

Molecular Phylogenetics and Taxonomy of the Genus *Boechea* and Related Genera (Brassicaceae: Boechereae)

Patrick J. Alexander,^{1,6} Michael D. Windham,² James B. Beck,² Ihsan A. Al-Shehbaz,⁴
Loren Allphin,⁵ and C. Donovan Bailey¹

¹Biology Department, MSC 3AF, New Mexico State University, Las Cruces, New Mexico 88003 U. S. A.

²Department of Biology, 139 Biological Sciences (Box 90338). Duke University, Durham, North Carolina 27708 U. S. A.

⁴Department of Monographic Studies, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166 U. S. A.

⁵Brigham Young University, Department of Plant and Wildlife Sciences, 275 Widtsoe Building, Provo, Utah 84602 U. S. A.

⁶Author for correspondence (paalexan@polyploid.net)

Communicating Editor: Andrea Weeks

Abstract—*Boechea* (Brassicaceae) is a diverse genus of ± 70 sexual diploid species and numerous apomictic hybrids concentrated in western North America. It is the largest genus in tribe Boechereae, which also includes seven other small genera. *Boechea* is closely related to *Arabidopsis* and is becoming a model genus for diverse studies, focusing particularly on apomixis and hybrid speciation. As part of an ongoing effort to clarify the taxonomy of the group, we present phylogenetic analyses of Boechereae, including all genera of the tribe and most of the sexual diploid species of *Boechea*. Ten loci are used, including two plastid loci, nrDNA ITS, and seven low-copy nuclear loci. These analyses indicate that *Boechea*, as currently circumscribed, is polyphyletic, comprising three main clades. Eastern North American species previously assigned to *Boechea* form a distinct clade with the Asian taxon *Borodinia macrophylla* and are herein transferred to the genus *Borodinia*, resulting in seven new combinations (*Borodinia burkii*, *Borodinia canadensis*, *Borodinia dentata*, *Borodinia laevigata*, *Borodinia missouriensis*, *Borodinia perstellata*, and *Borodinia serotina*). *Boechea repanda*, a morphologically aberrant species endemic to the Sierra Nevada, is recognized in the new genus *Yosemitea* (as *Yosemitea repanda*). A primarily western North American clade comprising all remaining species is strongly supported and retains the name *Boechea*. Although resolution within *Boechea* sensu stricto is limited, a number of well-supported clades are identified.

Keywords—*Borodinia*, cytonuclear incongruence, hybrid speciation, low-copy nuclear loci, molecular systematics, *Yosemitea*.

Boechea Á. Löve & D. Löve recently has become a model system for a diversity of plant evolutionary studies. It is relatively closely related to *Arabidopsis thaliana* (L.) Heynh. and, with ± 70 sexual diploid species and numerous apomictic hybrids, allows the genetic insights gained from this model species to be applied to a large and evolutionarily complex genus that occurs across a wide range of habitats (Mitchell-Olds 2001; Rushworth et al. 2011). Much of the research on *Boechea* focuses on hybridization, apomixis, and polyploidy (Böcher 1951, 1954, 1969; Roy and Rieseberg 1989; Roy 1995; Naumova et al. 2001; Sharbel and Mitchell-Olds 2001; Koch et al. 2003; Dobeš et al. 2004a, 2004b, 2006, 2007b; Sharbel et al. 2004, 2005, 2009, 2010; Schranz et al. 2005, 2006; Kantama et al. 2007; Aliyu et al. 2010). These issues are interrelated in *Boechea* because nearly all hybrids examined to date are apomictic and many of these hybrids are triploid, although *Boechea* also includes apomictic diploid hybrids (Beck et al. 2012). Other foci of research in *Boechea* include infraspecific adaptation, genetic diversity, and phylogeography (McKay et al. 2001; Dobeš et al. 2004a; Knight et al. 2006; Song et al. 2006; Song and Mitchell-Olds 2007; Kiefer et al. 2009a, 2009b); evolution of genes and genomes (Bishop et al. 2000; Windsor et al. 2006; Dobeš et al. 2007a; Kantama et al. 2007; Schranz et al. 2007); plant-pathogen interactions (Bishop et al. 2000; Roy and Raguso 1997; Roy 2001); and life history ecology (Bloom et al. 1990; Bloom et al. 2001).

The intensive research interest in *Boechea* is, however, complicated by a poor understanding of the taxonomy of the genus and extensive misapplication of names. For example, the name *B. holboellii* (Hornem.) Á. Löve & D. Löve has been applied to many samples used in a variety of research projects. However, recent taxonomic work indicates that this “species” represents an artificial, polytypic assemblage, that includes five morphologically distinct, sexual diploids and a diversity of apomictic hybrid lineages (Windham and

Al-Shehbaz 2006). *Boechea holboellii* s. s. is an apomictic triploid only known from Greenland and, with the exception of Böcher’s research in Greenland (Böcher 1951, 1954, 1969), it appears that none of the previous studies citing this species has actually sampled *B. holboellii* s. s. This makes it difficult to interpret previous research efforts, which are not based on a precise understanding of species boundaries and hybrid origins. A thorough exploration of *Boechea* taxonomy and phylogenetic relationships is therefore required if the genus is to reach its full potential as a model system.

Introduction to *Boechea*—As circumscribed in the recent *Flora of North America* treatment (Al-Shehbaz and Windham 2010), *Boechea* includes 110 species found in North America, Greenland, and the Russian Far East. It is most diverse in the western U. S. A., particularly in the state of California. Members of the genus are found from near sea level to ca. 4,400 m elevation, in habitats ranging in temperature and precipitation from arid rocky slopes to alpine tarns. Most *Boechea* species are perennials, with at least some forked to dendritic trichomes. The fruits are narrow, latiseptate (flattened parallel to the septum), and are erect, strictly reflexed, or anything in between. Morphological separation of *Boechea* from other genera, particularly *Arabis* L., is not always straightforward (Al-Shehbaz 2003).

Historically, *Boechea* species were included within a broadly circumscribed *Arabis* (e.g. Rollins 1941, 1993). The establishment of *Boechea* to accommodate species with a base chromosome number of seven (rather than eight, for species maintained in *Arabis*) was first proposed by Löve and Löve (1976). However, these authors did not discuss other differences between the two genera and their proposed segregation of *Boechea* from *Arabis* was not followed in Rollins’ (1993) authoritative work on North American Brassicaceae. Since that time, a series of phylogenetic analyses have confirmed that the two taxa are not closely related and that generic segregation is warranted (Koch et al. 1999,

2000, 2001; Bailey et al. 2006; Beilstein et al. 2006, 2008). This prompted the transfer of most North American *Arabis* species to *Boechera* (Al-Shehbaz 2003), and the recognition of the latter as a distinct genus in most recent taxonomic treatments (Dorn 2001; Holmgren 2005; Windham and Al-Shehbaz 2006, 2007a, 2007b, 2012; Al-Shehbaz and Windham 2010). Broad phylogenetic analyses of Brassicaceae by Bailey et al. (2006) and Beilstein et al. (2006, 2008) have led to a major tribal reorganization of the family (Al-Shehbaz et al. 2006; Warwick et al. 2010) that further highlights the divergence between *Arabis* and *Boechera*. Under this revised classification, *Arabis* (along with its sister genus *Draba* L.) is retained in the tribe Arabideae DC. *Boechera*, on the other hand, is assigned to the tribe Boechereae Al-Shehbaz, Beilstein, & E. A. Kellogg, along with the monospecific genera *Anelsonia* J. F. Macbr. & Payson, *Borodinia* N. Busch, *Nevada* N. H. Holmgren, *Phoenicaulis* Nutt., and *Polyctenium* Greene, as well as the ditypic genera *Cusickiella* Rollins and *Sandbergia* Greene.

Previous Phylogenetic Analyses of Boechereae and Boechera—There have been just two previous phylogenetic analyses of Boechereae that included more than 10 taxa from the tribe. Bailey et al. (2006) included 30 taxa of Boechereae as part of a global phylogenetic analysis of Brassicaceae using the nuclear ribosomal ITS region. Kiefer et al. (2009b) included 27 taxa of Boechereae and presented separate nuclear ITS and plastid *trnL-F* analyses. In both cases, resolution within Boechereae was limited. Kiefer et al. (2009b) noted that there was conflict between topologies resulting from analyses of plastid and nuclear loci and found that *Boechera* was not monophyletic in either plastid or ITS analyses. Several additional phylogenetic studies using *trnL-F* and/or ITS were dominated by samples of *Boechera stricta*, *B. divaricarpa* (A. Nelson) Á. Löve & D. Löve, and *B. holboellii* s. l., with little representation of other members of the genus (Dobeš et al. 2004a, 2004b; Schranz et al. 2005). These studies yielded little resolution and are difficult to interpret due to the polytypic nature of both *B. divaricarpa* and *B. holboellii* (Windham and Al-Shehbaz 2006, 2007a, 2007b).

Kiefer et al. (2009a) presented a plastid haplotype network with extensive sampling in *Boechera* (1,287 accessions) and more resolution than in previous studies. Unfortunately, drawing phylogenetic conclusions from this network is complicated by the lack of confidence values for groupings and the inability to assess monophyly in an unrooted network. However, Kiefer et al. (2009a) indicate that speciation and haplotype differentiation may be unlinked in the genus. This suggests that there may be fundamental problems with the use of plastid data in phylogenetic reconstruction in *Boechera* (see Discussion).

Goals of the Current Study—We present phylogenetic analyses of Boechereae using seven low-copy nuclear loci (alcohol dehydrogenase, chalcone synthase, *Dpa1*, *luminidependens*, *Mps35*, *Nuo*, and *pistillata*), nuclear ribosomal ITS, and two plastid loci (*rps16-trnK* and *trnL-F*). Members of all recognized genera in Boechereae are included, as are 57 of the 71 diploid *Boechera* species recognized in the *Flora of North America* treatment (Al-Shehbaz and Windham 2010) and several additional taxa either unrecognized in that treatment or treated as subspecies. These analyses are intended to address three issues: 1) resolution of the boundaries of the genus *Boechera*; 2) identification of clades within *Boechera*; and 3) examination of the utility of plastid data in phylogenetic analyses of *Boechera*.

MATERIALS AND METHODS

Sampling and DNA Isolation—Leaf material for DNA isolation was obtained from collections made by the authors and from recent herbarium specimens. A few extracted DNA samples were provided by other researchers. Samples were chosen in an effort to represent all genera of Boechereae and as many of the divergent diploid species of *Boechera* as possible. A total of 95 specimens are used, including 81 *Boechera* specimens, 11 other members of Boechereae, and three outgroups. Taxonomy follows the *Flora of North America* treatment (Al-Shehbaz and Windham 2010). Voucher information, including GenBank accession numbers, is given in Appendix 1. Data matrices are available on TreeBASE (study number S12814). Twenty-two species are represented by multiple individuals from different populations to allow limited evaluation of incongruence between phylogenetic results and existing species-level taxonomy. DNA from 82 samples was isolated following the procedures of Alexander et al. (2007), except that 10mm Tris-HCl in 70% EtOH was used instead of 70% EtOH when washing contaminants from the silica columns at step 13. The remaining DNA samples isolated for this study used a modified high-throughput CTAB approach similar to that presented in Mace et al. (2003).

Exclusion of Hybrids—Considering the prevalence of hybridization within *Boechera* (see Windham and Al-Shehbaz 2007a, 2007b) and the confounding effects of this process on phylogenetic analyses (McDade 1990; Linder and Rieseberg 2004), considerable effort was invested to identify and exclude hybrids. Many hybrid lineages in *Boechera* are triploid and show a distinctive pollen morphology (ovoid, irregularly colpate grains rather than the narrowly ellipsoid, tricolpate grains typical of most Brassicaceae) that allows them to be readily identified from flowering herbarium specimens (Windham and Al-Shehbaz 2006). All specimens exhibiting this pollen morphology were automatically excluded from our phylogenetic analyses. However, recent microsatellite analyses have identified previously unknown, apomictic diploid hybrids (Beck et al. 2012) that are more difficult to detect using pollen. To confirm their taxonomic assignment and non-hybrid status, all samples belonging to the “*Boechera* clade” (see Results) also were included in microsatellite analyses that examined 15 loci for 2,400 samples (Windham et al. unpubl. data). All but one of our “*Boechera* clade” samples showed allelic patterns (i.e. low heterozygosity and alleles derived from a single sexual species) congruent with their interpretation as sexual, non-hybrid diploids. The sole exception, *B. tiehmii*, is discussed in more detail below.

Amplification and Sequencing—Eight nuclear-encoded loci were sequenced: alcohol dehydrogenase (*adh*; primers Adh259F and Adh1043R, Slotte et al. 2006), chalcone synthase (*chs*; primers CS-F1 and CS-R4, Koch et al. 2000), *Dpa1* (primers Dpa1-F and Dpa1-R, Song and Mitchell-Olds 2007), the nrDNA ITS region (primers ITS5 and ITS4, White et al. 1990), *luminidependens* (primers LD-D1F and LD-XC4R, Slotte et al. 2006), *Mps35* (primers Mps35-F and Mps35-R, Song and Mitchell-Olds 2007), *Nuo* (primers Nuo-F and Nuo-R, Song and Mitchell-Olds 2007), and *pistillata* intron I (primers pi504a and pi1254r, Bailey and Doyle 1999). Additionally, two plastid loci were sequenced: *rps16-trnK* (primers rps16x2F2 and trnK(UUU)x1, Shaw et al. 2007) and *trnL-F* (primers trnC and trnF, Taberlet et al. 1991).

Amplifications were conducted in 25 μ L reactions with 1 μ L of template DNA, 1.5 units *Taq* polymerase, 0.5 μ M of each primer, 0.1 mM of each dNTP, 60 mM betaine, 20 μ M KCl, 1.5 mM MgCl₂, and 10 mM Tris-HCl. For amplifications of *chs*, 7.5 nM bovine serum albumin was included as well. Thermal cycler programs generally follow those of the authors listed for each primer above, although cycling conditions were sometimes modified to deal with recalcitrant samples. The PCR products were cleaned either using the Qiagen QIAquick® PCR purification protocol (Qiagen, Valencia, California) or by 15 minute digestion at 37°C with five units exonuclease I and one unit shrimp alkaline phosphatase (both from Affymetrix, Cleveland, Ohio) per 25 μ L PCR reaction. Sequencing reactions were carried out at the University of Chicago Cancer Research Center's DNA Sequencing Facility.

Direct sequencing of *adh* yielded highly polymorphic reads, in which the majority of the sequence was unintelligible for \pm 20 samples. This prompted concern that the primers used were amplifying multiple copies. To evaluate this possibility, *adh* was cloned using Invitrogen (Carlsbad, California) TOPO TA Cloning® for four such samples (017a *Boechera platysperma*, 023a *B. sparsiflora*, 085 *Phoenicaulis cheiranthoides*, and B103 *B. cusickii*). Eight to 10 cloned sequences were generated from each sample.

Alignment, Matrices, and Phylogenetic Analyses—Each locus was aligned automatically using ClustalW (Thompson et al. 1994) under default parameters. The resulting alignments were then checked and refined manually using Se-Al (Rambaut 2002). Gap characters were

scores using the simple indel coding method of Simmons and Ochoterena (2000) as implemented in SeqState (Müller 2005).

Ten different matrices were analyzed: each nuclear locus separately, and two combined matrices (referred to as the “plastid matrix” and “nuclear matrix”). The two plastid loci were not analyzed individually because, as subsets of a non-recombining genome, they are not independent. *Adh* was excluded from the nuclear matrix due to paralogy problems (see Results) and the remaining seven nuclear loci were concatenated. The nuclear matrix also excludes *Boecheira tiehmii* due to evidence of a hybrid origin of this species (see Results and Discussion).

Phylogenetic analyses were conducted with both parsimony and maximum likelihood approaches. Parsimony analyses involved heuristic searches in NONA (Goloboff 2000) spawned from WINCLADA (Nixon 1999) with 500 random addition sequence replicates with tree bisection and reconnection (TBR), holding 20 trees per replicate, followed by further TBR searching to a maximum of 10,001 trees. Clade support was estimated with 1,000 jack-knife resampling replicates with a removal probability of 0.36. Jack-knife replicates were conducted using default settings for the “new technology search” in TNT (Goloboff et al. 2008), using parsimony ratchet (Nixon 1999), sectorial search, tree-drifting, and tree-fusing techniques (Goloboff 1999).

Maximum likelihood (ML) analyses were conducted with RAXML (Stamatakis 2006; Stamatakis et al. 2008) via the online CIPRES portal (Miller et al. 2010), which uses the GTR + Γ model when conducting a heuristic search and the GTR + CAT model when computing bootstrap support. The best tree was inferred and support was estimated from 1,000 bootstrap replicates. Gap characters were removed prior to ML analyses, as the applicability of available models of evolution to gap characters is not clear. For the combined matrices, model parameters were estimated separately for each locus.

All analyses were rooted on the branch connecting the clade of *Crucihimalaya wallichii* and *Transberingia bursifolia* to the remaining samples. Topologies were not constrained to enforce reciprocal monophyly of these outgroups and the remaining taxa. *Crucihimalaya* and *Transberingia* are both members of tribe Camelinae, and this choice of rooting is based on previous studies demonstrating a sister relationship between members of Camelinae and a clade of Halimolobeae (represented here by *Halimolobos jaegeri*) plus Boechereae (Beilstein et al. 2006, 2008; Oyama et al. 2008).

RESULTS

Aligned lengths, numbers of parsimony-informative nucleotide characters, number of parsimony-informative gap characters, and completeness of sampling for each locus are shown in Table 1. Trees resulting from single-locus analyses of *Dpa1* and *pistillata* are shown in Figs. 1 and 2, respectively, while trees from *adh*, ITS, *luminidependens*, *Mps35*, and *Nuo* are available as supplementary Figs. S1–6. Trees resulting from analyses of the plastid matrix and nuclear matrix are shown in Figs. 3 and 4, respectively. Distinct groups within *Boecheira* s. l. identified by the nuclear matrix analysis (i.e. *Boecheira* s. s., *Borodinia*, and *Yosemitea*) are indicated in all figures.

Parsimony vs. Maximum Likelihood—Results from parsimony and ML analyses were generally congruent. With few

exceptions, all nodes receiving greater than 50% jackknife support in parsimony analyses also occurred on the best ML tree. Maximum likelihood analyses generally provided greater resolution than parsimony analyses, but this additional resolution received uniformly poor support (not shown).

***Adh* Clones**—Divergent placements of cloned *adh* sequences for accessions 017a, 023a, 085, and B103 indicate that the primers (from Slotte et al. 2006) amplify paralogous copies in *Boecheira* (Supplementary Fig. 1). The possibility that these individuals are actually hybrids was ruled out through microsatellite analyses (see Materials and Methods). This suggests that there is unrecognized paralogy in the uncloned accessions as well, so *adh* is not included in further analysis or discussion.

Nuclear vs. Plastid Resolution—Plastid and nuclear loci resolved substantially different topologies. Notably, *Boecheira* s. s. is recovered with high support in analyses of the nuclear matrix (Fig. 4; 99% parsimony jackknife / 97% maximum likelihood bootstrap), but not in analyses of the plastid matrix. This clade is also recovered in single-locus analyses of *chs*, *Dpa1*, ITS, *luminidependens*, *Mps35*, *Nuo*, and *pistillata* (Figs. 1 and 2; supplementary Figs. S2–6), with the exception of divergent placements of *B. tiehmii* (see Resolution in *Boecheira* and Boechereae, below) and some instability in the placement of *Boecheira davidsonii*. However, in the plastid topology this grouping is paraphyletic, with *Nevada*, *Anelsonia*, and most members of the *Borodinia* clade included within *Boecheira* s. s. (Fig. 3). Topological differences between nuclear and plastid topologies are also clearly evident in examination of species represented by more than one accession. In all but one case, if a species is represented by multiple accessions in the nuclear matrix topology, these accessions grouped together with strong support (the lone exception is *Boecheira fernaldiana*, the two subspecies of which are supported as distinct species by microsatellite analyses and reexamination of morphology, Windham et al. unpubl. data). This is in sharp contrast to the plastid matrix topology, in which ten species (*Boecheira breweri*, *B. canadensis*, *B. collinsii*, *B. fendleri*, *B. gracilipes*, *B. laevigata*, *B. lyallii*, *B. pendulocarpa*, *B. perennans*, and *B. serpenticola*) have two accessions placed separately in the plastid topology.

Resolution in *Boecheira* and Boechereae—Due to concerns with paralogy in *adh* sequences and anomalous results of plastid data, the nuclear matrix topology (which includes seven nuclear loci; Fig. 4) is considered to provide the most accurate reconstruction of relationships in Boechereae. Monophyly of Boechereae is strongly supported (100/99),

TABLE 1. Summary of variation among the ten loci used and the two concatenated matrices. Sequences were not recovered for 3% of the total 10 loci for 95 individuals, with missing data concentrated primarily in *adh*.

	Aligned length	Parsimony-informative characters	Parsimony-informative gap characters	Number of accessions	Percent missing data
<i>adh</i>	654	119	36	77	5.1%
<i>chs</i>	1,089	131	18	94	4.4%
<i>Dpa1</i>	759	112	13	95	1.2%
ITS	676	98	23	95	3.8%
<i>luminidependens</i>	615	97	16	95	1.8%
<i>Mps35</i>	830	133	21	91	1.5%
<i>Nuo</i>	704	50	0	92	2.4%
<i>pistillata</i>	942	182	64	91	1.4%
nuclear matrix	5,615	803	155	95	2.4%
<i>rps16-trnK</i>	921	86	23	95	1.6%
<i>trnL-F</i>	1,129	120	27	95	0.6%
plastid matrix	2,050	206	50	95	1.1%

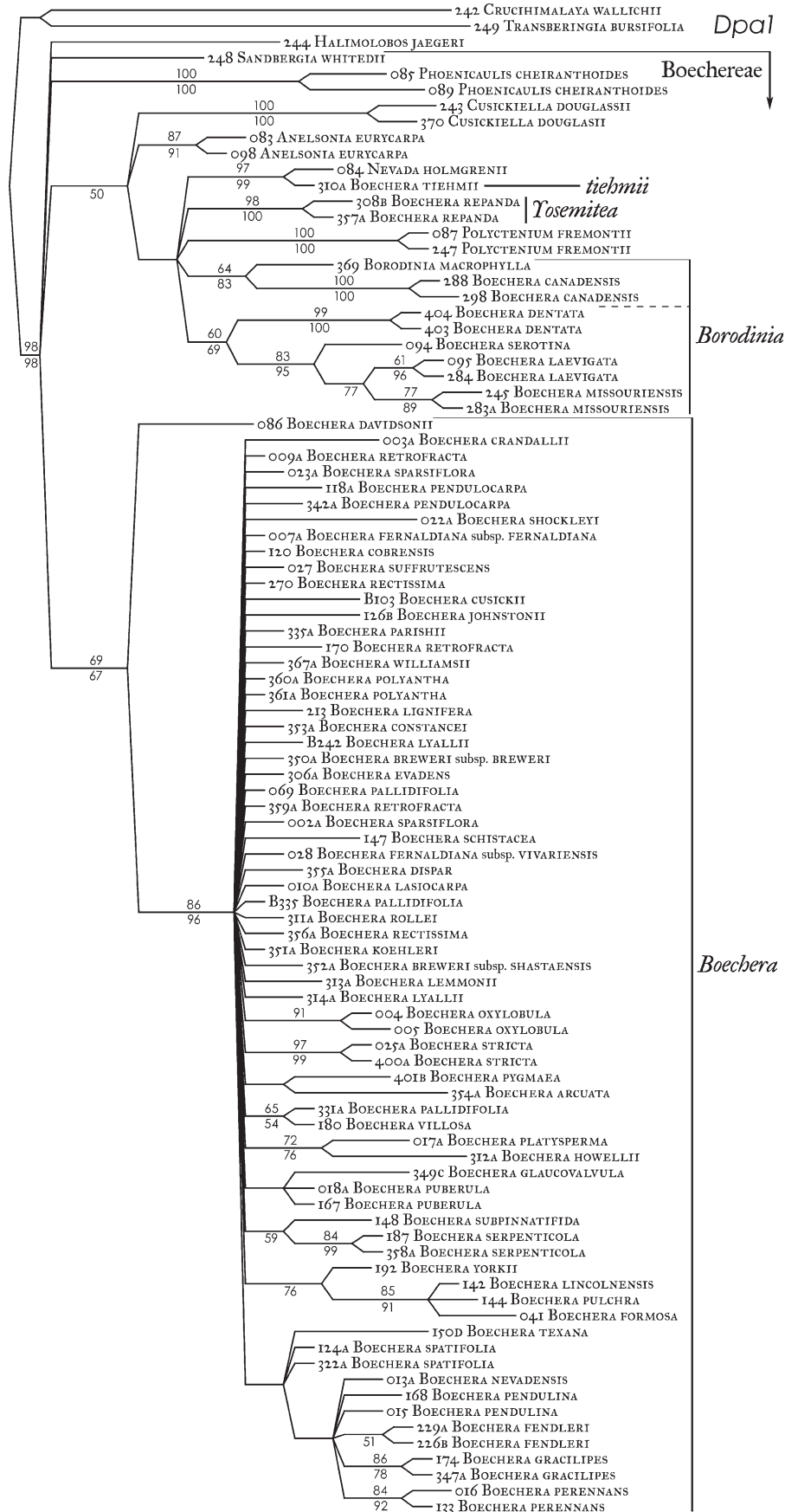


FIG. 1. Strict consensus phylogram of 10,001 most parsimonious trees (length = 316, CI = 0.83, RI = 0.87) from parsimony analysis of *DpaI* sequences. Numbers above branches indicate parsimony jackknife support, while numbers below branches indicate maximum likelihood bootstrap support. Support values below 50 are not shown, and a “-” indicates that the node in question did not occur on the best tree from maximum likelihood analysis.

Delivered by Publishing Technology to: New Mexico State University IP: 128.123.253.108 on: Mon, 18 Mar 2013 00:39:19 Copyright (c) American Society for Plant Taxonomists. All rights reserved.

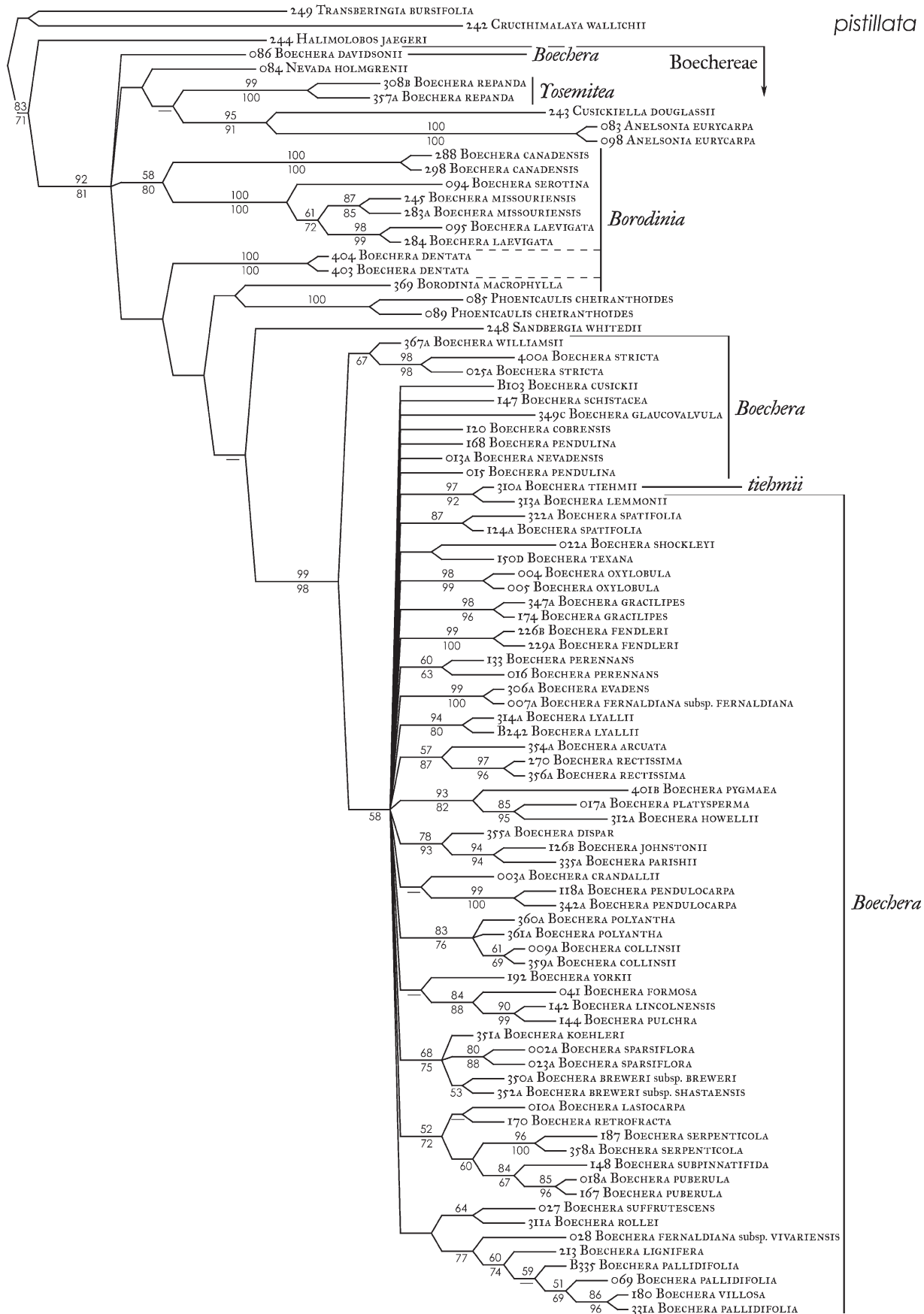


FIG. 2. Strict consensus phylogram of 38 most parsimonious trees (length = 758, CI = 0.75, RI = 0.81) from parsimony analysis of *pistillata* sequences. Numbers above branches indicate parsimony jackknife support, while numbers below branches indicate maximum likelihood bootstrap support. Support values below 50 are not shown, and a “-” indicates that the node in question did not occur on the best tree from maximum likelihood analysis.

Delivered by Publishing Technology to: New Mexico State University IP: 128.123.253.108 on: Mon, 18 Mar 2013 00:39:19 Copyright (c) American Society for Plant Taxonomists. All rights reserved.

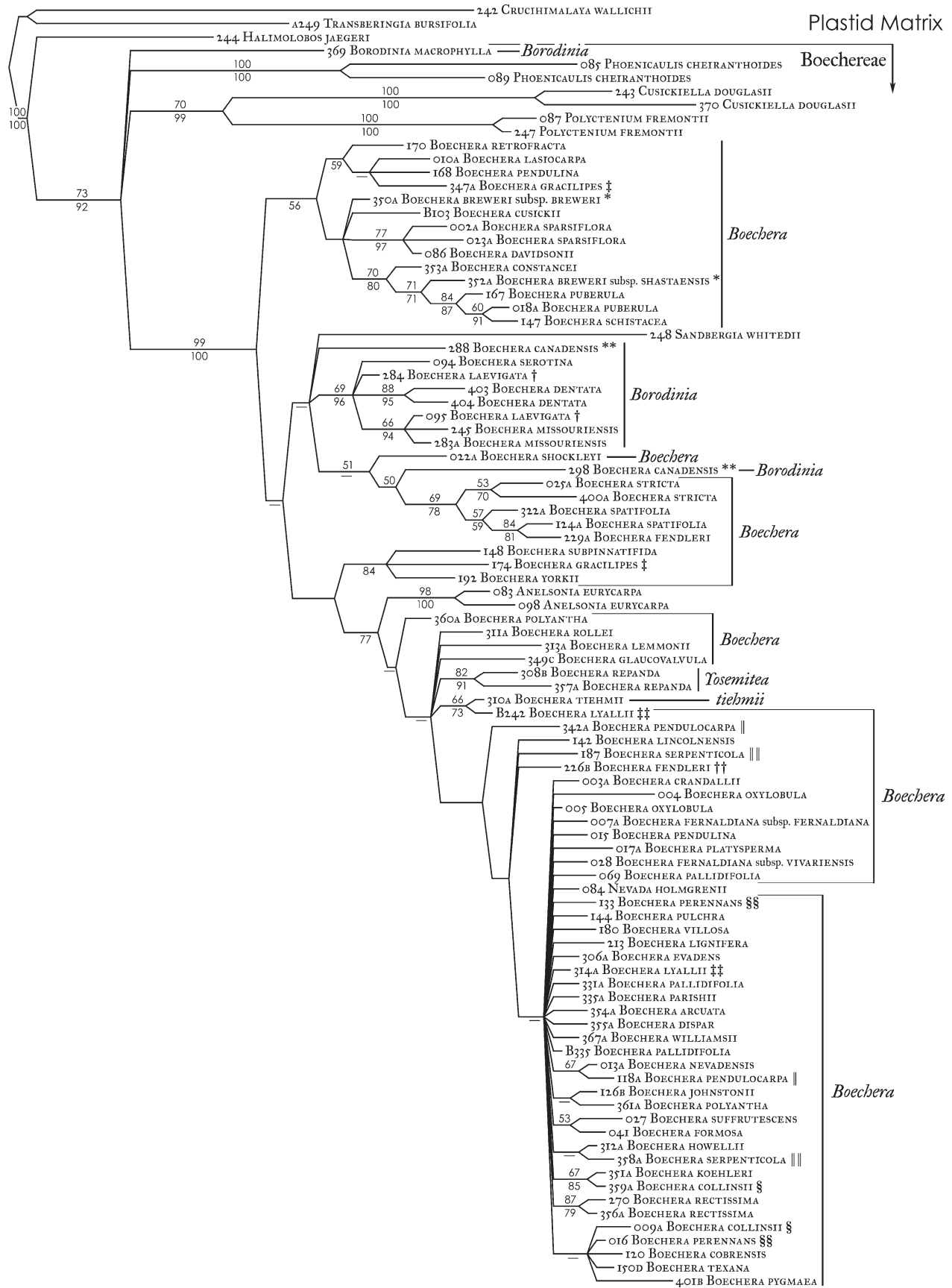


FIG. 3. Strict consensus phylogram of 10,001 most parsimonious trees (length = 912, CI = 0.63, RI = 0.76) from parsimony analysis of the plastid matrix. Numbers above branches indicate parsimony jackknife support, while numbers below branches indicate maximum likelihood bootstrap support. Support values below 50 are not shown, and a “-” indicates that the node in question did not occur on the best tree from maximum likelihood analysis. Accessions of a single species that are resolved separately are indicated by matching typographical symbols following the binomial.

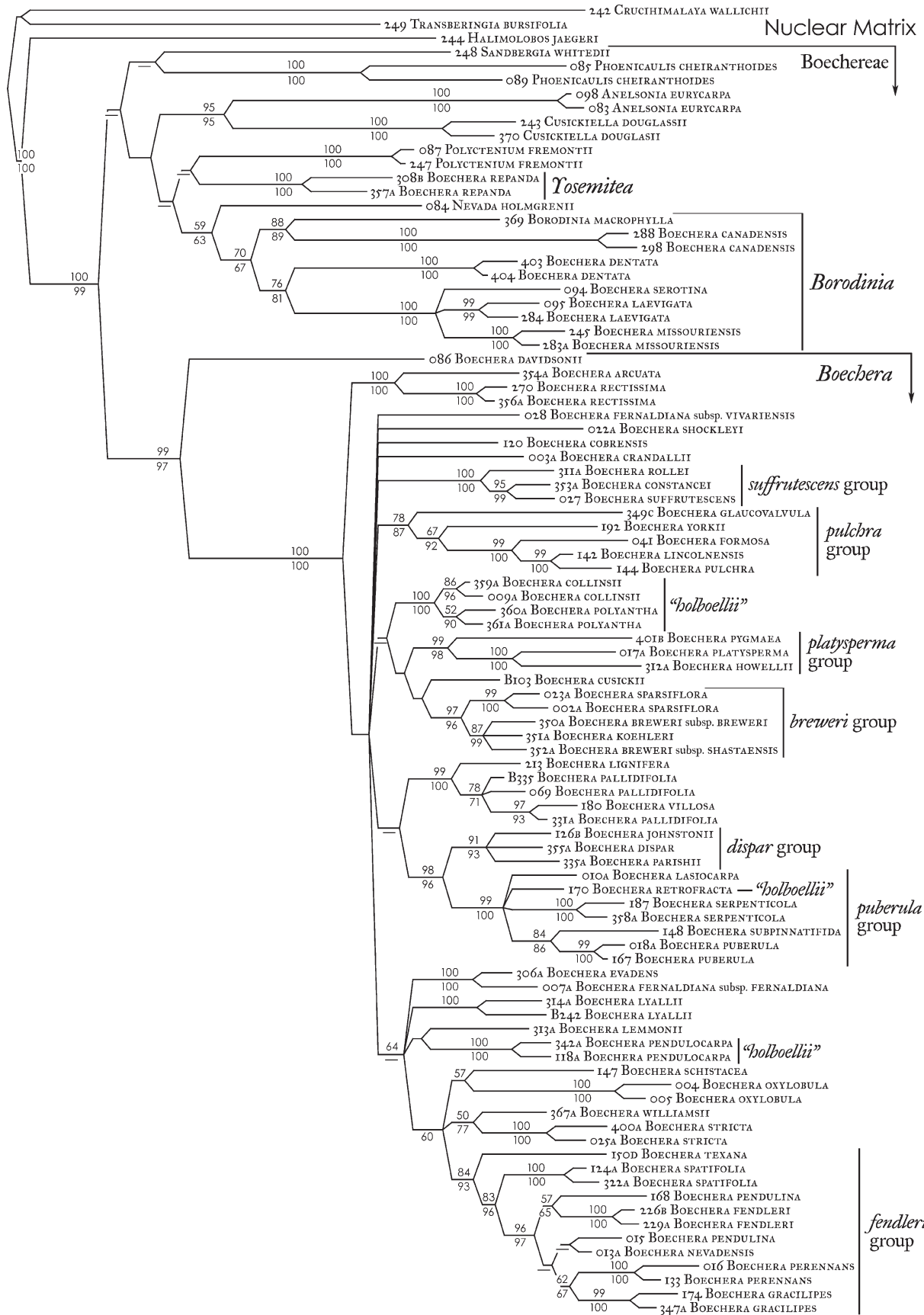


FIG. 4. Strict consensus phylogram of 480 most parsimonious trees (length = 2,905, CI = 0.74, RI = 0.80) from parsimony analysis of the nuclear matrix (loci *chs*, *Dpa1*, ITS, *luminiidependens*, *Mps35*, *Nuo*, and *pistillata*). Numbers above branches indicate parsimony jackknife support, while numbers below branches indicate maximum likelihood bootstrap support. Support values below 50 are not shown, and a “-” indicates that the node in question did not occur on the best tree from maximum likelihood analysis.

Delivered by Publishing Technology to: New Mexico State University IP: 128.123.253.108 on: Mon, 18 Mar 2013 00:39:19 Copyright (c) American Society for Plant Taxonomists. All rights reserved.

although limited outgroup sampling does not allow a robust assessment of tribal monophyly. Within Boechereae, each of the monotypic or ditypic genera represented by more than one sample (i.e. *Anelsonia*, *Cusickiella*, *Phoenicaulis*, and *Polycytenium*) receive maximum support, but relationships among the genera are largely unresolved. The only intergeneric relationships receiving > 50% support are *Anelsonia* plus *Cusickiella* (95/95) and *Nevada* plus the *Borodinia* clade (59/63). *Boechera* s. l. is not monophyletic in the nuclear matrix analysis and forms three groups: *Boechera* s. s. (comprising all but one of the western North American species); the *Borodinia* clade (*Borodinia macrophylla* plus five eastern North American species of *Boechera* s. l.); and *Yosemitea* (*Boechera repanda*). Geographic distributions of these groups are shown in Fig. 5. A number of well-supported groups of two to eight species recovered within *Boechera* s. s. are labeled in Fig. 4 and discussed below.

Boechera tiehmii varies markedly in its placement in single-locus nuclear analyses (Figs. 1 and 2 and supplementary Figs. S1–6). Two loci, ITS and *pistillata*, group *B. tiehmii* with *Boechera lemmonii*, with moderate to strong support (ITS: 79/87; *pistillata*: 97/92). A third locus, *Dpa1*, grouped *B. tiehmii* with *Nevada holmgrenii* with strong support (97/99). Analyses of two other loci, *chs* and *Mps35*, group *B. tiehmii* with *N. holmgrenii* in either the strict consensus tree from parsimony analyses (*Mps35*) or in the best tree from ML analyses (*chs*), but with weak support (< 50). In the remaining single-locus nuclear analyses, the position of *B. tiehmii* is unresolved relative to other members of the tribe.

DISCUSSION

Incongruence Between Nuclear and Plastid Loci—Results from our phylogenetic analyses of the nuclear matrix (Fig. 4) are generally congruent with both morphology and analyses of an extensive microsatellite data set (Windham et al. unpubl. data; see also Resolution within *Boechera* s. s. and Taxonomic Treatment, in which morphologically cohesive genera and clades within *Boechera* s. s. are described). By contrast, inferred plastid relationships in Boechereae (Fig. 3) appear to be at least partially independent of morphological divergence, nuclear relationships, and speciation. This is highlighted in the paraphyly of *Boechera* s. s. and divergent placements of members of a single species. *Boechera* s. s. is a morphologically cohesive entity, yet the plastid topology suggests that the morphologically distinct genera *Anelsonia*, *Nevada*, and *Sandbergia* are nested within it (see Taxonomic Treatment for morphological distinctions between these genera). The sampled sexual diploid species within *Boechera* s. s. are, with rare exceptions (e.g. *B. fernaldiana*), strongly supported as real entities by a combination of the nuclear topology, in which multiple accessions from within a single species are grouped together (Fig. 4), morphological evaluation (Windham and Al-Shehbaz 2006, 2007a, 2007b), and extensive microsatellite sampling (Windham et al. unpubl. data). Nonetheless, the plastid topology is inconsistent with these strongly-supported species circumscriptions. More extensive plastid sampling shows that a pattern of haplotype sharing among species coupled with haplotype divergence within species is widespread in the genus (Kiefer et al. 2009b). There are two plausible explanations for this: incomplete lineage sorting and plastid capture. Plastid loci should coalesce more rapidly than nuclear loci due to the lower effective population size for the plastid genome (Birky et al.

1983), so incomplete lineage sorting should result in over-resolution of plastid loci relative to nuclear loci. This is not consistent with the combination of extensive plastid haplotype sharing between species and divergent haplotypes within species that is observed in *Boechera* s. s. (Fig. 3 and Kiefer et al. 2009b). Plastid capture (i.e. introgression biased towards movement of plastid rather than nuclear genes between species; see Tsitrone et al. 2003; Chan and Levin 2005; Hedtke and Hillis 2011) seems to be a more likely explanation for incongruence between plastid and nuclear loci in Boechereae. Plastid capture could result in the observed pattern of species that are genetically cohesive at nuclear loci but not at plastid loci. Frequent hybridization between species, and the production of unreduced gametes in many members of *Boechera* s. s. (Naumova et al. 2001; Windham and Al-Shehbaz 2007a; Dobeš et al. 2007b), provide opportunities for plastid capture via hybridization followed by repeated backcrossing to the paternal species. Androgenesis, an additional mechanism that would allow for plastid capture, was recently proposed by Hedtke and Hillis (2011). In this scenario, an unreduced (2x) sperm uniting with a reduced (x) egg leads to replacement of the egg nucleus by the sperm nucleus rather than fusion of the two, producing offspring with a paternal nuclear genome but maternal plastid genome. Further research is needed to establish the mechanism by which plastid capture occurs in Boechereae. Regardless, it is clear that reliance on plastid data is likely to provide misleading estimations of species boundaries and phylogenetic relationships in *Boechera* s. s. and other members of Boechereae.

Generic Boundaries in Boechereae—The tribe Boechereae exhibits a familiar pattern with respect to generic delimitation. This involves a species-rich, poorly-defined genus (in this case *Boechera* s. l.) intimately associated with (and often paraphyletic to) an assortment of smaller, relatively well-defined satellite genera. This situation has been encountered in numerous groups, including asplenoid ferns (Schneider et al. 2004), flowering plants such as *Draba* s. l. (Jordon-Thaden et al. 2010), *Euphorbia* s. l. (Bruyns et al. 2006), and *Senecio* s. l. (Pelser et al. 2007) and even animals such as *Drosophila* s. l. (van der Linde et al. 2007). To achieve a phylogenetically congruent classification in such cases, one of two options must be pursued: 1) either the boundaries of the large genus must be expanded to an appropriately supported node that encompasses some or all of the segregates, or 2) the large genus must be split into smaller, well-supported monophyletic genera.

In the case of Boechereae, there are compelling taxonomic and nomenclatural reasons to favor Option 2. The only well-supported node that includes all species assigned to *Boechera* s. l. is the node corresponding to Boechereae (see Fig. 4). A genus circumscribed by this node would be extremely variable, encompassing characters typically used to distinguish tribes in the Brassicaceae. It would include both major fruit types characteristic of the family (siliques and silicles), both cotyledon positions (accumbent and incumbent), and both fruit compression types (latiseptate and angustiseptate). Such variation has rarely been accommodated in a single tribe of Brassicaceae, much less within a genus. In fact, most smaller genera currently assigned to Boechereae have only recently been transferred there as a series of molecular analyses (e.g. Bailey et al. 2006; Beilstein et al. 2006, 2008) have posited their true relationships. Prior to these studies,

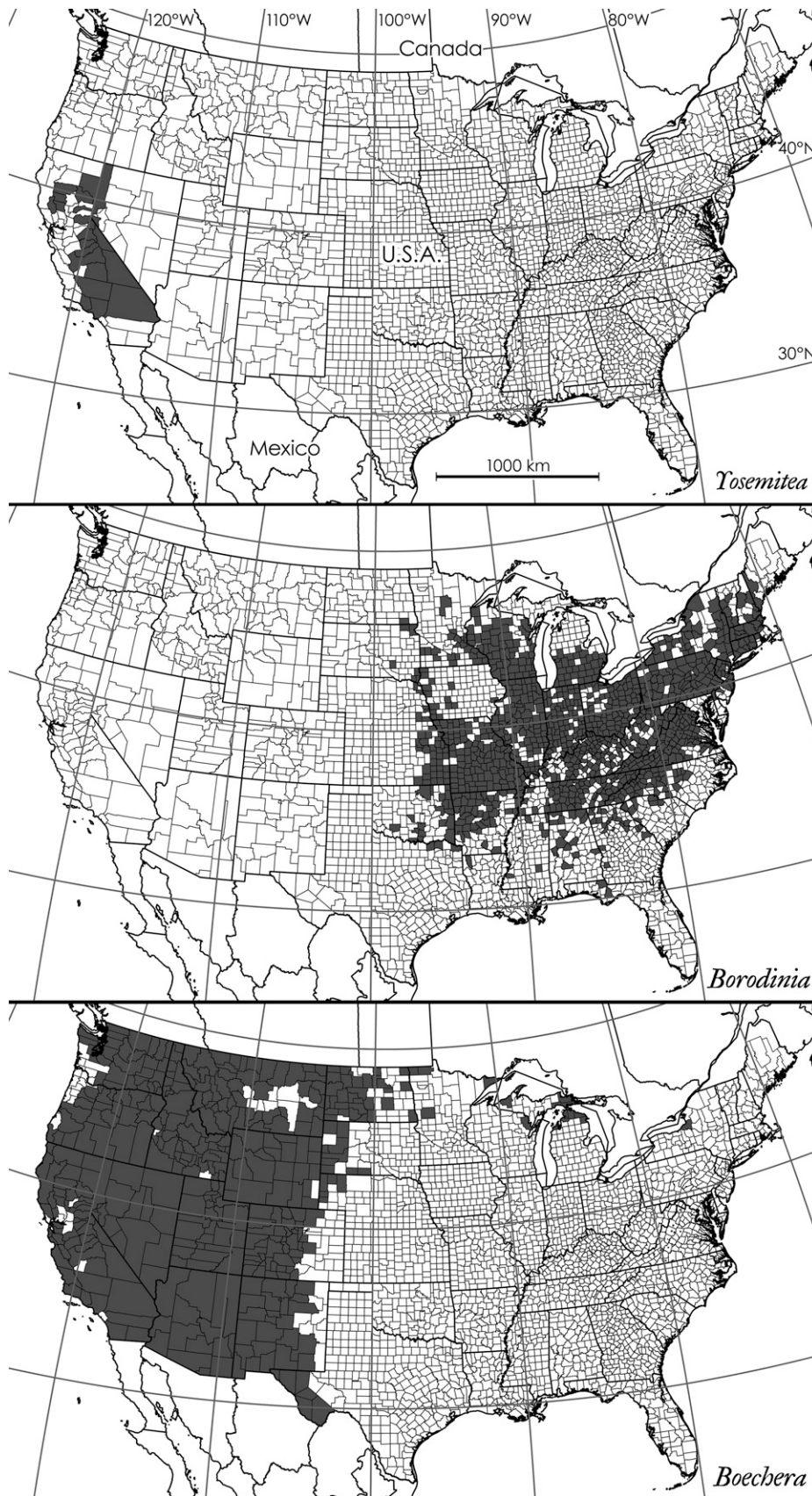


FIG. 5. Distribution of the three groups within *Boecheera* s. l.: *Boecheera* s. s., *Borodinia*, and *Yosemitea* in the continental U. S. A.. Distributions are based on herbarium specimens examined from BRY, CAS, DUKE, E, GH, JEPS, MO, NDG, NMC, NY, RM, RSA, UC, US, and WS, supplemented with distribution information from the Biota of North America Program (Kartesz 2011). Note that outside of the mapped area, the distribution of *Boecheera* s. s. extends through much of Canada and extends into the Russian Far East (*Boecheera falcata*). The distribution of *Borodinia* extends peripherally into Ontario and Québec, with *Borodinia macrophylla* disjunct in the Russian Far East.

Nevada (until recently part of *Smelowskia*) was assigned to Smelowskieae, *Sandbergia* (recently removed from *Halimolobos*) was included in the Halimoloboeae, and *Cusickiella* was included in the genus *Draba* (now Arabideae). Both *Anelsonia* and *Polyctenium* are long-standing genera with no previous association with *Boechera* or *Arabis* s. l.

Beyond our taxonomic reservations regarding the creation of a single, hyper-diverse genus equivalent to Boechereae lie the negative nomenclatural consequences of such a move. *Boechera* is a recent nomenclatural innovation, predated by nearly every other generic name in the tribe. The oldest available name is *Phoenicaulis* Nuttall, which, in its broadest application, has included just two of the ca. 120 species currently ascribed to the tribe. Transferring all members of the Boechereae into one genus would thus require ca. 118 new combinations. In consideration of these facts, we advocate splitting *Boechera* s. l. into three genera that are: 1) moderately to strongly supported by the nuclear matrix analysis (Fig. 4), 2) morphologically and geographically discrete, and 3) require the recognition of just one new genus and a total of eight new combinations at the species level. These genera are characterized as follows:

YOSEMITEA—The two accessions of *B. repanda* form a strongly supported (100/100) group whose relationship to other genera is unresolved. This taxon, endemic to the Sierra Nevada and adjacent ranges, is unique among the western North American species assigned to *Boechera* s. l. Its large (10–50 mm wide), repand to coarsely dentate basal leaves are strikingly different from the much smaller (2–12 mm wide), entire to shallowly dentate leaves characteristic of *Boechera* in this region. Morphologically anomalous and excluded from *Boechera* s. s. on molecular grounds, *B. repanda* is a species without a genus. Though morphologically most similar to the eastern North American clade discussed below, none of our phylogenetic analyses support a close relationship between the two. In consideration of these facts, we recognize *B. repanda* in a new monospecific genus, *Yosemitea*.

BORODINIA—This clade includes five sampled species of *Boechera* s. l.: *B. canadensis*, *B. dentata*, *B. laevigata*, *B. missouriensis*, and *B. serotina*. All are found east of the Great Plains, generally in deciduous forest (Fig. 5). Two morphologically similar species not included in our analyses, *B. burkii* (Porter) Windham & Al-Shehbaz and *B. perstellata* (E. L. Braun) Al-Shehbaz, also occur in this area. *Boechera perstellata* was included in previous phylogenetic analyses of ITS data in which it formed a clade with *B. dentata* with strong support (90% parsimony bootstrap; Kiefer et al. 2009a). *Boechera burkii* has not been included in any published phylogenetic analyses but is similar enough to *B. laevigata* that it is often treated as a variety of that species (Hopkins 1937; Rollins 1993; Windham and Al-Shehbaz 2007b). Nested among this group of eastern North American taxa is the type species of the monospecific Russian Far East genus *Borodinia*, which is strongly supported (88/89) as sister to *B. canadensis*. The *Borodinia* clade as a whole receives relatively weak support (70/67) but, like *Yosemitea*, it clearly does not belong to *Boechera* s. s. (Fig. 4). Based on these results, the seven members of *Boechera* s. l. restricted to eastern North America are transferred to the genus *Borodinia*. This appears to be yet another example of the eastern Asian/eastern North American floristic disjunction, which has been reported in at least 65 other genera (Boufford and Spongberg 1983; Xiang et al. 1998; Wen 1999).

BOECHERA s. s.—This clade includes the majority of species previously assigned to *Boechera* s. l., which occur in open rocky habitats, chaparral, or coniferous woodland primarily west of the Great Plains (Fig. 5). A few of these western species have ranges that extend into the Great Lakes and St. Lawrence River regions, and there are two eastern endemics, one in Quebec (*B. quebecensis* Windham & Al-Shehbaz) and one in Greenland (*B. holboellii* s. s.) (Al-Shehbaz and Windham 2010). *Boechera falcata* (Turcz.) Al-Shehbaz of the Russian Far East is also included in this clade in the ITS topology of Kiefer et al. (2009a), although with low support (56% parsimony bootstrap). The type species of *Boechera* is *B. holboellii*, typified on a distinctive apomictic triploid taxon only known in Greenland (Böcher 1951, 1954, 1969; Windham and Al-Shehbaz 2006). *Boechera holboellii* has a confusing taxonomic history in *Boechera* research (see Introduction) and, though many previous studies (e.g. Dobeš et al. 2004a; Dobeš et al. 2004b; Schranz et al. 2005) include samples identified as “*B. holboellii*,” these samples were all collected outside the known range of *B. holboellii* s. s. and probably represent a variety of sexual and apomictic segregates from *B. holboellii* s. l. (Windham and Al-Shehbaz 2006). As an apomictic triploid, *B. holboellii* s. s. is not appropriate for inclusion in phylogenetic analyses, but there are two lines of evidence that support its assignment to the clade under consideration. First, we have included four North American segregates of *B. holboellii* s. l. in our analyses (*B. collinsii*, *B. pendulocarpa*, *B. polyantha*, and *B. retrofracta*; Windham and Al-Shehbaz 2006) and all are robustly placed in this clade (Fig. 4). Second, we have obtained microsatellite data from *B. holboellii* s. s. (Windham et al. unpubl. data). Preliminary analyses indicate that this apomictic triploid is a hybrid and that one of the parents is *B. retrofracta*, a species that is robustly placed within *Boechera* s. s. Consequently, the generic name *Boechera* is retained for this clade.

Although *B. tiehmii* is tentatively retained in *Boechera* s. s., it may be necessary to revisit this classification in the near future. Differing placements of this species in single-locus nuclear analyses suggest that it may have originated as an intergeneric hybrid between *N. holmgrenii* and *B. lemmonii*. *Boechera tiehmii* has a narrow distribution in alpine habitats in Mono County, California and Washoe County, Nevada. Although *Nevada holmgrenii* has not been collected in these counties, it co-occurs with *B. lemmonii* in nearby Nye County, Nevada, rendering hybridization geographically plausible. However, a more thorough understanding of the origin of *B. tiehmii* and a final decision regarding its generic disposition await the collection of additional microsatellite data.

Resolution within *Boechera* s. s.—The nuclear matrix analysis shown in Fig. 4 strongly supports (99/97) a sister relationship between *B. davidsonii* and a clade comprising all other sampled members of *Boechera* s. s. This sister clade to *B. davidsonii* is highly supported (100/100), emphasizing the morphological and genetic gap between the two lineages. *Boechera davidsonii* is distinctive in that it has thickened caudex branches, is completely glabrous (a condition rarely encountered in just two other species), and apparently is uninvolved in the rampant hybridization that connects nearly every other taxon of *Boechera* s. s. (Windham and Al-Shehbaz 2006). Aside from the early divergence of *B. davidsonii*, deep relationships within *Boechera* s. s. receive little or no support. However, there is finer resolution that provides additional information. First, there is support for the polytypic nature of

B. holboellii s. l. Of the four sexual diploid segregates of *B. holboellii* included in our sampling (labeled “*holboellii*” in Fig. 4), only two (*B. collinsii* and *B. polyantha*) are placed within the same clade and one (*B. retrofracta*) is nested within a strongly supported clade of non-“*holboellii*” taxa. *Boechera pendulocarpa*, the most distinctive segregate morphologically, is weakly supported (64/–) as a member of the large, non-“*holboellii*” clade that includes the *B. fendleri* group, with which it shares widely pendent fruits and often biseriate seeds. Beyond providing some insight into the *B. holboellii* complex, the nuclear matrix analysis also identifies several clades that correspond to previously recognized morphological groups. Brief discussions of some of these well-supported groups of diploid species follow.

SUFFRUTESCENS GROUP—This strongly supported (100/100) clade includes three sexual diploid taxa. *Boechera suffrutescens* is a relatively common species distributed in an arc from the central Sierra Nevada through the east slope of the Cascade Range and northern Intermountain region to central Idaho. *Boechera constancei* and *B. rollei* are rare species found in the northern Sierra Nevada and Klamath Mountains, respectively. All three have relatively wide (2.5–6 mm), pendent fruits containing a single row of broadly winged (0.3–1.5 mm) seeds per locule. In the nuclear matrix analysis, the larger-flowered *B. rollei* (petals 8–11 mm) is well supported (95/99) as sister to a clade containing the two smaller-flowered species (petals 4.5–8 mm), which are, in turn, easily distinguished by differences in style length (styles 2.5–5 mm in *B. constancei* and 0.4–1.2 mm in *B. suffrutescens*). In terms of substrate preferences, *B. constancei* and *B. rollei* are obligately serpenticolous, whereas *B. suffrutescens* occurs on a variety of substrates, including serpentine. The placement of serpenticolous species in three distinct groups (*suffrutescens* group, *breweri* group, and *puberula* group) in the phylogeny suggests independent origins for this edaphic specialization.

PULCHRA GROUP—This moderately supported (78/87) clade includes five species with pendent to reflexed fruits occurring in the Mojave, Great Basin, and Colorado Plateau regions. *Boechera glaucovalvula*, a Mojave Desert endemic with distinctive glabrous fruits >5 mm wide, is sister to a clade comprising the other four species, all of which have narrower, pubescent fruits. Within this clade, *B. yorkii*, a rare taxon with unique yellow to brick-red flowers, is sister to a clade of three sexual diploids (*B. formosa*, *B. lincolnensis*, and *B. pulchra*) with white to purple flowers. These three species, formerly treated as varieties of *B. pulchra*, are allopatrically or parapatrically distributed from southern California through Nevada to the Four Corners region. *Boechera formosa*, a largely white-flowered taxon endemic to the Colorado Plateau, is sister to the primarily lavender/purple-flowered species of Nevada and California. Though closely related, *B. lincolnensis* and *B. pulchra* are easily distinguished by pedicel and fruit orientation (Windham and Al-Shehbaz 2006).

PLATYSPERMA GROUP—This strongly supported (99/98) clade includes three species, all of which have relatively wide (3–7 mm), ascending to erect fruits containing a single row of broadly winged (0.8–2.5 mm) seeds per locule. *Boechera pygmaea* is sister to a strongly supported (100/100) clade comprising *B. howellii* and *B. platysperma*. *Boechera pygmaea*, a rare endemic of the southern Sierra Nevada, is distinguished from the other members of the group by its narrow petals and non-undulate fruits that contain the smallest number of seeds (8–12) observed in the genus. *Boechera howellii* and

B. platysperma are more broadly distributed in the Sierra Nevada and southern Cascade Range, and are separable based on pubescence, which is confined to the basal leaf margins in *B. howellii* and scattered over the stems, leaves, and sepals in *B. platysperma*.

BREWERI GROUP—This strongly supported (97/96) clade includes three species: *B. breweri*, with two subspecies in western California and southwestern Oregon; *B. koehleri*, a facultatively serpenticolous species of northwestern California and southwestern Oregon; and *B. sparsiflora*, a widely distributed species occurring from the Great Basin northward to eastern Washington and adjacent Idaho. In the nuclear matrix analysis, the two accessions of *B. sparsiflora* are grouped together sister to a polytomy encompassing *B. koehleri* and the two subspecies of *B. breweri*. *Boechera cusickii*, a fourth species with clear morphological affinities to the *breweri* group, is placed sister to it, though without support. These four species are united by having ascending pedicels with predominantly simple trichomes and relatively long, arcuate fruits. Although the southern California taxon *B. arcuata* (formerly treated as a variety of *B. sparsiflora*) shares many of these features, the pedicel trichomes are different. This species is strongly supported as sister to *B. rectissima*, validating the recent recognition of *B. arcuata* and *B. sparsiflora* as distinct species (Windham and Al-Shehbaz 2006).

DISPAR GROUP—This strongly supported (91/93) clade includes three species: *Boechera dispar*, *B. johnstonii*, and *B. parishii*. All have lavender/purple flowers, divaricate-ascending fruits, and entire, densely pubescent (pannose) basal leaves with highly divided (6–14-rayed) dendritic hairs. The absence of resolution within the *dispar* group is somewhat surprising given that they exhibit major differences in petal size, style length, and ovule number. Based on these features, we suspect that *B. johnstonii* and *B. parishii* are sister species. *Boechera dispar* occurs sporadically in and around the western Mojave Desert; *B. johnstonii* and *B. parishii* are narrow endemics in southern California, the former occurring in the Cuyamaca and San Jacinto Mountains while the latter is limited to the San Bernardino Mountains.

PUBERULA GROUP—This strongly supported (99/100) clade includes: *Boechera lasiocarpa*, *B. puberula*, *B. retrofracta*, *B. serpenticola*, and *B. subpinnatifida*. All have closely pendent to reflexed fruits that are more or less pubescent (mostly glabrous in *B. retrofracta*). *Boechera puberula* and *B. subpinnatifida* form a clade, but relationships among species within the *puberula* group are otherwise unresolved. *Boechera puberula* is widely distributed in the Great Basin and southern Snake River Plains; *B. lasiocarpa* and *B. serpenticola* are rare species endemic to the Wasatch Mountains of Utah and the North Coast Ranges of California, respectively. *Boechera retrofracta*, one of the most widespread species in the genus, is involved in a particularly diverse array of hybrid lineages (Windham and Al-Shehbaz 2007a; Windham and Al-Shehbaz 2007b) and is the focus of much of the ongoing evolutionary ecology research in *Boechera* (Aliyu et al. 2010; Sharbel et al. 2010; Rushworth et al. 2011). The placement of *B. retrofracta* in the *puberula* group is anomalous compared to results of preliminary microsatellite analyses (Windham et al. unpubl. data) which indicate *B. retrofracta* is genetically similar to, or even conspecific with, *B. polyantha*. A better understanding of the situation awaits further research.

FENDLERI GROUP—This well supported (84/93) clade includes seven species, all of which exhibit widely pendent

fruits and at least some forked (2-rayed) trichomes. In addition, five of the seven have biseriate seeds arranged in two rows per locule. This is a widespread species group, occurring from southern California through southern Nevada, Utah, southern Wyoming, Colorado, New Mexico, western Texas, and Arizona. Clarification of species boundaries and the origin of hybrids in this group are the subject of ongoing research (Alexander et al. unpubl. data).

TAXONOMIC TREATMENT

Yosemitea P. J. Alexander & Windham, gen. nov.—TYPE: *Arabis repanda* S. Watson, Proc. Amer. Acad. Arts 11: 122. 1875.

Herbs, short- to long-lived perennials; caudices mostly not woody; trichomes stalked, 2–6-rayed, rarely simple. Stems usually 1 per caudex branch, arising near ground surface from center of basal rosettes. Basal leaves rosulate, broadly oblanceolate to obovate, repand to coarsely dentate or rarely entire; cauline leaves petiolate, not auriculate. Racemes ebracteate; fruiting pedicels erect to divaricate-ascending. Sepals glabrous or sparsely pubescent; petals white; ovules 34–50 per fruit. Fruits dehiscent, linear, latiseptate siliques, glabrous or pubescent; septum complete; stigma entire. Seeds uniseriate, winged; cotyledons accumbent.

Yosemitea repanda (S. Watson) P. J. Alexander & Windham, comb. nov. *Arabis repanda* S. Watson, Proc. Amer. Acad. Arts 11: 122. 1875; *Boechera repanda* (S. Watson) Al-Shehbaz, Novon 13(4): 388. 2003.—TYPE: U. S. A. California: Mariposa Co.: Yosemite Valley. 1866, *H. N. Bolander 4881* (holotype: GH; isotype: UC).

BORODINIA N. Busch in Bot. Mater. Gerb. Glavn. Bot. Sada RSFSR 2: 137. 1921.—TYPE: *B. baicalensis* N. Busch [= *Draba macrophylla* O. E. Schulz, *B. macrophylla* (Turcz.) O. E. Schulz].

Borodinia burkii (Porter) P. J. Alexander & Windham, comb. nov. *Arabis laevigata* (Muhl. ex Willd.) Poir. var. *burkii* Porter, Bull. Torrey Bot. Club 17: 15. 1890; *Arabis burkii* (Porter) Small, Man. Fl. Southeast. U.S. 572. 1933; *Boechera burkii* (Porter) Windham & Al-Shehbaz, Harvard Pap. Bot. 12: 237. 2007.—TYPE: U. S. A. Pennsylvania: Franklin Co.: Mercersburg, 1852, *I. Burk s. n.* (holotype: PH, isotype: GH).

Borodinia canadensis (L.) P. J. Alexander & Windham, comb. nov. *Arabis canadensis* L., Sp. Pl. 2: 665. 1753; *Boechera canadensis* (L.) Al-Shehbaz, Novon 13(4): 384. 2003.—

TYPE: *J. Clayton 400*, left-hand specimen (lectotype, designated by Reveal in Cafferty and Jarvis, Taxon 51(3): 521. 2002: LINN; isotype: BM).

Borodinia dentata (Raf.) P. J. Alexander & Windham, comb. nov. *Shortia dentata* Raf., Autik. Bot. 17. 1840; *Iodanthus dentatus* (Raf.) Greene, Pittonia 3: 254. 1897; *Arabis dentata* Torrey & A. Gray, Fl. N. Amer. 1: 80. 1838, non Clairville, Man. herbor. Suisse 223. 1811; *Arabis perstellata* E. Braun var. *shortii* Fernald, Rhodora 48: 208. 1946; *A. shortii* (Fernald) Gleason, Phytologia 4: 23. 1952; *Boechera shortii* (Fernald) Al-Shehbaz, Novon 13: 389.2003, nom. superfl.; *Boechera dentata* (Raf.) Al-Shehbaz & Zarucchi, Harvard Pap. Bot. 13: 293. 2008.—TYPE: U. S. A. Kentucky: sandy banks of the Ohio River, *C. W. Short s. n.* (lectotype, designated by Mulligan, Rhodora 97: 143. 1995: DWC, isolectotype: GH).

Borodinia laevigata (Muhl. ex Willd.) P. J. Alexander & Windham, comb. nov. *Turritis laevigata* Muhl. ex Willd., Sp. Pl. 3(2): 543. 1801; *Arabis laevigata* (Muhl. ex Willd.) Poir., Encycl. Suppl. 1: 411. 1810; *Boechera laevigata* (Muhl. ex Willd.) Al-Shehbaz, Novon 13(4): 386. 2003.—TYPE: U. S. A. Pennsylvania: without locality, *G. H. E. Muhlenberg s. n.* (holotype: PH).

Borodinia missouriensis (Greene) P. J. Alexander & Windham, comb. nov. *Arabis missouriensis* Greene, Repert. Sp. Nov. Regni Veg. 5: 244. 1908; *Boechera missouriensis* (Greene) Al-Shehbaz, Novon 13(4): 387. 2003.—TYPE: U. S. A. Missouri: Montier, 15 May 1894, *B. F. Bush 31* (holotype: NDG).

Borodinia perstellata (E. Braun) P. J. Alexander & Windham, comb. nov. *Arabis perstellata* E. Braun, Rhodora 42: 47. 1940; *Boechera perstellata* (E. Braun) Al-Shehbaz, Novon 13(4): 388. 2003.—TYPE: U. S. A. Kentucky: Franklin Co.: Elkhorn Creek, wooded hillsides, 6 May 1936, *E. L. Braun 1226* (holotype: GH).

Borodinia serotina (Steele) P. J. Alexander & Windham, comb. nov. *Arabis serotina* Steele, Contr. U.S. Natl. Herb. 13: 365. 1911; *Boechera serotina* (Steele) Windham & Al-Shehbaz, Harvard Pap. Bot. 12: 249. 2007.—TYPE: U. S. A. Virginia: Bath Co.: Alleghany Mts., vicinity of Millboro, disintegrating shale, 500 m, 21 August 1907, *E. S. Steele s. n.* (holotype: US).

Under this revised generic circumscription, Boechereae contains nine genera (*Anelsonia*, *Boechera*, *Borodinia*, *Cusickiella*, *Nevada*, *Phoenicaulis*, *Polyctenium*, *Sandbergia*, and *Yosemitea*) that can be distinguished using the following key:

KEY TO GENERA OF BOECHEREAEE

1. Fruits angustiseptate; leaves pectinate, rigid, persisting in subsequent years as pectinate spines *Polyctenium*
1. Fruits latiseptate, terete, or quadrangular; leaves undivided or rarely pinnatifid, soft, not persisting in subsequent years as spines 2
 2. Fruits ovoid siliques; ovules/seeds 4 per ovary/fruit *Cusickiella*
 2. Fruits linear to lanceolate siliques, rarely (*Anelsonia*) narrowly ovate siliques; ovules/seeds (6–)12–250 per ovary/fruit 3
 3. Plants scapose; stems leafless; seeds silvery papillate; lateral veins of fruit valves anastomosing *Anelsonia*
 3. Plants not scapose; stems leafy; seeds smooth or minutely reticulate; lateral veins of fruit valves not anastomosing (except *Phoenicaulis*) 4
 4. Cotyledons incumbent; cauline leaves not auriculate; seeds wingless, plump 5
 5. Trichomes exclusively simple; ovules/seeds 6–12 per ovary/fruit *Nevada*
 5. Trichomes branched; ovules/seeds 12–30 per ovary/fruit *Sandbergia*
 4. Cotyledons accumbent; cauline leaves auriculate or not; seeds winged or rarely wingless, flattened 6

6. Trichomes finely dendritic throughout; lateral sepals saccate at base; fruit valves with a prominent midvein and lateral veins; seeds/ovules 6–16(–16) per ovary/fruit *Phoenicaulis*
6. Trichomes absent, simple, or a combination of variously forked/stellate and simple; lateral sepals not saccate at base; fruit valves with obscure veins or rarely with a prominent midvein; seeds/ovules usually 20–250 per ovary/fruit (except a few *Boechera* and *Borodinia*) 7
7. Usually biennials, rarely perennials with caudex; glabrous or with simple (rarely branched) trichomes; eastern North America, mostly south of the U. S. A./Canada border (except *Borodinia macrophylla* in the Russian Far East) *Borodinia*
7. Perennials with well-developed caudex or woody foot; trichomes usually simple and/or branched; western North America and eastern North America mostly north of the U. S. A./Canada border (except *Boechera falcata* in the Russian Far East) 8
8. Basal leaves linear to narrowly oblanceolate or rarely obovate, (0.2–)0.5–9(–2) cm wide, entire or rarely dentate or pinnatifid; cauline leaves auriculate or rarely not; marginal fruit veins usually obscure; throughout western U. S. A., Canada, Alaska, and Russian Far East *Boechera*
8. Basal leaves broadly obovate to broadly oblanceolate, 1–5 cm wide, coarsely dentate or repand; cauline leaves not auriculate; marginal fruit veins usually prominent; Sierra Nevada and Transverse Ranges in California and Carson Range in Nevada *Yosemitea*

ACKNOWLEDGMENTS. We would like to thank the following institutions for loans of specimens and for allowing removal of material for DNA isolation: Harvard University (GH), Illinois Natural History Survey (ILLS), University of California (JEPS), Missouri Botanical Garden (MO), and Utah Museum of Natural History (UT). We would also like to thank Mark Beilstein and Eric Schranz for providing DNA samples, and Robert McEldery for providing leaf material for DNA isolation. This research was supported by NSF grant DEB-0817033.

LITERATURE CITED

- Al-Shehbaz, I. A. 2003. Transfer of most North American species of *Arabis* to *Boechera* (Brassicaceae). *Novon* 13: 381–391.
- Al-Shehbaz, I. A., M. A. Beilstein, and E. A. Kellogg. 2006. Systematics and phylogeny of the Brassicaceae (Cruciferae): an overview. *Plant Systematics and Evolution* 259: 89–120.
- Al-Shehbaz, I. A. and M. D. Windham. 2010. *Boechera*. Pp. 347–412 in *Flora of North America north of Mexico Vol 7.*, eds. Flora of North America Committee. New York and Oxford: Oxford University Press.
- Alexander, P. J., G. Rajanikanth, C. D. Bacon, and C. D. Bailey. 2007. Rapid inexpensive recovery of high quality plant DNA using a reciprocating saw and silica-based columns. *Molecular Ecology Notes* 7: 5–9.
- Aliyu, O. M., M. E. Schranz, and T. F. Sharbel. 2010. Quantitative variation for apomictic reproduction in the genus *Boechera* (Brassicaceae). *American Journal of Botany* 91: 1719–1731.
- Bailey, C. D. and J. J. Doyle. 1999. Potential phylogenetic utility of the low-copy nuclear gene *pistillata* in dicotyledonous plants: comparison to nrDNA ITS and *trnL* intron in *Sphaerocaradum* and other Brassicaceae. *Molecular Phylogenetics and Evolution* 13: 20–30.
- Bailey, C. D., M. Koch, M. S. Mayer, K. Mummenhoff, S. L. O’Kane Jr., S. I. Warwick, M. D. Windham, and I. A. Al-Shehbaz. 2006. Toward a global phylogeny of the Brassicaceae. *Molecular Biology and Evolution* 23: 2142–2160.
- Beck, J. B., P. J. Alexander, L. Allphin, I. A. Al-Shehbaz, C. Rushworth, C. D. Bailey, and M. D. Windham. 2012. Does hybridization drive the transition to asexuality in diploid *Boechera*? *Evolution* 66: 985–995.
- Beilstein, M. A., I. A. Al-Shehbaz, and E. A. Kellogg. 2006. Brassicaceae phylogeny and trichome evolution. *American Journal of Botany* 93: 607–619.
- Beilstein, M. A., I. A. Al-Shehbaz, S. Mathews, and E. A. Kellogg. 2008. Brassicaceae phylogeny inferred from phytochrome A and *ndhF* sequence data: tribes and trichomes revisited. *American Journal of Botany* 95: 1307–1327.
- Birky, C. W. Jr., T. Maruyama, and P. Fuerst. 1983. An approach to population and evolutionary genetic theory for genes in mitochondria and chloroplasts, and some results. *Genetics* 103: 513–527.
- Bishop, J. G., A. M. Dean, and T. Mitchell-Olds. 2000. Rapid evolution in plant chitinases: Molecular targets of selection in plant-pathogen coevolution. *Evolution* 97: 5322–5327.
- Bloom, C. T., C. C. Baskin, and J. M. Baskin. 1990. Germination ecology of the facultative biennial *Arabis laevigata* variety *laevigata*. *American Midland Naturalist* 124: 214–230.
- Bloom, T. C., J. M. Baskin, and C. C. Baskin. 2001. Ecological life history of the facultative woodland biennial *Arabis laevigata* var. *laevigata* (Brassicaceae): survivorship. *The Journal of the Torrey Botanical Society* 128: 93–108.
- Böcher, T. W. 1951. Cytological and embryological studies in the amphipomictic *Arabis holboellii* complex. *Biologiske Skrifter Kongelige Danske Videnskaberne Selskab* 6: 1–59.
- Böcher, T. W. 1954. Experimental taxonomic studies in the *Arabis holboellii* complex. *Svensk Botanisk Tidskrift* 48: 31–44.
- Böcher, T. W. 1969. Further studies in the *Arabis holboellii* complex. *Botanisk Tidsskrift* 64: 141–161.
- Boufford, D. E. and S. A. Spongberg. 1983. Eastern Asian-eastern North American phylogeographical relationships—a history from the time of Linnaeus to the twentieth century. *Annals of the Missouri Botanical Garden* 70: 423–439.
- Bruyns, P. V., R. J. Mapaya, and T. J. Hedderson. 2006. A new subgeneric classification for *Euphorbia* (Euphorbiaceae) in southern Africa based on ITS and *psbA-trnH* sequence data. *Taxon* 55: 397–420.
- Chan, K. M. A. and S. A. Levin. 2005. Leaky prezygotic isolation and porous genomes: rapid introgression of maternally inherited DNA. *Evolution* 59: 720–729.
- Dobeš, C., C. Kiefer, M. Kiefer, and M. A. Koch. 2007a. Plastidic *trnF_{UUC}* pseudogenes in North American genus *Boechera* (Brassicaceae): Mechanistic aspects of evolution. *Plant Biology* 9: 502–515.
- Dobeš, C., M. Koch, and T. Sharbel. 2006. Embryology, karyology, and modes of reproduction in the North American genus *Boechera* (Brassicaceae): a compilation of seven decades of research. *Annals of the Missouri Botanical Garden* 93: 517–533.
- Dobeš, C., T. Mitchell-Olds, and M. A. Koch. 2004a. Intraspecific diversification in North American *Boechera stricta* (= *Arabis drummondii*), *Boechera* × *divaricarpa*, and *Boechera holboellii* (Brassicaceae) inferred from nuclear and chloroplast markers—an integrative approach. *American Journal of Botany* 91: 2087–2101.
- Dobeš, C. H., T. Mitchell-Olds, and M. A. Koch. 2004b. Extensive chloroplast haplotype variation indicates Pleistocene hybridization and radiation of North American *Arabis drummondii*, *A. × divaricarpa*, and *A. holboellii* (Brassicaceae). *Molecular Ecology* 13: 349–370.
- Dobeš, C., T. F. Sharbel, and M. Koch. 2007b. Towards understanding the dynamics of hybridization and apomixis in the evolution of the genus *Boechera* (Brassicaceae). *Systematics and Biodiversity* 5: 321–331.
- Dorn, R. 2001. *Vascular plants of Wyoming*, ed. 3. Cheyenne: Mountain West Publishing.
- Goloboff, P. A. 1999. Analyzing large data sets in reasonable times: solutions for composite optima. *Cladistics* 15: 415–428.
- Goloboff, P. A. 2000. NONA (NO NAME) ver. 2. Tucumán: Published by the author.
- Goloboff, P. A., J. S. Farris, and K. C. Nixon. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24: 774–786.
- Hedtke, S. M. and D. M. Hillis. 2011. The potential role of androgenesis in cytoplasmic-nuclear phylogenetic discordance. *Systematic Biology* 60: 87–109.
- Holmgren, N. H. 2005. Brassicaceae. Pp. 174–418 in *Intermountain Flora: Vascular plants of the Intermountain West*, Vol. 2, part B, eds. N. H. Holmgren, P. K. Holmgren, and A. Cronquist. Bronx: New York Botanical Garden Press.
- Hopkins, M. L. 1937. *Arabis* in eastern and central North America. *Rhodora* 39: 63–98, 106–148, 155–186.
- Jordon-Thaden, I., I. Hase, I. A. Al-Shehbaz, and M. A. Koch. 2010. Molecular phylogeny and systematics of the genus *Draba* (Brassicaceae) and identification of its most closely related genera. *Molecular Phylogenetics and Evolution* 55: 524–540.
- Kantama, L., T. F. Sharbel, M. E. Schranz, T. Mitchell-Olds, S. de Vries, and H. de Jong. 2007. Diploid apomicts of the *Boechera holboellii* complex display large-scale chromosome substitutions and aberrant chromosomes. *Proceedings of the National Academy of Sciences USA* 104: 14026–14031.

- Kartesz, J. T. and The Biota of North America Program (BONAP). 2011. North American plant atlas. Chapel Hill, North Carolina URL: <http://www.bonap.org/MapSwitchboard.html> [accessed January 2011].
- Kiefer, C., C. Dobeš, and M. A. Koch. 2009a. *Boecheera* or not? Phylogeny and phylogeography of eastern North American *Boecheera* species (Brassicaceae). *Taxon* 58: 1109–1121.
- Kiefer, C., C. Dobeš, T. F. Sharbel, and M. A. Koch. 2009b. Phylogeographic structure of the chloroplast DNA gene pool in North American *Boecheera* - A genus and continental-wide perspective. *Molecular Phylogenetics and Evolution* 52: 303–311.
- Knight, C. A., H. Vogel, J. Kroymann, A. Shumate, H. Witsenboer, and T. Mitchell-Olds. 2006. Expression profiling and local adaptation of *Boecheera holboellii* populations for water use efficiency across a naturally occurring water stress gradient. *Molecular Ecology* 15: 1229–1237.
- Koch, M. A., J. Bishop, and T. Mitchell-Olds. 1999. Molecular systematics and evolution of *Arabidopsis* and *Arabis*. *Plant Biology* 1: 529–537.
- Koch, M. A., C. Dobeš, and T. Mitchell-Olds. 2003. Multiple hybrid formation in natural populations: concerted evolution of the internal transcribed spacer of nuclear ribosomal DNA (ITS) in North American *Arabis divaricarpa* (Brassicaceae). *Molecular Biology and Evolution* 20: 338–350.
- Koch, M. A., B. Haubold, and T. Mitchell-Olds. 2000. Comparative evolutionary analysis of chalcone synthase and alcohol dehydrogenase loci in *Arabidopsis*, *Arabis*, and related genera (Brassicaceae). *Molecular Biology and Evolution* 17: 1483–1498.
- Koch, M. A., B. Haubold, and T. Mitchell-Olds. 2001. Molecular systematics of the Brassicaceae: Evidence from coding plastidic *matK* and nuclear *Chs* sequences. *American Journal of Botany* 88: 534–544.
- Linder, C. R. and L. H. Rieseberg. 2004. Reconstructing patterns of reticulate evolution in plants. *American Journal of Botany* 91: 1700–1708.
- Löve, Á. and D. Löve. 1976. Nomenclatural notes on arctic plants. *Botaniska Notiser* 128: 497–523.
- Mace, E. S., H. K. Buhariwalla, and J. H. Crouch. 2003. A high-throughput DNA extraction protocol for tropical molecular breeding programs. *Plant Molecular Biology Reporter* 21: 459–460.
- McDade, L. 1990. Hybrids and phylogenetic systematics I. Patterns of character expression in hybrids and their implications for cladistic analysis. *Evolution* 44: 1685–1700.
- McKay, J. K., J. G. Bishop, J. Z. Lin, J. H. Richards, A. Sala, and T. Mitchell-Olds. 2001. Local adaptation across a climatic gradient despite small effective population size in the rare sapphire rockcress. *Proceedings of the Royal Society Biological Sciences Series B* 268: 1715–1721.
- Miller, M. A., M. T. Holder, R. Vos, P. E. Midford, T. Liebowitz, L. Chan, P. Hoover, and T. Warnow. 2010. The CIPRES Portals. CIPRES. URL: <http://www.phylo.org/portal2/> [accessed December 2010 to March 2011].
- Mitchell-Olds, T. 2001. *Arabidopsis thaliana* and its wild relatives: a model system for ecology and evolution. *Trends in Ecology & Evolution* 16: 693–700.
- Müller, K. 2005. SeqState: primer design and sequence statistics for phylogenetic DNA datasets. *Applied Bioinformatics* 4: 65–69.
- Naumova, T. N., J. van der Laak, J. Osadchij, F. Matzk, A. Kravtchenko, J. Bergervoet, K. S. Ramulu, and K. Boutilier. 2001. Reproductive development in apomictic populations of *Arabis holboellii* (Brassicaceae). *Sexual Plant Reproduction* 14: 195–200.
- Nixon, K. C. 1999–2002. WinClada ver. 1.0000. Ithaca: Published by the author.
- Oyama, R. K., M. J. Clauss, N. Formanová, J. Kroymann, K. J. Schmid, H. Vogel, K. Weniger, A. J. Windsor, and T. Mitchell-Olds. 2008. The shrunken genome of *Arabidopsis thaliana*. *Plant Systematics and Evolution* 273: 257–271.
- Pelster, P. B., B. Nordenstam, J. W. Kadereit, and L. E. Watson. 2007. An ITS phylogeny of tribe Senecioneae (Asteraceae) and a new delimitation of *Senecio* L. *Taxon* 56: 1077–1104.
- Rambaut, A. 2002. Se-Al v.2.0a11. Edinburgh: Published by the author.
- Rollins, R. C. 1941. A monographic study of *Arabis* in western North America. *Rhodora* 43: 289–325, 348–411, 425–485.
- Rollins, R. C. 1993. *The Cruciferae of continental North America*. Palo Alto: Stanford University Press.
- Roy, B. A. 1995. The breeding systems of six species of *Arabis* (Brassicaceae). *American Journal of Botany* 82: 869–877.
- Roy, B. A. 2001. Patterns of association between crucifers and their flower mimic pathogens: host jumps are more common than coevolution or cospeciation. *Evolution* 55: 41–53.
- Roy, B. A. and R. A. Raguso. 1997. Olfactory versus visual cues in a floral mimicry system. *Oecologia* 109: 414–426.
- Roy, B. A. and L. H. Rieseberg. 1989. Evidence for apomixis in *Arabis*. *Heredity* 80: 506–508.
- Rushworth, C. A., B.-H. Song, C.-R. Lee, and T. Mitchell-Olds. 2011. *Boecheera*, a model system for ecological genomics. *Molecular Ecology* 20: 4843–4857.
- Schneider, H., S. Russell, C. Cox, F. Bakker, S. Henderson, F. Rumsey, J. Barrett, M. Gibby, and J. Vogel. 2004. Chloroplast phylogeny of asplenoid ferns based on *rbcl* and *trnL-F* spacer sequences (Polypodiidae, Aspleniaceae) and its implications for biogeography. *Systematic Botany* 29: 260–274.
- Schranz, M. E., C. Dobeš, M. Koch, and T. Mitchell-Olds. 2005. Sexual reproduction, hybridization, apomixis, and polyploidization in the genus *Boecheera* (Brassicaceae). *American Journal of Botany* 92: 1797–1810.
- Schranz, M. E., L. Kantama, H. de Jong, and T. Mitchell-Olds. 2006. Asexual reproduction in a close relative of *Arabidopsis*: a genetic investigation of apomixis in *Boecheera* (Brassicaceae). *The New Phytologist* 171: 425–438.
- Schranz, M. E., A. J. Windsor, B.-H. Song, A. Lawton-Rauh, and T. Mitchell-Olds. 2007. Comparative genetic mapping in *Boecheera stricta*, a close relative of *Arabidopsis*. *Plant Physiology* 144: 286–298.
- Sharbel, T. F. and T. Mitchell-Olds. 2001. Recurrent polyploid origins and chloroplast phylogeography in the *Arabis holboellii* complex (Brassicaceae). *Heredity* 87: 59–69.
- Sharbel, T. F., T. Mitchell-Olds, C. Dobeš, L. Kantama, and H. de Jong. 2005. Biogeographic distribution of polyploidy and B chromosomes in the apomictic *Boecheera holboellii* complex. *Cytogenetic and Genome Research* 109: 283–292.
- Sharbel, T. F., M.-L. Voigt, J. M. Corral, G. Galla, J. Kumlehn, C. Klukas, F. Schreiber, H. Vogel, and B. Rotter. 2010. Apomictic and sexual ovules of *Boecheera* display heterochronic global gene expression patterns. *The Plant Cell* 22: 655–671.
- Sharbel, T. F., M.-L. Voigt, J. M. Corral, T. Thiel, A. Varshney, J. Kumlehn, H. Vogel, and B. Rotter. 2009. Molecular signatures of apomictic and sexual ovules in the *Boecheera holboellii* complex. *The Plant Journal* 58: 870–882.
- Sharbel, T. F., M.-L. Voigt, T. Mitchell-Olds, L. Kantama, and H. de Jong. 2004. Is the aneuploid chromosome in an apomictic *Boecheera holboellii* a genuine B chromosome? *Cytogenetic and Genome Research* 106: 173–183.
- Shaw, J., E. B. Lickey, E. E. Schilling, and R. L. Small. 2007. Comparison of whole chloroplast genome sequences to choose noncoding regions for phylogenetic studies in angiosperms: The tortoise and the hare III. *American Journal of Botany* 94: 275–288.
- Simmons, M. P. and H. Ochoterena. 2000. Gaps as characters in sequence-based phylogenetic analyses. *Systematic Biology* 49: 369–381.
- Slotte, T., A. Ceglitis, E. Neuffer, H. Hurka, and M. Lascoux. 2006. Intrageneric phylogeny of *Capsella* (Brassicaceae) and the origin of the tetraploid *C. bursa-pastoris* based on chloroplast and nuclear DNA sequences. *American Journal of Botany* 93: 1714–1724.
- Song, B.-H. and T. Mitchell-Olds. 2007. High genetic diversity and population differentiation in *Boecheera fecunda*, a rare relative of *Arabidopsis*. *Molecular Ecology* 16: 4079–4088.
- Song, B.-H., M. J. Clauss, A. Pepper, and T. Mitchell-Olds. 2006. Geographic patterns of microsatellite variation in *Boecheera stricta*, a close relative of *Arabidopsis*. *Molecular Ecology* 15: 357–369.
- Stamatakis, A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688–2690.
- Stamatakis, A., P. Hoover, and J. Rougemont. 2008. A rapid bootstrap algorithm for the RAxML web-servers. *Systematic Biology* 75: 758–771.
- Taberlet, P., L. Gielly, G. Pautou, and J. Bouvet. 1991. Universal primers for amplification of three non-coding regions of chloroplast DNA. *Plant Molecular Biology* 17: 1105–1110.
- Thompson, J. D., D. G. Higgins, and T. J. Gibson. 1994. CLUSTAL W: improving the sensitivity of progressive sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research* 22: 4673–4680.
- Tsitroni, A., M. Kirkpatrick, and D. A. Levin. 2003. A model for chloroplast capture. *Evolution* 57: 1776–1782.
- van der Linde, K., G. Bächli, M. J. Toda, W.-X. Zhang, T. Katoh, Y.-G. Hu, and G. S. Spicer. 2007. *Drosophila* Fallén, 1832 (Insecta, Diptera): proposed conservation of usage. *Bulletin of Zoological Nomenclature* 64: 238–242.
- Warwick, S. I., K. Mummenhoff, C. A. Sauder, M. A. Koch, and I. A. Al-Shehbaz. 2010. Closing the gaps: phylogenetic relationships in the Brassicaceae based on DNA sequence data of nuclear ribosomal ITS region. *Plant Systematics and Evolution* 285: 209–232.
- 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.

- White, T. J., T. Bruns, S. Lee, and J. Taylor. 1990. Amplification and direct sequencing of fungal ribosomal RNA gene for phylogenetics. Pp. 315–322 in *PCR protocols: a guide to methods and applications*, eds. M. Innis, D. Gelfand, J. Sninsky, and T. J. White. San Diego: Academic Press.
- Windham, M. D. and I. A. Al-Shehbaz. 2006. New and noteworthy species of *Boechera* (Brassicaceae) I: sexual diploids. *Harvard Papers in Botany* 11: 61–88.
- Windham, M. D. and I. A. Al-Shehbaz. 2007a. New and noteworthy species of *Boechera* (Brassicaceae) II: apomictic triploids. *Harvard Papers in Botany* 11: 257–274.
- Windham, M. D. and I. A. Al-Shehbaz. 2007b. New and noteworthy species of *Boechera* (Brassicaceae) III: additional sexual diploids and apomictic hybrids. *Harvard Papers in Botany* 12: 235–257.
- Windham, M. D. and I. A. Al-Shehbaz. 2012. *Boechera*. Pp. 521–533 in *The Jepson Manual: Vascular Plants of California*, 2nd edition, eds. B. G. Baldwin, D. H. Goldman, D. J. Keil, R. Patterson, T. J. Rosatti, and D. H. Wilken. Berkeley: University of California Press.
- Windsor, A. J., M. E. Schranz, N. Formanová, S. Gebauer-Jung, J. G. Bishop, D. Schnabelrauch, J. Kroymann, and T. Mitchell-Olds. 2006. Partial shotgun sequencing of the *Boechera stricta* genome reveals extensive microsynteny and promoter conservation with *Arabidopsis*. *Plant Physiology* 140: 1169–1182.
- Xiang, Q.-Y., D. E. Soltis, and P. S. Soltis. 1998. The eastern Asian and eastern and western North American floristic disjunction: congruent phylogenetic patterns in seven diverse genera. *Molecular Phylogenetics and Evolution* 10: 178–190.

APPENDIX 1. Voucher information and GenBank accessions for samples used in this study. For each sample, GenBank accessions are listed with loci in the following order: *chs*, *Dpa1*, ITS, *luminidependens*, *Mps35*, *Nuo*, *pistillata*, *rps16-trnK*, *trnL-F*, *adh*. When multiple *adh* clones were sequenced, they are identified by the prefixes used in Supplementary Fig. 1 (e.g., “A1”). Loci not successfully sequenced for a sample are indicated by “no sequence.” All samples are represented by herbarium vouchers except for seven samples isolated from greenhouse material and provided by E. Schranz.

All genera except Boechera, Borodinia, and Yosemitea. **083 Anelsonia eurycarpa** (A. Gray) J. F. Macbr. & Payson, U. S. A.: California: Mono County: On the southeast facing slope of White Mountain, near the saddle, nestled in rocky soil, 13,670 ft., *M. D. Beilstein* 2001-72, 27 Jun 2001 (MO) [DNA sample provided by M. Beilstein], JX146740, JX146834, JX146929, JX146545, JX146453, JX146362, JX146271, JX146176, JX146081, JX146651.

098 Anelsonia eurycarpa, U. S. A.: California: Mono County: White Mountains, near Barcroft Station, *M. Beilstein* 26299, 2001 (MO) [DNA sample provided by M. Beilstein], JX146748, JX146842, JX146937, JX146553, JX146461, JX146370, JX146278, JX146184, JX146089, JX146666.

242 Crucihimalaya wallichii (Hook. f. & Thompson) Al-Shehbaz, O’Kane, & R. A. Price, DNA sample provided by E. Schranz, JX146771, JX146865, JX146960, JX146576, JX146483, JX146393, JX146301, JX146207, JX146112, JX146689.

370 Cusickiella douglasii (A. Gray) Rollins, U. S. A.: Utah: Box Elder County: NNE of Etna on isolated peak south of Dry Creek Basin, ca. 3.92 km SE of the summit (7,013) of Beatty Mountain, 6,525 ft., *M. D. Windham* 3362, 4 May 2005 (NMC), JX146810, JX146905, JX147000, JX146616, JX146521, JX146430, no sequence, JX146247, JX146152, JX146718.

243 Cusickiella douglasii, DNA sample provided by E. Schranz, JX146772, JX146866, JX146961, JX146577, JX146484, no sequence, JX146302, JX146208, JX146113, JX146690.

244 Halimolobos jaegeri (Munz) Rollins, DNA sample provided by E. Schranz, JX146773, JX146867, JX146962, JX146578, JX146485, JX146394, JX146303, JX146209, JX146114, JX146691.

084 Nevada holmgrenii (Rollins) N. H. Holmgren, U. S. A.: Nevada: Nye County: Near crest of the Toiyabe Range at head of Last Chance Creek ca. 1.02 km NW of the summit (10,895) of South Toiyabe Peak, 10,050 ft., *M. D. Windham* 2186, 8 Jun 2000 (NMC), JX146741, JX146835, JX146930, JX146546, JX146454, JX146363, JX146272, JX146177, JX146082, JX146652.

085 Phoenicaulis cheiranthoides Nutt. in Torr. & A. Gray, U. S. A.: Nevada: Humboldt County: On ridge just SW of Hinkley Summit in the Santa Rosa Range ca. 3.32 km E of the summit (9732) of Granite Peak, 7,900 ft., *M. D. Windham* 99-22, 13 Jun 1999 (NMC), JX146742, JX146836, JX146931, JX146547, JX146455, JX146364, JX146273, JX146178, JX146083, A1: JX146653, A2: JX146654, A3: JX146655, A4: JX146656, A5: JX146657, A6: JX146658, A7: JX146659, A9: JX146660.

089 Phoenicaulis cheiranthoides, U. S. A.: Nevada: Storey County: N of Virginia City near NV 341 on ridge above Long Valley ca. 1.57 km E of the summit (7,438) of Orleans Hill, 6,475 ft., *M. D. Windham* 3108, 29 May 2004 (NMC), JX146745, JX146839, JX146934, JX146550, JX146458, JX146367, JX146275, JX146181, JX146086, JX146663.

087 Polycytenium fremontii (S. Watson)

Greene, U. S. A.: Idaho: Gooding County: NW of Shoshone along tributary of Thorn Creek ca. 5.27 km NE of the summit (5,567) of Flat Top Butte, 5,535 ft., *M. D. Windham* 2055, 9 May 2000 (NMC), JX146744, JX146838, JX146933, JX146549, JX146457, JX146366, no sequence, JX146180, JX146085, JX146662.

247 Polycytenium fremontii, DNA sample provided by E. Schranz, JX146775, JX146869, JX146964, JX146580, JX146487, JX146396, no sequence, JX146211, JX146116, JX146693.

248 Sandbergia whitedii (Piper) Greene, DNA sample provided by E. Schranz, JX146776, JX146870, JX146965, JX146581, JX146488, JX146397, JX146305, JX146212, JX146117, JX146694.

249 Transberingia bursifolia (DC.) Al-Shehbaz & O’Kane, DNA sample provided by E. Schranz, JX146777, JX146871, JX146966, JX146582, JX146489, JX146398, JX146306, JX146213, JX146118, JX146695.

Boechera. **354a Boechera arcuata** (Nutt.) Windham & Al-Shehbaz, U. S. A.: California: Santa Barbara Co.: Santa Ynez Mountains, Los Padres National Forest, East Camino Cielo 0.5 road miles W of Romero Saddle, 2.2 miles ENE of Montecito Peak, 6.7 miles NE of Antioch University in Santa Barbara [near the type locality of *Arabis arcuata* Nutt.], 3,250 ft., *P. J. Alexander* 1001A, 10 Apr 2009 (NMC), JX146801, JX146895, JX146990, JX146606, JX146513, JX146422, JX146329, JX146237, JX146142, JX146713.

350a Boechera breweri (S. Watson) Al-Shehbaz subsp. *breweri*, U. S. A.: California: Contra Costa Co.: Mount Diablo State Park, on North Peak 0.2 miles west of the summit, 8.8 miles east of central Walnut Creek [type locality of *Arabis breweri* S. Watson], 3,320 ft., *P. J. Alexander* 969A, 30 Mar 2009 (DUKE), JX146797, JX146891, JX146986, JX146602, JX146509, JX146418, JX146326, JX146233, JX146138, JX146710.

352a Boechera breweri (S. Watson) Al-Shehbaz subsp. *shastaensis* Windham & Al-Shehbaz, U. S. A.: California: Shasta Co.: Shasta National Forest, north of Lake Shasta, 2.6 miles E of Nosoni Mountain on the west side of North Fork Squaw Creek along F. R. 35N18A, 2.5 road miles from the (unmarked) junction with F. R. 35N18 (at 40.9319°N, 122.1452°W), which is 5.2 road miles from the junction with F. R. 27 (at 40.9120°N, 122.1763°W) [type locality of *B. breweri* subsp. *shastaensis*], 2,700 ft., *P. J. Alexander* 993A, 7 Apr 2009 (NMC), JX146799, JX146893, JX146988, JX146604, JX146511, JX146420, JX146328, JX146235, JX146140, no sequence.

009a Boechera collinsii (Fernald) A. Löve & D. Löve, U. S. A.: Idaho: Elmore Co.: ESE of Idaho City along Middle Fork of the Boise River ca. 1.05 km E of its confluence with Browns Creek, 4,000 ft., *M. D. Windham* 2375, 30 Apr 2001 (NMC), JX146726, JX146820, JX146915, JX146531, no sequence, JX146348, JX146257, JX146162, JX146067, JX146626.

359a Boechera collinsii, U. S. A.: Idaho: Boise Co.: E of Boise on slope above Deer Creek along road on N side of Boise River ca. 0.6 road miles NW of Arrowrock Dam, 3,150 ft., *M. D. Windham* 3638A, 25 Apr 2009 (NMC), JX146806, JX146900, JX146995, JX146611, JX146518, no sequence, JX146334, JX146242, JX146147, JX146715.

120 Boechera cobrensis (M. E. Jones) Dorn, U. S. A.: Nevada: Elko Co.: SW of Montello in Goshute Valley on low hill near Cobre Siding ca. 3.46 km SSW of Cobre Well, 5,935 ft., *M. D. Windham* 3094, 27 May 2004 (NMC), JX146751, JX146845, JX146940, JX146556, JX146464, JX146373, JX146281, JX146187, JX146092, JX146673.

353a Boechera constancei (Rollins) Al-Shehbaz, U. S. A.: California: Plumas Co.: Central Sierra Nevada, Plumas National Forest, N side of F. R. 24N20 above East Branch Rock Creek, 1.0 road miles from the junction with 24N28, 1.1 miles NE of Deanes Valley Campground, 4.3 miles WSW of central Quincy, 4,270 ft., *P. J. Alexander* 997A, 8 Apr 2009 (NMC), JX146800, JX146894, JX146989, JX146605, JX146512, JX146421, no sequence, JX146236, JX146141, JX146712.

003a Boechera crandallii (B. L. Rob.) W. A. Weber, U. S. A.: Colorado: Gunnison Co.: ESE of Gunnison at mouth of Cabin Creek along IS 50 ca. 1.6 rd mi WNW of the junction w/CO 114, 7,850 ft., *M. D. Windham* 2102, 17 May 2000 (NMC), JX146722, JX146816, JX146911, JX146527, JX146436, JX146344, JX146253, JX146158, JX146063, JX146622.

B103 Boechera cusickii (S. Watson) Al-Shehbaz, U. S. A.: Oregon: Wasco Co.: WSW of Shaniko near Shaniko Summit along U. S. Route 97 ca. 7.0 road miles NE of its junction with U. S. Route 197, 11,400 ft., *M. D. Windham* 3662, 26 Apr 2009 (DUKE), JX146749, JX146843, JX146938, JX146554, JX146462, JX146371, JX146279, JX146185, JX146090, A1: JX146667, A2: JX146668, A9: JX146669, AC1: JX146670, AC2: JX146671.

086 Boechera davidsonii (Greene) N. H. Holmgren, U. S. A.: Nevada: Humboldt Co.: Along road SSW of Hinkley Summit in the Santa Rosa Range ca. 3.13 km ESE of the summit (9732) of Granite Peak, 7,450 ft., *M. D. Windham* 99-223, 13 Jun 1999 (NMC), JX146743, JX146837, JX146932, JX146548, JX146456, JX146365, JX146274, JX146179, JX146084, JX146661.

355a Boechera dispar (M. E. Jones) Al-Shehbaz, U. S. A.: California: San Bernardino Co.: San Bernardino Mountains, San Bernardino National Forest, Cushenbury Canyon, east side of California Hwy. 18 at the Cactus Flats turnout, 3.8 miles NE of California Hwy. 18 in central Big Bear City, 1.8 miles SE of Whiskey Springs [type locality of *Arabis juniperina* M. E. Jones, a synonym of *B. dispar*], 6,150 ft., *P. J. Alexander* 1004A, 12 Apr 2009 (NMC), JX146802, JX146896, JX146991, JX146607, JX146514, JX146423, JX146330, JX146238, JX146143, no sequence.

306a Boechera evadens

Windham & Al-Shehbaz, U. S. A.: California: Tulare Co.: East side of a small hill on the N side of Sherman Pass Rd., near the jct. with Woodpecker Tr. & Rattlesnake Tr., 1.4 miles W of the lookout on Bald Mountain, southern Sierra Nevada, Sequoia National Forest [type locality of *B. evadensis*], 8,300 ft., *P. J. Alexander* 836B, 4 Jul 2008 (NMC), JX146783, JX146877, JX146972, JX146588, JX146495, JX146404, JX146312, JX146219, JX146124, JX146700.

226b *Boecheera fendleri* (S. Watson) W. A. Weber, U. S. A.: New Mexico: Santa Fe Co.: Along New Mexico 475 at the boundary of Santa Fe National Forest, about 5 miles NE of Santa Fe, 7,800 ft., *P. J. Alexander* 225B, 16 Jun 2005 (NMC), JX146768, JX146862, JX146957, JX146573, JX146480, JX146390, JX146298, JX146204, JX146109, JX146686.

229a *Boecheera fendleri*, U. S. A.: New Mexico: Taos Co.: On the W side of New Mexico 522 near Garrapata Creek, Carson National Forest, about 15 miles N of Taos, 7,440 ft., *P. J. Alexander* 229A, 17 Jun 2005 (NMC), JX146769, JX146863, JX146958, JX146574, JX146481, JX146391, JX146299, JX146205, JX146110, JX146687.

007a *Boecheera fernaldiana* (Rollins) W. A. Weber subsp. *fernalidiana*, U. S. A.: Nevada: Nye Co.: Near crest of the Toiyabe Range at head of Last Chance Creek ca. 1.02 km NW of the summit (10895) of South Toiyabe Peak, 10,000 ft., *M. D. Windham* 2185, 8 Jun 2000 (NMC), JX146725, JX146819, JX146914, JX146530, JX146439, JX146347, JX146256, JX146161, JX146066, JX146625.

028 *Boecheera fernaldiana* (Rollins) W. A. Weber subsp. *vivariensis* (S. L. Welsh) Windham & Al-Shehbaz, U. S. A.: Utah: Uintah Co.: ESE of Vernal along tributary of Cliff Creek on Blue Mountain ca. 2.50 km NNE of Davis Spring, 7,650 ft., *M. D. Windham* 2744, 3 Jun 2003 (NMC), JX146737, JX146831, JX146926, JX146542, JX146450, JX146359, JX146268, JX146173, JX146078, JX146648.

041 *Boecheera formosa* (Greene) Windham & Al-Shehbaz, U. S. A.: Utah: Uintah Co.: N of Vernal on hill above Steinaker Reservoir near Utah 44 ca. 4.4 road miles N of its junction with U.S. 40., 5,550 ft., *M. D. Windham* 2733, 2 Jun 2003 (UT), JX146738, JX146832, JX146927, JX146543, JX146451, JX146360, JX146269, JX146174, JX146079, JX146649.

349c *Boecheera glaucovalvula* (M. E. Jones) Al-Shehbaz, U. S. A.: California: Inyo Co.: Death Valley National Park, western Darwin Mesa, southern Santa Rosa Hills, 2.5 miles NNE of the junction of Saline Valley Rd. & California Hwy. 190, 3.2 miles NW of the head of Rainbow Canyon [type locality of *Arabis glaucovalvula* M. E. Jones], 4,880 ft., *P. J. Alexander* 965A, 27 Mar 2009 (NMC), JX146796, JX146890, JX146985, JX146601, JX146508, JX146417, JX146325, JX146232, JX146137, no sequence.

174 *Boecheera gracilipes* (Greene) Dorn, U. S. A.: Utah: Washington Co.: Along Leeds Creek on SE slope of the Pine Valley Mts., ca. 2.68 km NW of Ash Grove Spring, 5,950 ft., *M. D. Windham* 2034, 5 May 2004 (UT), JX146763, JX146857, JX146952, JX146568, JX146475, JX146385, JX146293, JX146199, JX146104, JX146683.

347a *Boecheera gracilipes*, U. S. A.: Arizona: Coconino Co.: Just NE of downtown Flagstaff on ridge above Switzer Canyon ca. 1.07 km NE of the junction of U. S. 66 and U. S. 180 [type locality of *Arabis gracilipes* Greene], 7,000 ft., *M. D. Windham* 3593, 31 May 2008 (NMC), JX146795, JX146889, JX146984, JX146600, JX146507, JX146416, JX146324, JX146231, JX146136, JX146709.

312a *Boecheera howellii* (S. Watson) Windham & Al-Shehbaz, U. S. A.: Oregon: Jackson Co.: East side of Mount Ashland, 50 yards SE of the top of the ski lift, ± 0.25 miles E of the summit, ± 4.5 miles W of Ogden Hill, ± 8.5 miles S of Ashland, Siskiyou Mountains, Rogue River National Forest [type locality of *Arabis howellii* S. Watson], 7,100 ft., *P. J. Alexander* 875A, 25 Jul 2008 (NMC), JX146787, JX146881, JX146976, JX146952, JX146499, JX146408, JX146316, JX146223, JX146128, JX146703.

126b *Boecheera johnstonii* (Munz) Al-Shehbaz, U. S. A.: California: Riverside Co.: SE of Lake Hemet in canyon above Kenworthy Station ca. 2.82 km WSW of the summit (6,868) of Lion Peak, 5,265 ft., *M. D. Windham* 2954, 31 Mar 2004 (NMC), JX146753, JX146847, JX146942, JX146558, JX146466, JX146375, JX146283, JX146189, JX146094, no sequence.

351a *Boecheera koehleri* (Howell) Al-Shehbaz, U. S. A.: Oregon: Josephine Co.: Siskiyou National Forest, NE side of the Illinois River above the Snailback Beach Trail, 0.8 miles NW of the confluence with Deer Creek, 4.1 miles W of Selma, 2.3 miles NW of the summit of Eight Dollar Mountain [near the type locality of *Arabis arbuscula* Greene, a synonym of *B. koehleri*], 1,200 ft., *P. J. Alexander* 985A, 3 Apr 2009 (DUKE), JX146798, JX146892, JX146987, JX146603, JX146510, JX146419, JX146327, JX146234, JX146139, JX146711.

010a *Boecheera lasiocarpa* (Rollins) Dorn, U. S. A.: Utah: Cache Co.: South end of Cache Valley on NE slope of James Peak ca. 5.89 km SSE of the summit (7,078) of Middle Mountain, 9,200 ft., *M. D. Windham* 2195a, 12 Jun 2000 (NMC), JX146727, JX146821, JX146916, JX146532, JX146440, JX146349, JX146258, JX146163, JX146068, no sequence.

313a *Boecheera lemmonii* (S. Watson) W. A. Weber, U. S. A.: Oregon: Douglas Co.: West side of the summit of Mount Thielsen, ± 150 meters miles WSW of the top of the spire, ± 15.5 miles WSW of Chemult, ± 12.5 miles N of the N shore of Crater Lake, southern Cascade Mountains, Umpqua National Forest, 8,850 ft., *P. J. Alexander* 879a, 26 Jul 2008 (NMC), JX146788, JX146882, JX146977, JX146593, JX146500, JX146409, JX146317, JX146224, JX146129, no sequence.

213 *Boecheera lignifera* (A. Nelson) W. A. Weber, U. S. A.: New Mexico: McKinley

Co.: NE of Navajo on slope overlooking Tohdildionih Wash ca. 2.28 km NNW of the summit (8574) of Zilditloi Mtn, 7,175 ft., *M. D. Windham* 3370, 7 May 2005 (NMC), JX146767, JX146861, JX146956, JX146572, JX146479, JX146389, JX146297, JX146203, JX146108, JX146685.

142 *Boecheera lincolnensis* Windham & Al-Shehbaz, U. S. A.: Nevada: Nye Co.: S of Lund on W slope of Egan Range near road to radio tower ca. 2.63 km ESE of Dee Gee Spring, 6,215 ft., *M. D. Windham* 3022, 2 May 2004 (NMC), JX146755, JX146849, JX146944, JX146560, JX146468, JX146377, JX146285, JX146191, JX146096, JX146676.

B242 *Boecheera lyallii* (S. Watson) Dorn, U. S. A.: California: Tulare Co.: West slope of the southern Sierra Nevada, south of Mineral King on the north side of Farewell Gap, ± 150 yards NW of the highest point on the Farewell Gap Trail, 1.6 miles ESE of White Chief Lake, Sequoia National Park, 10,540 ft., *P. J. Alexander* 1107, 9 Jul 2009 (DUKE), JX146770, JX146864, JX146959, JX146575, JX146482, JX146392, JX146300, JX146206, JX146111, JX146688.

314a *Boecheera lyallii*, U. S. A.: Washington: Skamania Co.: North side of Mount Adams on the Killen Creek Trail below the Pacific Crest Trail, ± 4.5 miles NNW of the summit, ± 30 miles SE of Randle, Cascade Mountains, 5,900 ft., *P. J. Alexander* 881A, 3 Aug 2008 (NMC), JX146789, JX146883, JX146978, JX146594, JX146501, JX146410, JX146318, JX146225, JX146130, JX146704.

013a *Boecheera nevadensis* (Tidestr.) Windham & Al-Shehbaz, U. S. A.: Nevada: Clark Co.: NW of Las Vegas along North Loop Trail in the Spring Mountains ca. 1.76 km WSW of Mummy Spring, 3,175 m, *M. D. Windham* 2159, 1 Jun 2000 (NMC), JX146728, JX146822, JX146917, JX146533, JX146441, JX146350, JX146259, JX146164, JX146069, JX146627.

004 *Boecheera oxylobula* (Greene) W. A. Weber, U. S. A.: Colorado: Park Co.: Just SE of Fairplay along U.S. 285 near South Platte River bridge ca. 4.37 km SW of the summit (10341) of Red Hill, 9,870 ft., *M. D. Windham* 2092, 16 May 2000 (NMC), JX146723, JX146817, JX146912, JX146528, JX146437, JX146345, JX146254, JX146159, JX146064, JX146623.

005 *Boecheera oxylobula*, U. S. A.: Colorado: Hinsdale Co.: WSW of Lake City near mouth of Alpine Gulch ca. 0.32 km ESE of Treasure Falls, 8,975 ft., *M. D. Windham* 2098, 17 May 2000 (NMC), JX146724, JX146818, JX146913, JX146529, JX146438, JX146346, JX146255, JX146160, JX146065, JX146624.

069 *Boecheera pallidifolia* (Rollins) W. A. Weber, U. S. A.: Utah: Duchesne Co.: W shore of Starvation Reservoir near Rabbit Gulch Campground ca. 0.93 km NNW of the U.S. 40 bridge (E end), 5,775 ft., *M. D. Windham* 3000A, 28 Apr 2004 (NMC), JX146739, JX146833, JX146928, JX146544, JX146452, JX146361, JX146270, JX146175, JX146080, JX146650.

331a *Boecheera pallidifolia*, U. S. A.: New Mexico: Taos Co.: East Chiflo Trail, Wild Rivers Recreation Area, about halfway up the east side of Rio Grande Canyon, ± 6.8 miles N of the confluence of the Rio Grande and Red River, ± 1.4 miles ESE of the highest point on Cerro Chiflo, ± 5.5 miles NW of Questa, 7,270 ft., *P. J. Alexander* 757A, 20 May 2008 (NMC), JX146791, JX146885, JX146980, JX146596, JX146503, JX146412, JX146320, JX146227, JX146132, JX146706.

B335 *Boecheera pallidifolia*, U. S. A.: Utah: San Juan Co.: South of Beef Basin near head of South Canyon at Moki Spring ca. 2.34 km N of Wild Cow Spring [type locality of *Arabis thompsonii* S. L. Welsh, a synonym of *B. pallidifolia*], 7,200 ft., *M. D. Windham* 3080, 17 May 2004 (UT), JX146792, JX146886, JX146981, JX146597, JX146504, JX146413, JX146321, JX146228, JX146133, JX146707.

335a *Boecheera parishii* (S. Watson) Al-Shehbaz, U. S. A.: California: San Bernardino Co.: ENE of Big Bear City on ridge overlooking Baldwin Lake, ca. 5.24 km WSW of Granite Spring [type locality of *Arabis parishii* S. Watson], 6,480 ft., *M. D. Windham* 3426, 26 Apr 2006 (NMC), JX146793, JX146887, JX146982, JX146598, JX146505, JX146414, JX146322, JX146229, JX146134, no sequence.

015 *Boecheera pendulina* (Greene) W. A. Weber, U. S. A.: Wyoming: Fremont Co.: WSW of South Pass City near Pine Creek ca. 1.37 km NNW of the State Route 28 bridge, 8,025 ft., *M. D. Windham* 99-145, 5 Jun 1999 (NMC), JX146729, JX146823, JX146918, JX146534, JX146442, JX146351, JX146260, JX146165, JX146070, JX146628.

168 *Boecheera pendulina*, U. S. A.: Arizona: Coconino Co.: Along tributary of Trail Canyon on the Kaibab Plateau near U. S. 89A ca. 4.5 road miles ENE of Jacob Lake, 7,300 ft., *M. D. Windham* 2349, 24 Apr 2001 (UT), JX146761, JX146855, JX146950, JX146566, JX146473, JX146383, JX146291, JX146197, JX146102, JX146681.

118a *Boecheera pendulocarpa* (A. Nelson) Windham & Al-Shehbaz, U. S. A.: Nevada: White Pine Co.: E of Ely near Success Summit in the Schell Creek Range ca. 3.65 km WSW of the summit (3,335) of Cleve Creek Baldy, 2,780 m, *M. D. Windham* 3023, 3 May 2004 (NMC), JX146750, JX146844, JX146939, JX146555, JX146463, JX146372, JX146280, JX146186, JX146091, JX146672.

342a *Boecheera pendulocarpa*, U. S. A.: Wyoming: Fremont Co.: WSW of South Pass City along Pine Creek ca. 1.70 km NW of the State Route 28 bridge, 8,025 ft., *M. D. Windham* 99-142, 5 Jun 1999 (NMC), JX146794, JX146888, JX146983, JX146599, JX146506, JX146415, JX146323, JX146230, JX146135, JX146708.

016 *Boecheera perennans* (S. Watson) W. A. Weber, U. S. A.: Utah: Washington Co.: Along tributary of Bulldog Canyon in the Beaver Dam Mts. ca. 8.75 km SW of the summit (6,529) of Jarvis Peak, 3,725 ft., *M. D. Windham* 2038, 6 May 2000 (NMC), JX146730, JX146824, JX146919, JX146535, JX146443, JX146352, JX146261,

JX146166, JX146071, JX146629. **133** *Boechera peremans*, U. S. A.: California: San Bernardino Co.: NNW of Yucca Valley in Water Canyon along Pioneerstown Rd. ca. 1.5 road miles NNW of its junction with California 62, 3,600 ft., *M. D. Windham* 2955, 1 Apr 2004 (NMC), JX146754, JX146848, JX146943, JX146559, JX146467, JX146376, JX146284, JX146190, JX146095, JX146675. **017a** *Boechera platysperma* (A. Gray) Al-Shehbaz, U. S. A.: California: Inyo Co.: ESE of Mt. Whitney below Mirror Lake in Lone Pine Canyon ca. 0.70 km SE of the summit (3,751) of Thor Peak, 3,200 m, *M. D. Windham* 2570, 15 Jun 2002 (NMC), JX146731, JX146825, JX146920, JX146536, JX146444, JX146353, JX146262, JX146167, JX146072, A1: JX146630, A2: JX146631, A4: JX146632, A5: JX146633, A7: JX146634, AC1: JX146635. **360a** *Boechera polyantha* (Greene) Windham & Al-Shehbaz, U. S. A.: Washington: Chelan Co.: WNW of Chasmere on E side of Peshastin Pinnacles ca. 50 meters N of Orchard Road, 1,200 ft., *M. D. Windham* 3668A, 30 Apr 2009 (NMC), JX146807, JX146901, JX146996, JX146612, no sequence, JX146426, JX146335, JX146243, JX146148, JX146716. **361a** *Boechera polyantha*, U. S. A.: Washington: Okanogan Co.: NNW of Omak on bluff above Robinson Flat along Duck Lake Road ca. 0.25 road miles NW of its junction with Ross Canyon Road, 1,150 ft., *M. D. Windham* 3672a-A, 1 May 2009 (NMC), JX146808, JX146902, JX146997, JX146613, no sequence, JX146427, JX146336, JX146244, JX146149, no sequence. **018a** *Boechera puberula* (Nutt.) Dorn, U. S. A.: Nevada: Nye Co.: E of Ione Summit along road to Austin in the Shoshone Range ca. 2.58 km SE of Bradley Spring, 7,200 ft., *M. D. Windham* 99-115, 26 May 1999 (NMC), JX146732, JX146826, JX146921, JX146537, JX146445, JX146354, JX146263, JX146168, JX146073, JX146636. **167** *Boechera puberula*, U. S. A.: Nevada: Elko Co.: SE side of Salmon Falls Creek along U.S. Route 93 ca. 18.5 road miles S of the Idaho border at Jackpot, 5,475 ft., *M. D. Windham* 99-101, 25 May 1999 (UT), JX146760, JX146854, JX146949, JX146565, no sequence, JX146382, JX146290, JX146196, JX146101, JX146680. **144** *Boechera pulchra* (M. E. Jones ex S. Watson) W. A. Weber, U. S. A.: California: San Bernardino Co.: SE of Lucerne near Cactus Flat in the San Bernardino Mts. ca. 1.13 km WNW of Top Spring, 6,035 ft., *M. D. Windham* 2959, 1 Apr 2004 (NMC), JX146756, JX146850, JX146945, JX146561, JX146469, JX146378, JX146286, JX146192, JX146097, JX146677. **401b** *Boechera pygmaea* (Rollins) Al-Shehbaz, U. S. A.: California: Inyo Co.: East slope of the southern Sierra Nevada, NE side of Horseshoe Meadows, 2.8 miles E of Cottonwood Pass, 1.2 miles N of Mulkey Pass, Inyo National Forest, 9,900 ft., *P. J. Alexander* 1060B, 2 Jul 2009 (DUKE), JX146812, JX146907, JX147002, JX146618, JX146523, JX146432, JX146340, JX146249, JX146154, no sequence. **270** *Boechera rectissima* (Greene) Al-Shehbaz, U. S. A.: California: Plumas Co.: Between U. S. Hwy. 89 and Lake Almanor, 14.5 km SE of Plumas County line, 4.5 km NW of junction to Almanor, 1,285 m, *R. W. Spellenberg* 13752, 23 Jun 2006 (NMC), JX146778, JX146872, JX146967, JX146583, JX146490, JX146399, JX146307, JX146214, JX146119, no sequence. **356a** *Boechera rectissima*, U. S. A.: California: Fresno Co.: West slope of the southern Sierra Nevada, on the east side of Dinkey Creek 0.6 miles S of the junction of Dinkey Creek Rd. & McKinley Grove Rd., 1.7 miles NNE of Dinkey Mountain, 9.7 miles ESE of the town of Shaver Lake, Sierra National Forest [type locality of *Arabis rectissima* Greene], 5,730 ft., *P. J. Alexander* 1026A, 22 May 2009 (NMC), JX146803, JX146897, JX146992, JX146608, JX146515, JX146424, JX146331, JX146239, JX146144, no sequence. **170** *Boechera retrofracta* (Graham) A. Löve & D. Löve, U. S. A.: Nevada: Lincoln Co.: NE of Atlanta in the Limestone Hills near Wells Summit ca. 8.79 miles NE of the summit (7805) of Atlanta Peak, 6,450 ft., *M. D. Windham* 3015, 2 May 2004 (NMC), JX146762, JX146856, JX146951, JX146567, JX146474, JX146384, JX146292, JX146198, JX146103, JX146682. **311a** *Boechera rollei* (Rollins) Al-Shehbaz, U. S. A.: California: Siskiyou Co.: Below the Pacific Crest Trail on the W side of Lilypad Lake, ± 0.55 miles S of Red Butte, ± 5.5 miles N of Seiad Valley, Siskiyou Mountains, Rogue River National Forest [type locality of *Arabis rollei* Rollins], 5,800 ft., *P. J. Alexander* 871A, 24 Jul 2008 (NMC), JX146786, JX146880, JX146975, JX146591, JX146498, JX146407, JX146315, JX146222, JX146127, JX146702. **147** *Boechera schistacea* (Rollins) Dorn, U. S. A.: Nevada: Nye Co.: WNW of Ophir Summit on ridge above Crane Canyon in the Toiyabe Range ca. 3.84 km NNW of the summit (10,895) of South Toiyabe Peak, 9,800 ft., *M. D. Windham* 3104, 28 May 2004 (NMC), JX146757, JX146851, JX146946, JX146562, JX146470, JX146379, JX146287, JX146193, JX146098, no sequence. **187** *Boechera serpenticola* Windham & Al-Shehbaz, U. S. A.: California: Shasta Co.: North Coast Ranges, near the summit of Bully Choop Mountain, 6,800 ft., *D. W. Taylor* 13690, 16 Jun 1993 (JEPS), JX146765, JX146859, JX146954, JX146570, JX146477, JX146387, JX146295, JX146201, JX146106, no sequence. **358a** *Boechera serpenticola*, U. S. A.: California: Trinity Co.: Klamath Ranges, N side of the North Yolla Bolly Mountains on Rattlesnake Ridge at the junction of F. R. 29N58 and F. R. 29, 15.4 miles SSW of Hayfork, Trinity National Forest, 4,420 ft., *P. J. Alexander* 1052A, 28 May 2009 (NMC), JX146805, JX146899, JX146994, JX146610, JX146517, no

sequence, JX146333, JX146241, JX146146, no sequence. **022a** *Boechera shockleyi* (Munz) Dorn, U. S. A.: Utah: Millard Co.: NE of Black Rock inhills E of Cricket Mountains ca. 9.46 km ESE of the summit (6126) of Red Pass, 5,460 ft., *M. D. Windham* 99-014, 21 Apr 1999 (NMC), JX146733, JX146827, JX146922, JX146538, JX146446, JX146355, JX146264, JX146169, JX146074, JX146637. **002a** *Boechera sparsiflora* (Nutt.) Dorn, U. S. A.: Idaho: Elmore Co.: ESE of Idaho City along Middle Fork of the Boise River ca. 1.05 km E of its confluence with Browns Creek, 4,000 ft., *M. D. Windham* 2374, 30 Apr 2001 (NMC), JX146721, JX146815, JX146910, JX146526, JX146435, JX146343, JX146252, JX146157, JX146062, JX146621. **023a** *Boechera sparsiflora*, U. S. A.: Nevada: Lander Co.: SW side of Dean Canyon in the Shoshone Range ca. 3.12 km N of the summit (9601) of Mt. Lewis, 6,600 ft., *M. D. Windham* 99-105, 26 May 1999 (NMC), JX146734, JX146828, JX146923, JX146539, JX146447, JX146356, JX146265, JX146170, JX146075, A1: JX146638, A2: JX146640, A3: JX146641, A4: JX146642, A5: JX146643, A8: JX146644, A9: JX146645, A11: JX146639. **124a** *Boechera spatifolia* (Rydb.) Windham & Al-Shehbaz, U. S. A.: Colorado: Costilla Co.: WSW of San Luis on slope overlooking Culebra Creek along CO 159 ca. 1.6 road miles WSW of the junction with CO 142, Sangre de Cristo Grant, 7,935 ft., *M. D. Windham* 3057, 14 May 2004 (NMC), JX146752, JX146846, JX146941, JX146557, JX146465, JX146374, JX146282, JX146188, JX146093, JX146674. **322a** *Boechera spatifolia*, U. S. A.: Colorado: Larimer Co.: Southwestern side of Knapp's Knob, E side of Crosier Mountain Trail, ± 6.4 miles NNE of the jct. of U. S. Hwy. 34 & U. S. Hwy. 36 in Estes Park, ± 0.4 miles SE of Glen Haven, Roosevelt National Forest [near type locality of *Arabis spatifolia* Rydb.], 7,700 ft., *P. J. Alexander* 824-1A, 20 Jun 2008 (NMC), JX146790, JX146884, JX146979, JX146595, JX146502, JX146411, JX146319, JX146226, JX146131, JX146705. **025a** *Boechera stricta* (Graham) Al-Shehbaz, U. S. A.: Utah: Piute Co.: NE of Kingston along Pole Creek on the Sevier Plateau ca. 4.58 km NNE of the summit (9,793) on Malmsten Peak, 8,075 ft., *M. D. Windham* 2128, 28 May 2000 (NMC), JX146735, JX146829, JX146924, JX146540, JX146448, JX146357, JX146266, JX146171, JX146076, JX146646. **400a** *Boechera stricta*, U. S. A.: Colorado: Rio Blanco Co.: Along West Branch Cow Creek ± 0.3 miles from its confluence with the main Cow Creek, ± 4.5 miles SW of Rio Blanco, ± 0.5 miles N of the Garfield County line, 7,300 ft., *P. J. Alexander* 811A, 16 Jun 2008 (NMC), JX146811, JX146906, JX147001, JX146617, JX146522, JX146431, JX146339, JX146248, JX146153, no sequence. **148** *Boechera subpinnatifida* (S. Watson) Al-Shehbaz, U. S. A.: Nevada: Humboldt Co.: NNE of Winnemucca near Hinky Summit in the Santa Rosa Range ca. 1.12 km S of the summit (8,017) of Chocolate Peak, 7,875 ft., *M. D. Windham* 3127, 31 May 2004 (NMC), JX146758, JX146852, JX146947, JX146563, JX146471, JX146380, JX146288, JX146194, JX146099, JX146678. **027** *Boechera suffrutescens* (S. Watson) Al-Shehbaz, U. S. A.: California: El Dorado Co.: ENE of Kyburz below Cup Lake near head of Tamarack Creek ca. 1.17 km SSE of the summit (9235) of Ralston Peak, 8,400 ft., *M. D. Windham* 2579, 18 Jun 2002 (NMC), JX146736, JX146830, JX146925, JX146541, JX146449, JX146358, JX146267, JX146172, JX146077, JX146647. **150d** *Boechera texana* Windham & Al-Shehbaz, U. S. A.: Texas: Jeff Davis Co.: Davis Mts. State Park, across the canyon from the lodge, 5,100 ft., *P. J. Alexander* 174D, 23 Apr 2005 (NMC), JX146759, JX146853, JX146948, JX146564, JX146472, JX146381, JX146289, JX146195, JX146100, JX146679. **310a** *Boechera tiehmii* (Rollins) Al-Shehbaz, U. S. A.: Nevada: Washoe Co.: W side of Church Peak, ± 0.8 miles NNW of the highest point on Mt. Rose, ± 1.6 miles NNE of Mt. Houghton, Carson Range ± 14 miles SW of central Reno, Toiyabe National Forest [type locality of *Arabis tiehmii* Rollins], 10,500 ft., *P. J. Alexander* 862A, 21 Jul 2008 (NMC), JX146785, JX146879, JX146974, JX146590, JX146497, JX146406, JX146314, JX146221, JX146126, no sequence. **180** *Boechera villosa* Windham & Al-Shehbaz, U. S. A.: New Mexico: Taos Co.: Bottom, Rio Grande Canyon, 2 mi N of confluence with Red River [holotype of *B. villosa*], 6,800 ft., *W. L. Baker* 1113, 17 May 1979 (NMC), JX146764, JX146858, JX146953, JX146569, JX146476, JX146386, JX146294, JX146200, JX146105, no sequence. **367a** *Boechera williamsii* (Rollins) Dorn, U. S. A.: Wyoming: Fremont Co.: NE of Farson on slope overlooking West Willow Creek along State Route 28 ca. 42.1 road miles NE of its junction with U. S. Route 191, 8,125 ft., *M. D. Windham* 3803B, 31 May 2009 (NMC), JX146809, JX146903, JX146998, JX146614, JX146519, JX146428, JX146337, JX146245, JX146150, JX146717. **192** *Boechera yorkii* S. Boyd, U. S. A.: California: Inyo Co.: Las Chance Range, on the N side of a canyon 440m S of Last Chance Mt. [isotype of *B. yorkii*], 7,910 ft., *D. York* 2611, 16 May 2001 (MO), JX146766, JX146860, JX146955, JX146571, JX146478, JX146388, JX146296, JX146202, JX146107, JX146684.

Borodinia. **288** *Borodinia canadensis* (L.) P. J. Alexander & Windham, U. S. A.: Oklahoma: McCurtain Co.: Broken Bow Lake; 18 miles N of Broken Bow; ca. 8.8 miles E of U. S. 259 from Mt. Herman One Stop; just outside the Holly Creek Campground, 730 ft., *R. McElderry* 544, 25 Apr 2005 (UARK), JX146781, JX146875, JX146970, JX146586, JX146493, JX146402, JX146310, JX146217, JX146122, JX146698. **298** *Borodinia*

canadensis, U. S. A.: Arkansas: Polk Co.: Ouachita Mountains, Ouachita National Forest, 12 miles SE of Mena, ca. 3.5 miles S of Arkansas 8 on CR 61, W 1.5 miles of 48320, E 1.2 miles on 48330, 1,185 ft., *R. McElderry* 1097, 31 May 2005 (UARK), JX146782, JX146876, JX146971, JX146587, JX146494, JX146403, JX146311, JX146218, JX146123, JX146699. **403** *Borodinia dentata* (Raf.) P. J. Alexander & Windham, U. S. A.: Illinois: Fayette Co.: Kankakee River Watershed, Wilmington Shrub Prairie Nature Preserve; 3 miles east of Braidwood (junction of Route 53 & 113) along Route 113, 1.5 mile north on Zlm Road, then 0.5 mile west, 560 ft., *M.J.C. Murphy* 2515, 2 May 2007 (ILLS), JX146813, JX146908, JX147003, JX146619, JX146524, JX146433, JX146341, JX146250, JX146155, JX146719. **404** *Borodinia dentata*, U. S. A.: Illinois: Will Co.: IDOT U.S. Route 51 Project Area; bluffs of the Kaskaskia River, 500 ft., *L. R. Phillippe* 39455, 24 Apr 2008 (ILLS), JX146814, JX146909, JX147004, JX146620, JX146525, JX146434, JX146342, JX146251, JX146156, JX146720. **095** *Borodinia laevigata* (Muhl. ex Willd.) P. J. Alexander & Windham, U. S. A.: Missouri: Christian Co.: Along the banks of Swan Creek where state route 125 crosses the creek, *M. Beilstein* 2001-06, 21 May 2001 (MO) [DNA sample provided by M. Beilstein], JX146747, JX146841, JX146936, JX146552, JX146460, JX146369, JX146277, JX146183, JX146088, JX146665. **284** *Borodinia laevigata*, U. S. A.: Arkansas: Montgomery Co.: Ouachita National Forest, Shirley Creek Float Camp on the N bank of the Ouachita River, ± 2.8 miles W of Oden, ± 22.5 miles E of the junction of U. S. Hwy 71 & Arkansas Hwy 8 on the E side of Mena, 770 ft., *P. J. Alexander* 722, 26 Mar 2008 (NMC), JX146780, JX146874, JX146969, JX146585, JX146492, JX146401, JX146309, JX146216, JX146121, JX146697. **369** *Borodinia macrophylla* (Turcz.) O. E. Schulz, Russia: Khabarovsk Territory: Ayno-Maik, confluence of the Borea and Odola Rivers with Omnya River, *V. Y. Barkalov s. n.*, 25 Jul 1989 (MO), no sequence, JX146904, JX146999, JX146615, JX146520, JX146429, JX146338,

JX146246, JX146151, no sequence. **245** *Borodinia missouriensis* (Greene) P. J. Alexander & Windham, DNA sample provided by E. Schranz, JX146774, JX146868, JX146963, JX146579, JX146486, JX146395, JX146304, JX146210, JX146115, JX146692. **283a** *Borodinia missouriensis*, U. S. A.: Arkansas: Montgomery Co.: Ouachita National Forest, Shirley Creek Float Camp on the N bank of the Ouachita River, ± 2.8 miles W of Oden, ± 22.5 miles E of the junction of U. S. Hwy 71 & Arkansas Hwy 8 on the E side of Mena, 770 ft., *P. J. Alexander* 721, 26 Mar 2008 (NMC), JX146779, JX146873, JX146968, JX146584, JX146491, JX146400, JX146308, JX146215, JX146120, JX146696. **094** *Borodinia serotina* (Steele) P. J. Alexander & Windham, U. S. A.: Virginia: Bath Co.: Base of steep, open shale barren at Ratcliff Hill, 0.8 miles east of Fort Lewis, *C. Keener* 3710, 14 Aug 1982 (GH), JX146746, JX146840, JX146935, JX146551, JX146459, JX146368, JX146276, JX146182, JX146087, JX146664.

Yosemitea. **308b** *Yosemitea repanda* (S. Watson) P. J. Alexander & Windham, U. S. A.: California: Inyo Co.: East shore of Lake Sabrina along the Lake Sabrina Trail, ± 0.2 miles south of the dam, ± 3.3 miles SE of the summit of Mt. Emerson, east slope of the Sierra Nevada, Inyo National Forest [type locality of *Arabis inamoena* Greene, a synonym of *B. repanda*], 9,200 ft., *P. J. Alexander* 845B, 6 Jul 2008 (NMC), JX146784, JX146878, JX146973, JX146589, JX146496, JX146405, JX146313, JX146220, JX146125, JX146701. **357a** *Yosemitea repanda*, U. S. A.: California: Mariposa Co.: West slope of the central Sierra Nevada, south side of Yosemite Valley, lower part of the former Ledge Trail 0.2 miles N of Glacier Point, 0.3 miles SSW of the restaurants & swimming pool at Curry Village, Yosemite National Park [type locality of *Arabis repanda* S. Watson], 4,800 ft., *P. J. Alexander* 1031A, 24 May 2009 (NMC), JX146804, JX146898, JX146993, JX146609, JX146516, JX146425, JX146332, JX146240, JX146145, JX146714.