Systematic Botany (2004), 29(3): pp. 737–751

A Phylogenetic Study of *Perideridia* (Apiaceae) Based on Nuclear Ribosomal DNA ITS Sequences

STEPHEN R. DOWNIE,[1] FENG-JIE SUN, DEBORAH S. KATZ-DOWNIE, and GINA J. COLLETTI

Department of Plant Biology, University of Illinois at Urbana-Champaign, Urbana, Illinois 61801
[1]Author for Correspondence (sdownie@life.uiuc.edu)

Communicating Editor: Alan Meerow

ABSTRACT. A phylogenetic study of the genus *Perideridia* (Apiaceae; tribe Oenantheae) was conducted to elucidate its circumscription, infrageneric relationships, and patterns in the evolution of available morphological, anatomical, and cytological characters. Nuclear rDNA ITS sequences were procured from 84 accessions of *Perideridia*, representing all 14 of its species and four of its six subspecies, and five outgroup taxa, and analyzed using maximum parsimony, maximum likelihood, and Bayesian inference methods. The trees recovered by each of these optimality criteria were congruent and generally quite robust. Upon the removal of the eastern Asian *Perideridia neurophylla*, previously referable to *Pterygopleurum neurophyllum*, the genus *Perideridia* is monophyletic and exclusively North American in distribution. Three major clades within *Perideridia* are inferred; the midwestern U.S. *Perideridia americana* is likely sister to all other species. With the exceptions of *Perideridia lemmonii* and *P. bolanderi* (where each species comprises two separate lineages), and *P. oregana* (whose limits are expanded to include tetraploid populations previously referred to as *P. leptocarpa*), all taxa were recovered as monophyletic. Optimization of 16 non-molecular characters on a phylogeny inferred by maximum parsimony analysis of combined ITS and non-molecular data revealed high instances of homoplasy, with the clade of *P. howellii* and *P. kelloggii*, taxa characterized by monostelic roots, supported by four of six synapomorphies. The occurrence of multistelic tuberous roots in all other species of *Perideridia* and in the unrelated *Pterygopleurum neurophyllum* suggests that this uncommon character among dicots has evolved twice in the family Apiaceae.

The genus *Perideridia* Rchb. (Apiaceae tribe Oenantheae Dumort.), as outlined by Chuang and Constance (1969), consists of 14 species and six subspecies (Table 1). Twelve species are indigenous to California and the Pacific Northwest, with one species restricted to the midwestern U.S., and another found only in Japan and Korea. All are slender, glabrous, herbaceous perennials arising from tuberous or fusiform to long, fibrous fascicled roots. These tuberous roots, arising singly or in small clusters, are a striking vegetative feature, for in most species each root consists of several to many separate steles with limited secondary growth. This multistelic type of vascular structure, apparently the fusion product of several individual roots, is unique among dicots, having been reported previously in only a few monocot species (Chuang 1970). These roots are quite nutritious and are widely consumed by Native Americans (Chuang and Constance 1969).

Making use of extensive herbarium and field collections, germination tests and seedling observations, comparative morphology and anatomy, and cytological, palynological, and phytochemical investigations, T.-I. Chuang and colleagues contributed greatly to a multidisciplinary systematic study of *Perideridia* (Chuang and Constance 1969; Chuang 1970; Giannasi and Chuang 1976). However, the discordance they observed between the grouping of species by major classes of flavonoids and those groups inferred from morphology (e.g., root structure and stylopodium shape) and anatomy (e.g., leaf mesophyll organization and number of vallecular vittae) led them to propose a reticulate mode of evolution for *Perideridia*, as these lines of evidence failed to show any consistent infrageneric pattern. A comparison of flavonoid chemistry, haploid chromosome number, and geographic distribution showed that the majority of species producing only flavonols are $n=19$ (the others being $n=20$ and 22) and are centered in California, whereas those species producing predominantly flavones are $n=20$ (or exact multiples of this number) and are concentrated in the Pacific Northwest and midwestern U.S. (Giannasi and Chuang 1976). Such a correlation, however, breaks down for that group of species having primarily flavonols and some flavones or traces of flavones; among these species, eight chromosome races are apparent, including four presumably diploid cytotypes ($n=8$, 9, 10, and possibly 13) and those with $n=17$, 18, 19, and 20. The probable origin and relationships among the dozen different chromosome numbers reported for the genus have yet to be explained, but it is of interest to note that ''the taxa at the assumed polyploid levels are mostly quite distinct and readily definable, while the diploid populations show essentially continuous variation'' (Chuang and Constance 1969). This is in contrast to those genera in other plant families manifesting extensive polyploidy, where the diploid species are most clearly defined morphologically and the polyploids, having lost their distinctiveness presumably through hybridization and gene flow, show a blurring of their boundaries (Chuang and Constance 1969; Giannasi and Chuang 1976).

Characteristics of the basal leaves, mature fruits, and roots are required for accurate identification of these plants. These leaves may be ternate, pinnate, or ternate-pinnately compound, with a few species exhibiting conspicuously dimorphic leaf divisions. Details of

TABLE 1. *Perideridia* taxa according to Chuang and Constance (1969) and their distributions according to The Biota of North America Program, North Carolina Botanical Garden, University of North Carolina.

Perideridia americana (Nutt. ex DC.) Rchb. - AL, AR, IL, IN, KS, KY, MI, MO, MS, OH, OK, TN
Perideridia bacigalupii T.I. Chuang & Constance - CA
Perideridia bolanderi (A. Gray) A. Nelson & J.F. Macbr. subsp. *bolanderi* - CA, ID, NV, OR, UT, WA, WY
Perideridia bolanderi subsp. *involucrata* T.I. Chuang & Constance - CA
Perideridia californica (Torr.) A. Nelson & J.F. Macbr. - CA
Perideridia erythrorhiza (Piper) T.I. Chuang & Constance - OR
Perideridia gairdneri (Hook. & Arn.) Mathias subsp. *gairdneri* - CA
Perideridia gairdneri subsp. *borealis* T.I. Chuang & Constance - AZ, CA, CO, ID, MT, NM, NV, OR, SD, UT, WA, WY; BC, ALTA, SASK
Perideridia howellii (J.M. Coult. & Rose) Mathias - CA, OR
Perideridia kelloggii (A. Gray) Mathias - CA
Perideridia lemmonii (J.M. Coult. & Rose) T.I. Chuang & Constance - CA, NV, OR
Perideridia leptocarpa T.I. Chuang & Constance - CA
Perideridia neurophylla (Maxim.) T.I. Chuang & Constance - Japan, Korea
Perideridia oregana (S. Watson) Mathias - CA, OR, WA
Perideridia parishii (J.M. Coult. & Rose) A. Nelson & J.F. Macbr. subsp. *parishii* - AZ, CA, NM
Perideridia parishii subsp. *latifolia* (A. Gray) T.I. Chuang & Constance - CA, NV
Perideridia pringlei (J.M. Coult. & Rose) A. Nelson & J.F. Macbr. - CA

the shape and size of the ultimate leaf divisions are also important. The fruits are rather unspecialized among umbellifers, range from orbicular to ellipsoid or oblong in shape, and vary in their type of ribs and number of vallecular and commissural vittae. The tuberous roots vary in number, shape, dimension, and color. Notwithstanding the mastery required to become familiar with many of these technical features, the foliage of most species is usually completely dried up by the time the fruit is mature, thus very few specimens are complete or have adequate material. Moreover, the deep-seated tuberous roots are easily detached from the fragile base of the stem and are often missing on herbarium collections.

Given the wealth of comparative data available (in addition to the incongruous nature of these data in demarcating similar groups of taxa), the uncertainty of some species delimitations, the difficulties encountered in identifying these plants, and the absence of detailed information on infrageneric relationships, further systematic study of the genus *Perideridia* is warranted. In this paper, we present results of a phylogenetic study of *Perideridia* based primarily on DNA sequence data. Different optimality criteria are considered and the resulting phylogenetic hypothesis is compared to the current disposition of species inferred previously on the basis of morphological, anatomical, cytological, and phytochemical studies. Chuang and Constance (1969) interpreted the supposedly monotypic and distinctive *Pterygopleurum* Kitag. of Japan and Korea as the single Asian representative of *Perideridia* based on the common possession of multistelic tuberous roots, and we evaluate its placement within *Perideridia*. Additionally, we use the resulting phylogeny to assess monophyly of species and infer trends in the evolution of specific morphological, anatomical, and cytological characters in an effort to underline their importance in species and clade delimitation.

MATERIALS AND METHODS

Complete sequences of the nuclear ribosomal DNA internal transcribed spacer (ITS) region were obtained from 84 accessions of *Perideridia* and combined with previously published sequence data from five outgroup representatives (Table 2). Material from two subspecies was not available for examination: *Perideridia gairdneri* subsp. *gairdneri* and *P. parishii* subsp. *parishii*. Subspecies *gairdneri* is restricted to several counties in California, primarily in coastal areas. It is listed as rare, and recent herbarium collections are unavailable. Subspecies *parishii* extends from the San Bernardino Mountains in southern California eastward to the mountains of Arizona and New Mexico. Herbarium specimens of this taxon are also old and few. DNA was extracted from one (*Perideridia neurophylla*) to 19 (*P. bolanderi* subsp. *bolanderi*) herbarium specimens for each of the remaining taxa. Duplicate herbarium specimens from the same population were examined when the plants differed or when there were doubts about their identification. In this paper, we follow the commonly used nomenclature of *Perideridia* provided by Chuang and Constance (1969).

Results of our prior, higher-level molecular systematic investigations of Apiaceae subfamily Apioideae and our on-going phylogenetic studies of tribe Oenantheae (S. Downie, unpublished data) revealed that the genus *Perideridia* is sister taxon to a clade comprising all other members of the tribe and that the *Conioselinum* clade (i.e., *Conioselinum scopulorum* (A. Gray) J. M. Coult. & Rose, *C. chinense* (L.) B. S. P., *Ligusticum canadense* (L.) Britton, and *L. porteri* J. M. Coult. & Rose) and tribe Pleurospermeae (e.g., *Physospermum cornubiense* (L.) DC.) are closely related to tribe Oenantheae, and are therefore suitable outgroups (Downie et al. 1998, 2001, unpublished data; Katz-Downie et al. 1999). All four members of the *Conioselinum* clade are native to North America (Kartesz 1994), whereas *Physospermum* is restricted to Eurasia.

Details of DNA extraction, PCR amplification and purification, and DNA sequencing are the same as provided elsewhere (Downie and Katz-Downie 1996; Downie et al. 2000a). Total genomic DNA was obtained from ca. 20 mg of dried, leaf tissue and PCR-amplified using primers "ITS4" and "ITS5" (White et al. 1990). Cycle sequencing reactions, using these same primers, were carried out on the purified PCR products using AmpliTaq DNA polymerase

(Invitrogen Life Technologies, Carlsbad, CA) and fluorescent dye-labeled terminators (ABI Prism BigDye Terminator vers. 3.0 Ready Reaction Cycle Sequencing Kit; Applied Biosystems, Foster City, CA), according to the manufacturer's protocol. Sequenced products were purified by passing the reaction through 800 μl Sephadex G-50 (Sigma-Aldrich Co., St. Louis, MO) spin columns, and then visualized using Applied Biosystem's 377A automated DNA sequencer. Both DNA strands were sequenced in their entirety.

The ITS sequences were edited as necessary and aligned manually. All newly acquired sequences have been deposited in GenBank (Table 2); the entire data matrix is available in TreeBASE (study accession number = S1009; matrix accession number = M1705). No data cells were scored as missing for *Perideridia*. Sequence data for two outgroup taxa (*Conioselinum scopulorum* and *Ligusticum canadense*), obtained from GenBank, were incomplete or missing for the 5.8S region. Uncorrected pairwise nucleotide differences were determined using PAUP* vers. 4.0 (Swofford 1998). The data matrix was first analyzed using PAUP* and maximum parsimony (MP), with gap states treated as missing data. Characters were treated as unordered and all character transformations were weighted equally. Heuristic MP searches were replicated 1000 times with random stepwise addition of taxa, tree-bisection-reconnection (TBR) branch swapping, and saving multiple trees (MulTrees). Bootstrap values (Felsenstein 1985) were calculated from 100 replicate analyses using TBR branch swapping and simple stepwise addition of taxa. The number of additional steps required to force particular taxa into a monophyletic group was examined using the constraint option of PAUP*. The Kishino-Hasegawa (parametric) and Templeton (non-parametric) tests, as implemented in PAUP*, were used to test for statistically significant differences in alternative tree topologies. The g1 statistic of skewed tree-length distribution was calculated from 10,000 random MP trees generated by PAUP*, compared to the critical values provided by Hillis and Huelsenbeck (1992), and used to assess the amount of nonrandom structure (i.e., phylogenetic signal) in the data.

A maximum likelihood (ML) analysis of these ITS data was subsequently performed, with the program Modeltest vers. 3.06 (Posada and Crandall 1998) used to select an appropriate model of DNA substitution and to estimate its parameters. A heuristic search using 10 random addition sequence replicates and TBR branch swapping under ML optimization was implemented using PAUP*. ML bootstrap analyses were aborted after 33 replicates and 11 days of processing on a Macintosh G4 computer. Subsequently, 1000 bootstrap replicate analyses were conducted using neighbor-joining searches with ML distance, and the likelihood settings estimated by Modeltest. Phylogenetic analysis was also carried out using MrBayes vers. 3.0 (Ronquist and Huelsenbeck 2003), a Bayesian inference of phylogeny program. Starting trees were chosen at random and one million generations were run with sampling occurring every 100 generations. The number of substitution types was set at six, as suggested by Modeltest, and the gamma shape parameter (reflecting among-site rate variation) was estimated automatically by MrBayes. Two thousand trees were discarded as ''burn-in'' prior to calculating the 50% majority rule tree, as the ln likelihood values for these trees had not stabilized.

Sixteen non-molecular characters from all taxa (save *Perideridia neurophylla*, discussed below) were also analyzed cladistically, in an effort to uncover synapomorphies and to assess patterns of character state change (Tables 3, 4). These characters were chosen based on their emphasis in previous taxonomic studies and those we thought would provide information useful in phylogenetic analysis. However, because many of the herbarium specimens examined were incomplete (as those plants with mature fruits often had withered or few leaves, and those with adequate basal leaves often possessed only flowers and (or) immature fruits) and several specimens lacked the deep-seated fusiform or tuberous roots characteristic of many species of the genus (for they are easily detached when collected), much of the information we used came from literature (Chuang and Constance 1969; Chuang 1970). For the majority of these characters, the determination of their character states was straightforward due to their qualitative nature. For the quantitative characters, character states were determined by detecting gaps in the character variation. Further explanation of the division of character states was either presented in previous morphological studies of Apiaceae (Spalik and Downie 2001; Spalik et al. 2001a) or, as in the case of haploid chromosome number, based on ploidy level designations provided by Chuang and Constance (1969). The tetraploids (n=17–22) were treated as four states, since they comprise the majority of the taxa; haploid numbers 18 and 19 were treated as a single state, as one taxon (*P. lemmonii*) possessed both of these tetraploid chromosome numbers. Treating chromosome numbers 18 and 19 as separate states resulted in no change to the resultant tree topology. These morphological, anatomical, cytological (haploid chromosome number), and ecological (habitat preference) data, each treated as an unordered character, were analyzed using MP and the heuristic search and bootstrap strategies described above. *Perideridia americana* was used to root these trees, based on the results of the MP and ML analyses of ITS sequences and the absence of anatomical data for *Physospermum* and members of the *Conioselinum* clade. Simultaneous parsimony analysis of combined ITS and non-molecular data (for 14 taxa, as molecular data were unavailable for *P. parishii* subsp. *parishii* and *P. gairdneri* subsp. *gairdneri*) was subsequently performed, with all characters weighted equally. The DNA accessions chosen to represent particular species in the ITS partition were selected arbitrarily. Patterns in the evolution of these phenotypic characters were evaluated by implementing the trace character function of MacClade vers. 4.03 (Maddison and Maddison 2002) on the maximally parsimonious trees.

RESULTS

Sequence Analysis. The ITS sequence from the single examined accession of *Perideridia neurophylla* was more divergent than any other accession of *Perideridia* or outgroup examined and, as a result, could not be aligned unambiguously. Uncorrected pairwise sequence divergence values between *P. neurophylla* and all other accessions (upon the exclusion of several small ambiguously aligned regions) ranged between 18.8 and 24.6%; among *Perideridia* accessions only, divergence estimates ranged from 21.5 to 24.6%. The results of preliminary phylogenetic analyses (discussed below) suggest that *P. neurophylla* should not be treated in *Perideridia*. As such, it was removed from all subsequent analyses.

The combined length of the entire ITS region (ITS-1, 5.8S, and ITS-2) for the 83 remaining accessions of *Perideridia* and five outgroup taxa ranged from 599 to 603 bp. The ITS-1 region was 211–218 bp in length, the 5.8S gene was 163 bp in length, and the ITS-2 region was 220–227 bp in length. Alignment of these 88 ITS sequences resulted in a matrix of 611 positions, with no positions excluded because of alignment ambiguity. The number of aligned positions parsimony informative was 227; the number of autapomorphic positions was 32. Uncorrected pairwise sequence divergence values for the entire ITS region and across all 88 accessions ranged from identity to 21.9% of nucleotides;

TABLE 2. Plant accessions from which ITS sequences were obtained, with corresponding DNA and GenBank accession numbers and voucher information. Taxon names and chromosome numbers are according to Chuang and Constance (1969). Two GenBank numbers per DNA accession indicate separate ITS-1 and ITS-2 sequences; a single GenBank number indicates a contiguous ITS-1, 5.8S, ITS-2 sequence. Herbarium acronyms are according to Holmgren et al. (1990).

Perideridia americana, 2018, USA, Illinois, Champaign Co., Hart Woods, 8 June 1960, *Sanderson s.n.* (ILLS 152162), AY246912; *P. americana,* 743, USA, Illinois, Champaign Co., Hart Woods, 14 June 1994, *Downie 743* (ILL), AY246908; *P. americana,* 2019, USA, Illinois, Fayette Co., Twelve Mile Prairie, 1 mi NE Farina, 19 May 1987, *Handel 36* (ILLS 189676), AY246913; *P. americana,* 2010, USA, Illinois, Ford Co., Gardner Prairie Restoration, Kempton, 31 May 1991, *Gardner 90* (ILLS 173778), AY246911; *P. americana,* 2121, USA, Illinois, Grundy Co., 1.6 mi W of Gardner, 29 May 1973, *Chuang & Chuang 7267* (ISU 7420), AY246915; *P. americana,* 2196, USA, Illinois, Grundy Co., 1.6 mi W of Gardner, *n*=20, 29 May 1973, *Chuang & Chuang 7267* (UC 1395573), AY246916; *P. americana,* 1938, USA, Illinois, Shelby Co., NE of Assumption, 2 June 1981, *Shildneck 12868* (ILL), AY246910; *P. americana,* 1803, USA, Illinois, Will Co., Shorewood, 10 June 1997, *Hill 29289* (ILLS 198118), AY246909; *P. americana,* 2017, USA, Missouri, Barry Co., E ca. 0.5 mi from Hwy. 86, 28 May 1978, *Young et al. 1576* (ILL), AY246914

Perideridia bacigalupii, 2030, USA, California, Mariposa Co., 1.5 mi SE of Mariposa, *n*=19, 30 June 1964, *Chuang & Constance 5954* (ISU 2588), AY246919; *P. bacigalupii,* 2029, USA, California, Nevada Co., 4 mi NW of Nevada City, *n*=19, 2 July 1964, *Chuang & Constance 5965* (ISU 2576), AY246918; *P. bacigalupii,* 2117, USA, California, Nevada Co., 5.5 mi NW of Nevada City, *n*=19, 2 July 1964, *Chuang & Constance 5966* (ISU 2579), AY246917

Perideridia bolanderi subsp. *bolanderi,* 2114, USA, California, Elko Co., road to Lake Lamoille, Ruby Range, 8 August 1978, *Chuang & Heckard 7734* (ISU 12732), AY246924; *P. bolanderi* subsp. *bolanderi,* 2170, USA, California, Harney Co., 3.4 mi E of Buchanan along U.S. Hwy. 20, *n*=19, 31 May 1963, *Raven 18460* (ISU 13414), AY246936; *P. bolanderi* subsp. *bolanderi,* 2115, USA, California, Sierra Co., 2 mi NW of Sattley, *n*=19, 22 June 1967, *Constance & Chuang 3780* (ISU 2603), AY246927; *P. bolanderi* subsp. *bolanderi,* 2026, USA, California, Trinity Co., 3 mi N of Junction City, 23 May 1965, *Cruden 964* (ISU 13386), AY246922; *P. bolanderi* subsp. *bolanderi,* 2027, USA, California, Trinity Co., 3 mi N of Junction City, 23 May 1965, *Cruden 964* (ISU 2598), AY246923; *P. bolanderi* subsp. *bolanderi,* 2187, USA, Idaho, Washington Co., Emmett-Indian Valley Rd., 6 mi SE of Crane Creek Reservoir, 25 May 1985, *Ertter 5708* (UC 1561612), AY246932; *P. bolanderi* subsp. *bolanderi,* 2182, USA, Nevada, Elko Co., Independence Mtns., Gance Creek, 20 June 1979, *Tiehm & Birdsey 5147* (UC 1441373), AY246926; *P. bolanderi* subsp. *bolanderi,* 2188, USA, Nevada, Elko Co., Tuscarora Mtns., E of Hot Creek crossing, 3 June 1987, *Pinzl 7927* (UC 1538775), AY246933; *P. bolanderi* subsp. *bolanderi,* 2021, USA, Nevada, Humboldt Co., 9 mi N of junction U.S. 40 and U.S. 95 at Winnemucca, 13 June 1967, *Gentry & Davidse 1509* (ILL), AY246920; *P. bolanderi* subsp. *bolanderi,* 2185, USA, Nevada, Humboldt Co., Jackson Mtns., road to Iron King Mine, 3 June 1979, *Tiehm & Birdsey 5005* (UC 1441379), AY246930; *P. bolanderi* subsp. *bolanderi,* 2179, USA, Nevada, Humboldt Co., Santa Rose Range, Three Mile Creek, 28 May 1987, *Tiehm 11109* (CAN 531099), AY246934; *P. bolanderi* subsp. *bolanderi,* 2189, USA, Nevada, Lander Co., Shoshone Range, Crum Canyon, 19 May 1987, *Pinzl 7878* (UC 1538773), AY246937; *P. bolanderi* subsp. *bolanderi,* 2184, USA, Nevada, Pershing Co., N end of Stillwater Range, Kitten Springs Rd., 22 May 1979, *Tiehm & Birdsey 4934* (UC 1441380), AY246929; *P. bolanderi* subsp. *bolanderi,* 2197, USA, Nevada, White Pine Co., S of Berry Creek Rd., main road through Schell Creek Range, 1 August 1978, *Williams & Tiehm 78-284* (UC 1441374), AY246938; *P. bolanderi* subsp. *bolanderi,* 2183, USA, Nevada, White Pine Co., Schell Creek Range, Success Summit Rd., 15 June 1977, *Williams 77-27-1* (UC 1441381), AY246925; *P. bolanderi* subsp. *bolanderi,* 2186, USA, Nevada, Washoe Co., Granite Range, Leadville Canyon along Hwy. 34, 24 May 1982, *Tiehm 6981* (UC 1485850), AY246931; *P. bolanderi* subsp. *bolanderi,* 2180, USA, Nevada, White Pine Co., road summit between Red Mtn. and White Pine Range, 23 June 1988, *Tiehm & Crisafulli 11786* (CAN 541881), AY246935; *P. bolanderi* subsp. *bolanderi,* 2022, USA, Oregon, Harney Co., below Jackman Park on Steens Mtn., 7 July 1976, *Lowry II 452* (ILL), AY246921; *P. bolanderi* subsp. *bolanderi,* 2198, USA, Oregon, Malheur Co., Barren Valley, 10 km N of Follyfarm, 30 May 1983, *Joyal 371* (UC 1468186), AY246928

Perideridia bolanderi subsp. *involucrata,* 2025, USA, California, Nevada Co., 1.9 mi S of Bridgeport, *n*=19, 2 July 1964, *Chuang & Constance 5968* (ISU 13411), AY246940; *P. bolanderi* subsp. *involucrata,* 2171, USA, California, Nevada Co., 1.9 mi S of Bridgeport, *n*=19, 2 July 1964, *Chuang & Constance 5968* (ISU 2615), AY246939

Perideridia californica, 2116, USA, California, Alameda Co., 1.1 mi SE of Rancho Los Mochos, 27 June 1967, *Constance et al. 3781* (ISU 2626), AY246943; *P. californica,* 2192, USA, California, Monterey Co., Los Bueyos Creek, Nacamiento River, 27 May 1984, *Branson s.n.* (UC 1508590), AY246941; *P. californica,* 2024, USA, California, Santa Clara Co., 16 mi S of Livermore on Mines Rd. to Mt. Hamilton, *n*=22, 7 June 1964, *Chuang 5952* (ISU 13316), AY246942; *P. californica,* 2207, USA, California, Santa Clara Co., 20 mi S of Livermore on way to Mt. Hamilton, *n*=22, 6 July 1965, *Chuang et al. 5985* (ISU 2627), AY246944

Perideridia erythrorhiza, 2120, USA, Oregon, Douglas Co., 5.6 mi E of Melrose, 16 July 1966, *Chuang & Mitchell 6052* (ISU 13283), AY246945; *P. erythrorhiza,* 2176, USA, Oregon, Douglas Co., 5.6 mi E of Melrose, 16 July 1966, *Chuang & Mitchell 6052* (ISU 2631), AY246948; *P. erythrorhiza,* 2174, USA, Oregon, Klamath Co., 1.6 mi SE of Odessa Marina, Klamath Falls, *n*=19, 23 August 1965, *Constance 3757* (ISU 13452), AY246946; *P. erythrorhiza,* 2175, USA, Oregon, Klamath Co., 1.6 mi SE of Odessa Marina, Klamath Falls, *n*=19, 23 August 1965, *Constance 3757* (ISU 2630), AY246947

Perideridia gairdneri subsp. *borealis,* 2178, Canada, Alberta, Waterton Lakes Natl. Park, Oil Bash, 2 August 1969, *Nagy 2572* (CAN 340194), AY246949; *P. gairdneri* subsp. *borealis,* 2181, Canada, Alberta, Waterton Lakes Natl. Park, Stoney Creek, 6 August 1969, *Nagy 2699* (CAN 340192), AY246954; *P. gairdneri* subsp. *borealis,* 1977, USA, California, Glenn Co., Plaskett Meadows campground, *n*=40, 8 July 1967, *Constance et al. 3786* (ISU 13425), AY246955; *P. gairdneri* subsp. *borealis,* 2047, USA, California, Glenn Co., Plaskett Meadows campground, *n*=40, 8 July 1967, *Constance et al. 3786* (ISU 2640), AY246952; *P. gairdneri* subsp. *borealis,* 2046, USA, California, Glenn Co., Plaskett Meadows, *n*=40, 8 July 1967, *Chuang et al. 6067* (ISU 2648), AY246951; *P. gairdneri* subsp. *borealis,* 2203, USA, Oregon, Benton Co., Long Tom River at south edge of Monroe, *n*=40, 30 July 1967, *Constance & Chuang 3808* (ISU 2632), AY246957; *P. gairdneri* subsp. *borealis,* 2204, USA, Oregon, Josephine Co., 2 mi S of Selma on Hwy. 199, 29 June 1965, *Chuang & Mitchell 5999* (ISU 2647), AY246958; *P. gairdneri* subsp. *borealis,* 2111, USA, Wyoming, Carbon Co., Ryan Park, Medicine Bow, *n*=20, 5 August 1973, *Chuang et al. 7305* (ISU 7630), AY246953; *P. gairdneri* subsp. *borealis,* 2193, USA, Oregon, Klamath Co., Pelican Barn near Upper Klamath Lake, 12 July 1991, *Rolle 374* (UC 1595835), AY246956; *P. gairdneri* subsp. *borealis,* 2190, USA, Wyoming, Carbon Co., North Brush Creek along Hwy. 130, *n*=20, 22 July 1971, *Crawford 354* (UC 1544121), AY246950

TABLE 2. Continued.

Perideridia howellii, 2195, USA, California, Butte Co., Concow Creek, 4 mi N of Concow, 31 July 1990, *Oswald & Ahart 4420* (UC 1562390), AY246960; *P. howellii,* 780, USA, California, Sonoma Co., Tin Barn Rd., 3.5 mi N of intersection with King Ridge Rd., *Raiche 30482* (UC), cult. UC Bot. Gard., Berkeley (no. 83.1080), collected 6 August 1992, AY246959

Perideridia kelloggii, 635, USA, California, Alameda Co., UC Bot. Gard., Berkeley, 6 August 1992, AY246961; *P. kelloggii,* 2051, USA, California, Fresno Co., 10 mi N of Parkfield, 5 July 1965, *Chuang et al. 5982* (ISU 13236), AY246965; *P. kelloggii,* 2200, USA, California, Humboldt Co., 1 mi S of Klamath River near Willow Creek, 4 July 1963, *Chuang et al. 5877* (ISU 13215), AY246968; *P. kelloggii,* 2050, USA, California, Humboldt Co., near Willow Creek, 4 July 1963, *Chuang et al. 5877* (ISU 2740), AY246964; *P. kelloggii,* 2199, USA, California, Mendocino Co., McDonald's Fork, 5 May 1963, *Chuang 5761* (ISU 13218), AY246967; *P. kelloggii,* 2109, USA, California, Sonoma Co., 3 mi S of Petrified Forest, 17 June 1975, *Chuang & Chuang 7487* (ISU 9335), AY246963; *P. kelloggii,* 778, USA, California, Sonoma Co., King Ridge Rd., 5 mi N of Cazadero, *Ornduff et al. s.n.* (UC), cult. UC Bot. Gard., Berkeley (no. 81.0521), collected 6 August 1992, U78373; *P. kelloggii,* 855, USA, California, Sonoma Co., King Ridge Rd., 5 mi N of Cazadero, *Ornduff et al. s.n.* (UC), cult. UC Bot. Gard., Berkeley (no. 81.0521), collected 6 August 1992, AY246962; *P. kelloggii,* 2052, USA, California, Sonoma Co., West Railroad Ave., 10 June 1971, *Chuang et al. 6892* (ISU 6452), AY246966

Perideridia lemmonii, 2210, USA, California, Nevada Co., 0.4 mi above U.S. Hwy. 49 on way to San Juan, *n*=18, 2 July 1964, *Chuang & Constance 5964* (ISU 13268), AY246978; *P. lemmonii,* 2038, USA, California, Nevada Co., 2 mi NW of Sattley, *n*=19, 22 June 1967, *Chuang & Constance 6059* (ISU 13271), AY246975; *P. lemmonii,* 2119, USA, California, Nevada Co., NE side of Lake Van Norden, Sierra Nevada, 7 September 1965, *Constance et al. 3763* (ISU 13449), AY246976; *P. lemmonii,* 2209, USA, California, Placer Co., 1.5 mi NW of Colfax, *n*=18, 2 July 1964, *Chuang & Constance 5962* (ISU 2677), AY246977

Perideridia leptocarpa, 2048, USA, California, Siskiyou Co., 5 mi NW of Cecilville, *n*=17, 15 June 1966, *Constance et al. 3768* (ISU 2754), AY246980; *P. leptocarpa,* 2031, USA, California, Siskiyou Co., above Trinity R. 5 mi NW of Cecilville, 22 July 1967, *Constance & Chuang 3802* (ISU 13493), AY246979; *P. leptocarpa,* 2049, USA, California, Siskiyou Co., above Trinity R. 5 mi NW of Cecilville, 22 July 1967, *Constance & Chuang 3802* (ISU 2748), AY246981

Perideridia neurophylla, KS131, Japan, Hondo, Koshigaya in Musashi, 6 September 1951, *Owhi 307* (MO), AY509127,

Perideridia oregana, 2043, USA, California, Glenn Co., Plaskett Meadows campground, *n*=10, 8 July 1967, *Constance et al. 3785* (ISU 13424), AY246985; *P. oregana,* 2042, USA, California, Humboldt Co., Grouse Mtn., on Clear Lake Rd., *n*=9, 30 June 1965, *Chuang & Mitchell 6002* (ISU 13380), AY246983; *P. oregana,* 2206, USA, California, Lassen Co., 1 mi NE of Nubieber, 19 July 1966, *Chuang & Mitchell 6056* (ISU 13311), AY246987; *P. oregana,* 2167, USA, California, Modoc Co., 5 mi W of Alturas, *n*=10, 23 August 1963, *Chuang & Gleason 5926* (ISU 2758), AY246984; *P. oregana,* 2112, USA, Oregon, Lane Co., 0.5 mi S of Spencer Butte Park, Eugene, *n*=10, 30 July 1967, *Constance & Chuang 3811* (ISU 2790), AY246982; *P. oregana,* 2205, USA, Oregon, Linn Co., overflow area of Calipooia River, 2.5 mi S of Tangent, *n*=10, 26 July 1967, *Constance & Chuang 3805* (ISU 13471), AY246986

Perideridia parishii subsp. *latifolia,* 2169, USA, California, Eldorado Co., Camp Sacramento, 3 mi NE of Strawberry, 25 August 1965, *Chuang 5948* (ISU 2823), AY246974; *P. parishii* subsp. *latifolia,* 2039, USA, California, Nevada Co., Soda Spring, 28 July 1973, *Heckard et al. 7292* (ISU 7625), AY246969; *P. parishii* subsp. *latifolia,* 2113, USA, California, Nevada Co., Soda Springs Resort, Sierra Nevada, 7 September 1965, *Constance & Chuang 3762* (ISU 2813), AY246973; *P. parishii* subsp. *latifolia,* 2040, USA, California, Trinity Co., above Trinity R. 16 mi S of Callahan, *n*=19, 22 July 1967, *Constance & Chuang 3798* (ISU 13496), AY246971; *P. parishii* subsp. *latifolia,* 2041, USA, California, Trinity Co., above Trinity R. 16 mi S of Callahan, *n*=19, 22 July 1967, *Constance & Chuang 3798* (ISU 2832), AY246972; *P. parishii* subsp. *latifolia,* 1975, USA, California, Trinity/Siskiyou Co. Line, Scott Mtn., *n*=19, 22 July 1967, *Constance & Chuang 3800* (ISU 2831), AY246970

Perideridia pringlei, 2122, USA, California, San Luis Obispo Co., California Polytechnical College Bot. Gard., 5 July 1965, *Chuang et al. 5979* (ISU 2834), AY246988; *P. pringlei,* 2177, USA, California, San Luis Obispo Co., California Polytechnical College Bot. Gard., *n*=20, 20 May 1963, *Rodin 7001* (ISU 2833), AY246989

Outgroups

Conioselinum chinense, 501, USA, California, San Mateo Co., San Bruno Mtn., *Raiche 30046;* cult. UC Bot. Gard., Berkeley (no. 83.0114), U78374; *C. scopulorum,* 1114, USA, Colorado, Garfield Co., Flat Tops Wilderness, *Vanderhorst 3883* (RM), AF008634, AF009113

Ligusticum canadense, 1056, USA, North Carolina, Jackson Co., Bull Pen Rd., *Hill 25934* (ILLS), AF008635, AF009114; *L. porteri,* 1091, USA, Colorado, Rio Blanco Co., Flat Tops/White River Plateau, *Vanderhorst 3763* (RM), U78375

Physospermum cornubiense, 879, Ukraine, Crimea, Alikat-Bogaz Pass, *Pimenov & Tomkovich s.n.* (MW), cult. Moscow State Univ. Bot. Gard., Russia, AF077904

considering *Perideridia* only, the maximum sequence divergence was 12.6%. Interspecific pairwise differences within *Perideridia* ranged from 2.5 to 12.6%. G & C content over the entire region ranged from 52.8 to 56.6%. Fourteen gaps, ranging between 1 and 5-bp in size, were introduced to facilitate alignment: ten were 1-bp in length; two were 2-bp in length; one was 4-bp in length; and one was 5-bp in length. Eleven of these gaps were parsimony informative. The g1 statistic for 10,000 random trees was −0.41. This value is significantly more skewed than random data (g1=–0.09 for 250 variable positions and 25 or more taxa; $P < 0.01$; Hillis and Huelsenbeck 1992), indicating that these ITS data contain significant amounts of phylogenetic signal. No evidence of obvious ITS length variants, representative of multiple rDNA repeat types, was observed.

Phylogenetic Analysis. MP analysis of 88 ITS sequences resulted in 32 minimal length trees, each of 524 steps (consistency indices (CI's) = 0.66 and 0.64, with and without uninformative positions, respectively; retention index (RI) = 0.93). The strict consensus of

TABLE 3. Non-molecular characters used in the phylogenetic analysis of *Perideridia* (based on Chuang 1970 and Chuang and Constance 1969).

1. Root type: 0, solitary; 1, fascicled, 2–6; 2, fascicled, 7–25
2. Multistelic tuberous roots: 0, absent or rare; 1, present (4–6 steles); 2, present (>12 steles)
3. Primary xylem strands in root arranged alternatively with secondary vascular tissue: 0, absent; 1, present
4. Basal leaf complexity: 0, ternate or biternate, or pinnate with no more than 2 pairs of pinnae; 1, pinnate with 3–5 pairs of pinnae; 2, bipinnately or tripinnately dissected
5. Basal leaf ultimate divisions: 0, narrowly linear, <1mm broad; 1, linear, 1–10 mm broad; 2, ovate to ovate-lanceolate, >10 (to 40) mm broad
6. Leaf divisions: 0, homomorphic; 1, dimorphic
7. Organization of mesophyll in leaf lamina: 0, dorsiventral; 1, isolateral
8. Accessory vascular bundle in leaf rachis transection: 0, absent; 1, present
9. Involucre at anthesis: 0, conspicuous; 1, inconspicuous or lacking
10. Fruiting rays: 0, subequal; 1, markedly unequal
11. No. of vittae in valleculae: 0, one; 1, more than one
12. No. of vittae in commissure: 0, two; 1, four to six; 2, >10
13. Stylopodium shape: 0, low conic (with long styles); 1, high conic (with short styles)
14. No. of veins in petals: 0, one; 1, three to seven
15. Haploid chromosome number: 0, diploids (8, 9, 10, and possibly 13); 1, 17; 2, 18 and 19; 3, 20; 4, 22; 5, >40 (octoploids and dodecaploids)
16. Habitat preference: 0, moist or wet; 1, xerophytic

these trees is presented in Fig. 1. For the 42 resolved nodes in the strict consensus tree, bootstrap values ranged from 35 to 100% (averaging 83.8%), with over half of these nodes supported by values > 90%. Of the 11 potentially informative alignment gaps, eight mapped without homoplasy on each of the 32 shortest trees (solid bars in Fig. 1). A 1-bp deletion occurred in *Ligusticum porteri*, *Conioselinum scopulorum*, and *Conioselinum chinense*, but not in *Ligusticum canadense* (open bar; Fig. 1). Another 1-bp deletion, arising twice independently, occurred in all accessions of *P. erythrorhiza* and *P. californica* (bars with diagonal striping; Fig. 1). A third 1-bp deletion occurred in all ingroup taxa, with reversals in *Perideridia howellii* and *P. pringlei* (stippled bars).

Based on the hierarchical likelihood ratio test statistic, Modeltest selected the TrN+G model of nucleotide substitution (Tamura and Nei 1993) as fitting these ITS data best (base frequencies: 0.2349, A; 0.2364, C; 0.2537, G; 0.2750, T; estimates of substitution rates: A↔C, 1; A↔G, 1.9931; A↔T, 1; C↔G, 1; C↔T, 5.9561; G↔T, 1; proportion of invariable sites = 0; gamma distribution shape parameter = 0.4919). Using these parameters, a single tree was recovered in PAUP*, with a −Ln likelihood score of 3605.11843 (Fig. 2). Bootstrap values, inferred using 1000 replicate neighbor-joining searches with ML distance, were generally high and comparable to those calculated by 33 replicate analyses under ML optimization, particularly so for the most well-supported nodes. Relationships inferred by Bayesian phylogenetic analysis (tree not shown) were identical to those estimated by the MP and ML

TABLE 4. Data matrix of character states indicated in Table 3 for use in the cladistic analysis of *Perideridia* morphological data. Polymorphic states are indicated in parentheses.

Species	Characters															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
P. americana	1	2	0	2	1	0	0	0	0	0	1	1	0	1	3	0
P. bacigalupii	1	1	0	2	1	0	1	0	0	1	0	0	0	0	2	1
P. bolanderi subsp. *bolanderi*	{0,1}	1	0	2	1	1	1	0	0	0	1	1	0	0	2	1
P. bolanderi subsp. *involucrata*	{0,1}	1	0	2	0	0	1	0	0	0	1	1	0	0	2	1
P. californica	1	1	0	2	1	1	0	1	0	0	0	{0,1}	0	0	4	0
P. erythrorhiza	1	1	0	1	0	0	1	0	1	1	1	1	0	1	2	1
P. gairdneri subsp. *borealis*	1	1	0	1	1	0	0	0	{0,1}	{0,1}	0	0	0	1	{3,5}	0
P. gairdneri subsp. *gairdneri*	0	1	0	1	1	0	1	0	1	{0,1}	0	0	0	0	2	1
P. howellii	2	0	1	2	2	0	0	1	0	0	0	0	1	1	3	0
P. kelloggii	2	0	1	2	1	0	1	1	0	0	0	0	1	0	3	1
P. lemmonii	0	1	0	0	1	0	1	0	1	1	0	0	0	0	2	1
P. leptocarpa	1	1	0	2	0	0	1	0	1	1	0	0	0	0	1	1
P. oregana	1	1	0	2	{0,1}	0	1	0	{0,1}	0	0	{0,1}	0	0	0	1
P. parishii subsp. *latifolia*	0	1	0	0	1	0	0	0	1	0	1	1	0	0	2	0
P. parishii subsp. *parishii*	0	1	0	0	1	0	0	0	1	1	1	1	0	0	2	0
P. pringlei	1	1	0	2	0	1	1	0	{0,1}	{0,1}	1	2	0	0	3	1

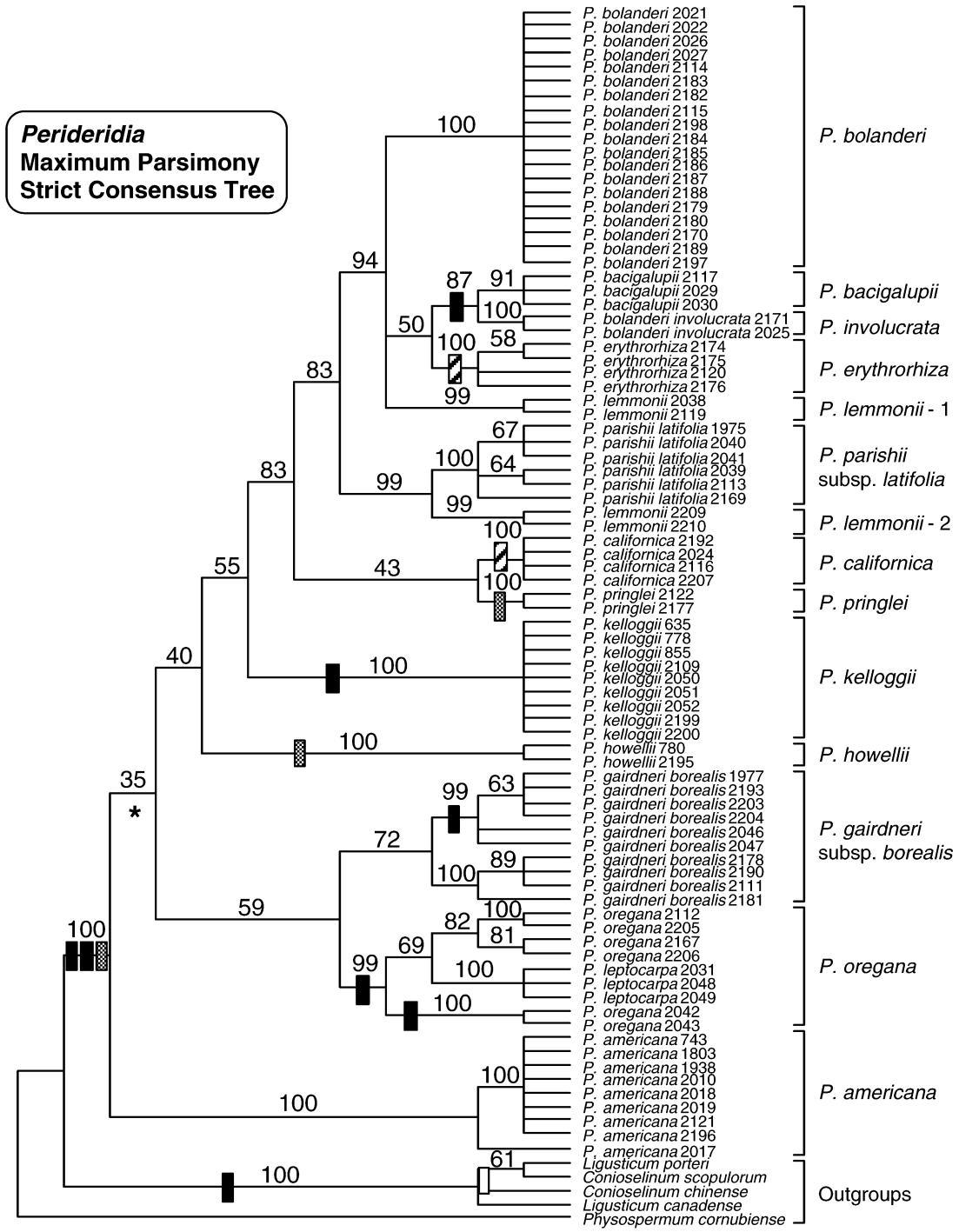

FIG. 1. Strict consensus tree of 32 minimal length 524-step trees derived from equally weighted maximum parsimony analysis of 88 ITS sequences (CI's = 0.66 and 0.64, with and without uninformative positions, respectively; RI = 0.93). Numbers at nodes are bootstrap estimates from 100 replicate analyses. Complete taxon names, including the ranks of infraspecific taxa which were omitted for brevity, are provided in Table 2. Bracketed clades indicate taxa recognized in this study. The distribution of 11 potentially informative alignment gaps is indicated: solid bars, synapomorphies; all other bars, homoplasies. The results of the Bayesian analysis were identical to those presented here, with the exception of the collapse of the single branch denoted by an asterisk.

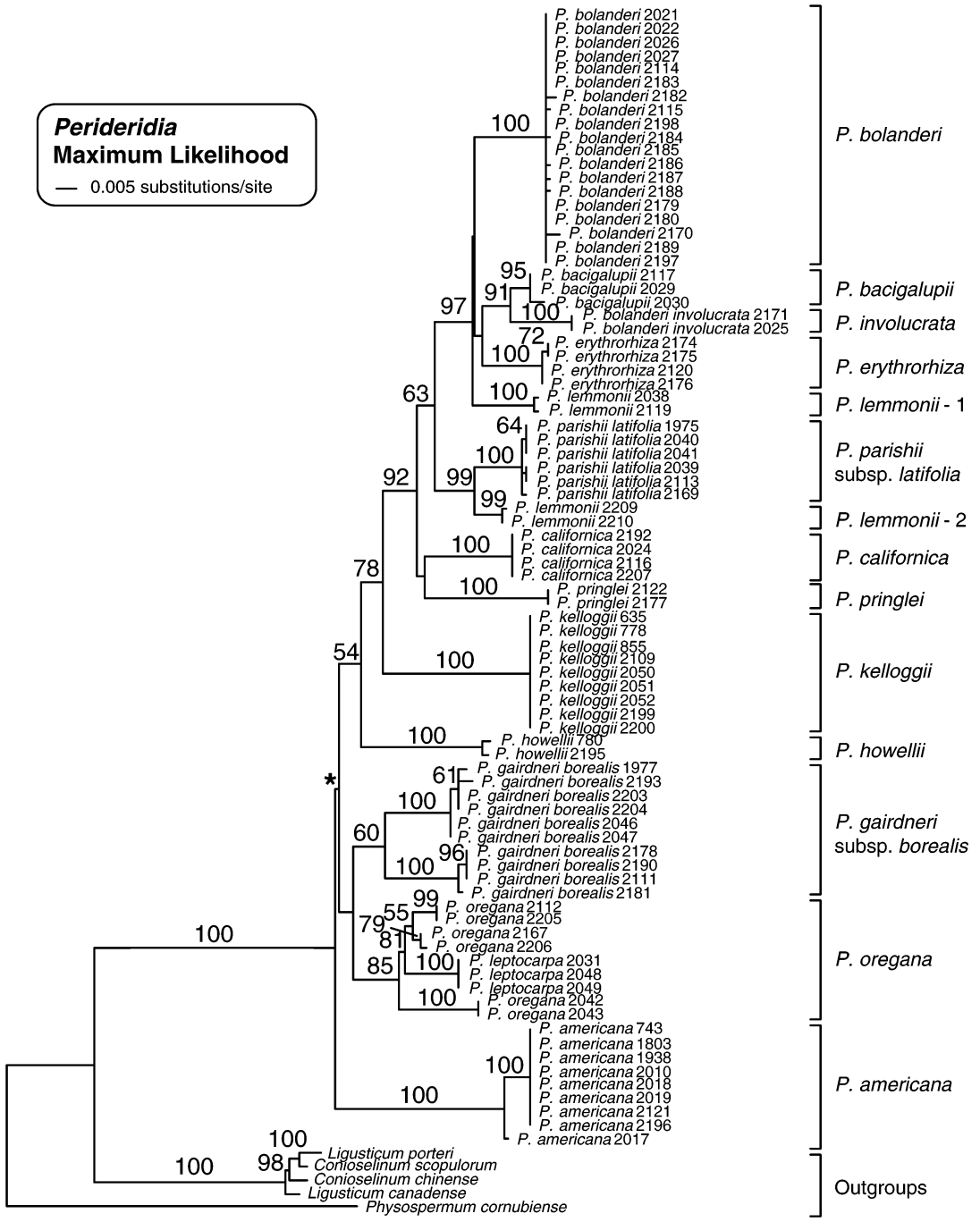

FIG. 2. Single tree derived from maximum likelihood analysis of 88 ITS sequences, under a TrN+G model of nucleotide substitution (–Ln likelihood = 3605.11843). Numbers at nodes represent bootstrap estimates calculated from 1000 replicate neighbor-joining analyses using maximum likelihood distance. Complete taxon names, including the ranks of infraspecific taxa which were omitted for brevity, are provided in Table 2. Bracketed clades indicate taxa recognized in this study. The results of the Bayesian analysis were identical to those presented here, with the exception of the collapse of the single branch denoted by an asterisk.

analyses, with the exception of the collapse of a single branch at the base of the tree yielding a trichotomy (indicated by asterisks in Figs. 1, 2). This collapsed branch is weakly supported in both the MP (35% bootstrap) and ML (< 50% bootstrap) trees. Bayesian posterior clade probabilities for 41 resolved nodes ranged from 53 to 100% (averaging 95.6%), with 36 of these nodes having posterior clade probabilities > 90%.

Phylogenetic Relationships. All trees resulted in a monophyletic and well-supported genus *Perideridia*. Conspecific populations of *Perideridia* (i.e., *P. bacigalupii*, *P. erythrorhiza*, *P. parishii* subsp. *latifolia*, *P. californica*, *P. pringlei*, *P. kelloggii*, *P. howellii*, *P. gairdneri* subsp. *borealis*, *P. leptocarpa*, and *P. americana*) constituted well-diagnosed groups, except for populations of *P. lemmonii*, *P. bolanderi*, and *P. oregana*. *Perideridia lemmonii* constituted two separate lineages (labeled as ''*P. lemmonii*-1'' and ''*P. lemmonii*-2,'' the latter arising as sister group to *P. parishii* subsp. *latifolia*). Constraining the four accessions of *P. lemmonii* to monophyly and repeating the MP analysis resulted in trees 15 steps longer (539 steps) than those most parsimonious (524 steps). Both suboptimal and optimal sets of trees were compared using the Kishino-Hasegawa and Templeton tests. These tests indicated that the suboptimal trees containing a monophyletic *P. lemmonii* are significantly different ($P < 0.05$) than the shortest trees recovered by the unconstrained analysis, suggesting that signal for *P. lemmonii* monophyly does not exist. *Perideridia bolanderi* is also not monophyletic, with populations from each of its two subspecies resolved as separate clades. *Perideridia bolanderi* subsp. *involucrata* (labeled as ''*P. involucrata*'') and *P. bacigalupii* are strongly supported sister groups, and are united by a synapomorphic 1-bp deletion in ITS-2 (Fig. 1). However, constraining all *P. bolanderi* accessions to monophyly resulted in trees only five steps longer than those most parsimonious, and the results of the Kishino-Hasegawa and Templeton tests did not indicate significant discordance between these sets of trees. Populations of *P. oregana* and *P. leptocarpa* constituted a well-supported clade (labeled as ''*P. oregana*''); however, the former species is paraphyletic, with a monophyletic *P. leptocarpa* arising from within it. These two species also share a unique 1-bp deletion in ITS-2; another 1-bp deletion is found in two accessions of *P. oregana* (accession nos. 2042 and 2043) from California (Fig. 1).

Three major clades are resolved in *Perideridia*, but support for only one of them (i.e., the *P. americana* clade) is strong. The first major clade constitutes species *P. bolanderi* (including subsp. *involucrata*), *P. bacigalupii*, *P. erythrorhiza*, *P. lemmonii*, *P. parishii*, *P. californica*, *P. pringlei*, *P. kelloggii*, and *P. howellii*. Bootstrap support values for the basal positions of *P. kelloggii* and *P. howellii* within this clade are weak (55 and 40%, respectively, in the MP tree (Fig. 1) and 78 and 54%, respectively, in the ML tree, Fig. 2). The second major clade constitutes species *P. gairdneri* and *P. oregana* (with included *P. leptocarpa*). This clade is also weakly supported, with bootstrap values of 59 and < 50% depending upon the analysis. In the MP and ML trees, the aforementioned two major clades are resolved as weakly supported sister groups. However, in the Bayesian tree (not shown), these two major clades form a basal trichotomy with *P. americana*, the third major clade. Support for the latter clade is strong, with 99–100% bootstrap or posterior probability values.

The relationships among these three major clades of *Perideridia* and the composition of the largest clade were affected by choice of outgroup. The exclusion of *Physospermum cornubiense* from subsequent MP searches and the rooting of the trees with the four North American members of the *Conioselinum* clade maintained *P. americana* as sister taxon to all other *Perideridia* taxa, but removed *P. kelloggii* and *P. howellii* from the first major clade, placing them as two branches of a four-branched polytomy (the other two branches representing the *P. bolanderi* through *P. pringlei* clade and the *P. gairdneri—P. oregana*/*P. leptocarpa* clade). Reinstating the Eurasian *Physospermum* but removing the four members of the *Conioselinum* clade in another round of MP analyses resulted in the placement of *P. howellii* as one of four basal branches within *Perideridia* (and maintained the three other major clades as outlined above for Fig. 1, but with the exclusion of *P. howellii* from the first major clade). Thus, as a result of different outgroup selection, the placements of *P. howellii* and *P. kelloggii* within the genus are not clear. These are the only two species of *Perideridia* possessing typical dicot monostelic roots; all other species possess multistelic tuberous roots.

With the exceptions of *Perideridia oregana* (including *P. leptocarpa*) and *P. gairdneri* subsp. *borealis*, where pairwise divergence estimates approached 4.5 and 6% of nucleotides, respectively, conspecific populations of *Perideridia* exhibited very little sequence divergence, if they varied at all. As examples, maximum pairwise sequence divergence values for *P. bolanderi* subsp. *bolanderi* (19 accessions), *P. kelloggii* (9 accessions), *P. americana* (9 accessions), *P. parishii* subsp. *latifolia* (6 accessions), and *P. erythrorhiza* (4 accessions) were 0.7%, 0%, 1.2%, 0.3%, and 0.2%, respectively. The eight accessions of *P. americana* from Illinois had identical ITS sequences, and only differed slightly from the single accession of *P. americana* from Missouri (accession no. 2017). The ten accessions of *P. gairdneri* subsp. *borealis* constituted two strongly-supported subclades, with one comprising populations from California (Glenn Co.) and Oregon (accession nos. 1977, 2193, 2203, 2204, 2046, and 2047) and the other comprising populations from Wyoming and Alberta (accession nos. 2178, 2190, 2111, and 2181). The first of these two subclades is

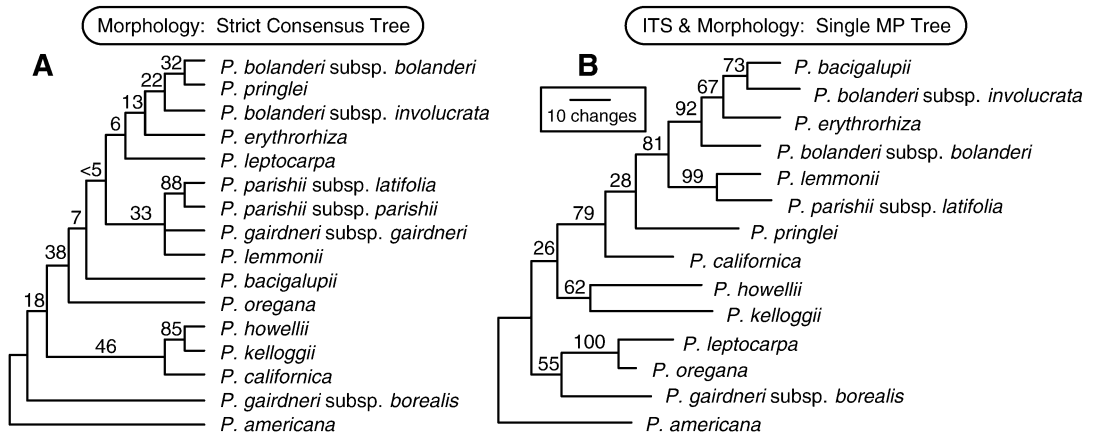

FIG. 3. A. Strict consensus tree of two minimal length 54-step trees derived from equally weighted maximum parsimony analysis of 16 morphological, anatomical, cytological, and ecological characters (CI = 0.67; RI = 0.67). B. Single tree of 342 steps derived from maximum parsimony analysis of combined ITS and non-molecular data (CI's = 0.70 and 0.55, with and without uninformative characters, respectively; RI = 0.58). Numbers at nodes in both trees are bootstrap estimates from 100 replicate analyses. ITS data were not available for *Perideridia gairdneri* subsp. *gairdneri* and *P. parishii* subsp. *parishii*, thus these taxa were not included in the combined analysis.

supported further by a shared 2-bp insertion in ITS-1 (Fig. 1). Geographic variation in ITS sequences was also apparent in populations of *P. oregana*, with those accessions from NE California (Modoc and Lassen Cos.) and Oregon (accession nos. 2112, 2205, 2167, and 2206) constituting a separate clade from those from NW and North Central California (Humboldt and Glenn Cos.; accession nos. 2042 and 2043). *Perideridia leptocarpa*, representing three accessions from Siskiyou Co., California, allies weakly with the NE California and Oregon populations of *P. oregana*. Variation in sequence divergence between the two separate lineages of *P. lemmonii* was approximately 6%. Of the nine populations represented by duplicate herbarium specimens, only one (*Perideridia gairdneri* subsp. *borealis*, accession nos. 1977 and 2047) exhibited dissimilar ITS sequences (with four nucleotide positions varying).

Morphological Analysis. Cladistic analysis of 16 morphological, anatomical, cytological, and ecological characters revealed two maximally parsimonious trees, each of 54 steps (CI = 0.67; RI = 0.67). However, the topology exhibited by the strict consensus of these trees (Fig. 3A) is highly unreliable, with only two nodes supported by bootstrap values ≥ 85% (*P. howellii* + *P. kelloggii*, and the two subspecies of *P. parishii*). All remaining nodes had bootstrap values < 50%. *Perideridia bolanderi* and *P. gairdneri* are each not monophyletic, and tests to evaluate differences in alternative tree topologies (where each of these species was constrained to be monophyletic and compared against non-constrained trees) showed no statistically significant differences. The exclusion of character 15 (haploid chromosome number) from subsequent MP searches resulted in a less resolved topology, with only clades *P. bolanderi* through *P. leptocarpa*, *P. parishii* subsp. *latifolia* + *P. parishii* subsp. *parishii*, and *P. howellii* through *P. californica* maintained, arising from a large, basal polytomy.

Simultaneous MP analysis of combined ITS and non-molecular data for 14 taxa resulted in a single, minimal length tree of 342 steps (CI's = 0.70 and 0.55, with and without uninformative characters, respectively; RI = 0.58; Fig. 3B). Bootstrap values ranged between 26 and 100%. While the relationships exhibited by this tree were highly consistent to those inferred using only molecular data from many more taxa, they differed by supporting (moderately, with a 62% bootstrap value) a union between *P. howellii* and *P. kelloggii*. The sister group relationship between *P. pringlei* and *P. californica*, as inferred (but supported weakly) by analyses of the large ITS data set, was not recovered in the combined analysis; however, trees uniting these two species were only two steps longer than those most parsimonious.

To see if the non-molecular characters tracked phylogeny, as inferred by the results of the analysis of combined ITS and non-molecular data, they were optimized on the resultant single, most-parsimonious 342-step cladogram. Six character states were synapomorphic. In *P. howellii* and *P. kelloggii*, these characters included a fascicle of 7–25 roots (character 1: state 2), monostelic roots (2:0), the occurrence of primary xylem strands in the root arranged alternatively with secondary vascular tissue (3:1), and a high conical stylopodium with short styles (13:1); *P. lemmonii* and *P. parishii* subsp. *latifolia* shared ternate or biternate basal leaves (4:0); and *P. bacigalupii*, *P. bolanderi*, *P. erythrorhiza*, *P. lemmonii*, and *P. parishii* subsp. *latifolia* shared a hap-

loid chromosome number of 18 or 19 (15:2). All other characters showed highly homoplastic distributions of their states across the phylogeny. Characters exhibiting the greatest homoplasy included narrowly linear basal leaf ultimate divisions (5:0), isolateral mesophyll organization (7:1), solitary vallecular vittae (11:0), two commissural vittae (12:0), and a xerophytic habitat preference (16:1).

Discussion

Perideridia neurophylla. The high ITS sequence divergence of *Perideridia neurophylla* relative to all other *Perideridia* ITS sequences suggested that this eastern Asian species may not belong within the genus. The results of preliminary phylogenetic analyses placed *Perideridia neurophylla* at the base of the trees, away from all other *Perideridia* species (results not shown). A search in GenBank using BLAST revealed the ITS sequence of *Perideridia neurophylla* to be most similar to those of members of tribe Aciphylleae M.F. Watson & S.R. Downie (Downie et al. 2000b). Maximum parsimony analysis of a much larger (and unpublished) data set than that presented here, including representatives of all major tribes and clades of Apiaceae subfamily Apioideae (Downie et al. 2001), revealed an affinity of *Perideridia neurophylla* to several accessions of *Spuriopimpinella* (H. Boissieu) Kitag. and *Pternopetalum* Franch., and to *Ligusticum scoticum* L. (tree not shown). This group is closely related to tribe Aciphylleae and distantly related to tribe Oenantheae. While the closest relative of *Perideridia neurophylla* has yet to be established, it is clear that this species should not be treated in *Perideridia*. The name *Pterygopleurum neurophyllum* (Maxim.) Kitag., previously applied to these plants, is maintained. These eastern Asian plants are indeed similar to North American *Perideridia* in habit and foliage type, but they differ most obviously in their prominent corky fruit ribs (*Pterygopleurum* means ''winged rib''), scaberulous inflorescences, and conspicuously ridged stems.

The genus *Perideridia* was cited by Constance (1972) as an example of the classic eastern Asian-North American disjunct distribution pattern. For many congeneric plants, such patterns of intercontinental biogeographic disjunctions have been reevaluated phylogenetically and show that some of these disjunct groups are erroneously circumscribed, as characterized by polyphyly of their corresponding taxa (reviewed in Wen 1999, 2001). The multistelic tuberous roots of *Pterygopleurum neurophyllum*—common in *Perideridia*, but ''unique'' among dicotyledons—led Chuang and Constance (1969) to transfer this species into *Perideridia* rather than to maintain it as a monotypic genus. On the basis of DNA evidence, we suggest that multistelic tuberous roots have evolved independently in two well-separated lineages of Apiaceae. Ontogenetic studies, however, are required to determine the exact mode of multistele formation in the tuberous roots of *Perideridia* and *Pterygopleurum*.

In addition to *Perideridia*, Constance (1972) lists four other genera of tribe Oenantheae (*Cicuta* L., *Cryptotaenia* DC., *Oenanthe* L., and *Sium* L.) demonstrating similar eastern Asian-North American disjunct distributional patterns. Our investigations are ongoing, but the results to date suggest that *Cryptotaenia*, *Oenanthe*, and *Sium* are also polyphyletic and that the taxonomic status of their disjunct members need to be redefined in light of these findings (Hardway et al. 2004; S. Downie and K. Spalik, unpublished data). Furthermore, we have shown that two additional Oenantheae genera having broader discontinuous distributions, *Berula* W.D.J. Koch and *Bifora* Hoffm., are also polyphyletic (Hardway et al. 2004). The high level of polyphyly noted for Oenantheae extends beyond the tribe, for many other genera of Apiaceae distributed widely in the northern hemisphere have been revealed to be polyphyletic through phylogenetic studies (Downie et al. 2000b, 2000c, 2002; Spalik et al. 2001b; Sun et al. 2004). The general phenotypic similarity of polyphyletic taxa, as exhibited by many umbellifers, is likely attributable to symplesiomorphies or convergence in distant but similar habitats (Wen 1999).

Phylogenetic Relationships and Character Evolution. Phylogenetic analyses of ITS sequence data under three different optimality criteria yielded a congruent and well-resolved hypothesis of relationships for the North American umbellifer genus *Perideridia*. Here, we use this phylogeny to assess monophyly of species and infer patterns in the evolution of specific morphological, anatomical, and cytological characters in an effort to underline their importance in species and clade delimitation.

Only two species of *Perideridia* have monostelic roots: *P. howellii* and *P. kelloggii*. These roots are generally quite long, fibrous or slightly thickened (rarely tuberous), and densely fascicled. They also have a distinctive anatomy, for each root is composed of four to five primary xylem elements arranged alternately with isolated strands of secondary vascular tissue (Chuang 1970). These characters, in addition to their unique leaf rachis anatomy and conspicuous stylopodia with short styles, serve to distinguish this group from all other species. However, some roots of *P. kelloggii* have one to several tubers near their tips that have the same multistelic type of vascular structure as found in other species of *Perideridia* (Chuang 1970). *Perideridia howellii* and *P. kelloggii* are both tetraploid ($n=20$) and share a similar geographic distribution. They unite as a moderately to strongly supported clade in the cladistic analyses of morphological and combined data. Separate analyses of molecular data, however, do not support their monophyly, although these two species are separated

by only one node in all inferred trees. Regardless of their respective relationship, they do not arise as basal in any of the trees, thus the presence of clustered fibrous or slightly thickened monostelic roots in *P. howellii* and *P. kelloggii* must be considered a reversal from ancestors bearing multistelic tuberous roots.

Perideridia americana (n=20) is the only species of *Perideridia* in the midwestern U.S. and is most abundant in Illinois and Missouri (Baskin and Baskin 1993). Along with *P. gairdneri* subsp. *borealis*, it is also unique in that it produces predominantly flavones, with flavonols occurring sporadically and only in trace amounts (Giannasi and Chuang 1976). All other species produce only flavonols, or mainly flavonols and a few flavones. Chuang and Constance (1969) described *P. americana* as being ''a tetraploid survivor at the border of Pleistocene glaciation.'' *Perideridia gairdneri* subsp. *borealis* is also tetraploid (with cytotypes of n=40 and 60 reported; Chuang and Constance 1969), and given their similar flavonoid chemistry, it was hypothesized that the current distribution of *P. americana* may represent a disjunct extension of the more northeasterly distributed *P. gairdneri* subsp. *borealis* (Giannasi and Chuang 1976). The results of the cladistic analyses presented here provide some support for the close affinity between these taxa. In the analyses of morphology or combined molecular and morphological data, *P. gairdneri* subsp. *borealis* is placed at or near the base of the trees (when *P. americana* is used to root the tree), whereas in the trees inferred from molecular data it is only two (weakly supported) nodes away from *P. americana*.

Perideridia gairdneri was described by Chuang and Constance (1969) as comprising two subspecies. The flavonoid chemistry of subsp. *gairdneri* (n=19) is quite distinct from that of subsp. *borealis*, and given further differences in their morphology, leaf anatomy, and haploid chromosome number, it was suggested that these taxa might represent different species (Giannasi and Chuang 1976; Cronquist 1997). While we were not able to include subsp. *gairdneri* in the molecular analysis because of its rarity, in the cladistic analysis of morphological data the two subspecies of *P. gairdneri* were not recovered as monophyletic. This result needs confirmation through molecular study. Subspecies *borealis* (=*Perideridia montana* sensu Cronquist 1997) is widely distributed, and is recognized by its once or occasionally twice pinnate leaves with 3–5 pairs of linear or lanceolate leaflets and globose fruits with solitary vallecular vittae. The two subclades of subsp. *borealis* recovered in the molecular-derived cladograms are geographically and cytologically differentiated, with one subclade comprising all examined populations from California and Oregon, and the other comprising populations from Wyoming and Alberta. For those accessions where chromosome numbers are available (Chuang and Constance 1969), those of the first subclade are n=40 (for 4 of 6 accessions) and those of the second are n=20 (2 of 4 accessions). A chromosome race of n=60, reported from Lake Co., Oregon (Chuang and Constance 1969), was not included in our study. However, Chuang and Constance (1969) reported both n=20 and 40 populations of subsp. *borealis* scattered randomly throughout the Willamette Valley, Oregon, so it is doubtful that further study will yield two cytologically distinct groups. Furthermore, morphological differences between the plants of these two subclades are not readily apparent upon examination of herbarium specimens.

Perideridia bolanderi is a morphologically heterogeneous species comprising two subspecies. Its tuberous roots may be solitary or clustered, its leaf divisions may be conspicuously dimorphic or homomorphic, and its bracts and bractlets may be deciduous or persistent. We have observed that herbarium specimens of *P. bolanderi* subsp. *bolanderi* are occasionally misidentified (usually as *P. parishii* subsp. *latifolia* or *P. gairdneri* subsp. *borealis*). A combination of characters is required to distinguish *P. bolanderi* from all other species, and we have not found any uniquely occurring non-molecular character supporting its monophyly. All plants have oblong-shaped fruits, bearing 2–4 vittae in the intervals and 4–6 on the commissure, and both subspecies share a haploid chromosome number of 19. However, this chromosome number is the most prevalent within the genus, and results from a recent study of other western North American apioid umbellifers have shown that fruit shape and vittae number are notoriously poor indicators of phylogenetic relationship (Downie et al. 2002). In all trees presented here (whether inferred using ITS sequences, morphology, or combined data), subspecies *bolanderi* and *involucrata* do not comprise a clade, although monophyly of the species in the molecular analyses was recovered in trees of only a few steps longer than those most parsimonious. *Perideridia bacigalupii*, with its many-flowered spherical umbellets, is confirmed as a distinct species sister to *P. bolanderi* subsp. *involucrata*. These plants grow sympatrically, have the same chromosome number (n=19), and share a synapomorphic 1-bp deletion in ITS-2.

Perideridia californica (n=22) and *P. pringlei* (n=20) constitute a weakly supported sister group in all ITS-derived trees, but do not form a clade upon consideration of morphology or combined data. They do, however, share several attributes, such as conspicuously dimorphic leaf divisions, long rays, and oblong-shaped large fruits. In addition to chromosome number, the species differ in habitat preference, tuber size and branching, leaflet size, leaf anatomy, and the number of vallecular vittae in the fruit intervals and commissure (Chuang and Constance 1969; Chuang 1970). Fur-

thermore, each species has a different deletion in the ITS region. We maintain each species as distinct.

Perideridia oregana ''is morphologically the most polymorphic species in the genus'' and occupies a broad range of habitats (Chuang and Constance 1969). Four different chromosome races are reported, three of which are presumably diploid ($n=8$, 9, and 10). The origin of the $n=13$ populations is unknown, but they are included in the aforementioned group on the basis of a similar vegetative morphology (Chuang and Constance 1969). The *Perideridia oregana* complex is quite difficult taxonomically for its races display essentially continuous variation in stature, dissection of foliage and segment size, ray number and length, and the number of commissural vittae (Chuang and Constance 1969; Chuang 1970). *Perideridia leptocarpa* ($n=17$), regarded initially as a tetraploid race of *P. oregana* owing to their similar morphology, was dubiously erected as a distinct species by Chuang and Constance (1969). The same authors postulated a hybrid origin of these plants because of their high degree of sterility, with some race of *P. oregana* suggested as one of the parental types. The results presented here, showing that *P. leptocarpa* arises from within a paraphyletic *P. oregana*, indicate that those collections of *P. leptocarpa* should be treated as *P. oregana*.

Perideridia lemmonii consists of two well-separated lineages. One of these (accession nos. 2038 and 2119) is strongly allied to *P. bolanderi*, *P. bacigalupii*, and *P. erythrorhiza*, whereas the other (accession nos. 2209 and 2210) is sister to *P. parishii* subsp. *latifolia*. This split is also reflected in a difference in chromosome number: accession no. 2038 is $n=19$; accession nos. 2209 and 2210 are both $n=18$ (Chuang and Constance 1969). Sequence divergence values among the accessions comprising these two clades are about 6%. *Perideridia lemmonii* and *P. parishii* subsp. *latifolia* grow together in meadows and open coniferous forests in California and Nevada and are very similar vegetatively (Cronquist 1997). Indeed, plants of both taxa are often included in the same collection (Chuang 1970). These taxa are differentiated primarily on the relative lengths of their fruiting rays and bractlets, the number of vittae in the intervals and commissure, and organization of the leaf mesophyll. In contrast, Chuang and Constance (1969) and Cronquist (1997) postulated a close relationship between *P. lemmonii* and *P. gairdneri* subsp. *gairdneri* on the basis of their single-veined petals, solitary tuberous roots, isolateral mesophyll organization, and ellipsoid to subglobose fruits. This association is supported, albeit weakly, in the analysis of morphological data. Material of *Perideridia gairdneri* subsp. *gairdneri* was unavailable for inclusion in the molecular analysis. We can see no obvious morphological differences between the collections comprising *P. lemmonii* lineages 1 and 2. (However, only one of these specimens has mature fruits, two are missing underground structures, and the basal leaves of all specimens, so critical for proper identification, are withered or poorly preserved.) Nevertheless, we accept *P. lemmonii*-2 as representing *P. lemmonii* sensu Chuang and Constance because of its position in the molecular-derived cladograms adjacent to *P. parishii* subsp. *latifolia*, a relationship in accordance with their sympatric distribution and highly similar vegetative morphology. We also believe that further study will reveal that *P. lemmonii*-1 is a new species. *Perideridia lemmonii*-1 is strongly supported as monophyletic and is quite distinct molecularly from putatively allied *P. bolanderi*, *P. bacigalupii*, and *P. erythrorhiza*.

In all molecular trees, *Perideridia erythrorhiza* constitutes a strongly supported clade (100% bootstrap and posterior probability values) that is allied weakly to *P. bacigalupii* + *P. bolanderi* subsp. *involucrata*. The monophyly of *P. erythrorhiza* is bolstered by a 1-bp deletion in ITS-1 (representing a loss of one G in a run of six G's in all other *Perideridia* species except *P. californica*, where this same deletion has occurred in parallel). *Perideridia erythrorhiza* is a rare species, restricted to three general locations in southwestern Oregon (Hipkins and Wilson 2001). A study of isozyme variation revealed that populations within and among these regions are highly differentiated (Hipkins and Wilson 2001), and other studies of the species using morphological, phenological, physiological, and genetic differences suggested that the Klamath and Douglas Cos. populations, located east and west of the Cascade Range, might actually represent different species (Meinke 1998, and unpublished data). We have examined ITS sequences from single populations from two of these regions (Klamath Co., accession nos. 2174 and 2175; Douglas Co., accession nos. 2120 and 2176) and report only one nucleotide difference between them (representing 0.2% sequence divergence). This conservation in DNA sequence does not support the recognition of two species, given that interspecific pairwise distances in *Perideridia* are at least ten-fold higher, ranging from 2.5% (between *P. leptocarpa* and *P. oregana*, taxa that are actually conspecific) to 12.6% (between *P. americana* and *P. bolanderi*). In general, conspecific populations of *Perideridia* exhibit very little sequence divergence, if they vary at all. Based on the inferred phylogeny, we speculate that the Klamath Co. populations may have had their origins from populations west of the Cascades. However, further sampling is necessary from each of the three localities in which *P. erythrorhiza* occurs (especially from the more genetically diverse southwesternmost populations in Josephine Co.; Hipkins and Wilson 2001) to confirm this speculation and the taxonomic status of these populations.

The similarity of the trees recovered by MP, ML, and Bayesian analyses indicates that phylogenetic signal in

Perideridia is relatively insensitive to the optimality criteria employed during tree searches. The results of each of these analyses support the integrity of most of the taxa in the genus, as outlined by Chuang and Constance (1969). *Perideridia bacigalupii*, *P. erythrorhiza*, *P. californica*, *P. pringlei*, *P. kelloggii*, *P. howellii*, and *P. americana* are each monophyletic species. *Perideridia parishii* subsp. *latifolia* and *P. gairdneri* subsp. *borealis* are also each evolutionarily distinct, but monophyly of their respective species must be confirmed upon the inclusion of subspp. *parishii* and *gairdneri* in a subsequent study. The four examined populations of *Perideridia lemmonii* comprise two separate lineages, and one of these may eventually be described as a new species upon further consideration. The two subspecies of *P. bolanderi* do not form a monophyletic group, but this separation is only weakly supported. If further studies confirm the separation of *P. bolanderi* subsp. *involucrata* from the typical subspecies, then the former should be treated as a distinct species, of which the name *P. involucrata* would apply. The species status of the narrowly distributed *P. leptocarpa* is rejected; it is best treated as a tetraploid race of *P. oregana*.

Lastly, while this study was not designed to find morphological characters synapomorphic for *Perideridia*, the taxa included are generally similar and share many common features (especially upon the removal of *P. neurophylla*). As an aid to identification of the genus, we provide a general description of *Perideridia*. The genus constitutes caulescent, glabrous, perennial herbs arising from one or a cluster of tuberous-thickened roots, of which the roots of many species are multistelic. These tuberous roots are the most distinctive vegetative character separating *Perideridia* from other genera which closely resemble it. Their leaves are pinnately or ternate-pinnately compound or dissected, with mostly narrow and elongate ultimate leaf divisions. The flowers are white when fresh. The fruits are glabrous, and orbicular to ellipsoid or oblong in shape; the ribs are generally inconspicuous. A stylopodium is evident, as is a prominent and persistent bifid carpophore. However, several members depart from this description. As examples, *P. howellii* and *P. kelloggii* have fibrous to slightly thickened, densely fascicled roots that are quite different anatomically from those of the other species, *P. bolanderi* subsp. *bolanderi*, *P. californica*, and *P. pringlei* exhibit dimorphic leaf divisions, and *P. howellii* bears conspicuously corky fruit ribs.

ACKNOWLEDGEMENTS. The authors thank the curators of the CAN, ILL, ILLS, ISU, MO, and UC herbaria and the Botanic Garden of the University of California for access to specimens; Carol Baskin, Sarah Malaby, and Paul Berrang for providing seeds; Mary Ann Feist for aiding in herbarium specimen selection; and Carolina Calviño, Changshook Lee, and Jun Wen for comments on an early draft of the manuscript. This work was supported by NSF grant DEB 0089452 and a NSF REU Award to Gina Colletti.

LITERATURE CITED

BASKIN, J. M. and C. C. BASKIN. 1993. The ecological life cycle of *Perideridia americana* (Apiaceae). *The American Midland Naturalist* 129: 75–86.

CHUANG, T.-I. 1970. A systematic anatomical study of the genus *Perideridia* (Umbelliferae-Apioideae). *American Journal of Botany* 57: 495–503.

CHUANG, T.-I. and L. CONSTANCE. 1969. A systematic study of *Perideridia* (Umbelliferae-Apioideae). *University of California Publications in Botany* 55: 1–74.

CONSTANCE, L. 1972. Patterns in the distribution of Japanese-American Umbelliferae. Pp. 93–99 in *Floristics and paleofloristics of Asia and Eastern North America,* ed. A. Graham. Amsterdam: Elsevier.

CRONQUIST, A. 1997. Apiaceae. Pp. 340–427 in *Intermountain flora: vascular plants of the Intermountain West, U. S. A.*, Vol. 3, part A, eds. A. Cronquist, N. H. Holmgren, and P. K. Holmgren. Bronx: The New York Botanical Garden.

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

———, ———, and K. SPALIK. 2000a. A phylogeny of Apiaceae tribe Scandiceae: evidence from nuclear ribosomal DNA internal transcribed spacer sequences. *American Journal of Botany* 87: 76–95.

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

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

———, S. RAMANATH, D. S. KATZ-DOWNIE, and E. LLANAS. 1998. Molecular systematics of Apiaceae subfamily Apioideae: phylogenetic analyses of nuclear ribosomal DNA internal transcribed spacer and plastid *rpoC1* intron sequences. *American Journal of Botany* 85: 563–591.

———, G. M. PLUNKETT, M. F. WATSON, K. SPALIK, D. S. KATZ-DOWNIE, C. M. VALIEJO-ROMAN, E. I. TERENTIEVA, A. V. TROITSKY, B.-Y. LEE, J. LAHHAM, and A. EL-OQLAH. 2001. Tribes and clades within Apiaceae subfamily Apioideae: the contribution of molecular data. *Edinburgh Journal of Botany* 58: 301–330.

———, R. L. HARTMAN, F.-J. SUN, and D. S. KATZ-DOWNIE. 2002. Polyphyly of the spring-parsleys (*Cymopterus*): Molecular and morphological evidence suggests complex relationships among the perennial endemic genera of western North American Apiaceae. *Canadian Journal of Botany* 80: 1295–1324.

FELSENSTEIN, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783–791.

GIANNASI, D. E. and T.-I. CHUANG. 1976. Flavonoid systematics of the genus *Perideridia* (Umbelliferae). *Brittonia* 28: 177–194.

HARDWAY, T. M., K. SPALIK, M. F. WATSON, D. S. KATZ-DOWNIE, and S. R. DOWNIE. 2004. Circumscription of Apiaceae tribe Oenantheae. *South African Journal of Botany* 70: 393–406.

HILLIS, D. M. and J. P. HUELSENBECK. 1992. Signal, noise, and reliability in molecular phylogenetic analyses. *Journal of Heredity* 83: 189–195.

HIPKINS, V. D. and B. L. WILSON. 2001. Genetic diversity in *Perideridia erythrorhiza*: a rare plant in southern Oregon. Final Report, Project #78, The National Forests Genetic Electrophoresis Laboratory, USDA Forest Service, Camino, CA. 15 pp.

HOLMGREN, P. K., N. H. HOLMGREN, and L. C. BARNETT. 1990. *Index herbariorum*. New York: The New York Botanical Garden.

KARTESZ, J. T. 1994. *A synonymized checklist of the vascular flora of the United States, Canada, and Greenland*, 2nd ed. Biota of the North American Program of the North Carolina Botanical Garden. Portland: Timber Press.

KATZ-DOWNIE, D. S., C. M. VALIEJO-ROMAN, E. I. TERENTIEVA, A. V. TROITSKY, M. G. PIMENOV, B.-Y. LEE, and S. R. DOWNIE. 1999. Towards a molecular phylogeny of Apiaceae subfamily Apioideae: additional information from nuclear ribosomal DNA ITS sequences. *Plant Systematics and Evolution* 216: 167–195.

MADDISON, D. R. and W. P. MADDISON. 2002. MacClade: analysis of phylogeny and character evolution, version 4. Sunderland: Sinauer Associates.

MEINKE, R. J. 1998. Taxonomic evaluation of the rare species *Perideridia erythrorhiza* (Apiaceae). Internal report to the USDA Forest Service and US Fish and Wildlife Service. 31 pp.

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

RONQUIST, F. and J. P. HUELSENBECK. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574.

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

———, A. WOJEWÓDZKA, and S. R. DOWNIE. 2001a. The evolution of fruit in Scandiceae subtribe Scandicinae (Apiaceae). *Canadian Journal of Botany* 79: 1358–1374.

———, ———, ———. 2001b. Delimitation of genera in Apiaceae with examples from Scandiceae subtribe Scandicinae. *Edinburgh Journal of Botany* 58: 331–346.

SUN, F.-J., S. R. DOWNIE, and R. L. HARTMAN. 2004. An ITS-based phylogenetic analysis of the perennial, endemic Apiaceae subfamily Apioideae of western North America. *Systematic Botany* 29: 419–431.

SWOFFORD, D. L. 1998. PAUP*. Phylogenetic analysis using parsimony (*and other methods). Version 4. Sunderland: Sinauer Associates.

TAMURA, K. and M. NEI. 1993. Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. *Molecular Biology and Evolution* 10: 512–526.

WEN, J. 1999. Evolution of eastern Asian and eastern North American disjunct distributions in flowering plants. *Annual Review of Ecology and Systematics* 30: 421–455.

———. 2001. Evolution of eastern Asian-eastern North American biogeographic disjunctions: a few additional issues. *International Journal of Plant Sciences* 162: 117–122 (supplement).

WHITE, T. J., T. BRUNS, S. LEE, and J. TAYLOR. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. Pp. 315–322 in *PCR protocols: a guide to methods and applications*, eds. M. A. Innis, D. H. Gelfand, J. J. Sninsky, and T. J. White. San Diego: Academic Press.