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Source: Systematic Botany, 40(2):572-596.
Published By: The American Society of Plant Taxonomists
URL: http://www.bioone.org/doi/full/10.1600/036364415X688745

Systematic Botany (2015), 40(2): pp. 572–596

DOI 10.1600/036364415X688745
Date of publication August 10, 2015

Weaving a Tangled Web: Divergent and Reticulate Speciation in *Boechera fendleri* sensu lato (Brassicaceae: Boechereae)

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Communicating Editor: Mark P. Simmons

Abstract—Hybrid speciation is relatively common in plants compared to other well-studied groups. Polyploidy and apomixis are strongly associated with hybrid speciation, presumably due to the opportunities they provide for both reestablishing reproductive function in hybrids with incomplete chromosomal homology and creating rapid reproductive isolation in sympatry. *Boechera*, a species-rich genus closely related to *Arabidopsis*, is a particularly fertile ground for the study of hybrid speciation. Thirty-eight apomictic triploid hybrid species are currently recognized in *Boechera*. Recent research has shown that apomictic diploid hybrids, although very rare in angiosperms, are common in *Boechera*. Given this complexity, focused studies of individual species complexes are critical to understanding speciation and diagnosing biodiversity in *Boechera*. Here we analyze DNA sequences from seven nuclear loci and multilocus genotypes from 15 microsatellite markers in a group of closely related taxa formerly included in *B. fendleri*. Our results support the recognition of four species previously segregated from *B. fendleri* s. l., including three genetically distinct, sexual diploids (*B. fendleri*, *B. spatifolia*, and *B. texana*) and one apomictic triploid hybrid (*B. porphyrea*). We also identify four novel apomictic diploid hybrid species (***B. carrizozoensis***, ***B. centrifendleri***, ***B. sanluisensis***, and ***B. zephyra***) and additional apomictic triploid hybrids. Our results reveal a complex network of relationships. Sexual diploid species can hybridize to form apomictic diploids, and members of these two groups can hybridize to form trigenomic, apomictic triploids.

Keywords—Apomixis, hybrid speciation, low-copy nuclear loci, microsatellite markers, molecular systematics.

Speciation involves both divergent and reticulate processes (Rieseberg and Willis 2007). In divergent speciation, diversifying selection toward multiple fitness peaks, along with genetic drift in geographically isolated populations, eventually produces genetically distinct and reproductively isolated descendant species. In reticulate speciation, hybridization among divergent taxa yields new species that are typically reproductively isolated via polyploidy and/or asexuality, rather than as a result of divergent adaptation. Although such hybrid speciation occurs throughout the tree of life, it is especially prevalent in plants (Hegarty and Hiscock 2005; Mallet 2007; Soltis and Soltis 2009).

Boechera Á. Löve & D. Löve, a genus closely related to *Arabidopsis* (DC.) Heynh., includes ca. 70 sexual diploid species (Al-Shehbaz and Windham 2010) that have arisen through divergent speciation within the last four million years (Beilstein et al. 2010). It also includes an unprecedented array of apomictic hybrids, which have made it a focal point for studies of hybridization, apomixis, and polyploidy (reviewed in Schranz et al. 2005; Dobeš et al. 2006; Rushworth et al. 2011). Unlike most groups showing extensive hybridization, *Boechera* has very few sexually reproducing polyploids. Recent taxonomic revisions (Windham and Al-Shehbaz 2006, 2007a, 2007b; Al-Shehbaz and Windham 2010) divide the genus into two major classes of species: sexual diploids resulting from divergent speciation (ca. 65% of named taxa) and apomictic triploids with reticulate evolutionary histories (35%). Extensive cytological and palynological studies of the genus (Beck et al. 2012; Windham et al. unpublished data) have established that these groups can be readily distinguished based on pollen morphology. The sexual diploids produce narrowly ellipsoid pollen grains, 13–16 μm wide, with three symmetrical colpi; the apomictic triploids exhibit spheroid grains, 22–30 μm wide, with asymmetrical colpi (Windham and Al-Shehbaz 2006). In triploid apomicts, the first division of meiosis is suppressed, resulting in the production of triploid microspores and megaspores via a single mitotic division (Roy 1995; Naumova et al. 2001; Windham and Al-Shehbaz 2006).

Despite their overall rarity in plants, apomictic diploid lineages that produce unreduced (2*x*) microspores and megaspores are also known in *Boechera* (Böcher 1951, 1969; Roy 1995; Naumova et al. 2001; Schranz et al. 2005). These have been reported primarily in the polytypic species *Boechera holboellii* (Hornem.) Á. Löve & D. Löve and in hybrids between the *holboellii* complex and *Boechera stricta* (Graham) Al-Shehbaz (generally included within *Boechera divaricarpa* (A. Nelson) Á. Löve & D. Löve s. l.). However, recent genus-wide microsatellite analyses of diploid *Boechera*, combined with additional chromosome counts and palynological observations, suggest that apomictic diploids are much more common throughout the genus than previously thought (Beck et al. 2012; Lovell et al. 2013). These apomictic diploids represent a third class of *Boechera* species, producing a mixture of: malformed, shrunken grains without cellular contents; well-formed, narrowly ellipsoid, symmetrically colpate grains like those of sexual diploids; and spheroid, irregularly colpate grains similar to (though smaller than) those of the apomictic triploids (Beck et al. 2012).

Although the frequency and importance of these apomictic diploids was not realized until recently and most of them are not addressed in recent taxonomic revisions of the genus (Windham and Al-Shehbaz 2006, 2007a, 2007b; Al-Shehbaz and Windham 2010), apomictic diploids are a major component of *Boechera* diversity and, therefore, critical to our understanding of evolution in the genus. Further, preliminary analyses of microsatellite data for nearly 4,000 accessions suggest that, contrary to previous hypotheses

based on morphology (e.g. Mulligan 1996), autopolyploids are rare and the vast majority of apomictic triploids in *Boechera* contain two or, more often, three divergent genomes derived from hybridization between sexual and apomictic diploid species (Windham et al. unpublished data). The complexity of speciation in *Boechera*, with divergent, sexual diploid species giving rise to apomictic diploids, which then serve as intermediaries in the formation of apomictic triploid hybrids, has produced unprecedented taxonomic confusion. Rigorous analysis of each species complex is essential to assess biodiversity, determine the origin of specific apomictic lineages, and provide a coherent evolutionary context for ongoing research in *Boechera*.

One of the most contentious species complexes within *Boechera* is the "*fendleri* group," which includes eight sexual diploid species, collectively occupying an area extending from west Texas north through New Mexico and Colorado to southern Wyoming, and west into Arizona, Utah, southern Nevada, eastern California, and northern Baja California. Recent phylogenetic analyses based on sequence data from seven nuclear loci (Alexander et al. 2013) indicate that these eight species form a well-supported clade. *Boechera fendleri* s. l. includes three of these sexual diploids (*Boechera fendleri* s. s., *Boechera spatifolia*, and *Boechera texana*) that were included within *B. fendleri* by most previous authors (e.g. Rollins 1993), but recently have been recognized as distinct species based on strong correlations between morphological variation and geography (Windham and Al-Shehbaz 2006). Another three species, *Boechera pendulina* (Greene) W. A. Weber s. s., *Boechera nevadensis* (Tidestr.) Windham & Al-Shehbaz, and an undescribed taxon provisionally referred to here as *B.* 'wyomingensis', have been combined under *B. pendulina* by most authors. Two of the sexual diploids in the group (*Boechera gracilipes* (Greene) Dorn and *Boechera perennans* (S. Watson) W. A. Weber) have been treated as distinct species for well over a century. Among the apomictic triploid taxa recognized by Al-Shehbaz and Windham (2010), only *Boechera porphyrea* belongs to the *fendleri* group, where it has usually been included in *B. fendleri* s. l. (e.g. Rollins 1993). Morphological comparisons suggest that *B. porphyrea* may represent a hybrid between *B. perennans* and *B. texana* (Windham and Al-Shehbaz 2007a). Although *B. porphyrea* is the only named hybrid previously ascribed to the *fendleri* group, preliminary microsatellite analyses and morphological observations suggested the existence of several additional hybrid lineages within *B. fendleri* s. l. In the present study, we use microsatellite and DNA sequence data to: 1) evaluate whether or not the three sexual diploid segregates of *B. fendleri* s. l. are genetically distinct; 2) delineate species within a set of apomictic hybrid lineages, including *B. porphyrea*, derived from sexual diploid *B. fendleri* s. l. ; and 3) examine the origins of these hybrid lineages.

Materials and Methods

Sampling and DNA Isolation—Samples were chosen to span the geographic ranges of *B. fendleri* s. s. and the sexual diploid (*B. spatifolia* and *B. texana*) and apomictic triploid (*B. porphyrea*) segregates recognized by Al-Shehbaz and Windham (2010). Our sampling also includes several unnamed apomictic diploid and triploid lineages derived from *B. fendleri* that were identified in preliminary morphological and microsatellite analyses. To ensure that the sexual diploid parents of these hybrid lineages are included in our sampling, initial hypotheses of hybrid parentage were generated using a microsatellite dataset that presently includes ca. 4000 individuals and all known diploid *Boechera* species (Beck et al. 2012; Windham et al. unpublished data). Potential parents were identified by automated searches for combinations of parents whose genotypes can account for the highest numbers of alleles in hybrids. Extensive sampling of *B. gracilipes* and *B. perennans* is included, based on these initial hypotheses. Sampling of hybrid lineages associated with *B. fendleri* s. l. is not exhaustive, however. To paraphrase Muir (1911), when we try to pick out any *Boechera* species by itself, we find it hitched to everything else in the genus. Due to rampant hybridization in *Boechera*, the set of all hybrids derived from *B. fendleri* s. l. and their parents includes much of the genus and would require sampling beyond what is feasible in the scope of the present study. Individuals from the type localities of *B. fendleri*, *B. gracilipes*, *B. perennans*, and *B. porphyrea* are included, as are samples of *B. spatifolia* collected ca. six miles northeast of the type locality.

Samples were drawn from recent collections by the authors (at BRY, DUKE, MO, NMC, and UT; 292 samples) and from previously collected specimens (at ASC, ASU, ARIZ, COLO, CS, GH, LL/TEX, RM, RSA, SJNM, SRSC, UNM, and WS; 82 samples). A total of 374 samples are included in microsatellite analyses, representing 214 populations. Populations are arbitrarily defined as individuals of the same species collected within ca. one mile of each other. The geographic distribution of all samples is shown in Fig. 1, and voucher information is provided on Dryad (doi:10.5061/dryad.7h5g1). In the following discussion, individuals are designated by population number. In cases where the population is represented by more than one individual, the population number is followed by a hyphen, the collector's initials, and collection number (e.g. 172-RCR2069). Letters following the collection number identify different individuals from the same collection event (e.g. 5-PJA1144A and 5-PJA1144B). Each population is represented by one to seven individuals, with the exception of population 132. In this case, 39 individuals were genotyped but only 9 (representing all unique genotypes and all individuals represented by herbarium specimens) are included in microsatellite analyses. In addition to the samples used in microsatellite analyses, *B. nevadensis*, *B. pendulina*, *B. stricta, Boechera williamsii* (Rollins) Dorn, and *B.* 'wyomingensis' are included in phylogenetic analyses (voucher information available in Alexander et al. 2013, sample numbers 013A, 015, 025A, 168, 367A, and 400A).

Leaf material for DNA isolation was taken from a single individual per herbarium specimen (marked by an asterisk or letter on the sheet). During fieldwork, leaf samples from additional, unvouchered individuals were sometimes collected along with herbarium specimens. Two DNA isolation methods were used. The protocol of Alexander et al. (2007), modified by the addition of 10 mM Tris-HCl to the 70% EtOH used to wash contaminants from the silica columns at step 13, was applied to 167 samples. The remaining 207 samples were extracted using a CTAB protocol modified for 96-well plates (Beck et al. 2012).

Microsatellite Amplification and Genotyping—Fifteen previously developed microsatellite loci were genotyped: ICE3, ICE14 (Clauss et al. 2002), a1, a3, b6, c8, e9 (Dobeš et al. 2004), Bdru266, BF3, BF9, BF11, BF15, BF18, BF19, and BF20 (Song et al. 2006). Forward primers for each locus were labeled with 6-FAM or HEX, and sets of two or three loci were simultaneously amplified using multiplex PCR as described in Beck et al. (2012). Samples were analyzed on a 3730xl DNA Analyzer (Applied Biosystems, Foster City, California) with a 500 ROX size standard. Electropherograms were sized and alleles determined with GENEMARKER v.1.9 (SoftGenetics, State College, Pennsylvania). All samples were successfully genotyped at a minimum of 13 of the 15 microsatellite loci. Summary statistics for microsatellite variation were calculated in GENODIVE 2.0b23 (Meirmans 2013). Complete microsatellite data and specimen citations are available on Dryad (doi:10.5061/dryad.7h5g1).

Assessing Ploidy and Reproductive Mode from Microsatellite Data—Individuals were assigned to three classes prior to further analysis: sexual diploids, apomictic diploid hybrids, and apomictic triploid hybrids (henceforth S2X, A2X, and A3X, respectively). This assignment was based on numbers of alleles per microsatellite locus per individual. Two of the 15 microsatellite loci (a3 and BF19) occasionally yielded anomalously high numbers of alleles in voucher specimens of known ploidy (Windham et al. unpublished data), suggesting they are present in multiple copies. These two loci were excluded from use in assigning individuals to S2X, A2X, and A3X classes. Samples with more than two alleles at one or more loci were assigned to the A3X class, except for two anomalous individuals (see Results). In genus-wide sampling of *Boechera*, plants with a maximum of two alleles per locus show a bimodal pattern of heterozygosity, as measured by the average across loci of the number of alleles per locus per individual. The mean value for S2X plants

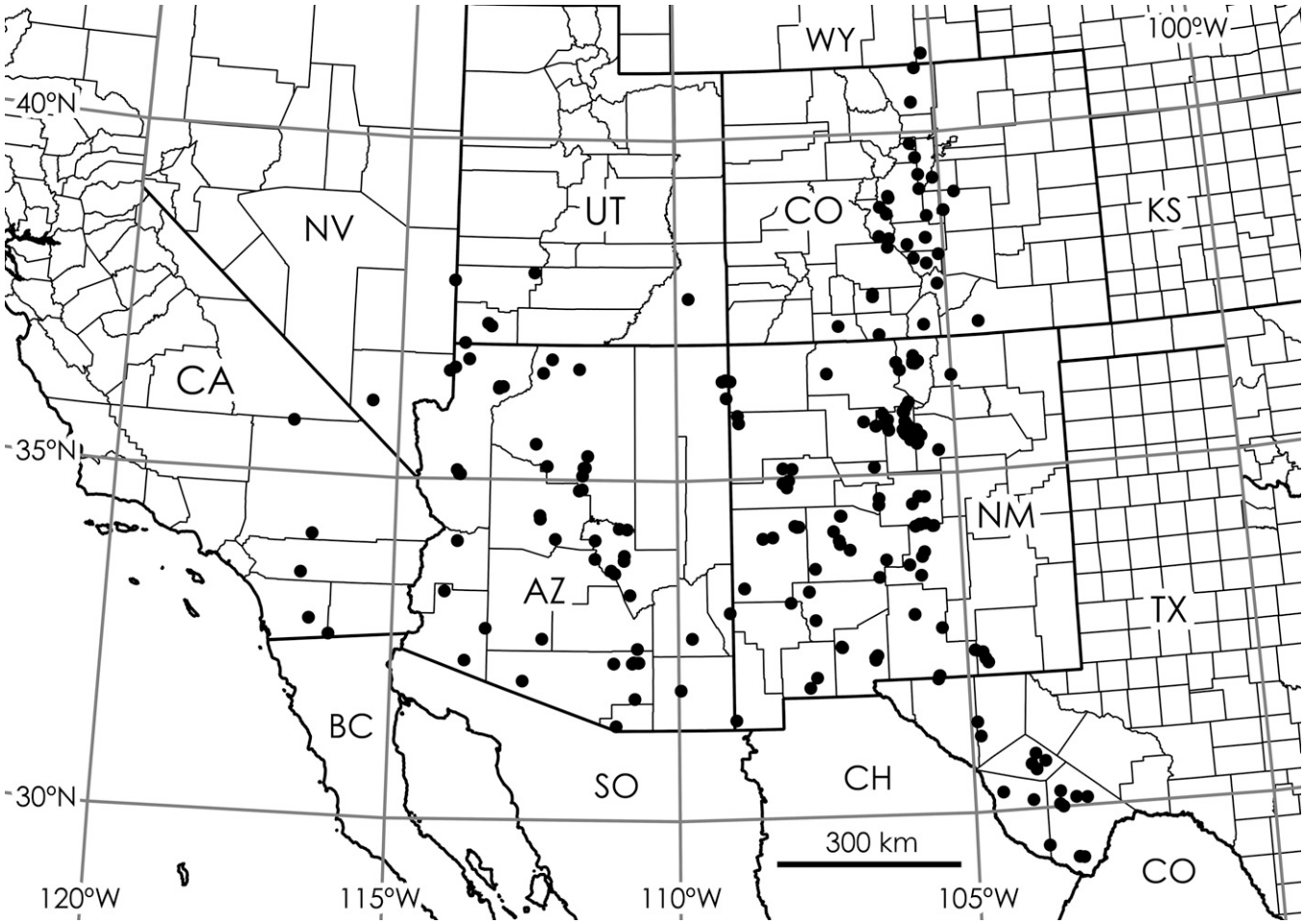

FIG. 1. Geographic distribution of all samples included in microsatellite analyses. This and all other maps were created in QGIS v.1.7.2 "Wroclaw" (Quantum GIS Development Team 2011).

approximates 1 (all loci homozygous), whereas the mean value for known A2X individuals is 1.75 (10 of 13 loci heterozygous; Beck et al. 2012). Although the distribution is bimodal, there are individuals spanning the range of intermediate values. With this in mind, all individuals with heterozygosity below 1.4 were assigned to the S2X class and all individuals with heterozygosity above 1.7 were assigned to the A2X class. Samples with intermediate heterozygosity were evaluated in preliminary analyses of the microsatellite data. Those placed within one of the S2X clusters were assigned to the S2X class and the remaining samples were assigned to the A2X class. After the number of species in the S2X and A2X classes and hybrid parentages in the A2X class were inferred as described below, separation of the two classes was reevaluated by examination of multi-dimensional scaling plots, with each plot including one A2X species and its inferred S2X progenitors. Correct class assignment was also assessed by checking pollen of flowering specimens available to the first author at NMC (total of 148) for consistency with the palynological categories found by Beck et al. (2012).

Assessing the Number of Species—Both non-parametric (AWCLUST: S2X, A2X, and A3X classes) and parametric (STRUCTURE: S2X only) approaches were used to analyze microsatellite data and assess the number of species within each class. Subsequent to these analyses, specimens were reevaluated to determine if the resulting clusters could be distinguished morphologically.

The program AWCLUST v.3.0 (Gao and Starmer 2008) provides a non-parametric approach to evaluating population structure based on allele-sharing distance, which does not include assumptions about reproduction and can be applied to both sexual and apomictic populations. AWCLUST estimates the number of clusters (K) in a set of data based on the gap statistic (Tibshirani et al. 2001). For gap-statistic analyses, 100 null simulations were run for values of K from one to 16. Individuals were assigned to clusters at the optimal K by AWCLUST's implementation of Ward's minimum variance hierarchical clustering. AWCLUST was also used to visualize microsatellite variation among individuals via multi-dimensional scaling (MDS) plots. These MDS plots provide a visual means of evaluating relative species cohesion and distinctness. Three matrices, each including all individuals from one of the three reproductive classes (S2X, A2X, and A3X), were analyzed in AWCLUST to infer the optimal K value and assign individuals to groups at the chosen value of K.

Commonly used parametric approaches, notably the widely used Bayesian approach implemented in the program STRUCTURE v.2.3.2 (Pritchard et al. 2000; Falush et al. 2003), involve assumptions that are problematic in apomictic lineages. STRUCTURE assumes that Hardy-Weinberg equilibrium (HWE) will exist in panmictic populations and deviations from HWE can therefore be attributed to partial or complete reproductive isolation between groups of individuals. In apomictic lineages, panmixia is excluded by default. Consequently, an expectation of HWE is unreasonable and the STRUCTURE model is inapplicable to delimiting species within the A2X and A3X classes. STRUCTURE was used to estimate the number of clusters (K) for S2X individuals only. STRUCTURE was run using the admixture model with default settings, 100,000 burn-in generations followed by 500,000 generations after burn-in, and four replicates for each value of K from one to nine. K was determined by the ΔK approach of Evanno et al. (2005) as implemented in the program STRUCTURE HARVESTER (Earl 2011).

Inferring Origins of Hybrids from Microsatellite Data—Two approaches were used to infer hybrid origins, a modification of the assignment test of Paetkau et al. (1995) and analyses in STRUCTURE using the USEPOPINFO setting.

The assignment test of Paetkau et al. (1995) is a commonly used method to assign an individual to one of several reference populations (k). For a genotype AA', the frequencies of A and A' in k are represented by f_{Ak} and $f_{A'k}$. For each locus, the probability of drawing genotype AA' from population k is $2f_{Ak}\ f_{A'k}$ and the probability of

drawing genotype AA is $(f_{Ak})^2$. The joint probability for a multilocus genotype is the product of the probabilities for each locus. This assignment test can be modified to pull alleles separately from two source populations (k and k'). The probability of drawing genotype AA' from source populations k and k' is then $f_{Ak} f_{A'k'} + f_{Ak'} f_{A'k}$; for AA it is $f_{Ak} f_{Ak'}$. Using this approach, diploid hybrid individuals are assigned to the pair of potential S2X parents from which there is the highest probability of pulling the individual's multilocus genotype. For triploid hybrids, three alleles are pulled from two source populations, one allele from a sexual diploid (k) and two alleles from a diploid hybrid (k''). In this case, the probability of drawing genotype $AA'A''$ is $f_{Ak} f_{A'k''} f_{A''k''} + f_{Ak''} f_{A'k''} f_{A''k} + f_{Ak''} f_{A'k} f_{A''k''}$, for AAA' it is $f_{Ak} f_{Ak''} f_{A'k''} + f_{Ak''} f_{Ak''} f_{A'k}$, and for AAA it is $(f_{Ak})(f_{Ak''})^2$. When two alleles are observed in our microsatellite data, we do not know which is present in two copies (i.e. whether the genotype is AAA' or $AA'A'$) and the probability of observing these two alleles thus includes each possibility: $(f_{Ak} f_{Ak''} f_{A'k''} + f_{Ak''} f_{Ak''} f_{A'k}) + (f_{Ak} f_{A'k''} f_{A'k''} + f_{Ak''} f_{A'k''} f_{A'k})$. Triploid hybrid individuals are then assigned to the pair of S2X and A2X parents from which there is the highest probability of pulling the individual's multilocus genotype. A difficulty with this approach arises when at least one allele in a hybrid individual is absent from all pairs of potential progenitors. This is the case for the majority of A2X and A3X individuals in our analyses and leads to probabilities of zero for all possible origins. Ideally a statistically rigorous method of estimating the probability of drawing a particular unsampled allele from a source species would be applied. However, none is available and instead a number of ad hoc methods have been used to circumvent this issue in traditional single-source assignment tests. In our analyses, we follow Guinand et al. (2002) by inserting a value of $0.1/2n$, where n is the number of individuals sampled from a potential source species, for all alleles not observed in a potential progenitor.

In STRUCTURE, the USEPOPINFO setting allows parameter estimation and population clustering based on a subset of the data while the remaining individuals are assigned, in whole or in admixture, to these clusters. Inappropriate HWE expectations for apomicts can be circumvented by estimating parameters and population structure based solely on S2X individuals, with admixture assignments of hybrids used to assess their parentage. Due to aberrant behavior of STRUCTURE analyses that include S2X, A2X, and A3X samples (results not shown), STRUCTURE analyses are used only to infer the ultimate S2X progenitors of A3X species and not to evaluate potential S2X × A2X pairings. For each putative hybrid taxon, a STRUCTURE analysis was conducted that included all individuals of the S2X species supplemented by all samples of the hybrid. Based on STRUCTURE's inferred value of $K = 5$ in S2X-only analyses, four runs at $K = 5$ were conducted, with 100,000 burn-in generations followed by 500,000 generations after burn-in, and hybrid admixtures in the run with the highest mean likelihood were examined.

Amplification and Sequencing for Phylogenetic Analyses—Phylogenetic analyses were used as a secondary means of inferring parentage for five of the seven hybrid lineages identified in analysis of the microsatellite data. Previously published data for seven nuclear-encoded loci (chalcone synthase, *Dpa1*, the ITS region, *luminidependens*, *Mps35*, *Nuo*, and *pistillata* intron 1) were used for sexual diploid samples (Alexander et al. 2013). These were supplemented with clone sequences generated for the locus *pistillata* (primers pi504a and pi1254r; Bailey and Doyle 1999; Bailey 2001). *Pistillata* was cloned for two individuals that are also included in the microsatellite sampling for each of the five hybrid lineages examined (GenBank accessions KM851232-KM851313). Amplification followed previously developed protocols (Alexander et al. 2013). The PCR products were cleaned using a 15-minute digestion at 37°C with five units exonuclease I and one unit shrimp alkaline phosphatase (both enzymes from Affymetrix, Santa Clara, California) per 25 µL PCR product. Cloning was conducted using Invitrogen (Carlsbad, California) TOPO TA cloning®. Clone sequences from an individual are designated by suffixes "P1", "P2", etc.; identical clones are analyzed as a single terminal.

Alignment and Matrices for Phylogenetic Analyses—Each locus was aligned using CLUSTALW 2.0.10 (Thompson et al. 1994) under default parameters. The resulting alignments were then checked and refined manually using SE-AL v.2.0a11 (Rambaut 2002) with the goal of minimizing the number of indel events (Zurawski and Clegg 1987). Gap characters were scored using the simple indel coding method of Simmons and Ochoterena (2000) as implemented in SeqState (Müller 2005). All matrices and trees are available on TreeBASE (S16561).

Six different matrices were analyzed. The first includes all seven loci for only the sexual diploid members of the *fendleri* group to evaluate relationships among these products of divergent speciation. Each of the remaining five matrices includes all seven loci for the sexual diploid samples, plus *pistillata* clone sequences for one of the five hybrid lineages in order to infer its parentage. We chose this approach because *pistillata*, despite being the most variable of the seven loci used, is not sufficiently informative on its own to resolve relationships among species in the *fendleri* group. By using seven loci for the divergently-related sexual diploid species, their relationships to each other are established using all available data. This reduces the burden on *pistillata* to provide all of the resolution and increases our ability to use it to group clone sequences from hybrids with those of their respective sexual diploid progenitors. This approach is intermediate between a single locus gene-tree analysis and a concatenated, multilocus analysis (a "species-tree" approach), and is therefore referred to as a "spene-tree" analysis (Govindarajulu et al. 2011).

Phylogenetic analyses were conducted using both parsimony (Fitch 1971) and maximum likelihood (Felsenstein 1973) approaches. All analyses were rooted on the branch connecting the *stricta/williamsii* clade to the *fendleri* group samples, based on genus-wide phylogenetic analyses indicating that these two species are closely related to the *fendleri* group (Alexander et al. 2013). Topologies were not constrained to enforce monophyly of any clades.

For parsimony analyses, heuristic searches were conducted using NONA (Goloboff 2000) spawned from WINCLADA v.1.0.08 (Nixon 1999–2002) 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 (Farris et al. 1996) resampling replicates with a removal probability of 0.36, using the "new technology search" in TNT v.VIII.2008 (Goloboff et al. 2008), with parsimony ratchet (Nixon 1999–2002), sectorial search, tree-drifting, and tree-fusing (Goloboff 1999) turned on and all other settings left their default values.

Maximum likelihood (ML) analyses were conducted with RAXML (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 replicates. Gap characters were removed, as it is not clear if these models of sequence evolution are applicable to gap characters. Model parameter values were estimated separately for each locus. The best tree was estimated and support values were generated from 1000 bootstrap replicates.

Results

Microsatellite Analyses—Summary statistics for the 15 microsatellite loci used in this study are provided for all specimens in Table 1 and for each of the inferred taxa in Table 2. Results of hybrid assignment tests and analyses in AWCLUST and

Table 1. For each microsatellite locus across all samples: number of alleles (A), effective number of alleles (A_e), observed heterozygosity (H_O), expected heterozygosity (H_E), inbreeding coefficient (F_{IS}), and one-sided p value for deviation of F_{IS} from HWE.

	A	A_e	H_O	H_E	F_{IS}	p value
ICE3	20	3.438	0.647	0.723	0.197	0.001
ICE14	5	1.210	0.339	0.177	–0.905	0.001
a1	5	1.284	0.250	0.226	0.206	0.004
a3	10	2.313	0.681	0.577	–0.268	0.001
b6	24	3.789	0.659	0.750	0.206	0.001
c8	24	2.320	0.636	0.580	0.007	0.240
e9	15	2.202	0.619	0.556	–0.001	0.719
Bdru266	36	4.881	0.610	0.811	0.339	0.001
BF3	31	4.827	0.699	0.808	0.225	0.001
BF9	26	2.051	0.534	0.522	0.093	0.001
BF11	3	1.392	0.495	0.288	–0.702	0.001
BF15	21	2.179	0.639	0.551	–0.094	0.028
BF18	6	1.299	0.282	0.235	0.114	0.038
BF19	20	2.581	0.545	0.633	0.131	0.001
BF20	23	2.982	0.680	0.678	0.116	0.001
Multi-locus	17.933	2.583	0.554	0.541	0.077	0.001

TABLE 2. For each inferred taxon across all microsatellite loci: average number of alleles per locus (A), average effective number of alleles per locus (A_e), observed heterozygosity (H_O), expected heterozygosity (H_E), inbreeding coefficient (F_{IS}), and one-sided p values for deviation of F_{IS} from HWE.

	A	A_e	H_O	H_E	F_{IS}	p value
			S2X			
B. fendleri	8.333	4.120	0.209	0.519	0.593	0.001
B. gracilipes	4.133	2.520	0.098	0.480	0.799	0.001
B. perennans	9.467	4.732	0.269	0.550	0.510	0.001
B. spatifolia	3.267	1.901	0.017	0.300	0.943	0.001
B. texana	5.467	3.145	0.197	0.441	0.560	0.001
Overall	16.000	2.550	0.158	0.458	0.611	0.001
			A2X			
B. carrizozoensis	5.000	3.344	0.710	0.553	–0.282	0.001
B. centrifendleri	6.200	3.232	0.800	0.607	–0.327	0.001
B. sanluisensis	5.400	2.625	0.759	0.541	–0.421	0.001
B. zephyra	3.533	2.625	0.763	0.528	–0.471	0.001
Overall	11.467	2.645	0.758	0.558	–0.369	0.001
			A3X			
B. 'CP'	7.267	4.832	0.994	0.764	–0.326	0.001
B. 'FST'	3.333	2.877	0.964	0.650	–0.510	0.001
B. porphyrea	3.333	2.670	0.873	0.563	–0.568	0.001
Overall	8.933	3.102	0.944	0.658	–0.493	0.001

STRUCTURE are described below as they relate to particular research questions.

Assessment of Ploidy and Reproductive Mode—Most samples were easily sorted into S2X, A2X, and A3X classes based on microsatellite data. Only minor overlap in heterozygosity (1.55–1.62) between S2X and A2X classes was found after evaluation of preliminary ordination plots. This categorization indicates that our total sampling includes 223 sexual diploids, 98 apomictic diploids, and 53 apomictic triploids. Only two of the 374 plants included in our analyses (187 and 214-PJA549a) do not conform to this classification scheme. Individual 187 is anomalous because it exhibits three alleles at two loci (indicative of triploidy) but is homozygous at nine (unexpected with hybridization). All other A3X plants in the analysis have at least six loci with three alleles and at most two homozygous loci. Individual 187 is morphologically assignable to *B. texana* and has just two unique alleles (both at locus Bdru266) relative to our sampling of S2X *B. texana*. Plant 187 is therefore included with *B. texana* in our other analyses. Individual 214-PJA549a has four alleles at seven loci and is apparently the lone tetraploid in our sampling. It is included with the A3X class in AWCLUST and STRUCTURE analyses, but is excluded from the hybrid assignment test due to the complicated array of potential origins for a tetraploid genotype.

Inferred Number of Species—Within the S2X class, both AWCLUST and STRUCTURE identify an optimal K of five. Based on morphology and placement of specimens at or near type localities, the resulting groups correspond with named species: *B. fendleri* (70 plants), *B. gracilipes* (28), *B. perennans* (58), *B. spatifolia* (39), and *B. texana* (28). An MDS plot (from AWCLUST) of plants in the S2X class is shown in Fig. 2A and their geographic distributions are shown in Figs. 3 and 4. Species clusters are well-separated on the first three axes, with the exception of individual 170, which is separated from the remaining *B. spatifolia* on axis 1, and intermediate between *B. spatifolia* and *B. perennans* on axis 3. This individual has no heterozygous loci and is strongly assigned to *B. spatifolia* in STRUCTURE analyses. STRUCTURE analyses indicate little introgression between species and most samples are assigned >95% to their respective species. Only 5 of 223 S2X samples (individuals 15 and 21, *B. fendleri*; 104, *B. gracilipes*; and 119 and 127, *B. perennans*) are found to have <85% assignment to a single species.

Within the A2X and A3X classes, AWCLUST gap-statistic analyses indicate an optimal K of four and three, respectively. Although one of the resulting clusters matches a previously recognized taxon (*B. porphyrea*), the remaining A2X and A3X clusters do not correspond with named species (see Discussion). Figures and subsequent discussion use novel names (see Taxonomic Account) or provisional designations for these putative species, as follows: in the A2X class: *Boechera carrizozoensis* (27 plants), *Boechera centrifendleri* (31), *Boechera sanluisensis* (21), and *Boechera zephyra* (19); in the A3X class: *Boechera* 'CP' (11) and *Boechera* 'FST' (11). The first three axes of MDS plots for the A2X and A3X classes are shown in Figs. 2B and 2C, and the geographic distributions of samples of each taxon are shown in Figs. 4 and 5. In the A2X class, putative species are well separated in MDS plots (except individual 205). In the A3X class, *B. porphyrea* is well separated from the remaining A3X samples. *Boechera* 'CP' and *B.* 'FST', however, are only separated from each other on axis 3, and *B.* 'CP' shows substantial genetic variation relative to the other two A3X clusters (Fig. 2C). These latter two putative taxa are also represented by comparatively few (11) plants and occur near each other in Santa Fe County, New Mexico. The lone tetraploid individual, 214-PJA549a (abbreviated 214a in Fig. 2C), is included within *B.* 'CP'.

Phylogenetic Analyses—Aligned lengths of the seven sequenced loci and the numbers of parsimony-informative characters they yield are listed in Table 3. A strict consensus tree resulting from parsimony analysis of the S2X samples is shown in Fig. 6A. Parsimony and ML analyses provide similar results, except that *B.* 'wyomingensis' and *B. nevadensis* form a clade in parsimony analyses, while *B.* 'wyomingensis' and *B. pendulina* are united in ML analyses. Both alternatives are poorly supported (<50% parsimony jackknife/ML bootstrap), and alternative resolution of these taxa is the primary source of conflict between phylogenetic methods in all analyses (with the exception of Fig. 6B). Figs. 6B, 6C, and 6D show results of spene-tree analyses for *B. carrizozoensis*, *B. sanluisensis*, and *B. zephyra*, respectively. Figure 7 shows results of spene-tree analyses for *B. porphyrea* (7A) and *B.* 'FST' (7B). *Pistillata* was not cloned from *B. centrifendleri* and *B.* 'CP'.

Parentage of Hybrids—Results of hybrid assignment tests are summarized in Suppl. Tables 1 and 2. Within each A2X species, hypotheses of parentage are consistent across samples with the exception of *B. carrizozoensis* and individual 205. Within the A3X class, only *B.* 'FST' shows consistent assignment of putative parentage across all samples. Results of STRUCTURE analyses assessing hybrid origins are shown in Fig. 8. With the exception of *B. carrizozoensis*, STRUCTURE yielded >85% assignment of each A2X sample to an admixture of two S2X species and >85% assignment of each A3X sample to an admixture of three S2X species. These are inferred to be the two proximate progenitors of A2X samples and the three ultimate progenitors of A3X samples. Phylogenetic analyses of A2X and A3X hybrids (Figs. 6 and 7) indicate that clone sequences from each of the sampled putative species represent two clades for A2X hybrids and three for A3X hybrids. Both STRUCTURE and

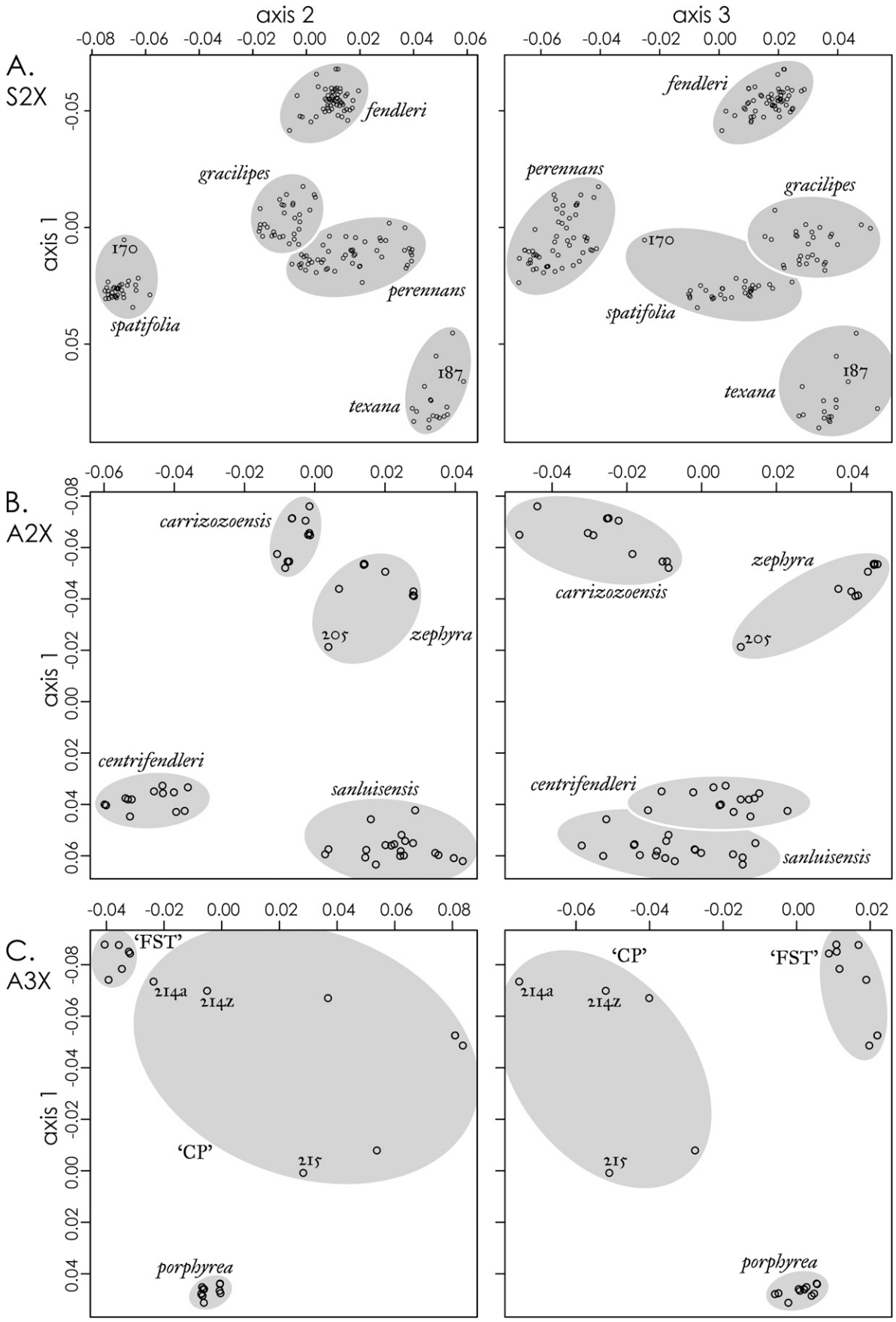

FIG. 2. First three axes of multi-dimensional scaling plots of microsatellite variation created in AWCLUST. Gray ellipses indicate groups identified by hierarchical clustering in AWCLUST at the inferred optimal value of *K*. A. Sexual diploid individuals, *K*=5. B. Apomictic diploid hybrid individuals, *K*=4. C. Apomictic triploid hybrid individuals, *K*=3. Additional axes (not shown) do not resolve additional clusters of individuals.

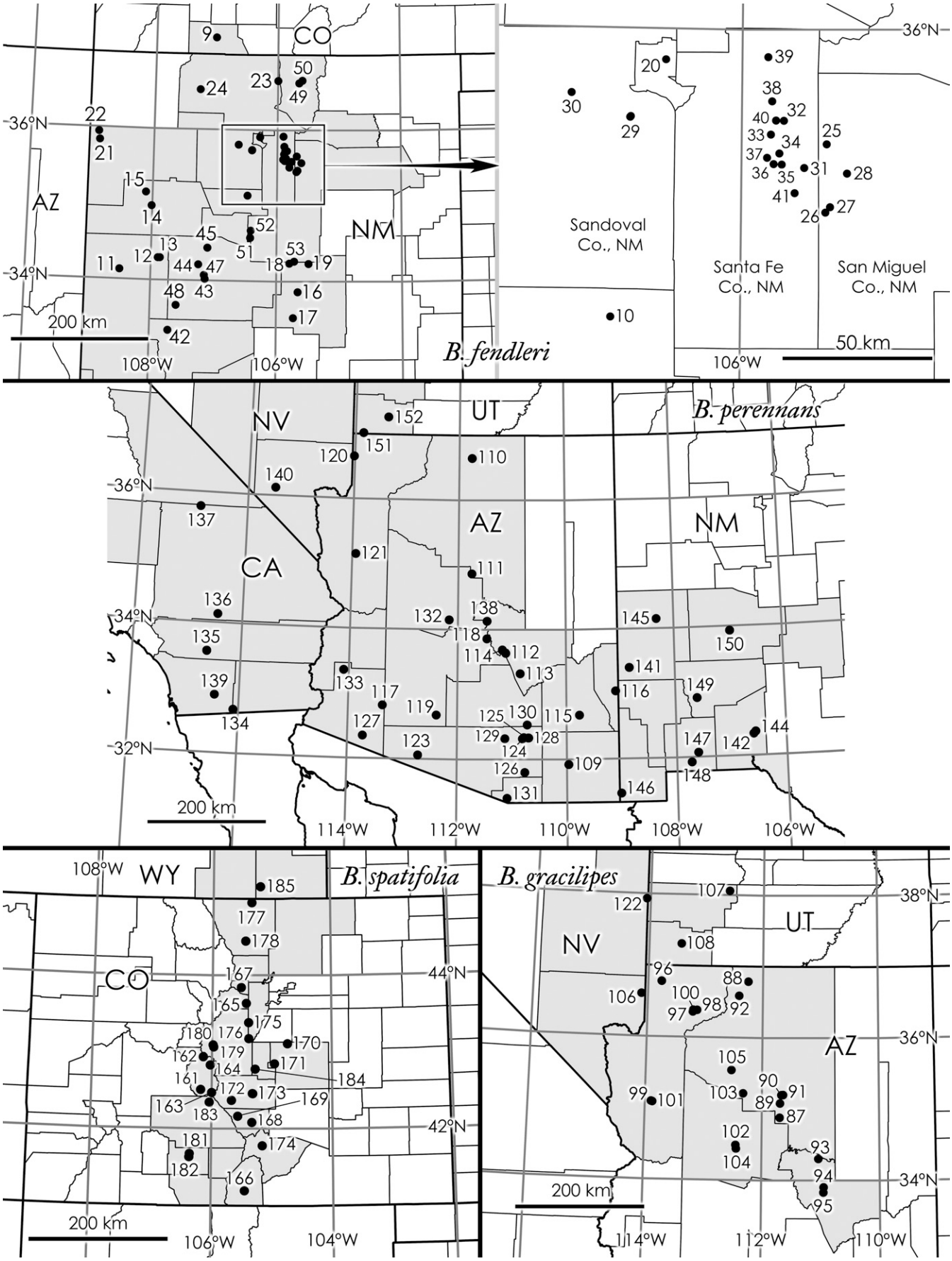

FIG. 3. Geographic distributions of sampled populations for *B. fendleri*, *B. gracilipes*, *B. perennans*, and *B. spatifolia*. The known county distribution of each taxon is shown in light gray.

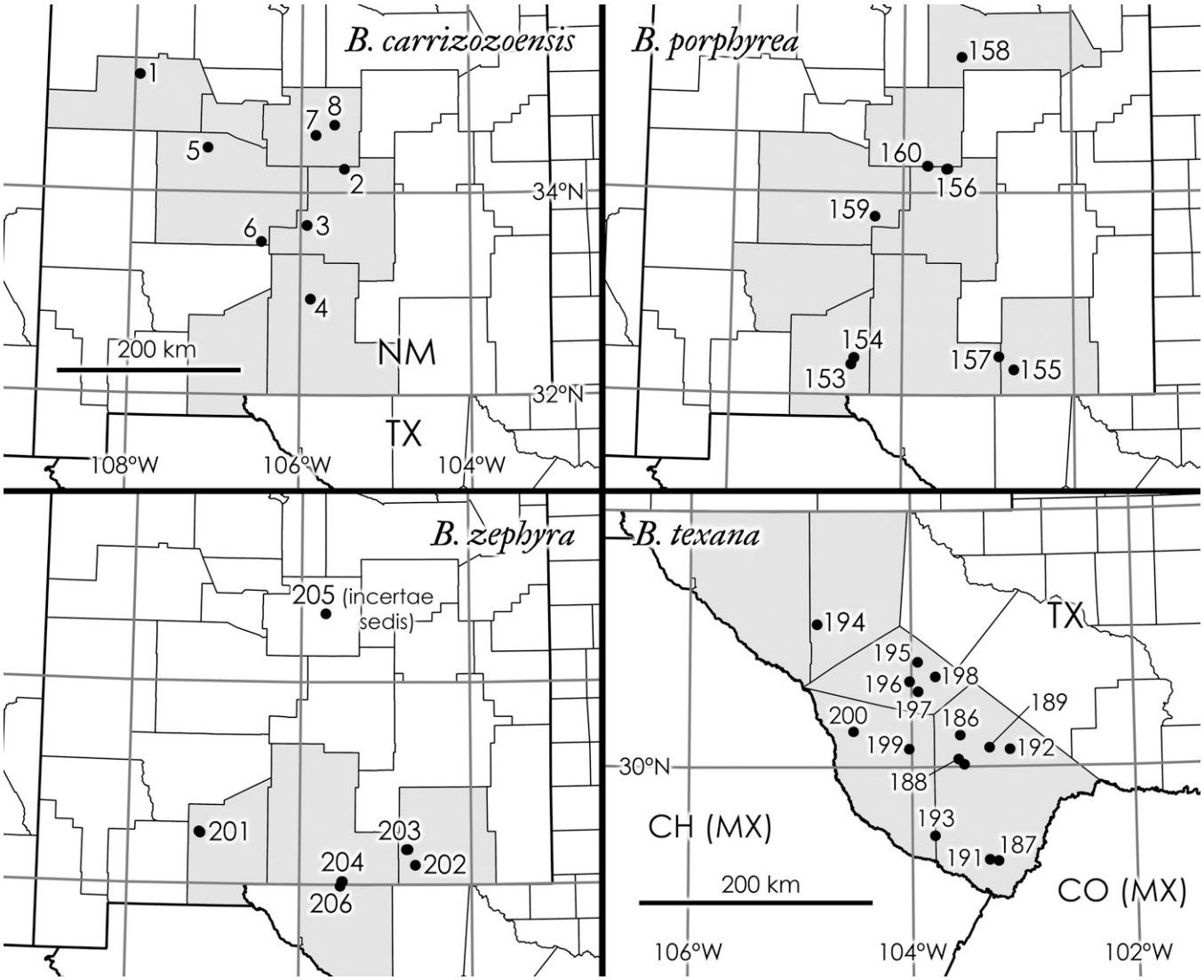

FIG. 4. Geographic distributions of sampled populations for *B. carrizozoensis*, *B. porphyrea*, *B. texana*, and *B. zephyra*. The known county distribution of each taxon is shown in light gray.

the phylogenetic results indicate that A2X hybrids contain two divergent genomes, while A3X hybrids contain three.

Within the A2X class, where the three methods (hybrid assignment, phylogenetic, and STRUCTURE) are directly comparable, they provide consistent results (with the exception of some uncertainty in *B. carrizozoensis*, described in more detail below). Within the A3X class, results of the three methods are not directly comparable. STRUCTURE and phylogenetic analyses both provide inferences of the ultimate S2X parents of hybrids, and results are consistent between the two analyses. Hybrid assignment tests provide the sole inference of proximate S2X × A2X origins.

Parentages of A2X Species—The separate analyses are strongly congruent regarding the hybrid origins and relative homogeneity of both *B. centrifendleri* and *B. sanluisensis*. The hybrid assignment test identifies an origin from *B. fendleri* × *gracilipes* for all 31 individuals of *B. centrifendleri*, and STRUCTURE indicates that it is an admixture of *B. fendleri* (48%) and *B. gracilipes* (38%; Fig. 8A). The hybrid assignment test identifies an origin from *B. fendleri* × *spatifolia* for all 21 individuals of *B. sanluisensis*, and STRUCTURE indicates it is an admixture of *B. fendleri* (49%) and *B. spatifolia* (45%; Fig. 8A). Although clone *pistillata* sequences from one individual of *B. sanluisensis* (81-PJA598F) were confined to the *B. fendleri* clade, those of a second accession (82-PJA739B) formed two groups: in a well-supported (85/73) clade with *B. spatifolia* and in a strongly supported (98/100) clade with *B. fendleri* (Fig. 6C).

The separate analyses also are congruent for *B. zephyra*. Eighteen of the 19 plants assigned to *B. zephyra* are identified as *B. perennans* × *texana* by the hybrid assignment test and as an admixture of *B. perennans* (42%) and *B. texana* (44%) by the STRUCTURE analysis (Fig. 8A). Clone *pistillata* sequences from two of these 18 individuals are placed in two groups: 1) a weakly supported (50/57) clade with *B. perennans* and 2) a strongly supported (86/94) clade with *B. texana* (Fig. 6D). Thus, both microsatellite and phylogenetic analyses suggest that nearly all of the plants assigned by AWCLUST to *B. zephyra* originated through hybridization between *B. perennans* and *B. texana*. The parents of the lone anomalous individual (205) are identified as *B. fendleri* and *B. texana* by both the hybrid assignment test and STRUCTURE.

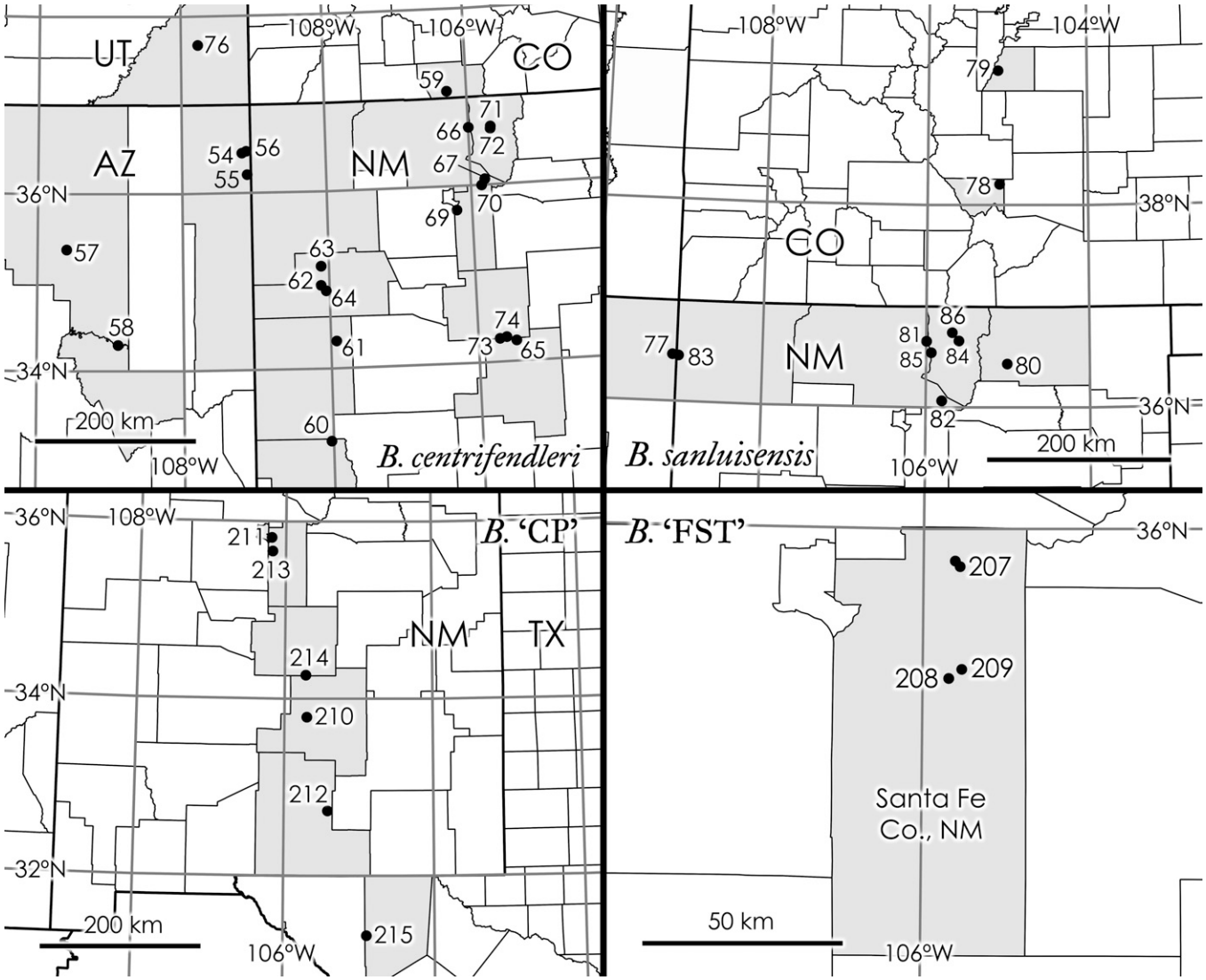

FIG. 5. Geographic distributions of sampled populations for *B. centrifendleri*, *B. sanluisensis*, *B.* 'FST', and *B.* 'CP'. The known county distribution of each taxon is shown in light gray.

The most problematic of the A2X hybrids is *B. carrizozoensis*. Results of the hybrid assignment test are variable, with samples assigned to either *B. fendleri* × *texana* (9 individuals) or *B. perennans* × *texana* (18 individuals). Although it is a confirmed diploid based on chromosome analyses (Windham et al. unpublished data), the STRUCTURE analysis identifies *B. carrizozoensis* as an admixture of three genomes: *B. texana* (51%), *B. perennans* (26%), and *B. fendleri* (19%; Fig. 8A). In the phylogenetic analysis (Fig. 6B), clones of *B. carrizozoensis* are found in two groups: 1) in a clade including *B. texana*; and 2) in a clade sister to *B. spatifolia*. The second group is well-supported as monophyletic (93/73), though its position as sister to *B. spatifolia* is poorly supported. These results all indicate that *B. texana* is one progenitor of *B. carrizozoensis*, but the second is uncertain.

TABLE 3. Aligned lengths and numbers of informative characters for low-copy nuclear loci used in phylogenetic analyses.

	Aligned length	Parsimony-informative characters	Parsimony-informative gap characters	Number of accessions
chs	1,089	10	2	15
Dpa1	759	10	1	15
ITS	676	7	2	15
luminidependens	615	5	1	15
Mps35	830	9	2	15
Nuo	704	9	0	15
pistillata	942	32	17	94
Combined	5,615	82	25	94

Parentages of A3X Species—STRUCTURE analysis indicates that the previously recognized triploid hybrid *B. porphyrea* is an admixture of *B. gracilipes* (25%), *B. perennans* (37%), and *B. texana* (23%; Fig. 8B). In the phylogenetic analysis (Fig. 7A), clones of *B. porphyrea* are found in three groups: 1) in a poorly supported (<50/<50) clade with *B. gracilipes*; 2) in a weakly supported (63/54) clade with *B. perennans*; and 3) in a well-supported (76/81) clade with *B. texana*. Both approaches suggest that the ultimate S2X progenitors of *B. porphyrea* are *B. gracilipes*, *B. perennans*, and *B. texana*. The hybrid assignment test is, however, unable to pinpoint a proximate origin for *B. porphyrea.* Half of the 30 plants

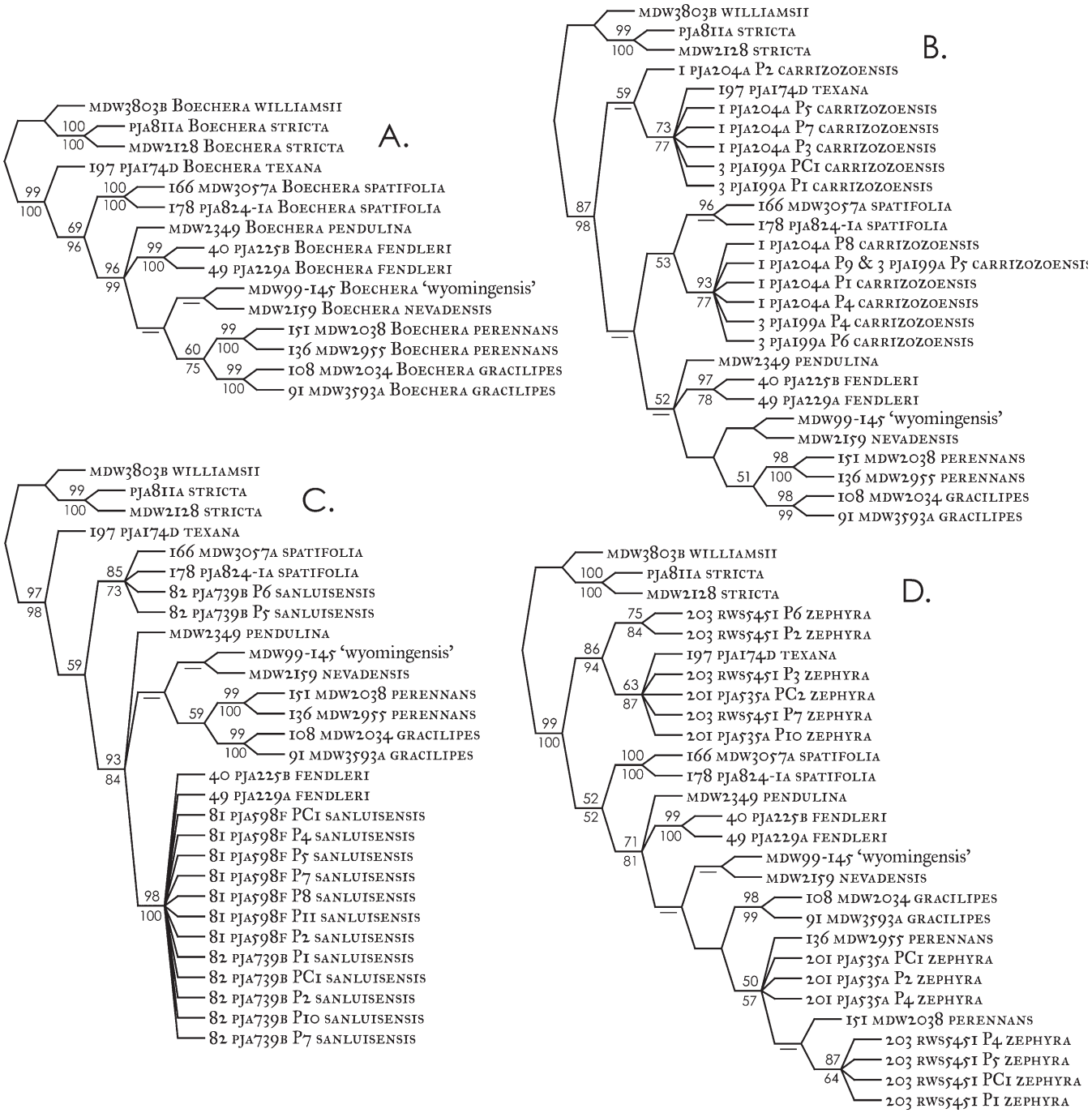

FIG. 6. Relationships among S2X species and spene-trees (see Materials and Methods) for A2X hybrids. Parsimony jackknife support is above branches, ML bootstrap support below branches. Values below 50 are not shown, and a "—" indicates a node not on the best ML tree. A. Sexual diploid species, strict consensus of two most parsimonious trees (length = 116, consistency index (CI) = 0.86, retention index (RI) = 0.94). B. *Boechera carrizozoensis* spene-tree, strict consensus of 12 most parsimonious trees (length = 131, CI = 0.74, RI = 0.84). C. *Boechera sanluisensis* spene-tree, strict consensus of eight most parsimonious trees (length = 124, CI = 0.78, RI = 0.92). D. *Boechera zephyra* spene-tree, strict consensus of six most parsimonious trees (length = 125, CI = 0.76, RI = 0.86).

analyzed are identified as possible hybrids between S2X *B. perennans* and A2X *B. carrizozoensis*. Eight others are assigned to *B. perennans* × *centrifendleri*, six to *B. texana* × *centrifendleri*, and one to *B. gracilipes* × *zephyra*. Only the latter is consistent with an ultimate origin from *B. gracilipes*, *B. perennans*, and *B. texana*.

With regard to the remaining apomictic polyploids, STRUCTURE analyses indicate that the plants assigned to *B.* 'FST' represent an admixture of *B. fendleri* (35%), *B. spatifolia* (29%), and *B. texana* (29%; Fig. 8B). Clone *pistillata* sequences from *B.* 'FST' (Fig. 7B) are placed in three groups: 1) in a poorly supported (<50/57) clade with *B. fendleri*; 2) in a poorly supported (<50/<50) clade with *B. spatifolia*; and 3) in a poorly supported (<50/<50) clade with *B. texana*. Analyses of both data sets indicate that the ultimate S2X progenitors of *B.* 'FST' are *B. fendleri*, *B. spatifolia*, and

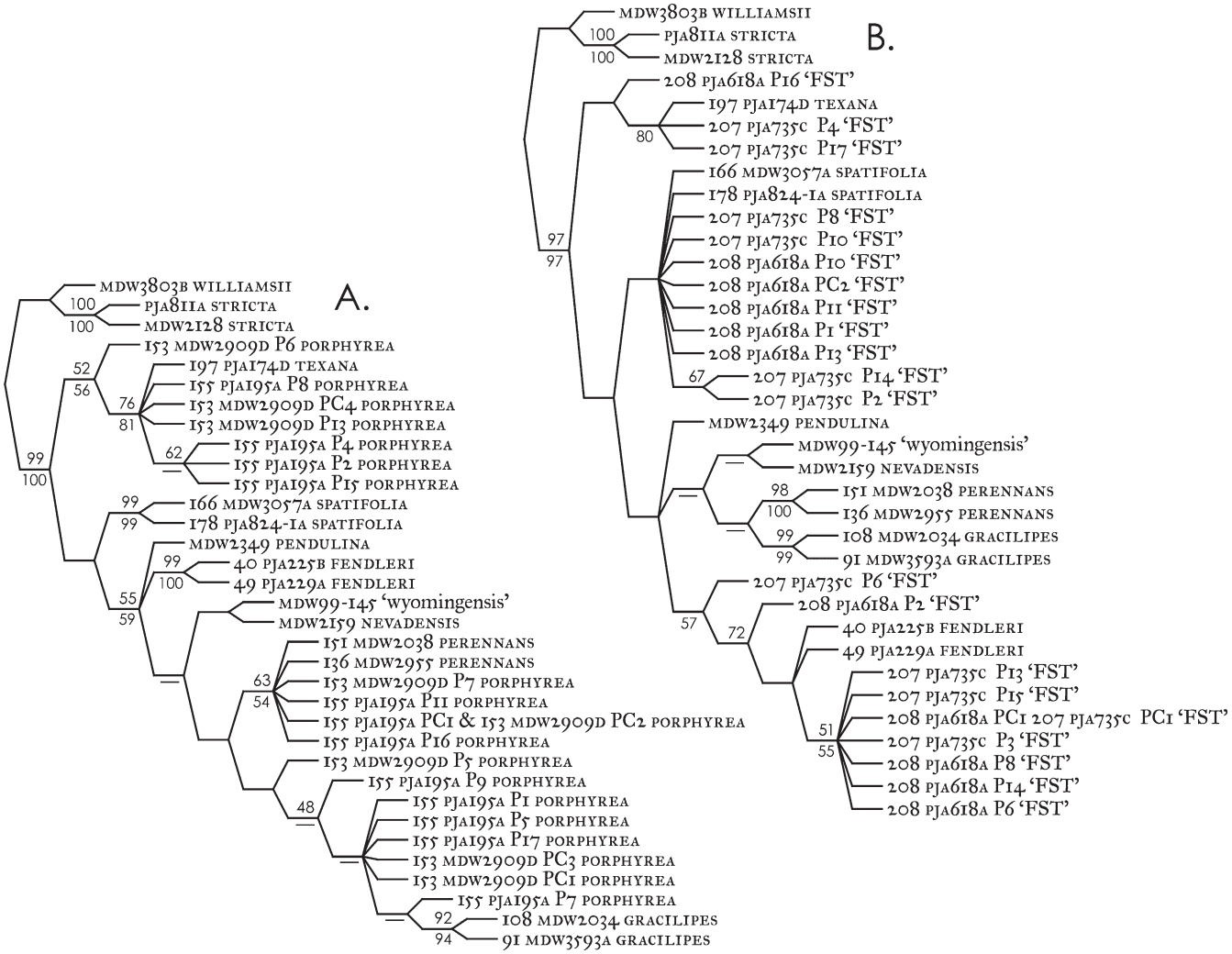

FIG. 7. Spene-trees (see Materials and Methods) for apomictic triploid hybrid putative species. Parsimony jackknife support is above branches, ML bootstrap support below branches. Values below 50 are not shown, and a "—" indicates a node not on the best ML tree. A. *Boechera porphyrea* spene-tree, strict consensus of four most parsimonious trees (length = 132, CI = 0.75, RI = 0.89). B. *Boechera* 'FST' spene-tree, strict consensus of 28 most parsimonious trees (length = 141, CI = 0.68, RI = 0.83).

B. texana. The hybrid assignment test finds a proximate origin involving S2X *B. texana* and A2X *B. sanluisensis* for all samples, consistent with the genomic composition based on STRUCTURE and phylogenetic analyses.

STRUCTURE analysis indicates that most plants ascribed to *B.* 'CP' represent an admixture of *B. fendleri* (29%), *B. perennans* (30%), and *B. texana* (25%; Fig. 8B). However, a few individuals depart from this pattern: 212-PJA1125 is an admixture of *B. fendleri* (26%), *B. gracilipes* (26%), and *B. perennans* (25%), while the tetraploid 214-PJA549a is an admixture of *B. fendleri* (30%), *B. perennans* (27%), *B. spatifolia* (21%), and *B. texana* (21%). As in the case of *B. porphyrea*, the hybrid assignment test is unable to confirm a specific proximate origin for *B.* 'CP'. Six plants are identified as putative hybrids between S2X *B. perennans* and A2X *B. carrizozoensis*, three to *B. fendleri* × *carrizozoensis*, and one (214-PJA549Z) to *B. fendleri* × *zephyra*.

Corroboration of the Assignment of Plants to S2X, A2X, and A3X Classes—Based on the number of species in the S2X and A2X classes and A2X hybrid origins described above, AWCLUST MDS plots showing each of the A2X species with its two most likely progenitors are shown in Fig. 9. Members of each A2X species form a distinct cluster well-separated from S2X plants, consistent with S2X and A2X class assignments. With the exception of *B. carrizozoensis*, A2X species are intermediate between their progenitors on the first axis. Given that only one parent (*B. texana*) can be confidently inferred for *B. carrizozoensis*, *B. spatifolia* was arbitrarily chosen as the second S2X species included in this plot. Replacement of *B. spatifolia* with other S2X species gives similar results (not shown).

Results of our microsatellite-based classification of S2X, A2X, and A3X groups are consistent with variation in pollen morphology, as described by Beck et al. (2012). S2X samples (76) have narrowly ellipsoid, regularly tricolpate pollen, rarely with a few malformed grains or small, round, ecolpate grains. A2X samples (45) have a mixture of ca. 50–75% narrowly ellipsoid, regularly tricolpate grains and 25–50% shrunken, malformed grains, except for one individual each of *B. centrifendleri* and *B. zephyra* (only narrowly ellipsoid pollen) and three of *B. sanluisensis* (pollen with a majority of ovoid, irregularly colpate grains

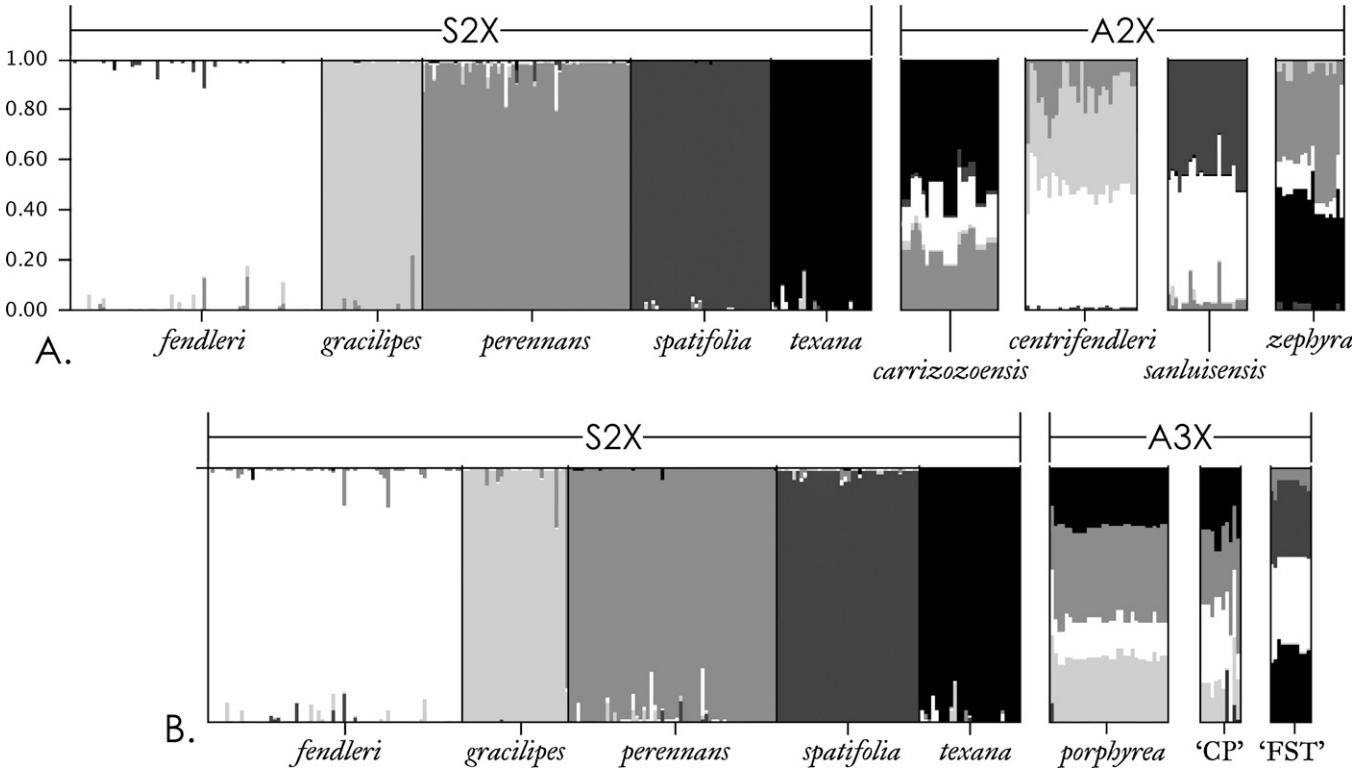

FIG. 8. Results of STRUCTURE analyses. Each putative hybrid species was run in a separate analysis with members of all sexual diploid species. Parameter estimation was limited to the sexual diploids. A. Apomictic diploid hybrids (A2X). B. Apomictic triploid hybrids (A3X).

mixed with shrunken, malformed grains). A3X samples (27) have uniformly ovoid, irregularly colpate pollen.

Discussion

Evaluation of Sexual Diploid Segregates from Boechera fendleri—Within the sexual diploid (S2X) class, five clusters are identified in both AWCLUST (Fig. 2A) and STRUCTURE analyses (Fig. 8) of multilocus genotypes. All five are strongly inbred (Table 2). The morphologies of individuals in each of these clusters correspond to the previously recognized species *B. fendleri*, *B. gracilipes*, *B. perennans*, *B. spatifolia*, and *B. texana*. With the exception of *B. texana*, our microsatellite analyses include individuals collected near the type locality of each named taxon and, in all cases, these topotypes are placed with their respective species. Three of these species, *B. fendleri*, *B. spatifolia*, and *B. texana*, were included within *B. fendleri* s. l. by Rollins (1993), but more recently have been segregated based on morphological differences and non-overlapping geographic ranges (Windham and Al-Shehbaz 2006; Al-Shehbaz and Windham 2010). Our results confirm that these taxa are genetically distinct as well. AWCLUST and STRUCTURE analyses both indicate that there is little introgression among these sexual diploids, indicating that hybridization rarely results in gene flow between S2X taxa.

Morphologically, the circumscription of *B. fendleri* based on microsatellite data differs somewhat from that of Al-Shehbaz and Windham (2010). In that treatment, *B. fendleri* was described as having flowering stems either single and arising centrally or one to seven and arising laterally from the basal rosette, while all individuals assigned to *B. fendleri* in microsatellite analyses have lateral flowering stems. Plants with single flowering stems terminating the rosettes assigned to *B. fendleri* by Al-Shehbaz and Windham (2010) represent apomictic diploid hybrids with *B. gracilipes* and are here treated as a distinct species, *B. centrifendleri*.

Apomictic Hybrid Species in Boechera fendleri s. l.—Although the commonly-used biological species concept of Dobzhansky (1935) and Mayr (1942) is conceptually inapplicable to apomictic lineages, "discontinuities are what everyone uses to distinguish species, and always did" (Mallet 2007). A process-neutral criterion of genetic discontinuity between species, the genotypic cluster species concept, is equally applicable to both sexual and apomictic lineages (Mallet 1995). Apomictic species "are genetically equivalent to sexual species in the biological species concept, but the mechanisms [. . .] are different" (Gastony and Windham 1989). Reproductive isolation between sexual lineages is, then, "a means of achieving speciation [. . .] rather than a definition of the species state itself" (Mallet 2007). We follow these authors in recognizing genetically cohesive groups of individuals that are genetically discontinuous from other such groups as species, regardless of their origin or mode of reproduction.

Among the apomictic diploid (A2X) and apomictic triploid (A3X) classes, four and three clusters are identified, respectively. All seven of these are strongly "outbred", with more observed heterozygosity than expected under HWE (Table 2). Only one corresponds to a previously named species, the A3X *B. porphyrea*. Though not previously recognized, the four A2X groups form cohesive clusters that are well separated from each other in genetic space (Fig. 2B). They are genetically discrete relative to their inferred parents and backcrossing is apparently absent (Figs. 8 and 9). Although the geographic ranges of these hybrids often overlap with one or both of their S2X progenitors, they are

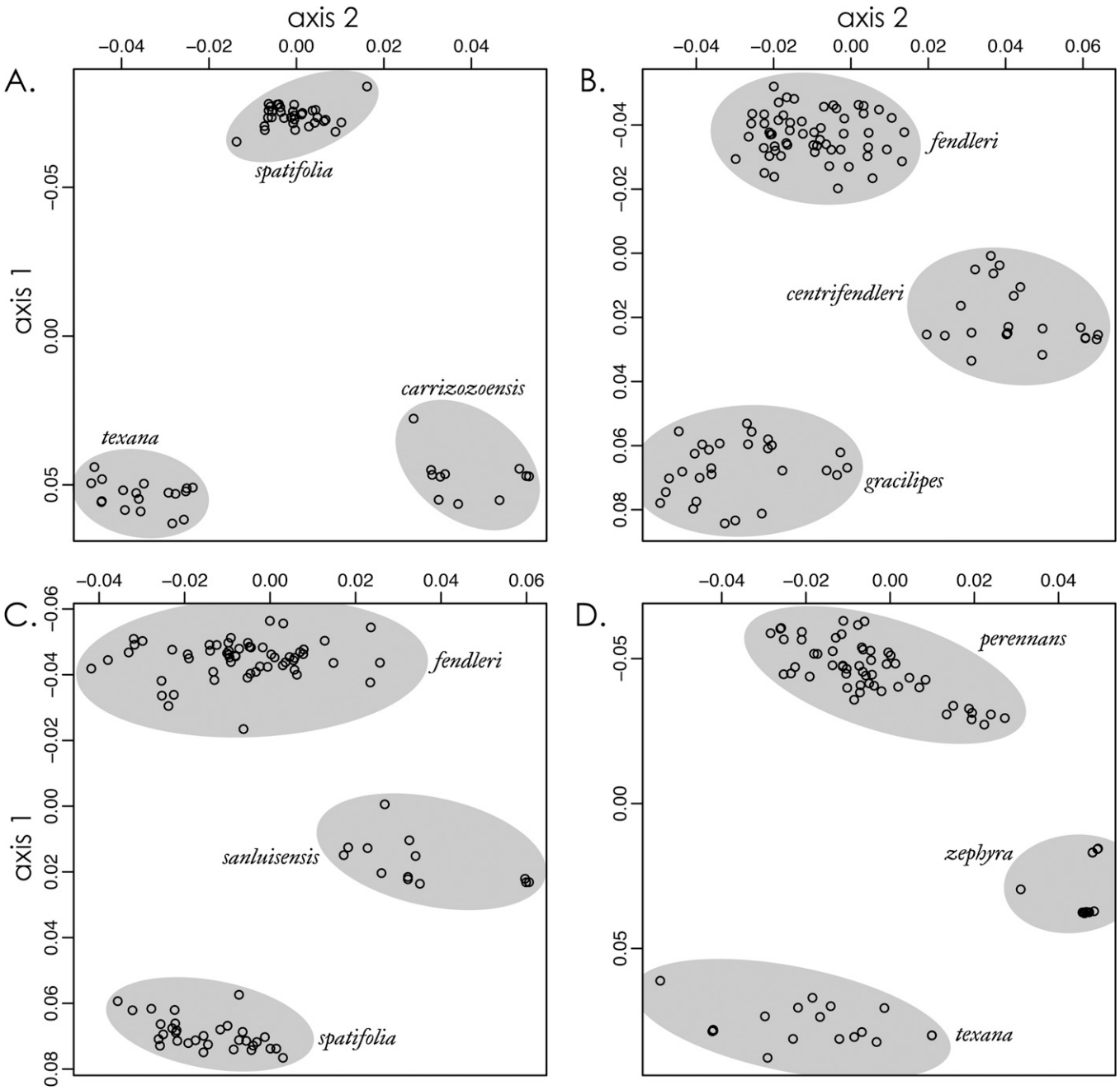

FIG. 9. First two axes of multi-dimensional scaling plots of microsatellite variation created in AWCLUST, each with one A2X species and two S2X species. Gray ellipses indicate groups identified by hierarchical clustering in AWCLUST at K=3. A. The A2X *B. carrizozoensis* with its progenitor *B. texana*; *B. spatifolia* is arbitrarily included as the second S2X species since the origin of *B. carrizozoensis* can be only partially determined. B. The A2X *B. centrifendleri* and its S2X progenitors, *B. fendleri* and *B. gracilipes*. C. The A2X *B. sanluisensis* and its S2X progenitors, *B. fendleri* and *B. spatifolia*. D. The A2X *B. zephyra* and its S2X progenitors, *B. perennans* and *B. texana*.

not limited to regions of parental sympatry—in fact, none of the pairs of S2X species giving rise to an A2X lineage are known to have overlapping ranges at present (Figs. 3 and 4)—indicating that they form populations that are reproductively independent of their parents. Specimens were reexamined to determine if the newly discovered A2X and A3X clusters are morphologically distinguishable from each other and from previously named species. The A2X clusters are readily distinguished from each other, but often very similar to one of their S2X progenitors. For example, *B. sanluisensis* shows slight morphological differentiation from *B. spatifolia*, while *B. zephyra* is only subtly distinct from *B. texana*. Nonetheless, these taxa can be reliably assigned to the hybrid A2X class by the abundance (25–50%) of malformed, inviable pollen grains mixed with narrowly ellipsoid (and occasionally unreduced spheroid) pollen. In addition, geographically these A2X hybrids are partially or completely separated from the parental species with which they are most easily confused. These observations are consistent with microsatellite analyses indicating that they form discrete genetic clusters and further support recognition of these four A2X lineages as species. They are described and formally named below (see Taxonomic Treatment).

Boechera porphyrea, the only apomictic member of the *fendleri* group previously recognized as a separate species, is genetically and morphologically distinct from the other two members of the A3X class. However, despite their clear genetic separation in Fig. 2C, the other two A3X clusters (*B.* 'FST' and *B.* 'CP') appear to be indistinguishable from one another morphologically. *Boechera* 'FST' is narrowly distributed, genetically cohesive, and can be confidently assigned to a single hybrid origin. It probably qualifies as a species. *Boechera* 'CP', on the other hand, consists of a small number of individuals from widely separated areas, includes much more genetic variation than either of the other two A3X species (Fig. 2C, Table 2), and may have arisen through several distinct hybridization events involving different parents. Due to the uncertain status of *B.* 'CP', the difficulty in distinguishing it from *B.* 'FST', and our limited sampling of both, they are provided with provisional designations to facilitate discussion but not formally named.

Inference of Apomixis and Hybrid Origin for the A2X and A3X Classes—The four A2X species are inferred to be apomictic, based on their pollen morphology and high heterozygosity. Genus-wide analysis of *Boechera* indicates that both of these features are strongly correlated with apomixis (Beck et al. 2012). Further support for apomixis includes the lack of allelic segregation in the A2X clusters (most individuals in a population share a single, highly heterozygous, multilocus genotype) and the apparent absence of introgression with their S2X progenitors (Figs. 8 and 9). This constellation of features would be difficult to explain in sexually reproducing hybrids, which would be expected to produce a wide range of genotypes through recombination, independent assortment, and backcrossing to one or both parental S2X species. Rapid ecological divergence and chromosomal rearrangement can reduce these expectations (Rieseberg 1997; Gross and Rieseberg 2005) but would not explain the maintenance of high heterozygosity in plants in the A2X class relative to the S2X class. The A3X clusters, on the other hand, are expected to be apomictic by default; normal meiosis is precluded by triploidy. Their occurrence at multiple sites lying outside areas of sympatry of their progenitors indicates that they are fertile despite the absence of normal meiosis.

That these apomicts are hybrids is strongly supported by analyses of both microsatellite and sequence data. Cloning of *pistillata* recovers two divergent copies in A2X samples and three divergent copies in A3X samples (Figs. 6 and 7). STRUCTURE analyses indicate that their genotypes are mixtures of two and three parental species, respectively, and not drawn solely from a single species (Fig. 8). Both lines of evidence indicate that members of the A2X class are digenomic hybrids, while members of the A3X class are trigenomic hybrids. This is consistent with the hypothesis of Beck et al. (2012) that diploid apomixis is generally triggered by hybridization. This conclusion contrasts with the hypothesis of Lovell et al. (2013) that diploid apomicts in *Boechera* are generally derived from within a single sexual diploid species. We agree with Lovell et al. (2013) that high heterozygosity does not, on its own, necessarily indicate a hybrid origin and could arise through other processes, such as the accumulation of mutations within an apomictic lineage. However, our conclusion that the apomictic diploids identified in this study are hybrids is not supported by high heterozygosity alone, but is confirmed by additional analyses of both microsatellite and sequence data. Similarly, Beck et al. (2012) demonstrated comparable levels of heterozygosity and genotypic additivity in two additional A2X lineages, *B. fendleri* × *B. stricta* and *B. retrofracta* (Graham) Á. Löve & D. Löve × *B. stricta*. The latter is often referred to as *Boechera* (or *Arabis*) *divaricarpa*, a taxon that has been shown to have multiple hybrid origins, many culminating in apomixis (Koch et al. 2003). The available evidence suggests that, although apomixis can arise in the absence of interspecific hybridization, the majority of apomictic diploid lineages examined to date in *Boechera* result from hybridization between divergent sexual diploid taxa. Additional focused studies of apomictic lineages and their parental species are needed to fully understand the relative importance of these alternative mechanisms.

Identification of Hybrid Parentages—A specific hybrid parentage is unambiguously inferred for four taxa, with strong agreement between hybrid assignment test, STRUCTURE, and phylogenetic results. Within the A2X class, *B. centrifendleri* is inferred to result from hybridization between *B. fendleri* and *B. gracilipes* (Fig. 8A). The parentage of *B. sanluisensis* is identified as *B. fendleri* × *spatifolia* (Figs. 6C and 8A), whereas *B. zephyra* is *B. perennans* × *B. texana* (Figs. 6D and 8A). Within the A3X class, *B.* 'FST' is inferred to be the product of hybridization between S2X *B. texana* and A2X *B. sanluisensis*, combining the genomes of three S2X species—*B. fendleri*, *B. spatifolia*, and *B. texana* (Figs. 7B and 8B).

Inferences of hybrid origins for the three remaining apomictic clusters (one A2X and two A3X) identified by this study are less straightforward. Individuals within each of the apomictic diploid and triploid clusters identified via AWCLUST are expected to share common hybrid origins. Violations of this assumption could be due to multiple parentages of a given taxon, the absence of one or both of its progenitors from the analysis, or a combination of these factors. For example, individual 205, although assigned to A2X *B. zephyra* by AWCLUST, is genetically and geographically isolated from other individuals of that species and is assigned a different hybrid combination (*B. fendleri* × *texana*). It probably represents a distinct, independently derived A2X taxon, although we are reluctant to reach this conclusion on the basis of a lone individual. Among the A3X clusters, *B.* 'CP' is variable among individuals with regards to both STRUCTURE admixture proportions (Fig. 8B) and hybrid assignments. Given that *B.* 'CP' also includes much more genetic variation than the other A3X species, it seems likely that it represents several lineages with different hybrid origins that are being erroneously grouped together by AWCLUST.

For A2X *B. carrizozoensis* and A3X *B. porphyrea* parentage can be only partially inferred. Both are genetically coherent, however, and the absence of a particular parent from the analysis is the most plausible explanation for these anomalous results. In the case of *B. carrizozoensis*, the hybrid assignment test, STRUCTURE, and phylogenetic results all identify *B. texana* as one of the two parents. The second parent is not confidently inferred by any of the analyses. However, *B. carrizozoensis* is genetically cohesive (Figs. 2B and 9A), morphologically distinctive, and its members share common ecological preferences (see Taxonomic Account), all strongly suggesting they share a common origin. It is noteworthy that *B. carrizozoensis* shows a higher proportion of "orphan alleles" (not traceable to any parent) than any

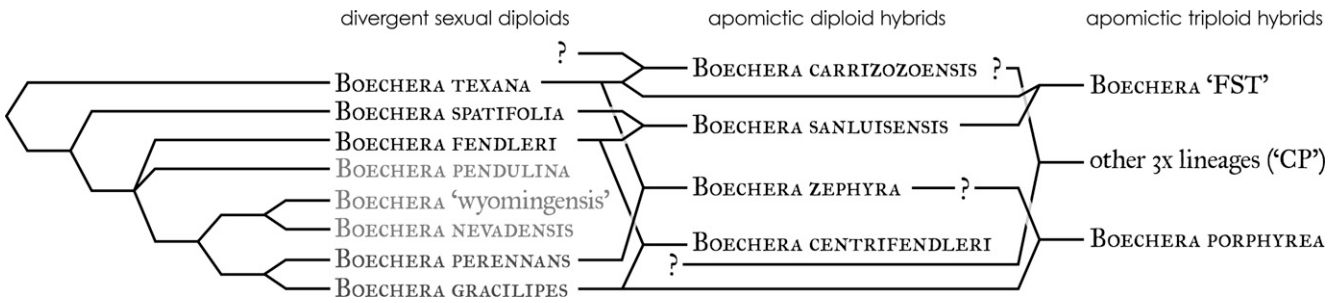

Fig. 10. Inferred relationships among segregates of *B. fendleri* s. l. (in black; other associated sexual diploid species are in gray), showing multiple levels of hybrid speciation.

other A2X taxon in our genus-wide microsatellite dataset (Windham et al. unpublished data). In light of this, we hypothesize that *B. carrizozoensis* arose through hybridization between *B. texana* and another sexual diploid that remains undiscovered and unsampled because it is very rare or perhaps extinct.

For *B. porphyrea*, an ultimate origin of *B. gracilipes* × *perennans* × *texana* is consistently inferred across individuals in both STRUCTURE and phylogenetic analyses (Figs. 7A and 8B). *Boechera zephyra* (*B. perennans* × *texana*) is the only sampled A2X species that could serve as a diploid intermediary for this origin. However, hybrid assignments include four different proximate parentages, and an origin from *B. gracilipes* × *zephyra* is inferred for only one of the 31 individuals of *B. porphyrea*. Unsampled *B. zephyra* genotypes could have been involved in the origin of the remaining *B. porphyrea* individuals or, alternatively, an A2X lineage not included in our analyses (either *B. gracilipes* × *perennans* or *B. gracilipes* × *texana*) could be the A2X parent of *B. porphyrea*.

Divergent and Reticulate Speciation in Boechera fendleri s. l.—Our results support the recent separation of *B. spatifolia* and *B. texana* from *B. fendleri* (Windham and Al-Shehbaz 2006; Al-Shehbaz and Windham 2010). These three species are divergently related sexual diploids that do not form a monophyletic group in our phylogenetic analyses (Fig. 6A; Alexander et al. 2013). They are quite distinct genetically (Figs. 2A and 8), morphologically recognizable (see Taxonomic Account), and peri- or allopatrically distributed (Figs. 3 and 4). These three sexual diploids have hybridized, among themselves and with the closely related species *B. gracilipes* and *B. perennans*, to produce a number of apomictic diploid and triploid hybrids. Although most of these hybrids are morphologically and genetically distinct, a few are of uncertain status. The apomictic diploid hybrids named herein (*B. carrizozoensis*, *B. centrifendleri*, *B. sanluisensis*, and *B. zephyra*) are particularly noteworthy, as very few are known in angiosperms. The frequency of this method of speciation in *Boechera* as a whole (Beck et al. 2012), and in the *fendleri* group in particular, is remarkable. Although apomictic triploid hybrids (represented here by *B. porphyrea*, *B.* 'FST', and *B.* 'CP') are reasonably common in angiosperms, those encountered in the *fendleri* group have fundamentally different genomic compositions and origins. Outside of *Boechera*, most triploid apomicts appear to be digenomic, arising from the union of unreduced and reduced gametes from two distinct sexual diploid progenitors (e.g. Harlan and deWet 1975). The triploid hybrids documented in our study are uniformly trigenomic, likely formed by hybridization between an apomictic diploid hybrid and a distinct sexual diploid. This process is analogous to the triploid bridge scenario for the origin of allotetraploids (Ramsey and Schemske 1998) but with a digenomic diploid bridge leading to trigenomic allotriploids. This combination of divergent speciation and hybridization at multiple ploidy levels creates a truly complicated network of relationships (Fig. 10).

Our analyses have shown that, within what was formerly considered a single species (*B. fendleri* s. l.), there are at least eight genetically distinct species and multiple levels of hybridization. Relationships in the *fendleri* group are a complicated network of divergent relationships among sexual diploid species, hybridization among these to form stable apomictic diploids, and subsequent hybridization between the apomictic diploid hybrids and sexual diploids to form apomictic triploid hybrids containing genomes from three different species (Fig. 10). Evolution has woven a tangled web; it must be carefully unraveled lest we be deceived.

Taxonomic Treatment

Previous morphological evaluations have indicated a number of morphological characters separating taxa formerly included within *B. fendleri* s. l. (summarized in Al-Shehbaz and Windham 2010). These include: number of basal rosettes and origin of flowering stems from the basal rosette(s); pubescence of flowering stems; number of cauline leaves; trichome form and distribution on leaves, stems, pedicels, and sepals; length of pedicels; pollen morphology; arrangement of seeds; and the width of the fruits.

Basal rosettes range from one to ten per plant, arising at ground level without a woody caudex or borne aboveground on a branched, woody caudex. Flowering stems may be single and terminating the basal rosette(s) or one to seven per rosette and arising laterally, with the basal rosette producing a sterile tuft of leaves beyond the bases of the inflorescences. Rarely, flowering stems terminating the basal rosette and arising laterally from it are present on a single plant. Variation in these characters is shown in Fig. 11. Lower parts of the flowering stems may be glabrous or pubescent with simple and forked trichomes. Basal leaves vary in size, shape, and pubescence (Figs. 12–14). Simple marginal trichomes are present on the petiole, and may extend to the apex of the leaf. Basal leaf surfaces are glabrous, sparsely pubescent near the margins, or pubescent throughout, with trichomes varying from simple to 6-rayed.

FIG. 11. Variation in rosette and flowering stem number in *B. fendleri* s. l.: A. a single basal rosette with three flowering stems arising laterally; B. a single basal rosette with one flowering stem arising centrally; C. three rosettes arising from a woody, branched caudex, each with a single flowering stem arising centrally.

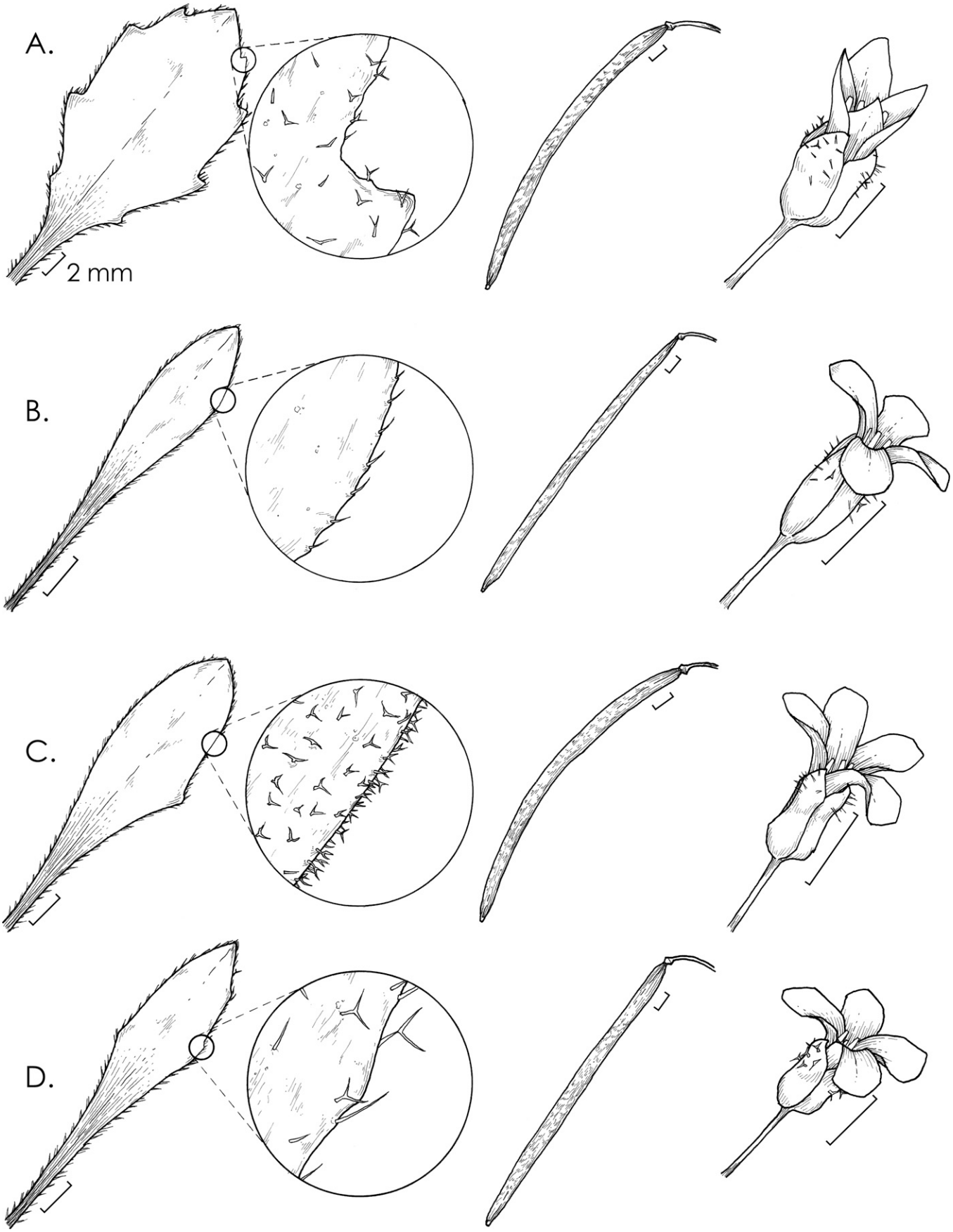

FIG. 12. Basal leaves, basal leaf pubescence, fruits, and flowers of: A. *Boechera fendleri*; B. *Boechera spatifolia*; C. *Boechera centrifendleri*; D. *Boechera sanluisensis*. All scale bars are 2 mm.

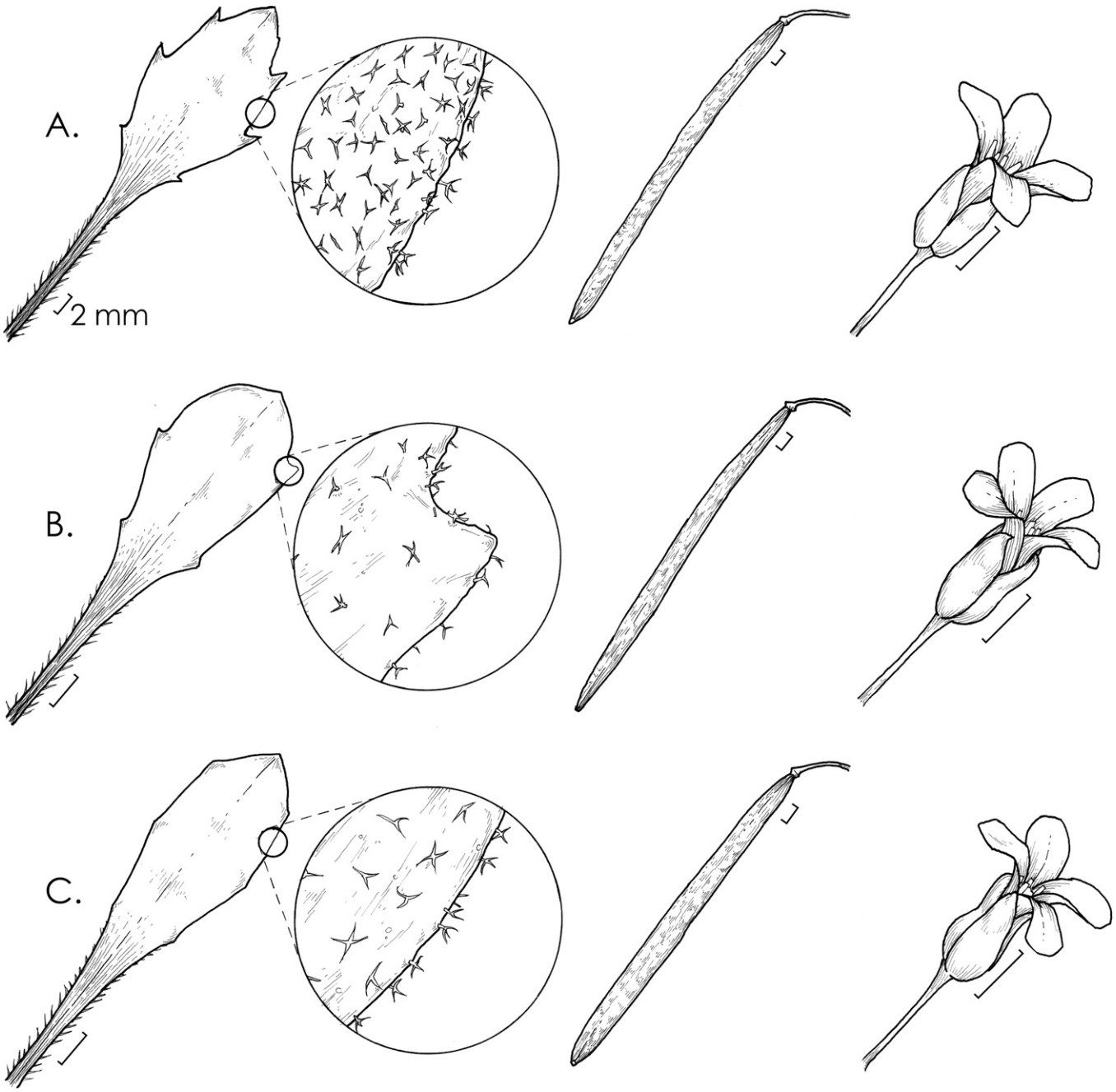

FIG. 13. Basal leaves, basal leaf pubescence, fruits, and flowers of: A. *Boechera porphyrea*; B. *Boechera zephyra*; C. *Boechera texana*. All scale bars are 2 mm.

Cauline leaves range from 5–27 in number and sometimes conceal the lower parts of the stems. Inflorescences may be either simple or branched. Fruiting pedicels vary from 4–27 mm in length and are either glabrous or with a few, scattered, mostly simple trichomes. Sepals may be either glabrous throughout or pubescent with simple or forked trichomes distally. Petals vary in color from white to lavender and may darken to purple with age. Pollen is either: narrowly ellipsoid and regularly colpate (S2X); spheroid and irregularly colpate (A3X); or a mixture of shrunken, malformed grains without cellular contents, narrowly ellipsoid grains, and, occasionally, some spheroid grains (A2X). Fruits vary from 1.3–3.0 mm in width, with seeds either in two partially overlapping rows (irregularly biseriate) or in two distinct rows (biseriate). Fruit orientation varies from closely pendent (held at a ca. 60° downward angle to ± parallel to the inflorescence axis) to widely pendent (held at a 15–45° downward angle). A number of other characteristics useful in distinguishing among species in *Boechera* as a whole are shared among members of the *fendleri* group. These species all have auriculate cauline leaves, glabrous fruits, and short (0.1–0.7 mm) styles. They never have dense, grayish pubescence obscuring leaf surfaces, pubescent petals, or secund fruits. Morphological descriptions of and a key to segregates from *B. fendleri* s. l. are provided below. These segregates can usually be distinguished from both each other and their parents based on macromorphology, but it is always advisable to examine

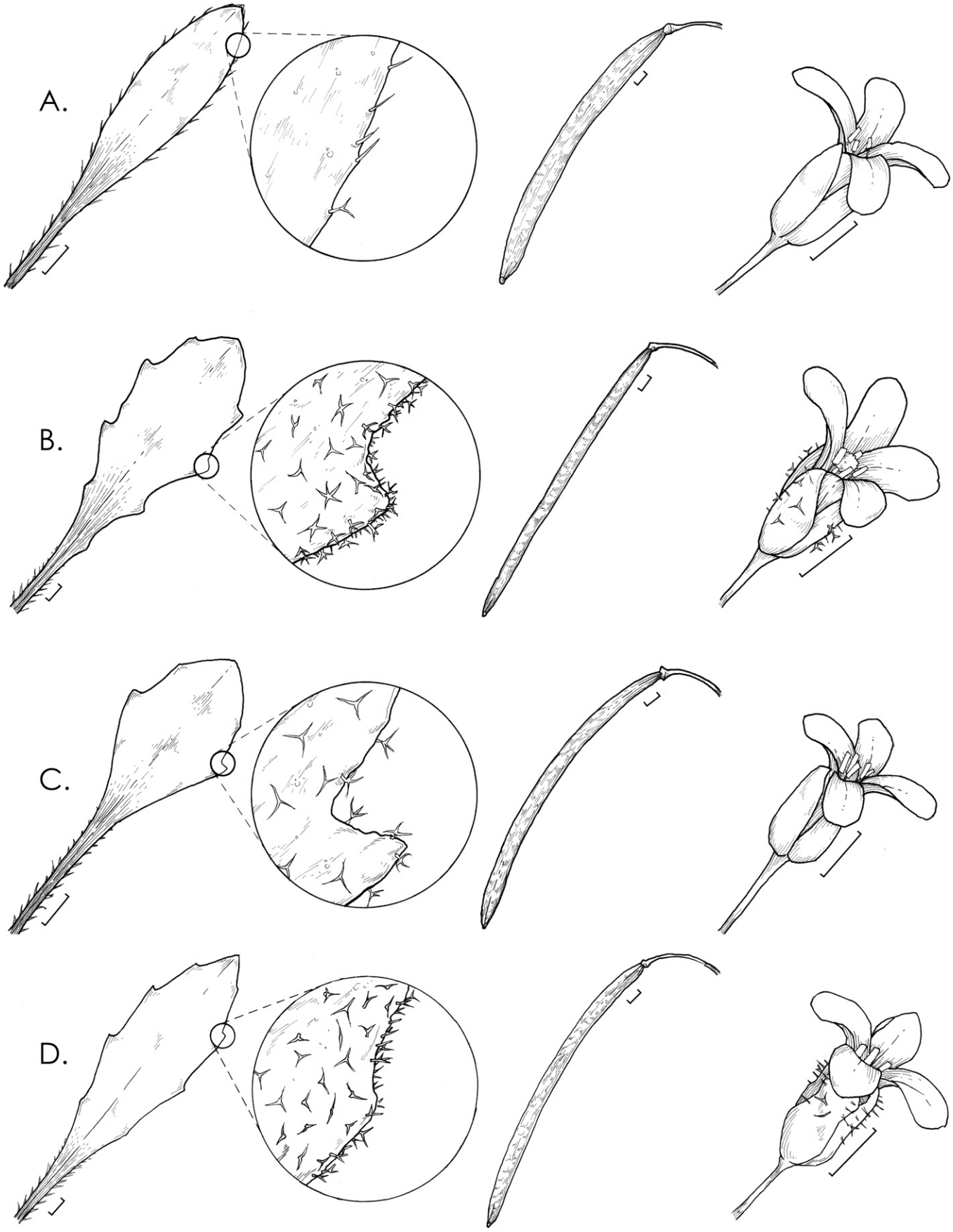

FIG. 14. Basal leaves, basal leaf pubescence, fruits, and flowers of: A. *Boechera carrizozoensis*; B. *Boechera perennans*; C. *Boechera* 'FST'; D. *Boechera gracilipes*. All scale bars are 2 mm.

pollen to ascertain the reproductive class (S2X, A2X, or A3X) to which a plant belongs. The key should be used with caution, as several morphologically similar hybrids (e.g. *B. gracilipes* × *perennans*, found in Arizona and peripherally in western New Mexico, and *B. fendleri* × *spatifolia* × *oxylobula*, found in central Colorado) have been found in preliminary analyses (Windham et al. unpublished data) but require further research and are not treated here.

1. Plants with several inflorescences borne laterally on the basal rosette (rarely, a single lateral inflorescence)
   2. Sepals glabrous; leaves with some 3- to 6-rayed trichomes ..... 2. *Boechera porphyrea* (in part)
   2. Sepals sparsely pubescent; leaves with simple and forked trichomes only
      3. Pollen narrowly ellipsoid; found throughout the western 2/3 of New Mexico ..... 1. *Boechera fendleri*
      3. Pollen a mixture of narrowly ellipsoid and 25–50% malformed, shrunken grains; sporadic from Taos County south to western Lincoln County, New Mexico ..... 6. *Boechera centrifendleri* (in part)
1. Plants with a single inflorescence terminating the basal rosette
   4. Sepals sparsely pubescent
      5. Basal leaves broadly oblanceolate, margins ciliate only towards the base and surfaces pubescent throughout; lower fruiting pedicels usually >12 mm long ..... 6. *Boechera centrifendleri* (in part)
      5. Basal leaves narrowly oblanceolate, margins prominently ciliate throughout their lengths and surfaces glabrous or with a few simple or forked trichomes near the margins; lower fruiting pedicels usually <12 mm long
         6. Fruits closely pendent; pollen narrowly ellipsoid ..... 3. *Boechera spatifolia*
         6. Fruits widely pendent; pollen a mixture of narrowly ellipsoid and 25–50% malformed, shrunken grains, or the well-developed grains spheroid and irregularly colpate ..... 7. *Boechera sanluisensis*
   4. Sepals glabrous
      7. Basal leaves narrowly oblanceolate, margins prominently ciliate throughout their lengths and surfaces glabrous or with a few simple or forked trichomes near the margins ..... 5. *Boechera carrizozoensis*
      7. Basal leaves broadly oblanceolate, margins prominently ciliate only towards the base and surfaces pubescent throughout
         8. Basal rosettes usually elevated above the ground on woody caudices; well-developed pollen grains narrowly ellipsoid (sometimes also with malformed, shrunken grains); plants of Trans-Pecos Texas and along the southern edge of New Mexico
            9. Fruits 2.5–3.0 mm wide, usually closely pendent; plants of Trans-Pecos Texas ..... 4. *Boechera texana*
            9. Fruits 2.0–2.4 mm wide, usually widely pendent; plants of the southern edge of New Mexico and barely entering Texas (in the Cornudas Mountains) ..... 8. *Boechera zephyra*
         8. Basal rosettes not elevated above the ground on woody caudices; well-developed pollen grains spheroid and irregularly colpate; plants of north-central to southern New Mexico, very rarely in Trans-Pecos Texas
            10. Basal leaves prominently and sharply dentate, the larger > 2.5 cm long, with at least some 4- to 6-rayed trichomes ..... 2. *Boechera porphyrea* (in part)
            10. Basal leaves shallowly dentate, the larger < 2.5 cm long, with forked and 3-rayed trichomes only ..... 9. other hybrids ('CP' and 'FST')

1. BOECHERA FENDLERI (S. Watson) W. A. Weber. Phytologia 51: 370. 1982. *Arabis holboellii* var. *fendleri* S. Watson in A. Gray, Synop. Fl. N. Amer. 1: 164. 1895. *Arabis fendleri* (S. Watson) Greene, Pittonia 3: 156. 1897.—TYPE: U. S. A. New Mexico: Santa Fe Co.: From Santa Fe E to Rabbit Ear Creek, 10–20 Aug 1847, *A. Fendler 27* (holotype: GH!; isotypes: MO!, NY!, UC!).

Plants short- to long-lived perennials, with 1–2(–6) basal rosettes usually at ground level, rarely borne above the ground on branched, woody caudices. Flowering stems 1–7 per rosette, arising laterally from the rosettes; lower parts hirsute with predominantly simple and a few forked trichomes, upper parts glabrous. Basal leaves broadly oblanceolate, 15–35 × 5–15(–20) mm, margins shallowly dentate; simple marginal trichomes present from petiole to leaf apex, mixed with forked hairs distally; blade surfaces pubescent with simple and forked trichomes or rarely glabrescent and with only sparse pubescence near the margins. Cauline leaves 7–14, not concealing the stem proximally. Inflorescences simple or rarely branched; lower fruiting pedicels 7–13(–17) mm, glabrous or with a few simple or forked trichomes. Flowers with sepals sparsely hirsute distally with simple and forked trichomes; petals white or rarely pale lavender, not darkening with age; pollen narrowly ellipsoid. Fruits 1.4–1.9 mm wide, closely pendent, with irregularly biseriate seeds. Figure 12A.

Distribution, Habitat, and Phenology—Found throughout the western two-thirds of New Mexico and peripherally in adjacent Colorado (Fig. 3) on rocky (usually igneous) slopes in ponderosa pine forest, pinyon-juniper woodlands, and scrub oak, from 1,900–2,600 m. Flowering Apr–Jun.

2. BOECHERA PORPHYREA (Woot. & Standl.) Windham, Al-Shehbaz & P. J. Alexander, Harvard Pap. Bot. 11: 272. 2007. *Arabis porphyrea* Woot. & Standl., Contr. U. S. Nat. Herb. 16: 123. 1913.—TYPE: U. S. A. New Mexico: Doña Ana Co.: In the Organ Mountains at the Cueva, 25 April 1907, *E. O. Wooton & P. C. Standley s. n.* (holotype: US!).

Plants mostly long-lived perennials, with 1–3 basal rosettes usually at ground level, occasionally borne above-ground on woody caudices. Flowering stems 1–5 per rosette, usually arising laterally from the rosettes, sometimes arising centrally and terminating the rosettes, or rarely with both central and lateral stems; lower parts glabrous or rarely with a few simple, forked, and 3-rayed trichomes, upper parts glabrous. Basal leaves broadly oblanceolate, (15–)25–60 × (4–)7–15 mm, margins sharply dentate; simple marginal trichomes present on petiole; blade surfaces pubescent with predominantly forked to 4-rayed (a few 5- or 6-rayed) trichomes. Cauline leaves 7–17(–21), often concealing the stem proximally. Inflorescences usually branched; lower fruiting pedicels (10–)15–27 mm, glabrous. Flowers with glabrous sepals; petals pale lavender at anthesis, darkening to purple with age; pollen spheroid. Fruits 1.8–2.5 mm wide, widely pendent, with irregularly biseriate seeds. Figure 13A.

Distribution, Habitat, and Phenology—Found primarily in southern New Mexico and sporadically to north-central

New Mexico (Fig. 4) on rocky (usually igneous) slopes in Chihuahuan desert scrub, scrub oak, and pinyon-juniper woodland; 1,350–2,100 m. Flowering Mar–May.

3. Boechera spatifolia (Rydb.) Windham & Al-Shehbaz, Harvard Pap. Bot. 11: 84. 2006. *Arabis spatifolia* Rydb., Fl. Rocky Mts. 361. 1917. *Arabis fendleri* (S. Watson) Greene var. *spatifolia* (Rydb.) Rollins, Rhodora 43: 394. 1941. *Boechera fendleri* (S. Watson) W. A. Weber subsp. *spatifolia* (Rydb.) W. A. Weber, Phytologia 51: 370. 1982. *B. fendleri* var. *spatifolia* (Rydb.) Dorn, Vasc. Pl. Wyoming, ed. 3. 375. 2001.—TYPE: U. S. A. Colorado: Larimer Co.: Estes Park, 20 July 1903, *G. E. Osterhout 2808* (holotype: NY!; isotype: RM!).

Plants mostly short-lived perennials, with 1(–3) basal rosettes at ground level, never on woody caudices. Flowering stems 1 per rosette, arising centrally and terminating the rosette; lower parts hirsute with predominantly simple (a few forked) trichomes, upper parts glabrous. Basal leaves narrowly oblanceolate, (7–)10–20(–28) × 2–4 mm, margins usually entire, sometimes sparingly dentate; simple marginal trichomes present from petiole to leaf apex; blade surfaces glabrous or rarely with a few simple and forked trichomes near the margins. Cauline leaves 10–18, sometimes concealing the stem proximally. Inflorescences usually simple; lower fruiting pedicels 4–10 mm, glabrous or with a few simple or forked trichomes. Flowers with sepals sparsely hirsute distally with simple and forked trichomes; petals white, not darkening with age; pollen narrowly ellipsoid. Fruits 1.2–1.8 mm wide, closely pendent, with irregularly biseriate seeds. Figure 12B.

Distribution, Habitat, and Phenology—Found throughout the Front Range in the Rocky Mountains of Colorado and peripherally in adjacent Wyoming (Fig. 3) on rocky slopes and gravelly soils in sagebrush, pinyon-juniper woodland, open ponderosa and other coniferous forests, and montane meadows; 2,200–3,000 m. Flowering May–Jul.

4. Boechera texana Windham & Al-Shehbaz, Harvard Pap. Bot. 11: 85. 2006.—TYPE: U. S. A. Texas: Culberson Co.: San Antonio Peak, Sierra Tinaja Pinta, 26 Apr 1961, *R. C. Rollins & D. S. Correll 61142* (holotype: GH!; isotype: LL!).

Plants mostly long-lived perennials, with (1–)2–4 basal rosettes usually elevated above-ground on branched, woody caudices. Flowering stems 1 per rosette, arising centrally and terminating the rosette; glabrous. Basal leaves broadly oblanceolate, 15–35 × 5–12 mm, margins shallowly dentate; simple marginal trichomes present on petioles only; blade surfaces with forked to 4-rayed trichomes. Cauline leaves 5–12, not concealing the stem proximally. Inflorescences usually simple; lower fruiting pedicels (7–)10–18(–20) mm, glabrous. Flowers with glabrous sepals; petals white or pale lavender, sometimes darkening with age; pollen narrowly ellipsoid. Fruits 2.5–3.0 mm wide, closely pendent or rarely widely pendent, with distinctly biseriate seeds. Figure 13C.

Distribution, Habitat, and Phenology—Current known only from the Trans-Pecos region of western Texas (Fig. 4), where it occurs on rocky (usually igneous) slopes in Chihuahuan desert scrub and evergreen oak woodland. Flowering Mar–Apr.

5. **Boechera carrizozoensis** P. J. Alexander, sp. nov.—TYPE: U. S. A. New Mexico: Socorro Co.: Northern Oscura Mountains, Garden Spring Canyon, slopes on the northwest side of Chicken Spring, 9.2 miles NNE of Oscura Peak, 29 Apr 2010, *P. J. Alexander 1160* (holotype: NMC!; isotypes: BRY!, DUKE!, MO!).

Plants mostly long-lived perennials, with (1–)2–6(–12) basal rosettes usually elevated above the ground on branched, woody caudices. Flowering stems 1 per rosette, arising centrally and terminating the rosette; glabrous. Basal leaves narrowly oblanceolate, (12–)25–45 × 2.5–5(–8) mm, margins entire or shallowly dentate; simple marginal trichomes present from petiole to leaf apex, often mixed with a few forked trichomes distally; blade surfaces glabrous or with sparse simple and forked trichomes near the margins. Cauline leaves 7–15, occasionally concealing the stem proximally. Inflorescences usually simple; lower fruiting pedicels 9–18 mm, glabrous. Flowers with glabrous sepals; petals lavender, not darkening with age; pollen a mixture of narrowly ellipsoid and malformed grains. Fruits 2.4–3.0 mm wide, closely pendent or occasionally widely pendent, with distinctly biseriate seeds. Figure 14A.

Distribution, Habitat, and Phenology—Found in central and southern New Mexico (Fig. 4) on rocky (usually sandstone or limestone) slopes in Chihuahuan desert scrub or at the lower extremes of pinyon-juniper woodland; 1,550–2,100 m. Flowering Mar–Apr.

Etymology—Named for the Carrizozo Malpais, where the first author first saw this species.

Comments—*Boechera carrizozoensis* is the most morphologically and ecologically distinctive of the hybrid species found in this study. It is found at lower elevations than most other *Boechera* in New Mexico and mostly on sedimentary substrates (90% of the specimens were collected on sandstone or limestone), while other members of *B. fendleri* s. l. are found primarily on igneous substrates. Morphologically, it shares several features with its known parent, *B. texana*, including wider fruits than other members of the *fendleri* group (2.4–3.0 mm vs. <2.0 mm for most other members of the group), glabrous flowering stems, and glabrous sepals. The combination of wide fruits and glabrous sepals readily distinguishes it from other members of the *fendleri* group in New Mexico except for other hybrids derived from *B. texana*. *Boechera carrizozoensis* is easily distinguished from both *B. texana* and these hybrids (*B. porphyrea*, *B. zephyra*, *B.* 'FST', and *B.* 'CP') by the narrowly oblanceolate basal leaves with prominent marginal cilia along their entire length but surfaces that are glabrous or sparsely pubescent with simple or forked trichomes. In basal leaf shape and pubescence, *B. carrizozoensis* most closely resembles *B. spatifolia* and *B. sanluisensis*.

Additional Specimens Examined—Specimens included in genetic analyses (population numbers are in bold): New Mexico: Cibola Co.: **1.** Zuni Canyon, just inside Cibola National Forest about 6 miles W of Grants, 27 May 2005, *P. J. Alexander 204* (NMC, UT). Lincoln Co.: **2.** Mesa Pasture, NMSU Corona Ranch, ±6 miles E of Corona, on the north slope of the mesa, 1 Apr 2007, *P. J. Alexander 553* (DUKE, NMC). **3.** Carrizozo Malpais, near the trail at the Valley of Fires campground, 14 May 2005, *P. J. Alexander 199* (NMC, UT). Valley of Fires Campground, E side of the Carrizozo Malpais, ±4 miles NW of Carrizozo, ±0.12 miles from US Hwy 380, 2 Apr 2007, *P. J. Alexander 562* (DUKE, NMC, SRSC). Otero Co.: **4.** On the NE side of the ridge separating Little Dry Canyon from Fresnal Canyon on the W side of the Sacramento Mts., about 4 miles NE of Alamogordo, 1 May 2005, *P. J. Alexander 156* (NMC, UT). Socorro Co.: **5.** West side of the Ladron Mountains, 2.1 miles west of Ladron Peak in an apparently nameless canyon, 18 Apr 2010, *P. J. Alexander 1144* (BRY, DUKE, MO, NMC, UNM). **6.** Northern San Andres Mountains,

north side of Mockingbird Canyon, 0.4 miles east-northeast of the summit of Mockingbird Mountain, 10.3 miles SSW of Oscura Peak, 23 Apr 2010, *P. J. Alexander 1158* (BRY, DUKE, NMC, WSMR). Torrance Co.: **7.** W side of the W peak of Rattlesnake Hill, ±6 miles S of Lucy, ±11.5 miles E of Willard, 31 Mar 2007, *P. J. Alexander 540* (NMC). **8.** 4 miles west of Negra, 6 Jun 1977, *W. L. Wagner 3056* (MO).

Specimens not included in the genetic analyses: New Mexico: Cibola Co.: Seis Allotment (southside pasture), 25 Apr 1975, *J. R. Lacey s. n.* (NMC); E of Grants about 1.5 miles E of junction of NM 117 with US 66, 20 May 1979, *R. W. Spellenberg 5134* (NMC); Doña Ana Co.: San Andres Mts., Ash Canyon, 25 Apr 1985, *K. W. Allred 2873* (NMCR); Lincoln Co.: 5 miles northwest of Carrizozo, 26 Apr 1969, *C. R. Hutchins 1777* (UNM); Otero Co.: Dry Cañon, from Highway 82, western escarpment Sacramento Mts., 12 Apr 1979, *W. H. Powers 991* (UNM); Fort Bliss Military Reservation, McGregor Range: Hueco Mountains, about 1.5 air miles NE of Bassett Ranch ruins and Wallbridge Tank at crest of mountain, 19 Apr 2007, *R. D. Worthington 34673* (NMC); Socorro Co.: Ca. 5 mi S of Bingham Post Office and US Hwy 380, N end of Oscura Mts., large canyon, 17 Apr 1977, *R. W. Spellenberg 4622* (NMC); West side of Chupadera Mesa in Hoot Owl Canyon along an apparently nameless road, 2.5 road miles southeast of the road from Bingham to Claunch, 4.3 miles ENE of Adobe, 20 Apr 2010, *P. J. Alexander 1156* (DUKE, MO, NMC); Valencia Co.: Gypsum hills south of White Ridge, 10 May 2012, *K. D. Heil 34072* (SJNM).

6. **Boechera centrifendleri** P. J. Alexander, sp. nov.—TYPE: U. S. A. New Mexico: Cibola Co.: Ojo Redondo in the eastern Zuni Mountains, 13 miles west of Grants, 1.3 miles south-southwest of Mount Sedgwick, 19 May 2014, *P. J. Alexander 1450* (holotype: NMC!; isotypes: ARIZ!, ASU!, BRY!, DUKE!, MO!, TEX!, UNM!).

Plants mostly short-lived perennials, with 1(–3) basal rosettes arising at ground level, not on woody caudices. Flowering stems 1(–3) per rosette, usually arising centrally and terminating the rosette; lower parts hirsute with predominantly simple and a few forked trichomes, upper parts glabrous. Basal leaves broadly oblanceolate, 12–30 × 4–9 mm, the margins usually shallowly dentate; simple marginal trichomes present from petiole to leaf apex, usually mixed with forked trichomes distally; blade surfaces pubescent with simple and forked trichomes or rarely glabrescent, with only sparse pubescence near margins. Cauline leaves (8–)15–27, usually concealing the stem proximally. Inflorescences usually simple; lower fruiting pedicels (7–)10–18(–23) mm, glabrous or with a few simple or forked trichomes. Flowers with sepals sparsely hirsute distally with simple and forked trichomes; petals usually pale lavender, not darkening with age; pollen a mixture of narrowly ellipsoid and malformed grains. Fruits 1.4–1.7 mm wide, closely or widely pendent, with irregularly biseriate seeds. Figure 12C.

Distribution, Habitat, and Phenology—Found from western New Mexico to northern Arizona and peripherally into southern Colorado and Utah in the Four Corners region (Fig. 5) on rocky (usually igneous) slopes and level openings in ponderosa pine forest, pinyon-juniper woodland, and scrub oak; 1,900–2,650 m. Flowering Apr–Jun.

Etymology—Named for the typical morphology of the species, which differs from *B. fendleri* in having flowering stems arising centrally rather than laterally from the basal rosettes.

Comments—*Boechera centrifendleri* is most similar to its parents, *B. fendleri* and *B. gracilipes*. It is usually distinguished from *B. fendleri* by its single, terminal flowering stems (vs. 1–7 lateral stems) and, on average, longer fruiting pedicels (10–18 vs. 7–13 mm). However, a few specimens of *B. centrifendleri* from the eastern extreme of its range, in New Mexico from Taos County south to Lincoln County, have lateral flowering stems and are difficult to distinguish from *B. fendleri*. In this area, careful examination of pollen may be necessary to distinguish the two. *Boechera centrifendleri* is more easily and reliably distinguished from *B. gracilipes*: it has fewer cauline leaves (15–27 vs. 30–65); shorter fruiting pedicels (10–18 vs. 20–47 mm); and only simple or forked trichomes on the basal leaf surfaces (vs. at least some 3-rayed).

Additional Specimens Examined—Specimens included in genetic analyses (population numbers are in bold): Arizona: Apache Co.: **54.** Navajo Nation, Chuska Mountains. Buffalo Pass, ca. 7.5 mi. E of the N12 junction on N13, 6 May 2004, *K. Christie 308* (ASC). **55.** Navajo Nation: ca. 10 mi S of Tsaile & ca. 200 yards N of Wheatfields Lake and W of Hwy. 12, 14 Apr 2003, *K. D. Heil 21213* (SJNM). **56.** SSW of Red Rock along road to Lukachukai in the Chuska Mts. ca. 1.89 km NW of the summit (9783′) of Roof Butte, 16 May 2004, *M. D. Windham 3073* (NMC, UT). Coconino Co.: **57.** NNE of Flagstaff on San Francisco Peaks along Lockett Meadow Rd. ca. 1.70 km ESE of Alto Spring, 31 May 2008, *M. D. Windham 3596* (DUKE, NMC). Gila Co.: **58.** Fulton Point on Mogollon Rim, 6 May 1967, *D. Keil 1864* (ASU). Colorado: Conejos Co.: **59.** On the W side of Aspen Glade Campground, Rio Grande National Forest, on the S side of CO Hwy 17 in the bottom of Conejos River Canyon ±5.8 miles SE of jct. with F.R. 250, 11 Jun 2008, *P. J. Alexander 763* (DUKE, MO, NMC). New Mexico: Catron Co.: **60.** W side of the Black Range, slopes of Black Canyon, 0.25 miles S of the canyon bottom along F.R. 150, 2 miles SW of the junction of Catron, Grant, and Sierra counties, 28 Aug 2005, *P. J. Alexander 265* (NMC). **61.** Datil Mountains, 1 Jun 1976, *R. Fletcher 207* (UNM). Cibola Co.: **62.** El Malpais National Monument: Cerro Rendija, 31 Jul 2006, *J. Coop 06JC351-F4* (UNM). **63.** Ojo Redondo Campground, about 12 miles W of Grants in Cibola National Forest, 27 May 2005, *P. J. Alexander 202* (NMC, UT). **64.** El Malpais National Monument: Cerro Encierro, 25 Jul 2006, *Y. Chauvin 06YC048-F8* (UNM). Lincoln Co.: **65.** Mesa Pasture, NMSU Corona Ranch, ±6 miles E of Corona, along a ravine on the N side of the mesa, 1 Apr 2007, *P. J. Alexander 552* (DUKE, NMC). Rio Arriba Co.: **66.** Carson National Forest, ±1.75 miles WNW of Tres Piedras, ±0.15 miles N of US Hwy 64, 9 May 2007, *P. J. Alexander 599* (leaves from an unvouchered individual). **67.** Santa Fe National Forest along F. R. 597 ± 0.7 miles N of Truchas, 18 May 2008, *P. J. Alexander 737* Y, Z (NMC). Santa Fe Co.: **69.** Caja del Rio Plateau along an unlabeled forest road 0.8 miles south of Montoso Peak, 2.8 miles SE of the confluence of the Rio de los Frijoles with the Rio Grande, 6 May 2010, *P. J. Alexander 1181* (BRY, DUKE, NMC). **70.** Southwestern foothills of the Sangre de Cristo Mountains, west side of Mesa Borrego, SW side of Forest Road 306, 0.1 road miles east from the junction with Forest Road 440, ±150 feet west of the road, 3.5 miles northeast of Cundiyo, 8 May 2010, *P. J. Alexander 1194* (BRY, DUKE, MO, NMC). Taos Co.: **71.** East side of Rio Grande Canyon on the trail from La Junta to Little Arsenic Springs, 0.6 miles NNE of the confluence of the Red River and Rio Grande, 17.1 miles NNW of Taos Pueblo, 9 May 2010, *P. J. Alexander 1195* (BRY, DUKE, NMC). **72.** Carson National Forest, E side of Rio Grande below Cebolla Mesa, ±1 mile S of the confluence with Red River, ±7.5 miles SW of Questa, ±16.5 miles NNW of Taos, 10 May 2007, *P. J. Alexander 610* (DUKE, NMC). Torrance Co.: **73.** NE base of Cougar Mountain, NE side of the Gallinas Mts., Cibola National Forest, ±7 miles W of Corona, 1 Apr 2007, *P. J. Alexander 548* (NMC). **74.** On the W side of NM Hwy 42, Cibola National Forest, ±2.5 miles NW of Corona, 1 Apr 2007, *P. J. Alexander 551* (DUKE, NMC). Utah: San Juan Co.: **76.** WNW of Blanding along road to Elk Ridge near Butts Canyon ca. 5.14 km NE of Keystone Arch, 17 May 2004, *M. D. Windham 3077* (DUKE, NMC, MO).

Specimens not included in genetic analyses: New Mexico: Catron Co.: Datil Mountains, Cibola National Forest, 27 May 1999, *J. A. R. Ladyman 052799–02* (UNM); Datil Mountains, Cibola National Forest, 15 Jun 1999, *J. A. R. Ladyman 061999–15–13* (UNM); Cibola Co.: Ojo Redondo campground, Cibola National Forest, 20 Jun 1999, *J. A. R. Ladyman 062099–16–01* (UNM); Just inside Cibola National Forest on the N side of the Zuni Mts., S side of Tuces Valley, ±6 miles S of Thoreau, ±0.9 miles from NM Hwy 12, 7 May 2007, *P. J. Alexander 578* (NMC); McKinley Co.: Western Mexican Springs Experimental Area, 22 Apr 1934, *B. S. Klinger 169* (169); Navajo Indian Reservation, 19 May 1935, *R. O. Baird s. n.* (NMC); Taos Co.: Carson National Forest, E side of Rio Grande Canyon below Cebolla Mesa on F. S. Trail 102, ±7 miles SW of Questa, ±17 miles NNW of Taos, 10 May 2007, *P. J. Alexander 607* (NMC); Carson National Forest, E side of Rio Grande below Cebolla Mesa, ±1.65 miles S of the confluence with Red River, ±7.5 miles SW of Questa, ±16.5 miles NNW of Taos, 10 May 2007, *P. J. Alexander 612* (NMC).

7. **Boechera sanluisensis** P. J. Alexander, sp. nov.—TYPE: U. S. A. New Mexico: Taos Co.: Carson National Forest, S side of F.R. 97 on the W side of US Hwy 285, ±7.5 miles SSE of Tres Piedras, 19 May 2008, *P. J. Alexander 752* (holotype: NMC!; isotypes: DUKE!, MO!).

Plants mostly short-lived perennials, with 1 basal rosette arising at ground level, not on a woody caudex. Flowering stems 1 per rosette, arising centrally and terminating the rosette; lower parts hirsute with predominantly simple and a few forked trichomes, upper parts glabrous. Basal leaves narrowly oblanceolate, 12–23 × 2–5 mm, the margins usually entire, sometimes shallowly dentate; simple marginal trichomes present from petiole to leaf apex; blade surfaces glabrous or with a few simple and forked trichomes distally. Cauline leaves (9–)12–19, rarely concealing the stem proximally. Inflorescences usually simple; lower fruiting pedicels 6–12(–16) mm, glabrous or with a few simple or forked trichomes. Flowers with sepals sparsely hirsute distally with simple and forked trichomes; petals white, not darkening with age; pollen a mixture of narrowly ellipsoid, spheroid, and malformed grains. Fruits 1.5–1.8 mm wide, widely pendent, with irregularly biseriate seeds. Figure 12D.

Distribution, Habitat, and Phenology—Found from central Colorado to northern New Mexico and peripherally into northeastern Arizona (Fig. 5) on rocky (usually igneous) slopes and in level openings in ponderosa woodland and in mixed coniferous forest, rarely in the upper margins of pinyon-juniper woodland; 2,200–2,900 m. Flowering May–Jul.

Etymology—Named for the distribution of the species. *Boechera sanluisensis* is most abundant in the vicinity of the southern San Luis Valley in north-central New Mexico.

Comments—*Boechera sanluisensis* is most similar morphologically to *B. spatifolia* and is readily distinguished from most other members of the *fendleri* group (excepting *B. carrizozoensis* and *B. spatifolia*) by the narrowly oblanceolate basal leaves with prominent marginal cilia along their entire length and surfaces glabrous or sparsely pubescent with simple or forked trichomes. It is readily distinguished from *B. carrizozoensis* by its narrower fruits (1.5–1.8 vs. 2.4–3.0 mm wide), sparsely pubescent (vs. glabrous) bases of the flowering stems, and sparsely pubescent (vs. glabrous) sepals. Distinguishing it from *B. spatifolia* can be difficult; the only reliable macromorphological character is the orientation of the fruits (widely pendent vs. closely pendent) and observation of pollen is often necessary for the two to be separated with confidence. Geography can also aid in distinguishing the two, as *B. sanluisensis* is found primarily to the south and southwest of the range of *B. spatifolia*.

Additional Specimens Examined—Specimens included in the genetic analyses (population numbers are in bold): Arizona: Apache Co.: **77.** Navajo Nation; along road to top of Roof Butte ca. 50 m from top, 20 May 2002, *K. D. Heil 18828* (SJNM). Colorado: Custer Co.: **78.** 2.0 mi S & 1.0 mi W Wetmore (from junction with Hwy 67 in Wetmore: 2.1 mi S on Hwy 96, then 0.4 mi W upslope on Cronk Gulch Road), 26 May 1999, *Morse 3143* (COLO). Douglas Co.: **79.** 15 mi SW of Sedalia, between Sedalia & Deckers, 6 Jul 1951, *R. C. Rollins 5148* (GH). New Mexico: Colfax Co.: **80.** Ridge S of Philmont Reservoir, Philmont Scout Ranch near Cimarron, 2 Jun 1968, *R. L. Hartman 1799* (RM). Rio Arriba Co.: **81.** Carson National Forest, ±1.75 miles WNW of Tres Piedras, ±0.15 miles N of US Hwy 64, 9 May 2007, *P. J. Alexander 598* (DUKE, NMC). Carson National Forest, ±1.75 miles WNW of Tres Piedras, ±0.15 miles N of US Hwy 64, 9 May 2007, *P. J. Alexander 599* A, D (NMC). **82.** Santa Fe National Forest along F. R. 597 ± 0.7 miles N of Truchas, 18 May 2008, *P. J. Alexander 738* (NMC). Santa Fe National Forest along F. R. 597 ± 0.7 miles N of Truchas, 18 May 2008, *P. J. Alexander 739* (NMC). San Juan Co.: **83.** Navajo Nation; Beautiful Mountain Road, S side of mtn. & near junction with road leading up mountain, 10 May 2000, *K. D. Heil 14536* (SJNM). Taos Co.: **84.** Carson National Forest, W base of the Taos Mountains along an unlabelled forest road, ±3 miles S of Questa, ±1.2 miles NE of Lama, 10 May 2007, *P. J. Alexander 616* (NMC). **85.** Carson National Forest, S side of F.R. 97 on the W side of US Hwy 285, ±7.5 miles SSE of Tres Piedras, 19 May 2008, *P. J. Alexander 752* (DUKE, NMC). **86.** East Chiflo Trail, Wild Rivers Recreation Area, just below the east rim 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, 20 May 2008, *P. J. Alexander 759* (DUKE, NMC).

Specimens not included in the genetic analyses: New Mexico: Colfax Co.: SE of Black Lake, on and about W facing edge of mesa overlooking Black Lake, 28 May 1979, *R. Soreng 256* (NMC); San Juan Co.: Navajo Nation, southwest side of Beautiful Mountain ca. 4.5 miles east of Roof Butte, 10 May 2008, *A. Clifford 00–198* (SJNM); Navajo Indian Reservation, Chuska Mountains, turnoff to the radar station, 14 Jun 1985, *J. M. Porter 1308* (SJNM); Taos Co.: Carson National Forest, NW side of Valle Escondido, ±0.35 miles S of US Hwy 64, ±10.5 miles E of Taos, 9 May 2007, *P. J. Alexander 601* (NMC); Carson National Forest, W side of Capulin Canyon ±5.5 miles ESE of Taos, ±0.5 miles NE from US Hwy 64, 9 May 2007, *P. J. Alexander 605* (NMC); Carson National Forest, E side of Rio Grande Canyon just below Cebolla Mesa on F. S. Trail 102, ±7 miles SW of Questa, ±17 miles NNW of Taos, 10 May 2007, *P. J. Alexander 606* (NMC).

8. **Boechera zephyra** P. J. Alexander, sp. nov.—TYPE: U. S. A. New Mexico: Otero Co.: Cornudas Mountains, NE side of Wind Mountain, 0.9 miles NE of the summit, 2.2 miles N of the Texas state line, 10 Apr 2010, *P. J. Alexander 1136* (holotype: NMC!; isotypes: BRY!, DUKE!, MO!, TEX!, UC!).

Plants mostly long-lived perennials, with (1–)3–6(–10) basal rosettes usually elevated on woody caudices. Flowering stems 1 per rosette, arising centrally and terminating the rosette; glabrous. Basal leaves broadly oblanceolate, 12–40 × 5–10(–14) mm, margins shallowly dentate; simple marginal trichomes present on petiole only; blade surfaces pubescent with forked to 4-rayed trichomes. Cauline leaves 9–14, not concealing the stem proximally. Inflorescences often branched; lower fruiting pedicels 11–19 mm, glabrous. Flowers with glabrous sepals; petals pale lavender at anthesis, usually darkening to purple with age; pollen a mixture of narrowly ellipsoid and malformed grains. Fruits 2.0–2.4 mm wide, usually widely pendent, with irregularly biseriate seeds. Figure 13B.

Distribution, Habitat, and Phenology—Found along the southern edge of New Mexico and peripherally into adjacent Texas (Fig. 4) on rocky slopes on igneous or limestone substrates in Chihuahuan desert scrub or at the lower extremes of pinyon-juniper-oak woodland; 1,350–1,850 m. Flowering Mar–Apr.

Etymology—The Greek "*zephyrus*" refers to west wind. The predominate winds at the type locality, Wind Mountain, are from the west.

Comments—*Boechera zephyra* is very similar to *B. texana*, with which it shares many features, most notably: basal rosettes usually elevated above-ground on woody caudices; single, terminal flowering stems; flowering stems glabrous; basal leaves pubescent on the surfaces with forked to 4-rayed trichomes; and glabrous sepals. However, *B. zephyra* has narrower fruits (2.0–2.4 vs. 2.5–3.0 mm) and has only been found north of the range of *B. texana*. *Boechera zephyra* could also be confused with *B. porphyrea*, from which it is distinguished by the following characters: flowering stems central and terminating the basal rosettes (vs. usually several and lateral); basal leaves shallowly (vs. sharply) dentate and

never with 5- or 6-rayed trichomes (vs. usually with a few 5- or 6-rayed trichomes). This is the most narrowly distributed of the apomictic diploid hybrid species discovered in this study, known from only six populations, and may be of conservation concern.

Additional Specimens Examined—Specimens in genetic analyses (population numbers are in bold): New Mexico: Doña Ana Co.: **201.** Sierra de las Uvas, just down-canyon from the entrance to the FAA site where Corralitos Rd. turns to dirt, 3 Apr 2005, *P. J. Alexander 138* (NMC, UT). Sierra de las Uvas, Kerr Canyon, ±1.7 miles N of the summit of Magdalena Peak, ±0.7 miles S of White Gap Tank, 26 Mar 2007, *P. J. Alexander 535* (DUKE, NMC). **202.** Guadalupe Mountains, south of NM Hwy. 137 1.0 miles NE of the confluence of Dark Canyon and Turkey Canyon, 4.7 miles (linear) east of Queen, 13.1 miles SSE of Three Forks, 9 Apr 2010, *P. J. Alexander 1130* (BRY, DUKE, MO, NMC). **203.** Guadalupe Mountains, south side of Rocky Arroyo, 1.5 miles east of Three Forks, 8.1 miles NNW of Sitting Bull Falls, 9 Apr 2010, *P. J. Alexander 1134* (BRY, DUKE, MO, NMC). Guadalupe Mountains, south side of Rocky Arroyo, 2.6 miles east of Three Forks, 7.9 miles NNW of Sitting Bull Falls, 9 Apr 2010, *P. J. Alexander 1135* (BRY, DUKE, MO, NMC). NW of Carlsbad in Rocky Arroyo, 1.5 mi E of Three Forks, 11 Apr 1980, *R. W. Spellenberg 5451* (NMC). Otero Co.: **204.** Cornudas Mountains, NE side of Wind Mountain, 0.9 miles NE of the summit, 2.2 miles N of the Texas state line, 10 Apr 2010, *P. J. Alexander 1136* B (NMC), C (DUKE; TEX). Cornudas Mountains, NE side of Wind Mountain, 0.7 miles NE of the summit, 2.3 miles N of the Texas state line, 10 Apr 2010, *P. J. Alexander 1138* A (NMC). Cornudas Mountains, NE bajada of Wind Mountain, 1.1 miles NE of the summit, 2.3 miles N of the Texas state line, 10 Apr 2010, *P. J. Alexander 1140* (NMC). Cornudas Mountains, NE bajada of Wind Mountain, 1.1 miles NE of the summit, 2.3 miles N of the Texas state line, 10 Apr 2010, *P. J. Alexander 1141* (NMC; UNM). Torrance Co.: **205.** [uncertain placement; included here based on AWCLUST results but probably representing a separate species] 15 miles W of Encino on the S side of US 60, 13 May 2005, *P. J. Alexander 196* (NMC, UT). Texas: Hudspeth Co.: **206.** Slope of Black Mountain in Cornudas Mountains, 7 Apr 1970, *D. S. Correll 38380* (LL).

Only one specimen not included in the genetic analyses is known: New Mexico: Otero Co.: Fort Bliss Military Reservation, McGregor Range: Hueco Mountains, "Red Mountain" about 2.1 air miles NW of Bassett Ranch ruins and Wallbridge Tank. *R. D. Worthington 34628* (NMC).

9. **Other Hybrids**—We have not found any morphological features that consistently separate *B.* 'FST' from *B.* 'CP'. Thus, although *B.* 'FST' appears to represent a genetically distinct species, we feel that formal recognition of this taxon is premature considering its morphological similarity to *B.* 'CP' and the fact that both are known from few specimens. A combined description of *B.* 'FST' and *B.* 'CP' is provided below to facilitate comparison with the other taxa recognized herein.

Plants mostly short-lived perennials, with 1–2 basal rosettes arising at ground level, not elevated on woody caudices. Flowering stems 1 per rosette, arising centrally and terminating the rosette; glabrous. Basal leaves broadly oblanceolate, 11–25 × 4–8 mm, margins entire or shallowly dentate; simple marginal trichomes present on petiole only; surfaces pubescent with forked and 3-rayed trichomes. Cauline leaves (7–)11–18(–23), sometimes concealing the stem proximally. Inflorescences usually simple; lower fruiting pedicels 9–17 mm, glabrous. Flowers with glabrous sepals; petals white or pale lavender at anthesis, usually darkening to purple with age; pollen spheroid. Fruits 1.6–2.0 mm wide, widely pendent, with irregularly biseriate seeds. Figure 14C.

Distribution, Habitat, and Phenology—Found in Santa Fe County in northern New Mexico and extending south in a line to Culberson County, Texas (Fig. 5) on rocky (usually igneous) slopes in pinyon-juniper woodland, 1,500–2,300 m. Flowering Apr–May.

Comments—These hybrids are most similar to *B. porphyrea* but can be distinguished from that species by the following characters: flowering stem single and terminal (vs. usually several and lateral); basal leaves relatively small (11–25 × 4–8 mm vs. usually 25–60 × 7–15 mm), entire or obscurely dentate (vs. sharply dentate), and with forked and 3-rayed trichomes on the surfaces (vs. at least some trichomes 4- to 6-rayed).

Specimens Examined—Specimens included in the genetic analyses (population numbers are in bold): ***Boechera* 'FST':** New Mexico: Santa Fe Co.: **207.** Southwestern foothills of the Sangre de Cristo Mountains, west side of County Road 123, 1.7 road miles south of NM Hwy 503, ±300 feet WSW of the road, 2.3 miles SSW of Cundiyo, 2.2 miles NNW of the summit of Cerro Piñon, 8 May 2010, *P. J. Alexander 1189* (DUKE, NMC). On the east side of C. R. 123, ±2.3 air miles south of NM Hwy. 503, ±5.3 miles SSE of Chimayo, ±14.5 miles N of Santa Fe, 18 May 2008, *P. J. Alexander 735* (DUKE, NMC). **208.** Santa Fe, ±1.6 miles SE of Santa Fe Plaza on the N side of Camino Lejo on Museum Hill, on land recently acquired by the Santa Fe Botanical Garden, 11 May 2007, *P. J. Alexander 618* (DUKE, NMC). **209.** Just E of the city of Santa Fe on slope above Santa Fe River ca. 1.32 km ESE of the summit (7617) of Cerro Gordo, 25 May 2009, *M. D. Windham 3755* (DUKE, NMC). ***Boechera* 'CP':** New Mexico: Lincoln Co.: **210.** Southern Jicarilla Mountains on the south side of Forest Road 483 1.9 road miles west of Forest Road 72, 1.7 miles ENE of the highest point on Castle Garden Mesa, 4.5 miles SSW of Ancho Peak, 19 Apr 2010, *P. J. Alexander 1151* (BRY, DUKE, MO, NMC). Los Alamos Co.: **211.** West side of the Rio Grande, southeast of White Rock on the Red Dot Trail, 4.7 miles SSE of the junction of NM Hwy 502 and NM Hwy 4, 4.3 miles NNE of Montoso Peak, 4 May 2010, *P. J. Alexander 1166* (DUKE, NMC). Otero Co.: **212.** Southeastern Sacramento Mountains, south side of Dog Canyon Road, 3.3 miles (linear) northeast of Avis, 3.1 miles E of the Bluewater Lookout Tower, 8 Apr 2010, *P. J. Alexander 1125* (NMC). Santa Fe Co.: **213.** Caja del Rio Plateau on the west side of Forest Road 25, 2.2 miles east of Colorado Peak, 8.6 miles NW of the junction of NM Hwy 599 and Interstate 25, 6 May 2010, *P. J. Alexander 1182* (BRY, DUKE, NMC). Torrance Co.: **214.** In the pass between Cougar Mt. and North Cougar Mt., on the SE side of the smaller of the two peaks of North Cougar Mt., NE side of the Gallinas Mountains, Cibola National Forest, ±7 miles W of Corona, 1 Apr 2007, *P. J. Alexander 549* (NMC). Texas: Culberson Co.: **215.** Down canyon from Headquarters 2.6 miles; near road on bank of creek; south fork of Victorio Canyon, 11 Mar 1962, *J. Read A-394* (SRSC).

Acknowledgments. We thank the following institutions for loans of specimens and permission to remove material for DNA isolation: Northern Arizona University (ASC), Arizona State University (ASU), University of Arizona (ARIZ), University of Colorado (COLO), Colorado State University (CS), Harvard University (GH), University of Texas at Austin (LL and TEX), University of Wyoming (RM), Rancho Santa Ana Botanic Garden (RSA), San Juan College (SJNM), Sul Ross State University (SRSC), University of New Mexico (UNM), Utah Museum of Natural History (UT), and Washington State University (WS). We would also like to thank Brook Milligan for assistance with the hybrid assignment test, Gerritt McGill for producing illustrations, and David Anderson, Gene Jercinovic, Chick Keller, and Lillis Urban for assistance with fieldwork. This research was supported by NSF grants DEB-0817033 and PGR MCA 1238731, and by a grant to the first author by the Otero Chapter of the New Mexico Native Plant Society.

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