* 63: 608–625.

Coulter, J.M. & Rose, J.N. 1887. Notes on Umbelliferae of the E. United States III. *Bot. Gaz.* 12: 73–76

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

Crawford, D.J. & Hartman, R.L. 1972. Chromosome numbers and taxonomic notes for Rocky Mountain Umbelliferae. *Amer. J. Bot.* 59: 386–392.

Downie, S.R. & Katz-Downie, D.S. 1996. A molecular phylogeny of Apiaceae subfamily Apioideae: Evidence from nuclear ribosomal DNA internal transcribed spacer sequences. *Amer. J. Bot.* 83: 234–251.

Downie, S.R., Katz-Downie, D.S. & Cho, K.-J. 1996. Phylogenetic analysis of Apiaceae subfamily Apioideae using nucleotide sequences from the chloroplast *rpoC1* intron. *Molec. Phylogenet. Evol.* 6: 1–18.

Downie, S.R., Katz-Downie, D.S. & Spalik, K. 2000a. A phylogeny of Apiaceae tribe Scandiceae: Evidence from nuclear ribosomal DNA internal transcribed spacer sequences. *Amer. J. Bot.* 87: 76–95.

Downie, S.R., Katz-Downie, D.S., Sun, F.-J. & Lee, C.-S. 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.

Downie, S.R., Katz-Downie, D.S. & Watson, M.F. 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. *Amer. J. Bot.* 87: 273–292.

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

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

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

Downie, S.R., Watson, M.F., Spalik, K. & Katz-Downie, D.S. 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. *Canad. J. Bot.* 78: 506–528.

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

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., Källersjö, M., Kluge, A.G. & Bult, C. 1995. Constructing a significance test for incongruence. *Syst. Biol.* 44: 570–572.

Feder, N. & O'Brien, T.P. 1968. Plant microtechnique: Some principles and new methods. *Amer. J. Bot.* 55: 123–42.

Feist, M.A.E. 2009. Clarifications concerning the nomenclature and taxonomy of *Oxypolis ternata* (Apiaceae). *J. Bot. Res. Inst. Texas* 3: 661–666.

Feist, M.A.E. 2010. The reinstatement of *Ptilimnium texense* (Apiaceae) and a new key to the genus. *J. Bot. Res. Inst. Texas* 4: 641–651.

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

Hall, T.A. 1999. BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucl. Acids Sym. Ser.* 41: 95–98.

Hardway, T.M., Spalik, K., Watson, M.F., Katz-Downie, D.S. & Downie, S.R. 2004. Circumscription of Apiaceae tribe Oenantheae. *S. African J. Bot.* 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. & Ronquist, F. 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. *Bot. J. Linn. Soc.* 63(Suppl. 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. & Meacham, C.A. (eds.), *Synthesis of the North American flora*, version 1.0. Chapel Hill: North Carolina Botanical Garden. CD-ROM.

Kral, R. 1981. Notes on some "quill-leaved" umbellifers. *Sida* 9: 124–134.

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

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

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

Liogier, H.A. & Martorell, L.F. 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., Plunkett, G.M., Lowry, P.P., Van Wyk, B.-E. & Tilney, P.M. 2006. The taxonomic value of fruit wing types in the order Apiales. *Amer. J. Bot.* 93: 1357–1368.

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

Magee, A.R., Calviño, C.I., Liu, M., Downie, S.R., Tilney, P.M. & Van Wyk, B.-E. 2010a. New tribal delimitations for the early diverging lineages of Apiaceae subfamily Apioideae. *Taxon* 59: 567–580.

Magee, A.R., Van Wyk, B.-E., Tilney, P.M. & Downie, S.R. 2009a. 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). *Syst. Bot.* 34: 580–594.

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

Magee, A.R., Van Wyk, B.-E., Tilney, P.M., Sales, F., Hedge, I. & Downie, S.R. 2009b. *Billburttia*, a new genus of Apiaceae (tribe Apieae) endemic to Madagascar. *Pl. Syst. Evol.* 283: 237–245.

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

Mathias, M. 1936. Studies in the Umbelliferae V. *Brittonia* 3: 239–245.

McNeill, J., Barrie, F.R., Burdet, H.M., Demoulin, V., Hawksworth, D.L., Marhold, K., Nicolson, D.H., Prado, J., Silva,P.C., Skog, J.E., Wiersema, J.H. & Turland, N.J. (eds.) 2006. *International code of botanical nomenclature (Vienna Code): Adopted by the Seventeenth International Botanical Congress Vienna, Austria, July 2005*. Regnum Vegetabile 146. Ruggell: Gantner.

Persoon, C.H. 1805. *Synopsis plantarum seu enchiridium botanicum*, vol. 1. Tübingen, Germany: J.G. Cotta.

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

Plunkett, G.M., Soltis, D.E. & Soltis, P.S. 1996. Evolutionary patterns in Apiaceae: Inferences based on *matK* sequence data. *Syst. Bot.* 21: 477–495.

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

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

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

Simmons, M.P. & Ochoterena, H. 2000. Gaps as characters in sequence-based phylogenetic analyses. *Syst. Biol.* 49: 369–381.

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

Spalik, K. & Downie, S.R. 2006. The evolutionary history of *Sium sensu lato* (Apiaceae): Dispersal, vicariance, and domestication as inferred from ITS rDNA phylogeny. *Amer. J. Bot.* 93: 76–95.

Spalik, K., Downie, S.R. & Watson, M.F. 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.

Swofford, D.L. 2003. PAUP*: Phylogenetic analysis using parsimony (*and other methods), version 4. Sunderland, Massachusetts: Sinauer.

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

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

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

Walter, T. 1788. *Flora Caroliniana*. London: J. Fraser.

Weakley, A.S. & Nesom, G.L. 2004. A new species of *Ptilimnium* (Apiaceae) from the Atlantic coast. *Sida* 21: 743–752.

Wen, J. & Zimmer, E.A. 1996. Phylogeny and biogeography of *Panax* L. (the ginseng genus, Araliaceae): Inferences from ITS sequences of nuclear ribosomal DNA. *Molec. Phylogenet. Evol.* 6: 167–177.

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

Winter, P.J.D., Magee, A.R., Phephu, N., Tilney, P.M., Downie, S.R. & Van Wyk, B.-E. 2008. A new generic classification for African peucedanoid species (Apiaceae). *Taxon* 57: 347–364.

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

U.S. Fish and Wildlife Service. 1988. Determination of *Ptilimnium nodosum* (harperella) to be an endangered species. *Fed. Reg.* 53: 37978–37982.

Appendix 1. Accessions from which nuclear rDNA ITS and cpDNA sequence data were obtained, with corresponding DNA accession and GenBank reference numbers and voucher information.

Taxon name — **DNA accession number;** voucher information; cpDNA GenBank accession number(s), ITS GenBank accession number. An asterisk (*) indicates sequences newly generated for this study; a number sign (#) indicates the *trnQ* and *trnK* sequences used were part of a longer sequence of the entire *psbI-trnK* region deposited to GenBank; a paragraph sign (§) indicates the *trnK* sequence used was part of a longer sequence of the *rps16* intron-*trnK* region deposited to GenBank.

Atrema americanum 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 & 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), JQ652503*, JQ652549*. **3411;** U.S.A., Texas, Bexar Co., San Antonio, 31 July 1921, *Schulz 594* (US 1087113); JQ652500*, JQ652550*, JQ652463*. **3412;** U.S.A., Texas, Hays Co., Wimberly, 5 July 1942, *Fisher s.n.* (F 1501788); JQ652501*, JQ652551*, JQ652464*. *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. Coult. & 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 & al. 99586I* (MO 3680921); EF185229#, EF177717. **2395;** U.S.A., Missouri, Stoddard Co., Otter Slough Conservation Area, 31 May 2000, *Brant & al. 4380* (MO 5186226); EF185230#, EF177720. *Limnosciadium pumilum* (Engelm. & A. Gray) Mathias & Constance — **3742;** U.S.A., Texas, San Ptricio Co., US 181 NW of Sinton, 5 Apr. 1984, *Ertter 5263* (NY); JQ652499*, JQ652548*, JQ652470*. *Neogoezia gracilipes* (Hemsl.) Hemsl. — **2270;** Mexico, Oaxaca, Nochixtlan, N of La Joya, 2 Oct. 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 Sept. 1984, *Nelson 3687* (NCU 537890); JQ652489*, JQ652540*, EF647756. **2747;** U.S.A., North Carolina, Scotland Co., McIntosh Carolina Bay, US 401 NE of Laurinburg, 13 Sept. 1992, *Sorrie 6946* (NCU 562048); JQ652490*, JQ652541*, EF647757. **2751;** U.S.A., South Carolina, Lee Co., just NE of Mt Pleasant Church, W of Lynchburg, 10 Sept. 1985, *Nelson 4271* (NCU 537512); JQ652491*, JQ652542*, EF647758. **2937;** U.S.A., South Carolina, Bamberg Co., Bamberg Bay Preserve, 28 Aug. 2005, *Feist, Molano-Flores & Glitzenstein 3193* (ILLS); JQ652492*, JQ652543*, EF647759. **2938;** U.S.A., South Carolina, Bamberg Co., Oxypolis Bay Preserve, 28 Aug. 2005, *Feist, Molano-Flores & Glitzenstein 3194* (ILLS); JQ652493*, JQ652544*, EF647760. *Oxypolis fendleri* (A. Gray) A. Heller — **2350;** U.S.A., Colorado, Boulder Co., Forth of July Canyon, 10 July 1962, *Jones 34084* (ILL); JQ652502*, JQ652552*, EF647767. **2351;** U.S.A., Colorado, Boulder Co., along Boulder Creek, 24 June 1962, *Jones 34450* (ILL); JQ652504*, JQ652553*, EF647768. **2368;** U.S.A., New Mexico, Rio Arriba Co., Ortega Mountains, 17 Aug. 1984, *Hill 15181* (UC 1508862); JQ652505*, JQ652554*. **2369;** U.S.A., Colorado, Chafee Co., CO 306, 14 mi W of Buena Vista, 2 Aug. 1973, *Haber & Given 2049* (CAN 370800); JQ652506*, 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 Sept. 1987, *Thomas 101486* (DAO 574521); JQ652494*, EF185240§, EF177736. **2713;** U.S.A., Florida, Alachua Co., Gainesville, N side of NE 39th Ave. N. just E of Main St., 9 Sept. 1987, *Alcorn 155* (FLAS 166610); JQ652495*, JQ652545*, EF177737. *Oxypolis filiformis* × *O. 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 Aug. 1980, *Judd & Perkins 2714* (FLAS 174297); JQ652498*, EF185242§, EF177739. *Oxypolis greenmanii* Mathias & Constance — **2717;** U.S.A., Florida, Bay Co., Tyndall Airforce Base, 15 Sept. 1979, *Judd & Perkins 2439* (FLAS 174274); JQ652496*, JQ652546*, EF177738. **2941;** U.S.A., Florida, Gulf Co., just E of Wetappo Creek and 3.6 mi S of FL 22, 2 Sept. 2005, *Feist & Molano-Flores 3244* (ILLS); JQ652497*, JQ652547*, 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), JQ652507*, JQ652555*, EF647784. **2756;** Canada. British Columbia: Queen Charlotte Islands, Graham Island, 2003, *Cheney s.n.* (ILLS), JQ652508*, JQ652556*, 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 Sept. 1997, *Oswald & Ahart 8863* (JEPS 94369), JQ652509*, JQ652557*, EF647789. **2927;** U.S.A., California: Sierra Co., ca. 1.25 mi N of Scales, ca. 2 mi (air) SE of Poverty Hill, 28 Sept. 2001, *Ahart 9295* (JEPS 102455), JQ652510*, JQ652558*, 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); JQ652511*, JQ652559*, EF647791. **2929;** U.S.A., Oregon, Klamath Co., near W boundary of Crater Lake Park, 24–29 Aug., *Wynd 1745* (ORE 64782); JQ652512*, JQ652560*, EF647785. **3376;** U.S.A., California, Kern Co., French Meadow, 3 Sept. 2007, *Feist & Molano-Flores FM-11;* JQ652513*, JQ652561*, JQ652465*. **3413;** Canada, Haida Guai, British Columbia, *Feist & Molano-Flores Site 4-2;* JQ652514*, JQ652562*. **3417;** U.S.A., California, Butte Co., 9 Sept. 2007, *Feist & Molano-Flores BTC-13;* JQ652515*, JQ652563*, JQ652466*. **3442;** U.S.A., Oregon, Lane Co., Quaking Aspen Swamp, 13 Sept. 2007, *Feist & Molano-Flores QAS-25;* JQ652516*, JQ652564*. **3464;** U.S.A., California, San Bernardino Co., Lemon Lily Springs, 2 Sept. 2007,

Appendix 1. Continued.

Feist & Molano-Flores LLS-24; JQ652517*, JQ652565*. **3465;** U.S.A., California, San Bernardino Co., Lemon Lily Springs, 2 Sept. 2007, *Feist & Molano-Flores LLS-16*; JQ652518*, JQ652566*. **3466;** U.S.A., California, San Bernardino Co., Lemon Lily Springs, 2 Sept. 2007, *Feist & Molano-Flores LLS-10*; JQ652519*, JQ652567*, JQ652467*. **3528;** U.S.A., California, Sierra Co., Scales, 25 Oct. 2007, *Feist & Molano-Flores S-11*; JQ652520*, JQ652568*, JQ652468*. **3532;** U.S.A., California, Tulare Co., Nelson Trail, 4 Sept. 2007, *Feist & Molano-Flores NT-16*; JQ652521*, JQ652569*, JQ652469*. ***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); JQ652522*, EF185245§, AY360255. **1998;** U.S.A., Louisiana, Winn Parish, along LA 126, 1.2 mi E of Jct. LA 1233, Kisatchie National Forest, 20 Sept. 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 Aug. 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 Oct. 1970, *Massey & Thomas 3480* (NCU 422851); JQ652523*, EF185248§, EF177745. **2738;** U.S.A., North Carolina, Pender Co., Holly Shelter Game Land, 3 Oct. 1997, *Horn & Dirig 362* (DUKE 363865); JQ652524*, 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 Sept. 2005, *Feist, Molano-Flores & Glitzenstein 3222* (ILLS); JQ652525*, JQ652570*, EF647809. ***Perideridia americana*** (Nutt. ex DC.) Reichenb. — **2033;** U.S.A., Illinois, Shelby Co., NE of Assumption, 2 June 1981, *Shildneck 12868* (ILL); JQ652526*, JQ652527*, JQ652471*. ***Perideridia kelloggii*** (A. Gray) Mathias — **778;** U.S.A., California, Sonoma Co., King Ridge Rd., 5 mi N. of Cazadero, 6 Aug. 1993, *Ornduff & al. s.n.* (UC), cult. University of California Botanical Garden, Berkeley (no. 81.0521); EF185251#, U78373. ***Ptilimnium ahlsii*** 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); JQ652472*, 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); JQ652473*, JQ652528*, 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); JQ652474*, JQ652529*, 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); JQ652475*, JQ652530*, EF647822. ***Ptilimnium costatum*** (Elliott) Raf. — **1646;** U.S.A., Illinois, Jackson Co., Shawnee National Forest, 20 Sept. 1989, *Stritch 2159* (ILLS 172136); EF185253#, EF177749. **1970;** U.S.A., Illinois: Jackson Co., Shawnee National Forest, 11 Sept. 1989, *Stritch 2124* (ILLS 172160); EF185254#, EF177750. **2402;** U.S.A., Missouri, Wayne Co., Hattie's Ford Fen Area, 12 Oct. 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 Oct. 1972, *Athey 2197* (NCU 473641); JQ652476*, JQ652531*. ***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); JQ652480*, JQ652533*, EF647843. **2784;** U.S.A., South Carolina, Aiken Co., *Maddox SC-7-4;* JQ652481*, EF185257§, EF177753. **2787;** U.S.A., Maryland, *Maddox MG-4,* JQ652482*, EF185258§, EF177754. **2900;** U.S.A., South Carolina, Saluda Co., near Hibernia, Saluda Highpond, 11 May 2005, *Feist & Molano-Flores 3287* (ILLS); JQ652483*, JQ652534*, EF647841. **2902;** U.S.A., Georgia, Greene Co., Siloam Outcrop, 12 May 2005, *Feist & Molano-Flores Siloam-5;* JQ652484*, JQ652535*, EF177754. **2930;** U.S.A., Arkansas, Yell Co., Ouachita Mountains, below the Hwy. 27 bridge over Irons Fork, 16 Oct. 1990, *Bates 10558* (UARK); JQ652485*, JQ652536*, 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); JQ652486*, JQ652537*, EF647853. **2934;** U.S.A., West Virginia, Berkeley Co., along Back Creek, 25 Aug. 2005, *Feist, Harmon & O'Malley 3285* (ILLS); JQ652487*, JQ652538*, EF647854. **2936;** U.S.A., North Carolina, Granville County, Tar River, 26 Aug. 2005, *Feist 3286* (ILLS); JQ652488*, JQ652539*, 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); JQ652478*, EF185260#, EF177758. **2623;** U.S.A., Illinois, Randolph Co., W of Sparta, 16 July 2003, *Feist 2510* (ILLS); JQ652477*, 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 Aug. 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 Oct. 1993, *Dubrule Reed 1354* (TAMU 24011); JQ652479*, JQ652532*, 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 2. Accessions from which fruit anatomical observations were made 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, *J. 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 & al. 4380* (MO 5186226). ***Limnosciadium pumilum*** (Engelm. & A. Gray) Mathias & Constance — U.S.A., Texas, Calhoun Co., vacant lot in Port O'Connel, 13 Apr. 1952, *Gentry 1996* (BRIT). — U.S.A., Texas, San Patricio Co., US 181 NW of Sinton, 5 Apr. 1984, *Ertter 5263* (NYBG). ***Oxypolis canbyi*** (J.M. Coult. & Rose) Fern. — U.S.A., South Carolina, Lee Co., W of Lynchburg, 10 Sept. 1985, *J. Nelson 4269* (USCH 032054). — U.S.A., Georgia, Lee Co., NE Leesberg, 22 Aug. 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, *G.N. Jones 20071* (ILL). ***Oxypolis filiformis*** (Walter) Britton — U.S.A., South Carolina, Charleston Co., Francis Marion N.F., 29 Aug. 2009, *Feist & Molano-Flores 3197* (ILLS). — U.S.A., Florida, Calhoun Co., 29 Aug. 1980, *Judd & Perkins 2729* (FLAS 174320). ***Oxypolis greenmanii*** Mathias & Constance — U.S.A., Florida, Gulf Co., 17 mi N of Port St. Joe, 7 Sept. 1955, *Godfrey 53756* (NCSC 52879). — U.S.A., Florida, Bay Co., Tyndall Airforce Base, 15 Sept. 1979, *Judd & Perkins 2439* (FLAS 174274). ***Oxypolis occidentalis*** J.M. Coult. & Rose — U.S.A., California, Lemon Lily Springs, 2 Sept. 2007, *Feist & Molano-Flores 4106* (ILLS). — U.S.A., Oregon, Lane Co., Quaking Aspen Swamp, 17 Sept. 2007, *Feist & Molano-Flores 4131* (ILLS). — U.S.A., California, Kern Co. Portuguese Meadow, 27 Sept. 1936, *L. Benson 8007* (POM 287809). ***Oxypolis rigidior*** (L.) Raf. — Canada, Ontario, Essex Co., 5.3 km E & 5.7 km N of Leamington, *Oldham 6994* (CAN 522163). — U.S.A., Indiana, Tippecanoe Co., Ross Biological Reserve, 2 Oct. 1958, *Webster & Webster 7206* (DUKE 147518). — U.S.A., Tennessee, Munroe Co., Cherokee N.F., 21 Sept. 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 Nov. 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 Oct. 1967, *Bozeman 11639* (NCU 303709). ***Ptilimnium ahlsii*** 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, *J. Nelson 13280* (USCH 58378). ***Ptilimnium costatum*** (Elliott) Raf. — U.S.A., Illinois, Washington Co., 25 Sept. 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 Aug. 2005, *Feist 3188* (ILLS) — U.S.A., Alabama, Tuscaloosa Co., North River, 15 mi N of Tuscaloosa, *Easterly Ala. 146* (WVA114892). ***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 Oct. 1949, *Shinners 11830* (SMU). — U.S.A., Texas, Tyler Co., ca. 2 mi E of Warren, 5 Oct. 1969, *Correll 3813* (LAF 46206).