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RESEARCH ARTICLE

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An in-depth investigation of cryptic taxonomic diversity in the rare endemic mustard *Draba maguirei*

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Abstract

Premise: Previously published evidence suggests that *Draba maguirei*, a mustard endemic to a few localities in the Bear River, Wellsville, and Wasatch Mountains of northern Utah, may represent a cryptic species complex rather than a single species. Conservation concerns prompted an in-depth systematic study of this taxon and its putative relatives.

Methods: Sampling most known populations of *D. maguirei* s.l. (*D. maguirei* var. *maguirei* and *D. maguirei* var. *burkei*), we integrate data from geography, ecology, morphology, cytogenetics and pollen, enzyme electrophoresis, and the phylogenetic analysis of nuclear internal transcribed spacer sequences to explore potential taxonomic diversity in the species complex.

Results: *Draba maguirei* var. *burkei* is shown here to be a distinct species (*D. burkei*) most closely related to *D. globosa*, rather than to *D. maguirei*. Within *D. maguirei* s.s., the northern (high elevation) and southern (low elevation) population clusters are genetically isolated and morphologically distinguishable, leading to the recognition here of the southern taxon as *D. maguirei* subsp. *stonei*.

Conclusions: Our study reveals that plants traditionally assigned to *D. maguirei* comprise three genetically divergent lineages (*D. burkei* and two newly recognized subspecies of *D. maguirei*), each exhibiting a different chromosome number and occupying a discrete portion of the geographic range. Although previously overlooked and underappreciated taxonomically, the three taxa are morphologically recognizable based on the distribution and types of trichomes present on the leaves, stems, and fruit. Our clarification of the diversity and distribution of these taxa provides an improved framework for conservation efforts.

KEYWORDS

Brassicaceae, conservation, cytogenetics, dysploidy, enzyme electrophoresis, ITS phylogeny, pollen, SEM, trichomes, Utah

Although originating in obscure, scholarly discussions (Sarkar, 2021), the term "biodiversity" is now ubiquitous in human communication. Because of our misuse of planetary resources, we find ourselves amid a biodiversity extinction crisis that has the potential to devastate life on Earth (Ceballos et al., 2020). Given our dependence on the vast, intricate web of life for our survival, we must combat the mass extinction our species has initiated (Díaz et al., 2006). One of the many challenges to these critical conservation efforts is the fact that we are making decisions based on patently incomplete inventories (Costello et al., 2013). Because we cannot appreciate or protect taxa of which we are unaware, systematic studies focused on the discovery of undetected biodiversity have become critical.

Although often referred to as "cryptic," genetically discrete taxa that are only subtly differentiated are no less foundational to the web of life than their showier congeners. Cryptic taxa are especially common in rapidly evolving lineages, i.e., those most likely to replenish depleted biodiversity in the shortest time. Despite being crucial in our quest to conserve biodiversity, cryptic taxa are a major challenge for taxonomists (Löve, 1964; Grant, 1981; Soltis et al., 2007) because their detection often requires more sophisticated tools than a hand lens or dissecting microscope. Deciphering a cryptic species complex is best achieved by integrating a broad set of systematic approaches (Scheen et al., 2002; Windham et al., 2022a, 2022b), and classifications based on a consensus of morphological,

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ecological, cytogenetic, and molecular characters are more likely to provide the higher levels of confidence required for protection under the Endangered Species Act (ESA) and other environmental laws (Haig et al., 2006). Here we apply this principle to resolving cryptic taxonomic diversity within the North American *Draba maguirei* complex (Brassicaceae).

The hyperdiverse genus *Draba* currently comprises >400 species (Al-Shehbaz, 2018), making it the most species-rich and demonstrably monophyletic genus in the mustard family (Jordon-Thaden et al., 2010; Hohmann et al., 2015). *Draba* exhibits frequent hybridization (Koch and Al-Shehbaz, 2002; Windham, 2003) and rampant polyploidization (Brochmann et al., 1992; Grundt et al., 2004; Jordon-Thaden and Koch, 2008). Some polyploidization events in the genus appear to have triggered additional rounds of speciation via aneuploidy or dysploidy (Beilstein and Windham, 2003). As a result, *Draba* is rife with undetected, cryptic species (Gustafsson et al., 2014), and has become a focus for the description of taxa new to science (Al-Shehbaz, 1989, 1991, 1994, 2009, 2012, 2014, 2016, 2018; Al-Shehbaz and Windham, 2007; Al-Shehbaz and Mulligan, 2014; Mulligan, 2021). *Draba* is most common at high latitudes in the Northern Hemisphere, but its primary centers of biodiversity lie farther south and are associated with the Tibetan Plateau, the northern Andes, and the central Rocky Mountains of North America. Just over 50% of *Draba* species are considered "narrowly distributed," and these rare, endemic taxa are almost equally divided among the three ecoregions listed above (Jordon-Thaden et al., 2013).

More than a quarter of all accepted *Draba* species are found in North America, with Rollins (1993) listing 104 species from the continent and Al-Shehbaz et al. (2010) reporting 121. Most of these are concentrated in the western third of the continent where suitable montane habitats are sporadically distributed across millions of hectares of inhospitable valleys, steppes, and deserts (Cronquist et al., 1972). The isolation of these habitat islands is conducive to rapid speciation in organisms with relatively low vagility (Brown, 1978), which may help explain the impressive diversity of *Draba* in the region. As botanical exploration of the mountains of western North America has intensified (Cronquist et al., 1972; Hartman and Nelson, 1998; Ertter, 2000), the number of recognized taxa has mushroomed. Roughly 20% of the *Draba* species Rollins (1993) attributed to this region were named in the preceding 60 years.

The discovery of new *Draba* taxa in western North America has continued unabated during the last 30 years, culminating in the recognition of more than a dozen additional species (Al-Shehbaz and Windham, 2007; Al-Shehbaz and Mulligan, 2014; Mulligan, 2021) as well as a proliferation of taxa at the varietal level (Welsh, 2015). Most of these taxa have very limited distributions and are poorly represented in herbaria. Not surprisingly, as the number of described taxa has increased, so has the diversity of taxonomic opinions about them. Continuing disputes over the significance of specific morphological characters (especially trichomes) have led to divergent classifications in regional and continental floristic treatments. This lack of consensus negatively affects the development of conservation strategies for the many rare taxa involved. The taxa herein referred to as the "*Draba maguirei* alliance" provide a prime example of this.

Draba maguirei was originally named and characterized in 1941 by C. L. Hitchcock (see Table 1), who described *D. maguirei* var. *maguirei* based on collections from Mt. Naomi in the Bear River Range of northern Utah (USA). Plants occurring in the Wellsville Mountains (across the Cache Valley to the southwest), which seemingly differed only in having unbranched trichomes on their leaves, were distinguished as *D. maguirei* var. *burkei*. Hitchcock (1941) also named *D. apiculata*, a taxon of uncertain relationship to *D. maguirei*, based on materials from the Uinta Mountains in northeastern Utah. Rollins' (1993) classification of this group is very similar to Hitchcock's original treatment (Table 1). He recognized the same two varieties of *D. maguirei* but remarked (Rollins, 1993: p. 432) that "var. *burkei* may prove worthy of specific rank once adequately studied." Rollins maintained Hitchcock's *D. apiculata* at the species level, but recognized it using the name *D. globosa*, which has nomenclatural priority by 24 years.

With the aim to clarify the taxonomy of *Draba maguirei* and other taxa occurring in the Intermountain region of western North America, Windham (2000, 2003) undertook cytogenetic analyses to supplement existing macromorphological data sets. A sample of *D. maguirei* var. *maguirei* yielded chromosome counts of $n = 16$ (Windham, 2000), whereas two populations representing the *burkei*

TABLE 1 Comparison of taxonomic treatments of *Draba maguirei* and allied taxa.

Hitchcock (1941)	Rollins (1993)	Holmgren (2005); Al-Shehbaz et al. (2010)	Welsh (2003, 2015)	Taxonomy adopted here
D. maguirei var. *maguirei*	*D. maguirei* var. *maguirei*	*D. maguirei*	*D. maguirei* var. *maguirei*	*D. maguirei* subsp. *maguirei* subsp. *stonei*
D. maguirei var. *burkei*	*D. maguirei* var. *burkei*	*D. burkei*	*D. maguirei* var. *burkei*	*D. burkei*
D. apiculata	*D. globosa*	*D. globosa*	*D. densifolia* var. *globosa*	*D. globosa*

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morphotype showed $n = 10$ (Windham, 2003). This difference in chromosome number, combined with geography and then-unpublished DNA data, led Windham (2003) to recognize *D. burkei* as a new species. As indicated in Table 1, this taxonomy was subsequently adopted by Holmgren (2005) and Al-Shehbaz et al. (2010). Departing from this developing consensus, Welsh (2015) maintained *D. burkei* as a variety of *D. maguirei* and treated *D. globosa* as a variety of *D. densifolia* without providing any evidence to support the relationships implied by this classification.

The choice between variety or species has profound implications for the conservation and continued survival of the taxa involved. Under the broad circumscription of Welsh (2015), *Draba maguirei* is a northern Utah endemic known from fewer than two dozen localities in the Bear River, Wellsville, and Wasatch Mountains. Even when *D. maguirei* is considered as a single panmictic taxon, the Utah endemic is regarded as globally imperiled (G2; NatureServe, 2022). However, if additional cryptic taxa are included within it, any or all entities may be threatened or endangered and require human intervention to ensure their long-term survival. The appropriate level of concern and the type of intervention required in this case cannot be determined without resolving the relationships and taxonomic status of *D. maguirei* var. *maguirei, D. maguirei* var. *burkei*, and the questionably related *D. globosa*. Here, we integrate data from biogeography, ecology, morphology (including scanning electron microscope [SEM] analyses), cytogenetic and pollen studies, enzyme electrophoresis, and phylogenetic analyses of internal transcribed spacer (ITS) sequences to investigate the distribution, taxonomy, and conservation status of *Draba maguirei* and allied taxa.

MATERIALS AND METHODS

Geography and ecology

Accurate distributional information is critical to determining the taxonomic status of *Draba maguirei* var. *burkei* (hereafter called *D. burkei* anticipating the outcome of this study). Both Hitchcock (1941) and Rollins (1993) implied that *D. maguirei* and *D. burkei* occupy nonoverlapping (allopatric) ranges. If this observation proves true for all known collections and populations, it will strengthen the argument for recognizing *D. burkei* at the species level. To this end, we examined all specimens of the *D. maguirei* complex housed in the regional herbaria at BRY, OGDF, UT, UTC, and WSCO (herbarium acronyms according to Thiers [2016]). These collections provided baseline data for geographic distributions, substrate preferences, and other important ecological parameters. This information was used to relocate known populations and identify comparable habitats to be examined in the field.

Field surveys were conducted over four summers (1995–1998) in the Bear River, Monte Cristo, Wellsville, Wasatch, Deep Creek, and western Uinta Mountains of Utah. Through the combined efforts of R. D. Stone, F. G. Smith, N. H. Holmgren, M. J. Windham, and M. D. Windham, most previously identified populations of *Draba maguirei* and its allies were relocated, and several new localities were discovered. For each site visited, detailed notes were taken regarding the number of plants present and their preferred habitats. At least five populations of each taxon (Table 2), covering most of the geographical range as well as the ecological and morphological variability, were chosen for additional study. Localities of specimens used in the study were mapped with the *ggmap* package (v.3.0.0; Kahle and Wickham, 2013) for *ggplot2* (v.3.3.6; Wickham, 2016) in R (R Core Team, 2022), using map tiles by Stamen Design (http://stamen.com) under a Creative Commons license (CC BY 3.0), with data by OpenStreetMap (http://openstreetmap.org) under Open Data Commons Open Database License (ODbL) (http://www.openstreetmap.org/copyright).

Morphology

Materials included in the morphological study consisted of whole plants and/or caudex branches broken off at ground level. These samples were kept fresh in moist paper towels in Ziploc bags stored in an ice chest until they could be returned to the lab (up to two days). In the lab, the plants were examined microscopically (see below) and assigned individual numbers. These numbers were used to ensure one-to-one correspondence between morphological and isozyme samples, facilitating the detection of any misidentified plants or cryptic taxa. Sample sizes for these analyses are listed in Table 2. Following the removal of material (usually a single leaf) for isozyme study, the morphological samples were placed in a standard plant press and air-dried for an average of two weeks.

After drying, each plant in a population sample was examined using a Wild dissecting microscope. All features traditionally used to distinguish *Draba* taxa occurring in Utah and adjacent states were observed. These included habit; flower color; style length; fruit shape; leaf size, shape, and arrangement; and the nature of the pubescence. Several discrete morphotypes were encountered during this analysis, and representative samples of each were prepared for examination using an SEM. Materials observed on the SEM included individual fruits, stems, and leaves removed from the air-dried plants discussed above. These were mounted on standard SEM stubs with double stick tape and sputter coated with a gold-palladium alloy (60/40). All specimens were examined on a Hitachi S-450 microscope at an accelerating voltage of 15 KeV. Characters useful for delineating taxa and their potential relationships were photographically documented using Polaroid Type 55 P/N film.

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TABLE 2 Populations used in morphological, cytogenetic, and enzyme electrophoretic studies of *Draba maguirei* and allied taxa. All collections from Utah (vouchers deposited at UT); duplicates are noted wherever available. Collection locality, *collector information*, chromosome number (*n*), and sample size for morphological studies indicated for each accession. * = populations also included in the DNA study.

***Draba maguirei* subsp. *maguirei* (northern)**		
Cache Co., ENE of Logan in the Bear River Mountains along Naomi Peak Trail, *Windham et al. 4531*	*n* = 16	6
Cache Co., S slope of Mt. Gog, Bear River Range, *Windham 95-156*	*n* = 16	18
*Cache Co., SE slope of Mt. Magog, Bear River Range, *Windham 95-161*	*n* = 16	36
***Draba maguirei* subsp. *stonei* (southern)**		
*Cache Co., ENE of Logan in the Bear River Mts, along U.S. Rte. 89, ~0.8 road miles ENE of the entrance to Woods Camp Campground, *Windham & Windham 97-118; Windham 4474, 4497*	*n* = 8	27
Cache Co., Card Canyon ~0.5 mi. SE of Logan Canyon, *Stone & Smith 1796*	*n* = 8	19
Cache Co., Monte Cristo Range near Mollens Hollow, *Stone & Smith 1804*	*n* = 8	12
Draba burkei		
Box Elder Co., Cottonwood Canyon, Wellsville Mountains, *Windham et al. 95-113*	*n* = 10	25
Box Elder Co., NW slope of Willard Peak, Wasatch Mountains, *Windham & Stone 95-163*	*n* = 10	22
Cache Co., first canyon N of Wide Hollow, Wellsville Mountains, *Windham & Windham 97-126*	—	12
*Cache Co., James Peak, S end of the Cache Valley, *Windham & Windham 97-134*	—	14
*Weber Co., Chicken Creek, E slope of the Wasatch Mountains, *Windham & Stone 95-116* (flowering); *Windham & Windham 97-128* (fruiting)	*n* = 10	32
*Weber Co., head of Upper Ogden Bowl, Mt. Ogden, *Windham et al. 95-168*	*n* = 10	22
Draba globosa		
*Duchesne Co., N slope of Murdock Mt., Uinta Mountains *Windham 95-219*	—	20
*Juab Co., E side of Haystack Peak, Deep Creek Mountains *Windham & Holmgren 95-189*	—	1
*Salt Lake Co., head of Peruvian Gulch, Wasatch Mountains *Windham & Windham 95-227*	—	33
Salt Lake Co., Wasatch Mountains, NE slope of Devils Castle, *Stone 1860*	—	24
Summit Co., SW slope of Bald Mt., Uinta Mountains *Windham 95-216*	—	27

Chromosome and pollen studies

Fieldwork was conducted early in the montane growing season (May–July) to facilitate the collection of materials for meiotic chromosome analyses. Samples consisted of young (preblooming) inflorescences that were picked fresh and placed in vials containing Farmer's fixative (3 parts ethanol/1 part glacial acetic acid). Materials fixed in this manner were kept at moderate temperatures (20–25°C) for 24 hr, then transferred to a standard freezer (–20°C) where they were stored in 70% ethanol for up to 27 years prior to analysis.

Chromosome slides were prepared following the detailed protocol of Windham et al. (2020) using buds <1 mm in diam. All stages of meiosis were studied, with chromosome counts derived from first division meiocytes at late prophase, metaphase, and anaphase. Representative cells were photographed using a Canon EOS Rebel T3i digital camera (Canon Inc., Japan) mounted on a Meiji MT5310L microscope (Meiji Techno, Japan). Pollen samples were obtained from undehisced anthers of recently opened flowers taken from the same inflorescences. Anthers were individually transferred to droplets of 1% acetocarmine stain and ruptured with the tip of a dissecting needle. When most pollen grains had settled on the slide surface in a single focal plane, pollen size and morphology (proportion of well-formed vs. malformed grains) were documented using the microscope–camera setup indicated above.

Enzyme electrophoresis

Active enzymes were extracted from fresh, field-collected material (the origin of which is discussed in the Morphology section above). For each plant analyzed, a small section (~25 mm^2) of leaf tissue was placed in a porcelain spot plate with 12 drops of grinding buffer and crushed with the base of a glass test tube. We used the phosphate-PVP grinding buffer of Soltis et al. (1983), modified by the addition of dimethylsulfoxide (DMSO) to a final concentration of 10% (v/v). The slurry produced by grinding was absorbed into

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Whatman 3MM chromatography paper wicks that were stored (up to two years) in an ultracold freezer at −70°C.

To separate the enzymes into their component isozymes, the samples were inserted into 12.5% starch gels prepared with an appropriate buffer system. Five different buffer systems were used to survey enzyme variability: systems 1 and 6 (from Soltis et al., 1983), systems 8 and 11 (as modified by Haufler [1985]), and system M, a pH 7.5 version of the morpholine-citrate system used by Odrzykoski and Gottlieb (1984). Whenever possible, enzymes were run on two or more buffer systems to ensure that comigration of bands in different individuals was a true reflection of genetic similarity. Ten enzymes were assayed (Table 3). The enzymes malate dehydrogenase (MDH) and phosphoglucomutase (PGM) were assayed using recipes provided by Werth (1985); all other staining schedules were adapted from Soltis et al. (1983).

Band patterns on the stained gels were photographed using Kodak Technical Pan 2415 film. Genotypes were inferred directly from electromorphs observed on the stained gels based on the assumption that enzyme substructure and compartmentalization in *Draba* are similar to those observed in other flowering plants (Gottlieb, 1981). For each enzyme, the loci coding for different isozymes were numbered sequentially from anode to cathode. The identities of isozymes between populations and species were verified by running samples side-by-side on the same gels.

DNA isolation, amplification, and sequencing

DNA sampling of the *Draba maguirei* alliance was designed to encompass the geographical, morphological, and chromosomal diversity encountered in the group (Table 2). Two samples of *D. maguirei* were included, one representing the northern cluster of populations and one the southern. The three *D. burkei* plants analyzed encompassed the high and low elevation extremes, much of the substrate diversity, and the geographic outlier on James Peak. *Draba globosa* was sampled from each of the three mountain ranges where it was known to occur in Utah (see Table 2).

The primary goal of the DNA sequence analysis was to estimate genetic divergence among members of the *D. maguirei* alliance and explore their phylogenetic relationships. Because this necessitated a broader sampling of *Draba* species, we included other species from the central Rocky Mountains and vicinity for which previously published cytogenetic data were available. All major *Draba* clades identified by the broad phylogenetic analysis of Jordon-Thaden et al. (2010) were included. Our analysis incorporated 16 samples representing their "Group II" (a largely New World dysploid clade), six samples from their "Group III" (a circumboreal euploid clade), and two samples of their "Group I" (a largely Eurasian euploid clade of questionable monophyly). *Draba verna*, a Eurasian native escaped in Utah, was included to represent the "less diverged *Draba* group" of Jordon-Thaden et al. (2010). All ITS sequences for *Draba* species were previously published, except for *D. maguirei* subsp. *stonei*, which was newly generated for this study. Published sequences of *Arabis alpina* and *A. nuttallii* provided outgroups for the analysis.

DNA samples consisted of 10–20 mg of leaf tissue gathered from air-dried (pressed) or silica-dried plants collected between 1995 and 1997. The DNA was obtained using a cetyltrimethyl ammonium bromide (CTAB) extraction protocol (Hillis et al., 1996) and diluted 1:10 and 1:20

TABLE 3 Enzymes surveyed during electrophoretic study of *Draba maguirei* and allied taxa with Enzyme Commission numbers in parentheses, acronyms, buffer systems providing the best resolution, number of loci resolved, and number of loci showing apparent duplications. * = loci at which *D. burkei* is more like *D. globosa* than it is to *D. maguirei*.

Enzyme (E.C. Number)	Acronym	Buffer system[1]	Loci resolved	Loci duplicated
Alcohol dehydrogenase (1.1.1.1)	ADH	8	1	0
Aldolase (4.1.2.13)	ALD	11	1	0
Isocitrate dehydrogenase (1.1.1.42)	IDH	M	1	1
*Leucine aminopeptidase (3.4.11.-)	LAP	8	1	0
Malate dehydrogenase (1.1.1.37)	MDH	M	4	3
Phosphoglucoisomerase (5.3.1.9)	PGI	6	2	1
Phosphoglucomutase (2.7.5.1)	PGM	6	2	1
6-Phosphogluconate dehydrogenase (1.1.1.44)	6-PGDH	1	2	1
*Shikimate dehydrogenase (1.1.1.25)	SkDH	1 & M	1	0
*Triosphosphate isomerase (5.3.1.1)	TPI	6	2	1

[1]Systems 1 and 6 taken from Soltis et al. (1983); Systems 8 and 11 as described by Haufler (1985); system M (morpholine) taken from Odrzykoski and Gottlieb (1984).

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in preparation for polymerase chain reaction (PCR). The ITS regions of nuclear ribosomal DNA were selected as the most appropriate subject for phylogenetic reconstruction in *Draba*. The two ITS regions (and the intercalated 5.8S gene) were PCR amplified using the primers ITS1 and ITS4 (White et al., 1990). Each 20 µl amplification reaction contained 13.7 µl H_2O, 2.0 µl 10× buffer, 1.4 µl $MgCl_2$, 0.4 µl dNTP's, 0.12 µl AmpliTaq, 1.0 µl of each primer, and 0.75 µl diluted DNA template, added in that order. We used a standard PCR amplification program beginning with a 2 min 30 s denaturation, followed by 35 cycles of denaturation for 20 s at 95°C, annealing for 30 s at 47°C, and extension for 1 min at 73°C. Following these cycles, the program terminated with a final extension period of 4 min at 73°C. All PCR products were cleaned using a QIAGEN QIAquick PCR purification kit and sequenced on an ABI 377 automated sequencer using dye-terminator chemistry. Both strands of the double-stranded PCR product were sequenced to ensure a complete and accurate reading in all taxa sampled.

The resultant nucleotide sequences were edited using Sequencher 3.0 (GeneCodes, Ann Arbor, MI). Edited sequences of all taxa were aligned in AliView v1.28 (Larsson, 2014). Ambiguously aligned regions, of which there were few, were excluded from the data set. Boundaries between the two ITS regions and the 5.8S subunit were established by comparison with a sequence of *Arabidopsis thaliana* (accession #X52320) downloaded from GenBank.

The best fitting substitution model for the ITS data set (SYM+I+G4) was selected using ModelTest- NG v0.1.6 (Darriba et al., 2020) based on the Akaike information criterion (Akaike, 1974). Maximum likelihood analyses were carried out in RAxML-NG v1.1.0 (Kozlov et al., 2019), with bootstrap support (MLBS) for the most likely tree calculated from 1000 replicates. Bayesian inference was performed using MrBayes v3.2.7 (Ronquist et al., 2012) in three independent runs, each with four chains (three heated, one cold). Chains were run for 10 million generations, with trees sampled every 1000 generations. Output parameters for each run were compared in Tracer v1.7.1 (Rambaut et al., 2018) to ensure runs reached convergence. The first 25% of sampled trees were discarded as burn-in, with the remaining trees used to generate a majority-rule consensus tree and calculate clade posterior probabilities (PP).

RESULTS

Geography and ecology

The habitats of *Draba maguirei* and *D. burkei* are superficially quite similar. Both taxa occur on rocky slopes or ledges at elevations from 1800–3000 m. They each favor shaded, north-facing slopes at lower elevations, and more exposed habitats of variable aspect at high elevations. Lists of associated (dominant) genera were nearly identical, including various combinations of *Acer, Pseudotsuga, Pinus, Abies, Juniperus, Cercocarpus, Poa, Agrostis*, and *Carex*. Ecologically, the superficially similar *Draba globosa* resembles high elevation populations of the other two, growing in rocky sites (usually close to late-melting snowbanks) in association with *Abies, Picea*, and a diversity of grasses and forbs. Unlike *D. maguirei* and *D. burkei*, this species occurs near timberline and was not found below 3000 m elevation.

Despite their general ecological similarities, *Draba maguirei* and its allies exhibited clear differences in geographic distribution and substrate preference. Intensive fieldwork associated with this project did not reduce the geographic distance between known populations of *D. maguirei* and *D. burkei*; they remained separated by a gap of 11.5 km (Figure 1). *Draba maguirei* is composed of three population clusters in the Bear River and Monte Cristo Ranges: (1) a high elevation (2500–3000 m) northern group tightly concentrated around the type locality on Mt. Naomi; (2) a low elevation (1800–2200 m) southern group found in Logan Canyon and its lower tributaries; and (3) an isolated, low elevation population situated 10 km to the southeast in the Monte Cristo Range.

Plants matching the description of *D. burkei* occurred in four areas (Figure 1) across the Cache Valley to the southwest: (1) a northern cluster that includes the type locality in the Wellsville Mountains; (2) a central group concentrated on Willard Peak and Mt. Ben Lomond; (3) a southern outlier occurring on Mt. Ogden; and (4) an eastern population cluster centered on James Peak. All plants of *D. burkei* were confined to the Wellsville and Wasatch Mountains, except for the last-mentioned cluster. Physiographically, James Peak is considered the southernmost summit of the Bear River Range. However, it lies just west of the main Cache Valley fault and is geologically more like the Wasatch Mountains located just 5 km to the southwest (Stokes, 1963). In Utah, *D. globosa* was found only in the Deep Creek, Wasatch, and Uinta Mountains, well south of the ranges of the other taxa. *Draba burkei* and *D. globosa* both occurred in the Wasatch Mountains, but their ranges were separated by 60 km.

Field observations of preferred geologic substrates revealed an interesting pattern to the distribution of *Draba maguirei* and allied taxa. Throughout its narrow range, *D. maguirei* occurred almost exclusively on dolomite, a rock whose unusual chemical composition produces nutrient-poor soils with high magnesium content (Mota et al., 2021). Indeed, the Bear River Range is well known for its endemic flora, including such species as *Primula maguirei, Erigeron cronquistii, Musineon lineare*, and *Viola frank-smithii*. Most of these are dolomite endemics with distributions very similar to that of *D. maguirei*. Herbarium labels frequently report *D. maguirei* growing on limestone, a substrate superficially like dolomite. Because some of these collecting sites were not revisited during this project, we cannot rule out the occasional occurrence of *D. maguirei* on limestone.

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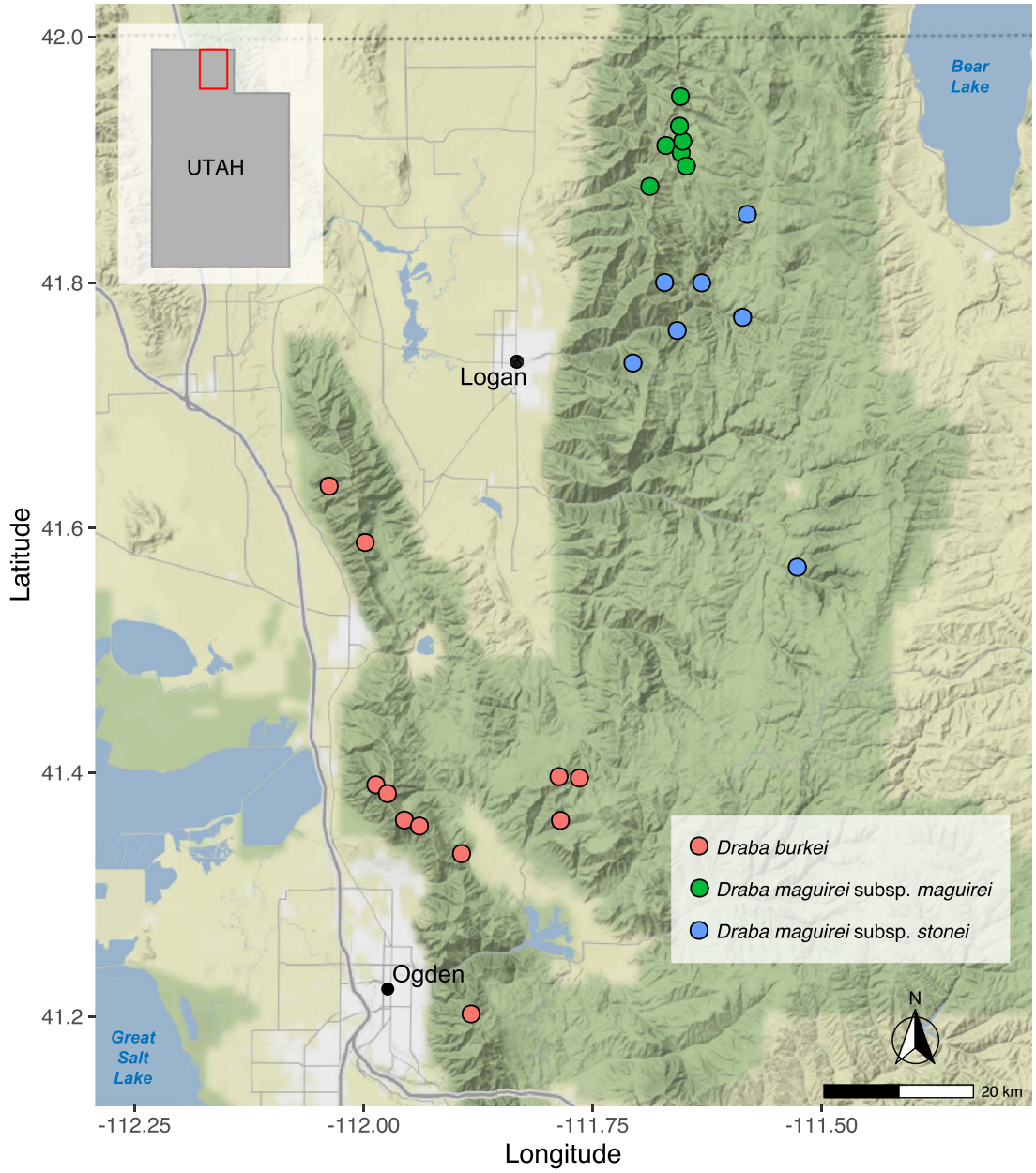

FIGURE 1 Geographic distributions of *Draba maguirei* and allied taxa as confirmed by study of herbarium specimens. Green dots = *D. maguirei* subsp. *maguieri*. Blue dots = *D. maguirei* subsp. *stonei*. Orange dots = *D. burkei*. Map tiles by Stamen Design, under CC BY 3.0. Data by OpenStreetMap, under ODbL.

The substrate preferences of *D. burkei* were markedly different. At the southern end of its range, it primarily occurred on quartzite. The isolated population on James Peak was found on quartzite as well. Plants of *D. burkei* in the northern and central portion of its range typically grew on limestone or calcareous shale outcrops. This taxon currently is not known to occur on dolomite. However, limestone and dolomite strata are closely associated in the Wellsville Mountains (Stokes, 1963), and it is possible that *D. burkei* eventually may be found on dolomitic substrates. It is interesting to note that the substrate preferences of *D. globosa* (quartzite and granitic rocks) are more like those of *D. burkei*.

Morphology

Among the characters included in our morphological study of the *Draba maguirei* alliance, several were invariant. All taxa possessed yellow flowers and oblong-oblanceolate leaves arranged in basal rosettes (i.e., the flowering stems were scapose). All three tended to be caespitose at higher elevations, though *D. maguirei* and *D. burkei* developed elongate, trailing caudex branches at lower elevations. Although fruit shape is commonly used to identify taxa within *Draba*, the variability encountered in the *D. maguirei* alliance appeared uncorrelated with geography. Variation in

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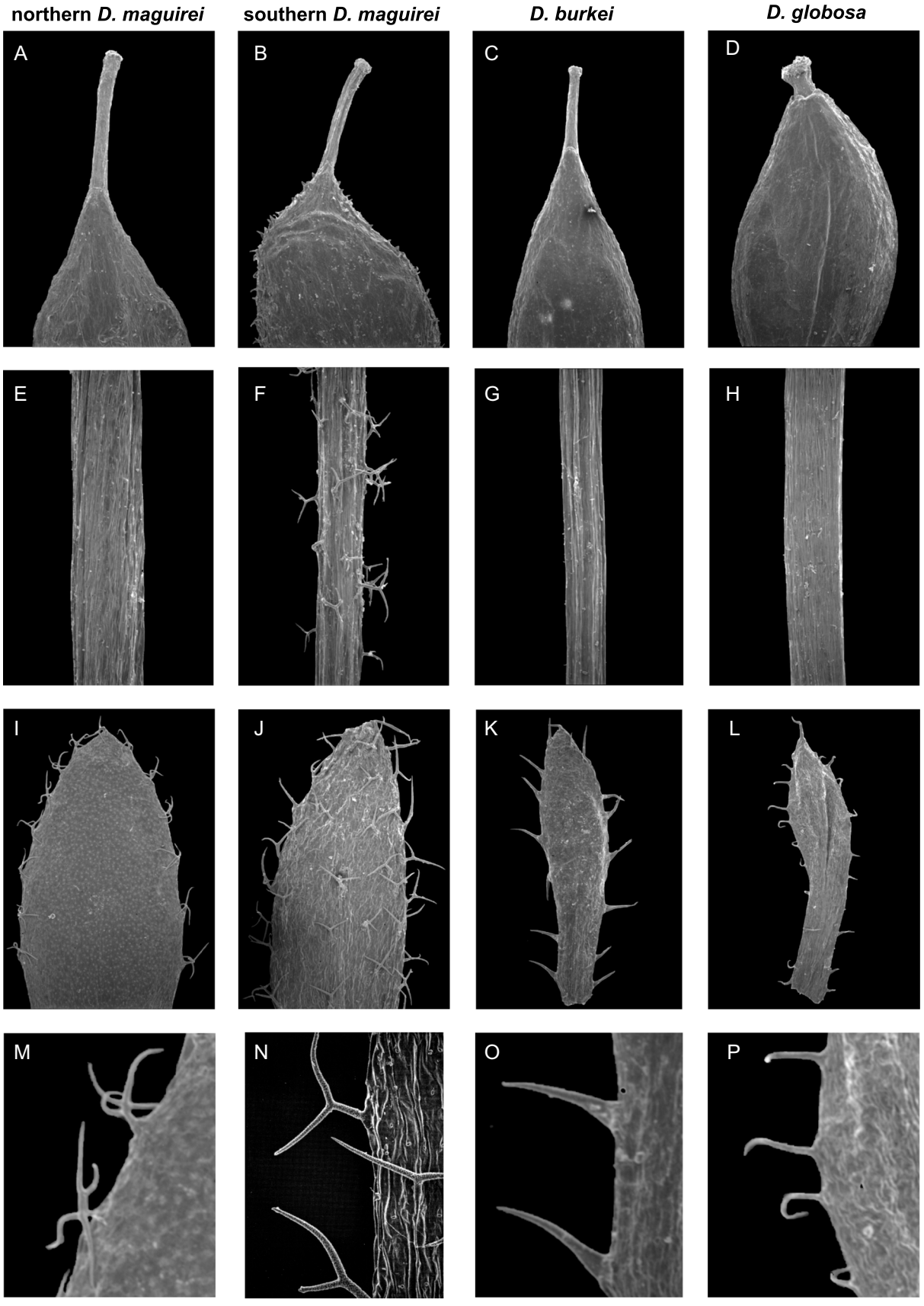

FIGURE 2 (See caption on next page)

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this character (Figure 2A–D) was likely a function of individual reproductive success, wherein fruits maturing different numbers of seeds exhibit somewhat different shapes.

The remainder of the morphological characters analyzed showed variation within the alliance that was geographically correlated. These features, some of which are potentially valuable indicators of relationships, are illustrated in Figure 2. SEM micrographs of developing fruits clearly display the differences in style length that have figured prominently in past taxonomic treatments of the alliance. *Draba maguirei* (Figure 2A, B) and *D. burkei* (Figure 2C) consistently had styles greater than 0.7 mm in length. The styles of *D. globosa* (Figure 2D) did not exceed 0.6 mm and tend to have a much more prominent stigma. Fruits in this alliance typically were glabrous, but many individuals among southern populations of *D. maguirei* produced fruits with very short, unbranched trichomes (Figure 2B). Micrographs of the proximal portions of flowering stems also showed taxonomically useful differences in trichomes. Flowering stems were consistently glabrous in *D. globosa* (Figure 2H) and largely so in *D. burkei* (Figure 2G) and northern *D. maguirei* (Figure 2E). By contrast, the southern populations of *D. maguirei* showed at least some branched trichomes on the stems of every individual examined (Figure 2F).

Although leaf shape and arrangement did not vary significantly among members of the *D. maguirei* alliance, taxonomically useful differences in leaf size and indument were documented. Apparently insensitive to elevational gradients, all plants of *D. maguirei* (Figure 2I, J) produced relatively large leaves two-to-three times longer than those of *D. globosa* and most plants of *D. burkei*. In *D. globosa* (Figure 2L), the leaves were consistently small, rarely exceeding 6 mm in length. *Draba burkei* was more variable, with high elevation populations (Figure 2K) more similar to *D. globosa*, but a few low elevation plants approaching the leaf size of *D. maguirei*. In addition to leaf size, there were clear differences in the distribution of trichomes on the rosette leaves. In *D. burkei* (Figure 2K) and *D. globosa* (Figure 2L), trichomes are confined to the margin of the leaf. This generally was true of northern *D. maguirei* as well (Figure 2I), although occasional plants exhibited a few trichomes on blade surfaces. By contrast, plants collected from the southern populations of *D. maguirei* always had trichomes on blade surfaces (Figure 2J).

Trichome differences among members of the *D. maguirei* alliance were not limited to their position of attachment on the leaves. Each of the taxa showed notable differences in the type of trichomes present. In northern *D. maguirei* (Figure 2M), most trichomes were of the short-stalked, cruciform type that branched to form four rays. Although this type also occurred on plants of southern *D. maguirei*, most trichomes observed on this taxon were of the bifurcate (2-rayed) type (Figure 2N). The trichomes of *D. burkei* (Figure 2O) and *D. globosa* (Figure 2P) were always unbranched. Even here, subtle distinctions emerged at higher magnifications. The marginal trichomes of *D. burkei* were broad-based and rather stiff, such that they did not collapse during drying. *Draba globosa*, on the other hand, exhibited trichomes that were more diminutive, with narrow bases and a tendency to collapse and curl when dried.

Chromosome and pollen studies

Cytogenetic analyses of *D. maguirei* and its allies reinforced the geographical and morphological distinctions observed. Chromosome numbers and the populations from which they were derived are listed in Table 2. The most easily interpreted chromosome squashes were obtained from *D. burkei* and the southern populations of *D. maguirei*. Four sampled populations of *D. burkei* consistently showed 10 bivalents at late prophase I (Figure 3A) and metaphase I (Figure 3B). In anaphase I, these bivalents separated into two daughter nuclei, each containing 10 chromosomes (Figure 3C). The second cell division of meiosis proceeded normally, resulting in the production of predominantly (>99%) well-formed, exclusively tricolpate pollen grains averaging 20 μm wide (Figure 3D). Cytogenetic data were also obtained from three populations of southern *D. maguirei* (Table 2). These samples exhibited eight bivalents at late prophase I (Figure 3E) and metaphase I (Figure 3F) and two daughter nuclei each with eight chromosomes at anaphase I (Figure 3G). The second cell division of meiosis proceeded normally, resulting in the production of predominantly (>95%) well-formed, exclusively tricolpate pollen grains averaging 22 μm wide (Figure 3H).

Meiosis in northern *D. maguirei* was more difficult to interpret, with different cells exhibiting variable numbers of multivalents, bivalents, and univalents during the first division. All cells formed at least a few multivalents, some of which were clearly discernable as quadrivalents at late prophase I (Figure 3I). A few cells formed as many as eight quadrivalents, which were most evident at metaphase I (Figure 3J). Cells with only multivalents and bivalents often divided symmetrically at anaphase I to form two daughter nuclei containing 16 chromosomes each (Figure 3K). In these cases, the second cell division of meiosis proceeded

FIGURE 2 Scanning electron microscope (SEM) micrographs of morphological features distinguishing *D. maguirei, D. burkei*, and *D. globosa*. (A–D) Distal portion of fruit illustrating differences in style and stigma morphology and pubescence; scale bars = 0.3 mm. (E–H) Lower portion of flowering stem showing variation in pubescence; scale bars = 0.5 mm. (I–L) Distal portion of basal leaves illustrating differences in leaf size and distribution of trichomes; scale bars = 1 mm. (M–P) Margins of basal leaves showing variation in trichome morphology; scale bars = 0.25 mm.

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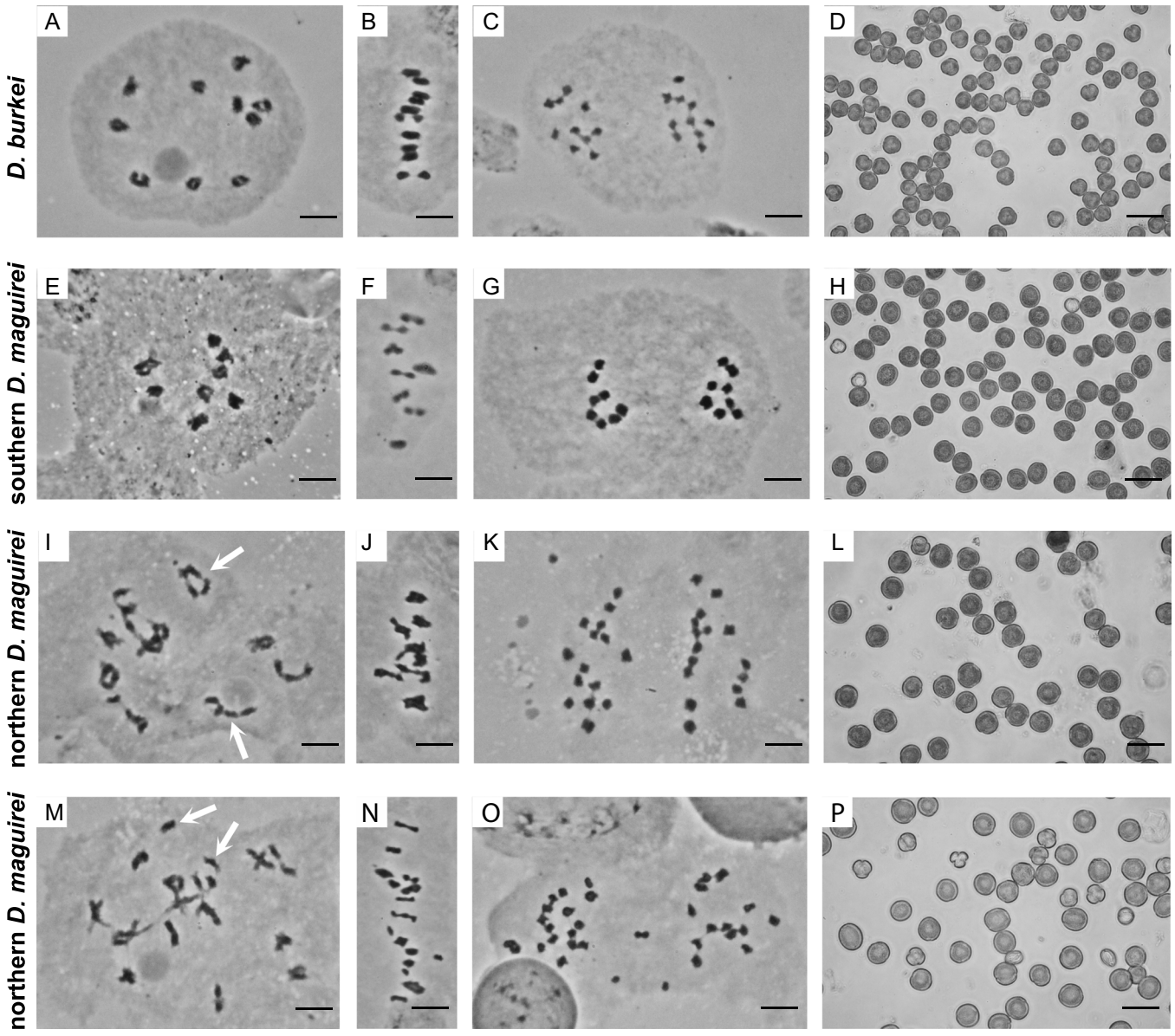

FIGURE 3 Microsporogenesis in *Draba burkei* and *D. maguirei*; scale bars = 20 μm for chromosome images and 50 μm for pollen images. (A–D) *D. burkei* showing 10 bivalents in meiosis I. (A) Late prophase I; (B) metaphase I; (C) anaphase I with even distribution of 10 chromosomes to each pole; (D) mature, well-formed pollen (none lacking cytoplasm). (E–H) southern *D. maguirei* exhibiting eight bivalents in meiosis I. (E) Late prophase I; (F) metaphase I; (G) anaphase I with even distribution of eight chromosomes to each pole; (H) mature, mostly well-formed pollen (<5% lacking cytoplasm). (I–L) Northern *D. maguirei* with mostly multivalents and bivalents in meiosis I. (I) Late prophase I; arrows identify apparent quadrivalents; (J) metaphase I cell with ± 8 quadrivalents; (K) anaphase I shows even distribution of 16 chromosomes to each pole; (L) mature, mostly well-formed pollen resulting from even distribution of chromosomes. (M–P) Northern *D. maguirei* with mostly bivalents and occasional univalents in meiosis I. (M) Late prophase I; arrows identify univalents; (N) metaphase I cell with bivalents (common), as well as univalents and multivalents (rare); (O) anaphase I showing uneven distribution of chromosomes (17 on the left, 13 on the right) and premature separation of chromatids in two laggard univalents; (P) mature pollen with ~40% of grains lacking cytoplasm.

normally, resulting in the production of predominantly (>95%) well-formed pollen grains averaging 24 μm wide (Figure 3L).

On the other hand, some samples of northern *D. maguirei* exhibited primarily bivalents and a few univalents at late prophase I (Figure 3M). Both paired and unpaired chromosomes migrated to the metaphase plate (Figure 3N), resulting in meiotic irregularities in subsequent phases. In the cell shown in Figure 3O, the chromosomes that formed bivalents and multivalents have dissociated and moved toward the poles, with 17 migrating toward the daughter nucleus on the left and 13 toward the right. The two chromosomes that did not pair lagged on the metaphase plate, triggering premature disjunction of chromatids (Figure 3O). The expected downstream consequences of this would be losses and gains of entire chromosomes in the

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pollen derived from these cells. Notably, these samples showed higher proportions (often >20%) of unfilled, inviable pollen (Figure 3P). The filled, presumably viable pollen grains produced by northern populations of *D. maguirei* (Figure 3L, P) were slightly larger than those of the southern populations (Figure 3H) and always included some tetracolpate grains that were not observed in the latter.

Cytogenetic studies of *D. globosa* were unsuccessful despite repeated attempts to obtain meiotic material at the appropriate stage. All samples gathered were postmeiotic, even those collected immediately after snow melt. Even if plants undergoing meiosis could be located in nature or raised in a greenhouse, it now seems unlikely that such material would provide interpretable counts given other observations on the reproductive biology of the species. Most relevant is the fact that the populations of *D. globosa* we studied produced little or no functional pollen but yielded abundant seed. This dichotomy suggests that *D. globosa* may reproduce via apomixis, which is strongly associated with triploidy and highly irregular meiosis in related species (Mulligan, 1976). Based on these observations, we suggest that future chromosome studies of this species should focus on mitotic analyses.

Enzyme electrophoresis

Electrophoretic analysis of 10 enzymes in *D. maguirei* and its allies yielded information on 17 putative gene loci (Table 3). Three of these loci (PGI-1, 6PGDH-1, and MDH-4) were represented by a single invariant band in all taxa; a fourth (MDH-2) exhibited an invariant, three-banded pattern throughout the complex. Although these four loci did not distinguish the taxa recognized by other data sets, they provided evidence that the sampled individuals were indeed closely related. The remaining 13 loci were variable within or among taxa; gel photos for several of these are provided in Figure 4.

In the enzyme SkDH, all samples of *D. maguirei* (both northern and southern population clusters) possessed a single, slow-migrating band that was best resolved on buffer system 1 (Figure 4A; lanes 1–10). By contrast, all samples of *D. burkei* and *D. globosa* shared a faster band that was best resolved on buffer system M (Figure 4A; lanes 11–20). In the enzyme TPI, all samples of *D. maguirei* shared a slow-migrating band that was absent from *D. burkei* and *D. globosa* (Figure 4B). Most individuals of the latter two taxa shared a fixed three-banded pattern for this enzyme, though some individuals of *D. globosa* appeared homozygous for the slowest migrating member of the triplet (Figure 4B; lanes 19–20). The enzyme PGM provided more taxonomic resolution than any other included in the study. All samples of *D. maguirei* shared a prominent, fast-migrating electromorph (labelled "1" in Figure 4C) that was absent or barely expressed in *D. burkei* and *D. globosa*. The latter two taxa were distinguished from one another by an exceptionally slow-migrating band at the PGM-2 locus consistently present in *D. burkei* (Figure 4C; lanes 11–16) but apparently absent in *D. globosa* (Figure 4C; lanes 17–20).

The band patterns resulting from our enzyme analyses were unexpectedly complex, with many bands per locus, evidence of fixed (nonsegregating) heterozygosity, and the frequent occurrence of genetically unbalanced heterozygotes. All these patterns are indicative of gene duplication, suggesting that the loci exhibiting these complex patterns are represented by more than one gene copy. Such patterns are characteristic of polyploids, and thus we expected to observe duplicated loci in northern *D. maguirei* because of its tetraploid chromosome number. The hypothesis that *D. globosa* produces seeds via apomixis (see Chromosome and pollen studies above) would also predict that this species might exhibit duplicated loci given that every apomictic *Draba* studied to date has proven to be polyploid (Mulligan, 1976).

The most unexpected result of this analysis was the discovery that the two supposed diploid taxa (southern *D. maguirei* with $n = 8$ and *D. burkei* with $n = 10$) exhibited levels of gene duplication equivalent to those observed in the confirmed and inferred polyploids. This was most easily visualized on gels representing the dimeric enzyme locus PGI-2 (Figure 4D). Among the many bands detected at this locus, no single taxon stands out as distinctive. However, the band patterns expressed by heterozygous individuals (i.e., those with more than one band at Locus 2) provided crucial information on gene duplication.

In a dimeric enzyme, heterozygotic diploid individuals should show a balanced three-banded pattern in which the heterodimer (middle band) is about twice as intense as either homodimer. The occurrence of either (1) more than three bands or (2) unbalanced three-banded heterozygotes (in which one of the homodimeric bands is darker and the other is very faint) indicates the presence of three or more gene copies. On the PGI gel shown here (Figure 4D), more than three PGI-2 bands were observed in one sample of northern *D. maguirei* (lane 5), two individuals of southern *D. maguirei* (lanes 7, 8), and two samples of *D. burkei* (lanes 14, 15). This gel also documented unbalanced heterozygosity in two individuals of northern *D. maguirei* (lanes 3, 4), two samples of southern *D. maguirei* (lanes 6, 9), and two individuals of *D. globosa* (lanes 19, 20). Table 3 provides a conservative estimate of the number of duplicated loci present among the 10 enzymes studied. We consider the estimate conservative because it is founded solely on the putative diploid taxa (southern *D. maguirei* and *D. burkei*). Based on a multiplicity of bands and the occurrence of unbalanced or apparently fixed heterozygosity, we estimate that eight of 17 loci (47%) were duplicated in these supposed diploids (see Table 3, last column).

ITS phylogenetic analysis

Sanger sequencing of targeted PCR products yielded a segment of DNA 622 base pairs long that was

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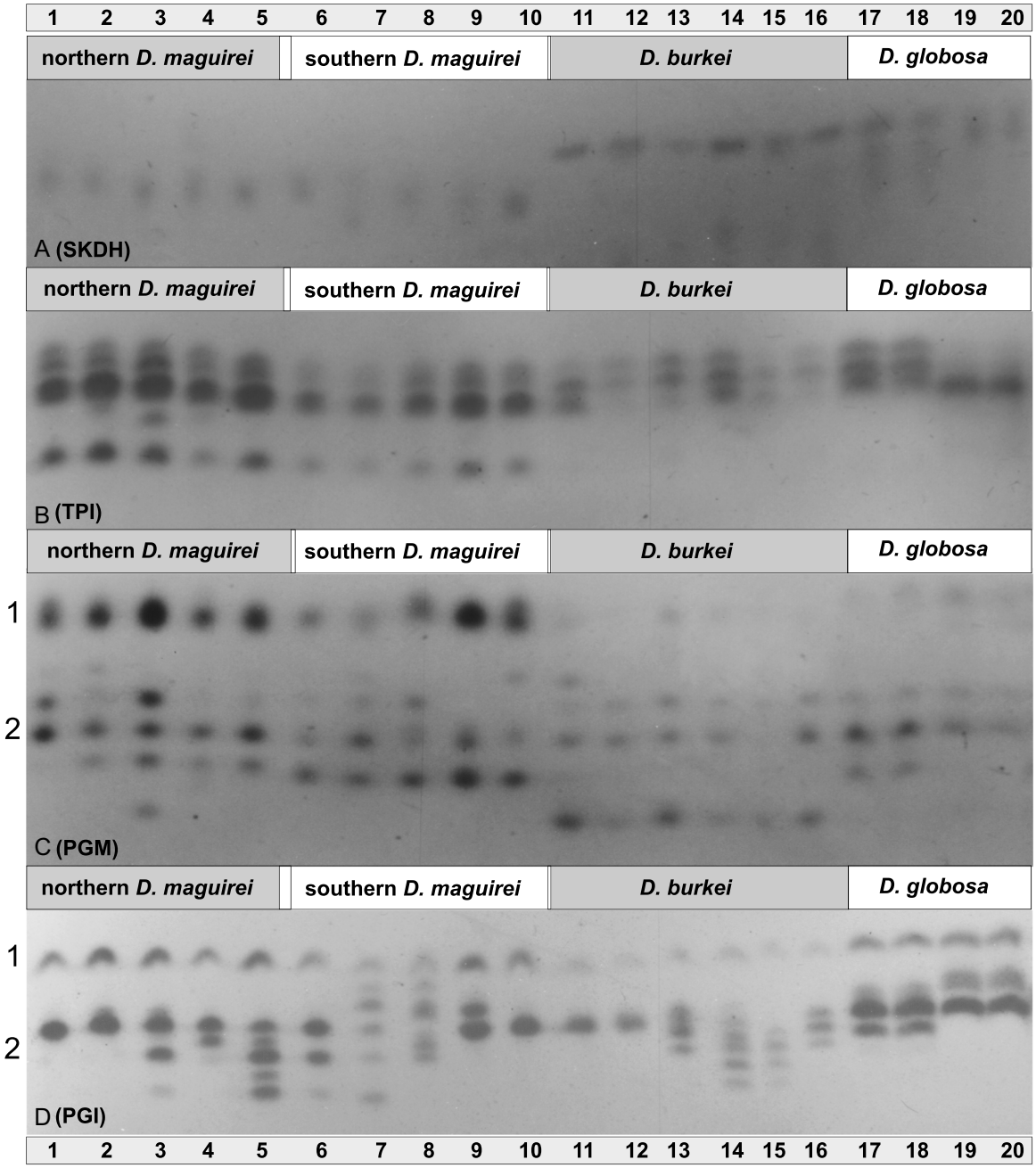

FIGURE 4 Isozyme gel photos showing variation within and among members of the *Draba maguirei* group. Each panel (A–D) represents a different enzyme: (A) SkDH; (B) TPI; (C) PGM; (D) PGI. Anode is toward the top of each panel. In all photos, lanes 1–5 are samples from the northern (high-elevation) populations of *D. maguirei* and lanes 6–10 are samples from the southern (low-elevation) populations, lanes 11–16 represent *D. burkei* and lanes 17–20 are samples of *D. globosa*.

reproducible in all samples. ITS1, ITS2, and the 5.8S subunit are composed of 272, 186, and 164 base pairs, respectively. Variability in ITS sequences was quite low. In *D. maguirei* s.s., the southern (n = 8) and northern (n = 16) populations exhibited identical sequences despite the apparent genetic discontinuity between the two cytotypes. ITS sequences from the three sampled populations of *D. burkei* (Table 2) were indistinguishable from one another, as were those of the three geographically isolated populations of *D. globosa*; consequently, we chose a single sequence to represent each of these taxa. Two other pairs of species in *Draba* Group II exhibited nearly identical ITS sequences (Figure 5). The first pair, *Draba albertina* and *D. densifolia*, which are very distinct morphologically but share a chromosome base number of x = 12, differ by a single two-base insertion in *D. densifolia*. The equally distinctive *D. sobolifera* and *D. subalpina* (both with x = 13) differed only in a single deletion in *D. subalpina*.

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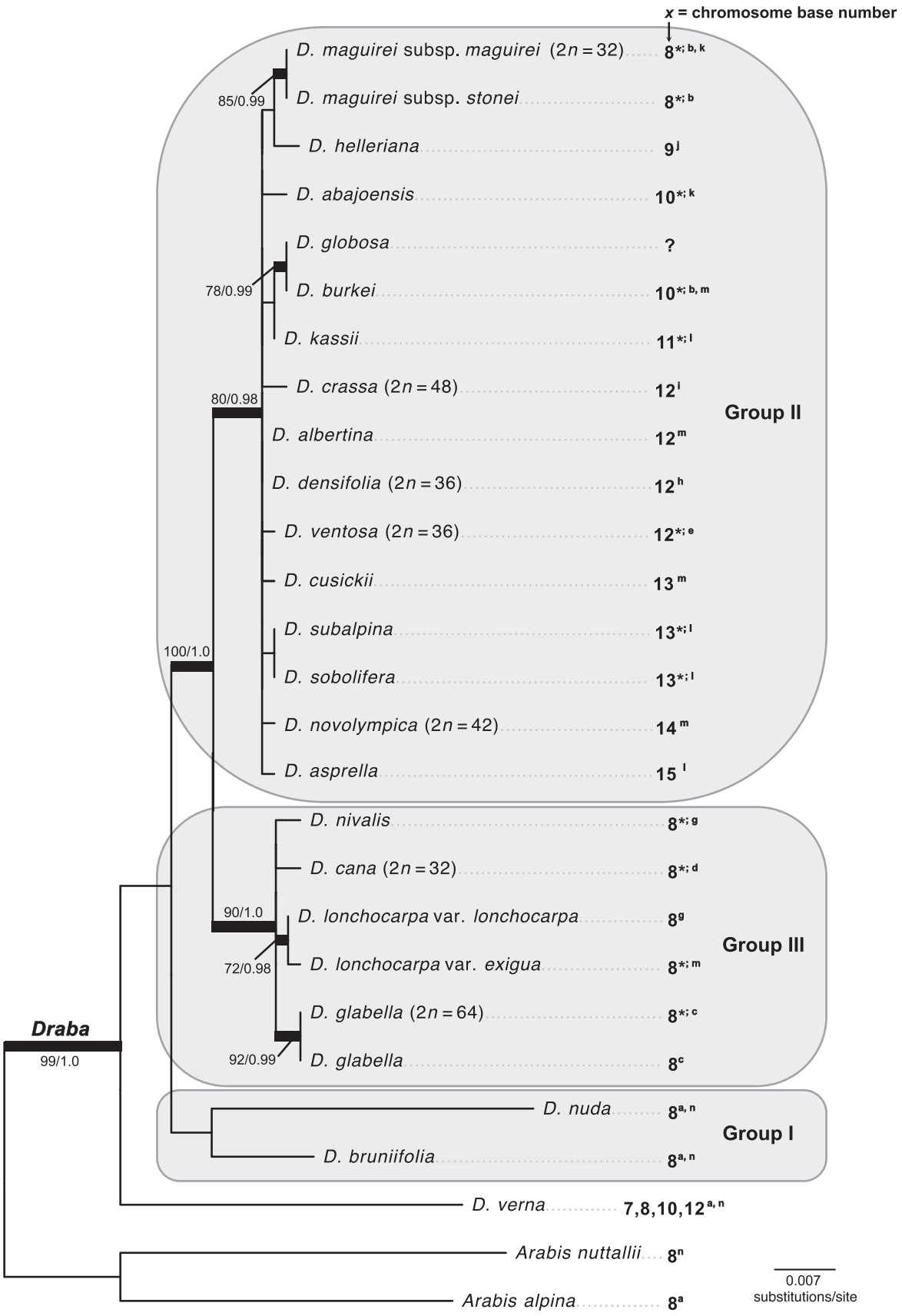

FIGURE 5 (See caption on next page)

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DISCUSSION

Phylogenetic analysis of select *Draba* ITS sequences (Figure 5) using *Arabis alpina* and *A. nuttallii* as outgroups recovered the same major clades identified by Jordon-Thaden et al. (2010) based on a much broader sampling of *Draba* (371 accessions representing ca. 45% of species diversity). The genus *Draba* as circumscribed by the latter authors was strongly supported in our analysis (MLBS 99/BPP 1.0), while *Draba* Group I remained weakly supported. *Draba* Groups II and III were strongly supported as sister lineages (MLBS 100/BPP 1.0), with both groups well supported as monophyletic (MLBS 80/BPP 0.98 and 90/1.0, respectively). Members of the *D. maguirei* alliance (all previously unsampled) were placed in Group II, along with 11 other species endemic to North America. Relationships within Group II were largely unresolved, though the northern and southern populations of *D. maguirei* were well supported (MLBS 85/BPP 0.99) as sister taxa, as were *D. burkei* and *D. globosa* (MLBS 78/BPP 0.99).

Phylogenetic patterns of chromosomal variation within *Draba*

As circumscribed by Jordon-Thaden et al. (2010), *Draba* Group II included ~25% of the species assigned to the genus, with the majority of these restricted to the Americas. Biogeographical analyses of the most comprehensive phylogenetic sampling of tribe Arabideae (approximately half the recognized species) by Karl and Koch (2013) identified North America as the most probable ancestral area for *Draba* Group II. This group is exceedingly diverse, and there are no evident morphological synapomorphies. However, there are intriguing correlations between the ITS-based phylogeny and observed chromosome numbers (Figure 5). Ongoing cytogenetic analyses of Group II species from western North America (Windham, 2000, 2003, and unpublished data) indicate that chromosome base numbers within the lineage are highly variable, forming a continuous series from $x = 9$ to 15. This continuous series is in sharp contrast to the predominantly euploid members of Groups I and III, which consist almost exclusively of diploids and polyploids based on $x = 8$ (Jordon-Thaden and Koch, 2008).

Mulligan (1976) was the first to propose an informal classification of North American *Draba* incorporating the cytogenetic data he had spent more than a decade generating (Mulligan, 1966, 1970, 1971a, 1971b, 1972, 1974, 1975). His classification separated the high latitude, yellow-flowered *Draba* species into two groups: one euploid and the other with exclusively noneuploid chromosome numbers. Subsequent phylogenetic analyses by Beilstein and Windham (2003) supported this use of chromosome base number as an indicator of species relationships. They showed that all sampled members of Mulligan's yellow-flowered noneuploid group were closely related and formed a well-supported clade with the only native, white-flowered, noneuploid species. The more recent discovery by Jordon-Thaden et al. (2010) that the North American noneuploid species are closely related to South American species with similarly variable chromosome numbers raises the possibility that the noneuploid species of *Draba* Group II may greatly outnumber the euploids.

Are the noneuploids of *Draba* Group II aneuploids or dysploids?

Throughout their paper, Beilstein and Windham (2003) referred to the noneuploid *Draba* species as "aneuploids", following the traditional terminology of Stebbins (1971) and Grant (1981), which did not consistently distinguish between aneuploidy (loss or gain of whole chromosomes and all associated genes) and dysploidy (changes in chromosome number resulting from fusion or fission with minimal loss or gain of genetic material). Aneuploidy, as more narrowly defined by recent authors, selectively deletes or duplicates linkage groups, usually resulting in unbalanced genomes (Torres et al., 2008) and nonviable or poorly adapted individuals (Siegel and Amon, 2012; Weiss-Schneeweiss and Schneeweiss, 2013). Given that the genetic consequences of true aneuploidy are cumulative (with each sequential deletion or addition compounding any negative effects), Guerra (2000) concluded that aneuploidy is unlikely to produce a stepwise series of chromosome numbers like that observed in *Draba* Group II (see Figure 5). Numerical series of this sort are now generally attributed to dysploidy—a process that maintains crucial genic content and balance despite major chromosomal rearrangements (Guerra, 2000).

Dysploid changes in chromosome number are characterized as either "ascending" (increasing via fission) or "descending" (decreasing via fusion). Empirical evidence

FIGURE 5 ITS-based phylogeny of *Draba* sampled across three major groups recognized by Jordon-Thaden et al. (2010) and analyzed by maximum likelihood (ML) and Bayesian Markov chain Monte Carlo (B/MCMC). Thickened branches indicate where ML bootstrap support (MLBS) is >70 and Bayesian posterior probability (PP) >0.95 [MLBS/BPP]. Groups II and III are each strongly supported as monophyletic and as reciprocal sister groups. All polyploid taxa are indicated by 2*n* chromosome number following taxon name in parentheses. Where available, chromosome base number (*x*) is indicated in far-right column. Chromosome base numbers followed by an asterisk indicate that the DNA sample used here originated from the same voucher used to obtain the chromosome data. Letter superscripts that follow chromosome base numbers indicate the published source(s) for those counts, as follows: (a) ccdb.tau.ac.il, (b) herein, (c) Mulligan, 1970, (d) Mulligan, 1971a, (e) Mulligan, 1971b, (f) Mulligan, 1971b (as *D. paysonii* var. *treleasii*), (g) Mulligan, 1974, (h) Mulligan, 1976, (i) Price, 1979, (j) Ward, 1983 (incorrectly attributed to var. *blumeri*), (k) Windham, 2000 (as *D. spectabilis* var. *spectabilis*), (l) Windham, 2000, (m) Windham, 2003, (n) Windham, unpublished data.

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indicates that descending dysploidy is much more common (Lysak, 2014), and this process has been documented in the Asteraceae (Senderowicz et al., 2021), Brassicaceae (Mandáková and Lysak, 2018), Fabaceae (Fonsêca et al., 2016), Malvaceae (Udall et al., 2019), Poaceae (Luo et al. 2009), Solanaceae (Chase et al., 2022), and many other plant families. Highlighting the evolutionary significance of dysploidy, Escudero et al. (2014) indicated that chromosomal changes arising from it often persist longer in evolutionary time than the changes caused by polyploidy. However, in most of the families cited above, the two processes operate in tandem, with polyploidy (i.e., whole genome duplication [WGD]) driving chromosome numbers up and descending dysploidy bringing them back down. Descending dysploidy is a key component of postpolyploid diploidization (Mandáková and Lysak, 2018), which is, in turn, thought to be a major contributor to the evolutionary success of angiosperms (Dodsworth et al., 2016).

Evidence of postpolyploid diploidization in *Draba* Group II

Polyploidy followed by descending dysploidy is especially well documented in the Brassicaceae (Mandáková et al., 2010, 2016, 2017, 2020), where it appears to be a primary driver of species diversification (Mandáková and Lysak, 2018). *Draba* Group II has not received a great deal of attention in this regard, but our analyses suggest that it may be one of the most extensive examples yet discovered. Cytotaxonomic studies by Mulligan (1966, 1970, 1971a, 1971b, 1972, 1974, 1975, 1976) and Windham (2000, 2003) previously demonstrated the existence of a continuous series of noneuploid chromosome base numbers extending from $x = 9$ to $x = 15$ in western North American *Draba*. Species exhibiting each of these base numbers are represented in our phylogenetic tree (Figure 5), where they are shown to be closely related to each other and to the broader clade that Jordon-Thaden et al. (2010) referred to as *Draba* Group II. In circumscribing this group, the latter authors noted that *Draba* Group II might also include species with euploid chromosome numbers. However, there was no direct evidence of this given that the individual plants sampled for their phylogenetic study were not subject to cytogenetic analysis.

Based on the results presented herein, *Draba maguirei* is key to understanding the evolutionary processes operating within *Draba* Group II. This species adds two new chromosome numbers ($n = 8$ and $n = 16$; Figures 3 and 5) to the continuous series previously documented for the group. Without additional information, these would likely be interpreted as euploid numbers based on $x = 8$. However, our isozyme data reveal that the southern populations of *D. maguirei* (supposedly diploid with $n = 8$) exhibit just as much gene duplication in the form of fixed or unbalanced heterozygosity (Figure 4) as the northern populations (apparently tetraploid with $n = 16$). The same is true of *D. burkei*, the other "diploid" taxon included in the isozyme analyses (Table 3), where the levels of fixed or unbalanced heterozygosity are comparable to those observed in *D. globosa* (its putatively triploid sister taxon).

Draba maguirei and related taxa seem to represent yet another mustard lineage in which "chromosome number per se is not a reliable indicator of ploidy level" (Mandáková et al., 2010: 2277). This apparent lack of correlation between gene duplication and chromosome number is precisely what we would expect if the majority of *Draba* Group II (or at least the North American lineage) had experienced a polyploidization event (WGD) resulting in a tetraploid ($n = 16$) common ancestor, whose descendants then diversified via descending dysploidy. It appears to be a textbook example of postpolyploid chromosomal diploidization (Mandáková and Lysak, 2018) in which most of the duplicated genes of the polyploid ancestor were retained while the DNA was reorganized through chromosomal fusion. Based on the information at hand, we hypothesize that a mesopolyploid North American lineage of *Draba* Group II experienced one or more waves of descending dysploidy (Levin, 2020), which generated a continuous series of chromosome numbers bridging the gap between diploid and tetraploid. In addition, we posit that the southern ($n = 8$) populations of *D. maguirei* are not true diploids. Instead, we believe that they represent a pseudodiploid taxon in which the plesiomorphic chromosome base number has been restored via descending dysploidy while the lineage has, in large part, remained genetically polyploid (Mandáková et al., 2016). Building on this scenario, we propose that the northern ($n = 16$) populations of *D. maguirei* represent the first step (chromosomal polyploidization) in a potential new round of evolution by descending dysploidy.

The evolutionary scenario outlined above has the potential to proceed very rapidly (Mandáková et al., 2010, 2017), which may well contribute to the lack of resolution among the species of *Draba* Group II seen in our ITS phylogeny (Figure 5). A similar inability to resolve relationships within the group was reported by Jordon-Thaden et al. (2010), whose ITS analysis of 124 terminals representing 66 species of *Draba* Group II yielded a Bayesian tree with just 14 well supported (≥0.95 BPP) branches. Separate and combined analyses of plastid *trnL-F* sequences by Jordon-Thaden et al. (2010) did little to improve phylogenetic resolution within *Draba* Group II. Clearly, additional loci will be needed to resolve the complex evolutionary history of *Draba* Group II.

TAXONOMIC CONSIDERATIONS

Draba burkei vs. *D. maguirei*

The data presented here indicate that *Draba burkei* cannot be submerged in, or even be closely associated with, *D.*

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maguirei. There is no geographic contact between the two taxa (Figure 1), and their substrate preferences are largely nonoverlapping. They are easily distinguished morphologically (Figure 2), with no evidence of intermediates or potential hybrids. If they were to hybridize, the differences in chromosome number (Figure 3) would almost certainly render the hybrids sterile. These genetic differences are also observed in the enzyme data presented (clearly distinct in three of the four enzymes shown in Figure 4) and in the nonsister relationship of *D. maguirei* and *D. burkei* in our phylogenetic tree (Figure 5). Instead, *D. burkei* and *D. globosa* have identical ITS sequences and are well supported as sister taxa (MLBS 78/BPP 0.98). Evidence of this close relationship is found in nearly every aspect of their biology, including substrate preferences, overall morphology (Figure 2), and isozyme similarities (Figure 4). In all cases where clear isozymic distinctions were observed, *D. burkei* was always more similar to *D. globosa* than to *D. maguirei*.

Given the clear distinctions between *D. maguirei* and *D. burkei* and the fact that these taxa are not sister to one another in our ITS phylogeny (Figure 5), we reject Welsh's (2015) conservative treatment of the latter as a variety of *D. maguirei*. We favor the recognition of monophyletic species whenever possible, and subsuming *D. burkei* within *D. maguirei* results in a taxon that is clearly paraphyletic. To have any chance of being monophyletic, this taxon would have to include *D. globosa* (Figure 5), and a species with this circumscription could not be called *D. maguirei* because *D. globosa* was published 24 years earlier by Payson (1917). Considering the limited sampling and lack of resolution among *Draba* Group II taxa in all phylogenies published to date (Figure 5; Beilstein and Windham, 2003; Jordon-Thaden et al., 2010; Karl and Koch, 2013), any lumping of previously recognized species (as done by Welsh, 2015) is almost certain to have adverse effects, both on monophyly and nomenclatural stability. We need to take all available information into account, building classifications based on a broad array of data sets (Haig et al., 2006), not just a few obvious morphological characters.

Draba burkei vs. *D. globosa*

Once *Draba burkei* is removed from *D. maguirei*, we have two options regarding the taxonomic treatment of *D. burkei*. It can be treated as a distinct species or combined with its apparent closest relative, *D. globosa*. Either option would be consistent with the results shown in the phylogenetic tree (Figure 5). Despite the evident relationship between *D. burkei* and *D. globosa*, the two taxa are amply distinct and clearly on separate evolutionary trajectories. There is no overlap between their geographic ranges, which are separated by 60 km. They differ in their ecological requirements as well, with *D. burkei* never found above 3000 m elevation and *D. globosa* never found below that level. The two taxa are immediately recognizable based on differences in style length (Figure 2C vs. Figure 2D) and show more subtle divergence in trichome type (Figure 2O vs. Figure 2P).

Preliminary analyses of reproductive behavior separate the taxa as well. *Draba burkei* appears to require cross pollination to set seed (Tait, 2002) and shows considerable genetic variation within and among populations (Johnson, 2002). *Draba globosa*, on the other hand, sets abundant seed despite having abortive anthers, and isozyme studies indicate that most populations are genetically invariant. These are hallmarks of apomixis (asexual seed production), which has been documented in four other species of North American *Draba* (Mulligan and Findlay, 1970; Mulligan, 1976). Apomixis in *Draba* (and most other taxa) is strictly associated with polyploidy (Mulligan, 1976). Typically, the taxa involved are triploids that fail to form normal pollen because the three sets of chromosomes are unable to align properly during meiosis. If this correlation between apomixis and polyploidy holds true in *D. globosa*, a difference in chromosome number would be added to the list of features that differentiate it from *D. burkei*.

Although the possibility that *D. globosa* is triploid remains conjectural, this hypothesis dovetails with the evidence from geography, ecology, morphology, and reproductive biology to favor the separation of *D. burkei* and *D. globosa* at the species level. Even taxonomic tradition can be cited in support of this position. Prior to this study, no taxonomist familiar with *Draba* has ever postulated a close relationship between these taxa, though Hitchcock (1941) noted some similarities. This separation was acknowledged even in the recent Welsh (2015) classification, where *D. burkei* and *D. globosa* were treated as varieties of *D. maguirei* and *D. densifolia*, respectively (Table 1). *Draba burkei* and *D. globosa* have been considered sufficiently distinct to be treated as different species for 80 years, and the discovery of a close relationship between them does nothing to detract from their traditional separation. Therefore, based on all the evidence before us, we have chosen to recognize *D. maguirei* var. *burkei* as a distinct species following Windham (2003). We also maintain *D. globosa* at the species level, explicitly rejecting its recent treatment as a variety of *D. densifolia* (Welsh, 2015). Typical material of *D. densifolia* was included in our phylogenetic sampling (Appendix 1), and it yielded ITS sequences nearly identical to those of *D. albertina*, which shares a chromosome base number of $x = 12$ (Figure 5). Although poorly resolved, the topology of the phylogenetic tree suggests that *D. globosa* is more distantly related to *D. densifolia* and should not be subsumed in the latter.

Northern vs. southern *Draba maguirei*

During this study, we encountered unexpected, geographically correlated variability within Hitchcock's *D. maguirei* var. *maguirei*. Most significantly, cytogenetic analyses revealed that the northern and southern population clusters (green and blue, respectively, in Figure 1) had different

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chromosome numbers. The northern plants were polyploid (Figure 3I–K, M–O), showing double the chromosome complement observed in southern populations (Figure 3E–G). Meiotic cells from the northern populations formed up to eight quadrivalents (Figure 3J), suggesting that the four chromosome sets present in these plants were largely homologous. Based on these observations, we hypothesize that the northern populations of *D. maguirei* s.s. were derived from the southern via autopolyploidy, an idea further supported by their very similar enzyme profiles (Figure 4) and identical ITS sequences (Figure 5).

Although the northern populations of *D. maguirei* may have arisen as an autopolyploid derivative of the southern, there is clear evidence of incipient divergence. Northern populations have predominantly four-rayed trichomes that are usually confined to the margins of the rosette leaves (Figure 2M). By contrast, southern populations have primarily bifurcate trichomes that extend onto leaf surfaces (Figure 2N). The most dependable distinguishing feature relates to the pubescence of the proximal portions of the scapose flowering stems. Whereas the stems of northern *D. maguirei* are almost always glabrous (Figure 2E), those of southern plants showed at least some branched trichomes on every individual examined (Figure 2F). The common occurrence of minute trichomes on fruits in southern populations (Figure 2B) helps to separate them from the glabrous-fruited northern populations (Figure 2A), and the regular presence of tetracolpate pollen grains in the northern plants (data not shown) help to distinguish them from the strictly tricolpate southern plants (Figure 3H). Interestingly, the de novo appearance of tetraaperturate pollen in autopolyploid fireweeds (Mosquin, 1967) also provided a useful character for distinguishing polyploids from their diploid progenitors.

The development of recognizable morphological differences between the northern and southern populations was likely driven by an abrupt reduction in gene flow, initiated by one or more polyploidization events and reinforced by subsequent ecological and phenological divergence. Based on extensive field surveys undertaken in the late 1990s (see "Geography and ecology" section of Materials and Methods), it appears that the habitats of the northern and southern populations of *D. maguirei* do not overlap. Where they grow in closest proximity (on the north side of Logan Canyon), they are separated by at least 3 km distance and 300 m elevation. The two taxa also flower at different times, presumably because of their elevational differences. When the plants on Mt. Naomi (2700 m) were in full bloom around the first of July, the plants in central Logan Canyon (1800 m) were already shedding seed. These phenological differences would greatly restrict genetic exchange between northern and southern populations. Any pollen movement that did occur likely would be ineffective because crosses between population clusters would produce reproductively impaired triploids.

Although northern and southern *D. maguirei* are closest relatives to one another (Figure 5) and show little genetic divergence at the enzyme loci studied (Figure 4), they represent different ploidies, occupy spatially discrete habitats, appear to be reproductively isolated by both intrinsic and extrinsic factors, and are morphologically distinguishable. Thus, they fit the definition of "distinct population segments" under the Endangered Species Act (Haig et al., 2006) and should not be treated as a single uniform taxon for conservation purposes. As noted by Soltis and Gitzendanner (1998, p. 473), "the ESA provides for the protection of unnamed populations or lineages of vertebrates only … invertebrates, plants, fungi, or microbes lacking taxonomic status cannot be protected under the ESA." To bring the cryptic subdivisions of *D. maguirei* to the attention of the scientific community and make them eligible for consideration under the ESA, we here recognize them as discrete, named taxa.

The appropriate hierarchical level for separating a diploid (in this case, pseudodiploid) taxon from a subtly distinct, presumed autopolyploid derivative has long been a source of contention. Löve (1951; 1964) strongly advocated for the recognition of such taxa as separate species, noting that their incipient, chromosomally based reproductive isolation made them biological species. In response, Lewis (1980, p. 135) stated that "anyone planning wholesale naming of thousands of cytotypes with specific epithets ought to reconsider this approach before flooding the taxonomic literature with impractical names simply to satisfy man's interpretation of a biological species concept." Lewis' position quickly gained primacy among plant systematists, with the result that diploids and their autopolyploid derivatives are rarely provided nomenclatural recognition. However, this approach has significant negative consequences, both for biodiversity conservation and our understanding of evolution itself. As noted by Soltis et al. (2007), autopolyploidy is a potent and prevalent evolutionary force and, by failing to account for it nomenclaturally, we may be seriously underestimating the biodiversity of Earth.

In dealing with *Draba maguirei*, we have attempted to find a middle ground between the species splitting often associated with phylogenetic species concepts ["taxonomic inflation" *sensu* Zachos (2015)] and the lumping (taxonomic ghosting) of evolutionarily significant entities by focusing too narrowly on easily observed morphological traits. Faced with an analogous situation in the circumboreal fireweed *Epilobium* (now *Chamerion*) *angustifolium* L., Mosquin (1966a, 1966b, 1967) chose to treat the two widespread "chromosome races" as subspecies. Diploid populations, confined to higher latitudes or elevations, were referred to *E. angustifolium* subsp. *angustifolium* whereas the more widely distributed polyploids (mostly tetraploids) were recognized as *E. angustifolium* subsp. *circumvagens* Mosquin. The most dependable morphological differences between these taxa (i.e., the distribution of trichomes and the presence or absence of tetraaperturate pollen) are remarkably like those distinguishing the northern and southern populations of *Draba maguirei* (see Results).

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Although the subspecies of *Epilobium angustifolium* show significant geographic overlap and production of triploid hybrids (neither of which is known to occur in *D. maguirei*), Husband and Sabara (2003) found that a combination of pre- and postzygotic barriers between *E. angustifolium* subsp. *angustifolium* and *E. angustifolium* subsp. *circumvagens* resulted in 99.7% reproductive isolation. With continued research, Mosquin's (1966a) taxonomic treatment of *Epilobium angustifolium* gained wide acceptance within the systematics community, and the subspecies were retained when the species was transferred to *Chamerion* by Hoch and Raven (1999).

In adopting a classification of *Draba maguirei* that is similar to the widely accepted subdivision of *Chamerion angustifolium* (L.) Holub, we aim to establish a middle ground between "taxonomic inflation" (Zachos, 2015) and "grossly underestimating" biodiversity (Soltis et al., 2007). We advocate for the more extensive use of the rank of subspecies as defined and operationalized by Huxley (1940) and van Steenis (1957). This involves identifying "species statu nascendi" (van Steenis, 1957), taxa with unique combinations of character states that show evidence of geographic or ecologic replacement but potentially incomplete reproductive isolation.

The approach advocated by Huxley and van Steenis avoids the mass proliferation of species names and acknowledges that speciation is a slow process usually requiring thousands of generations to produce morphologically recognizable, fully isolated, end products. To this end, Huxley (1940, p. 36) stated that "the principle of replacement should, whenever possible, be adopted, thus reducing the number of species while increasing the number of subspecies. Similar principles of ecological or genetic replacement should be reserved for natural groups of the same general nature as species but exhibiting a lower degree of morphological differentiation and/or reproductive isolation." For his part, van Steenis (1957, p. 228) opined that "the rank of subspecies should be reserved for, and confined to, replacing partial populations, i.e., natural groups of the same general nature as species but exhibiting a lower degree of morphological differences and/or reproductive isolation and for morphologically slightly distinct polyplotypes." The latter term, rarely used in the recent literature, indicates that van Steenis considered this approach especially relevant to classifying polyploid complexes. Given the strong correlation between chromosome numbers, geography, phenology, and the morphological features that distinguish the northern and southern population clusters of *D. maguirei*, we conclude that these "cytotypes" represent species statu nascendi, the archetype of subspecies as defined by Huxley (1940) and van Steenis (1957). Because the type specimens represent the northern cluster, this is the population system that bears the name *D. maguirei* subsp. *maguirei*. We here propose to recognize the southern taxon as *D. maguirei* subsp. *stonei*.

TAXONOMIC TREATMENT

Draba maguirei C. L. Hitchc., Revis. Drabas W. N. Amer. 70, plate 5, Figures 37a-c. 1941.

Draba maguirei C. L. Hitchc. subsp. ***maguirei***. Type: U.S.A. Utah. Cache Co.: Bear River Range, east slope of Mt. Naomi, subalpine, rocky soil at 9600 ft., 20 July 1936, *Maguire et al. 14161* (holotype: WTU 51784; isotypes GH, NY 185302 photo!, UTC 22118!).

Draba maguirei C. L. Hitchc. subsp. ***stonei*** Windham, subsp. nov. (Appendix S1). Type: U.S.A. Utah. Cache Co.: ENE of Logan in the Bear River Range near U.S. Route 89 ~0.8 road miles ENE of the entrance to Wood Camp Campground. Lat./Long.: 41.7999N 111.6311W (WGS84 Datum), 5850 ft. elev., in gravelly (dolomite) soil on NW-facing ridgetop with *Pinus, Juniperus, Pseudotsuga, Cercocarpus*, and *Lomatium*. 27 April 2018, *M.D. Windham 4474* (holotype: DUKE 408063!; isotypes BRY!, COLO!, MO!, NY!, RM!, UC!, US!, UT!, UTC!).

Similar to subsp. *maguirei* but differing in: (1) rosette leaves with trichomes common on margins and surfaces (vs. usually sparse on margins and absent on surfaces); (2) leaf trichomes mostly 2- to 3-rayed (vs. many 4-rayed); (3) fruits and proximal portion of flowering stems usually sparsely pubescent (vs. mostly glabrous); (4) chromosome number of $2n = 16$ (vs. 32); and 5) occurrence in low- to mid-montane habitats <2450 m elevation (vs. high-montane to subalpine habitats >2450 m).

Perennials with branched caudices forming loose, spreading mats to 20 dm in diam.; caudex branches terminating in leaf rosettes that produce either leafy, sterile, short shoots or scapose flowering stems in later growing seasons. **Rosette leaves** appressed to ground surface or slightly recurved, oblanceolate, 0.5–1.2 cm × 1.5–3 mm; margins with stalked, mostly 2- and 3-rayed trichomes to 0.7 mm long; leaf surfaces (especially abaxial) with scattered trichomes. **Sterile short shoots** unbranched, to 2 cm long, leafy, with sparse, mostly 2- and 3-rayed trichomes to 0.7 mm long; short shoot leaves alternate and recurved proximally, tufted and ascending distally, narrower and more pubescent than rosette leaves. **Flowering/fruiting stems** unbranched, scapose, 0.4–1.3 dm, sparsely hirsute proximally with simple and/or 2- and 3-rayed, short-stalked trichomes to 0.7 mm long. **Racemes** 5–19-flowered, ebracteate, elongating in fruit; rachises straight to slightly flexuous, glabrous. **Fruiting pedicels** divaricate-ascending to ascending, gently upcurved or straight, the lowermost 5–12(20) mm long, glabrous. **Flowers**: sepals elliptic, 3–4 × 1.2–2 mm, glabrous or with rare, mostly simple trichomes; petals yellow, oblanceolate, often shallowly bilobed at apices, 5–7 × 1.2–2 mm; anthers broadly sagittate, 0.5–0.9 × 0.4–0.5 mm when shedding pollen. **Fruits** ± flattened parallel to the septum, not twisted, ovate to lanceolate, bilaterally symmetric to slightly falcate, styles 0.5–1.4 mm, mature ovaries 3–7.5 × 2–3.3 mm; valves with scattered, simple trichomes to 0.3 mm long (occasionally glabrous);

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ovules 4–10 per ovary. **Seeds** ovoid to oblong, 1.6–2 × 1.3–1.6 mm. **Chromosome number** $2n = 16$.

Paratypes

Fruiting paratypes from type population: 2 June 2018, *M.D. Windham 4497* (DUKE!, MO!, NY!, UT!); 8 July 1997, *M.D. Windham & M.J. Windham 97-118* (DUKE!); flowering paratypes from type population: 23 May 1998, *M.D. Windham & M. Beilstein 98-202* (DAO!; DUKE!)

Distribution, Habitat, and Phenology

Known only from the Bear River Range in Cache Co., Utah. Shaded dolomite outcrops and adjacent rocky slopes; 1600–2440 m. Flowering April–June.

Etymology and additional comments

This taxon is named in honor of R. Douglas Stone, who participated in many phases of this project and was the first to point out the distinctive nature of the southern populations of *D. maguirei*. Conservation status: *Draba maguirei* s.s. (i.e., excluding *D. burkei*) is a Utah endemic that has not been found in adjacent Idaho (Moseley, 1991); it is ranked as globally imperiled (G2; NatureServe, 2022). Known populations of *D. maguirei* s.s. are about equally divided between *D. maguirei* subsp. *maguirei* and *D. maguirei* subsp. *stonei*, effectively halving the distribution and population numbers of both taxa.

AUTHOR CONTRIBUTIONS

This study was conceived of and organized by M.D.W. Field samples were gathered by M.D.W. Data collection and analyses were conducted by M.D.W., K.T.P., and K.M.P. All authors discussed the results and contributed to the final manuscript.

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DATA AVAILABILITY STATEMENT

DNA sequences used in this study are deposited in GenBank (Appendix 1).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Holotype of *Draba maguirei* subsp. *stonei* in the Duke University Herbarium.

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APPENDIX 1: SAMPLE INFORMATION FOR SPECIMENS INCLUDED IN MOLECULAR PHYLOGENETIC ANALYSES. TAXON, COLLECTION DATA, COLLECTOR (VOUCHER LOCATION), ITS GENBANK ACCESSION NO.

Arabis alpina L.: Romania, *O'Kane & Dihoru 3618* (MO), AF137559. ***Arabis nuttallii*** (Kuntze) B.L. Rob.: U.S.A., Montana, *O'Kane 3672* (MO), AF137562. ***Draba abajoensis*** Windham & Al-Shehbaz: U.S.A., Utah, San Juan Co., La Sal Mountains, *Windham et al. 95-170* (UT), AY047682 (as *D. spectabilis* Greene). ***Draba albertina*** Greene: U.S.A., Utah, Juab Co., Mt. Nebo, *Windham 96-206* (UT), AY047661. ***Draba asprella*** Greene: U.S.A., Arizona, Coconino Co., tributary of Bear Wallow Canyon E of Sedona. *Windham et al. 98-002* (UT), AY047662. ***Draba bruniifolia*** Steven: Armenia, Pambakski Mountains, Mt. Kerogli, *Chandjian s.n.* (UT), AY047664. ***Draba burkei*** (C.L. Hitchc.) Windham & Beilstein: U.S.A., Utah, Box Elder Co., Wellsville Mountains, Cottonwood Canyon, *Windham et al. 95-113* (UT), AY047684. ***Draba cana*** Rydb.: Canada, Alberta, WSW of Banff, *Mulligan & Crompton 3261* (DAO), AY047665 (Mulligan, 1971a). ***Draba crassa*** Rydb.: U.S.A., Colorado, Summit Co., Hoosier Ridge, *O'Kane & Weber 11063* (DAO), DQ467634. **Draba *cusickii*** B.L. Rob. ex O.E. Schulz.: U.S.A., Oregon, Harney Co., Steens Mtn., *Chambers 2406* (DAO), DQ467622 (as *D. sphaeroides* Payson). ***Draba densifolia*** Nutt.: U.S.A., Utah, Salt Lake Co., Wasatch Mountains, S of Alta, *Windham & Windham 97*-138 (UT), AY047667. ***Draba glabella*** Pursh 1: Canada, Northwest Territories, E end of Great Slave Lake, *Cody 15818* (DAO), AY047668 (Mulligan, 1970). ***Draba glabella*** 2: Canada, Québec, Gaspé Peninsula, Cap Chat, *Hellquist* 14777 (UT), AY047669. ***Draba globosa*** Payson: U.S.A., Utah, Salt Lake Co., Wasatch Mountains *Windham & Windham 95-227* (UT), AY047670. ***Draba helleriana*** Greene: U.S.A., New Mexico, vicinity of Santa Fe Canyon, *Arsène & Benedict 16924* (BM), DQ467533. ***Draba kassii*** S.L. Welsh: U.S.A., Utah, Tooele Co., Deep Creek Range, Goshute Canyon, *Windham 98-211* (UT), AY047672. ***Draba lonchocarpa*** Rydb. var. ***exigua*** O.E. Schulz: U.S.A. Utah, Summit Co., Uinta Mountains, Bald Mt., *Windham 95-215a* (UT), AY047673. ***Draba lonchocarpa*** Rydb. var. ***lonchocarpa***: U.S.A., Utah, Cache Co., Bear River Range, W of Crescent Lake, *Windham & Stone 95-199* (UT), AY047674. ***Draba maguirei*** C.L. Hitchc. subsp. ***maguirei***: U.S.A., Utah, Cache Co., Bear River Range, Mt. Magog, *Windham 95-161* (UT), AY047675. **Draba *maguirei*** C.L. Hitchc. subsp. ***stonei*** Windham: U.S.A., Utah, Cache Co., Logan Canyon, *Windham 97-118* (UT), OQ161093. ***Draba nivalis*** Lilj.: Canada, Northern Territories, Baffin Island, *Parmelee & Seaborn 4177* (DAO), AY047677 (Mulligan, 1974). ***Draba novolympica*** Payson & H. St. John: U.S.A., Utah, Juab Co., Deep Creek Mountains, Haystack Peak, *Windham & Holmgren 95-191* (UT), AY047679 (as *D. paysonii* J.F. Macbr. var. *treleasei* (O.E. Schulz) C.L. Hitchc.). ***Draba nuda*** (Bél.) Al-Shehbaz & M. Koch: Iran, *Rechinger 54514* (M), AF137577. ***Draba sobolifera*** Rydb.: U.S.A., Utah, Piute Co., Tushar Mountains, Bullion Canyon, *Windham & Stone 95-201* (UT), AY047681. ***Draba subalpina*** Goodman & C.L. Hitchc.: U.S.A., Utah, Garfield Co., Paunsaugunt Plateau, Coyote Hollow, *Windham 98-129* (UT), AY047683. ***Draba ventosa*** A. Gray: Canada, Alberta, N of Banff, *Mulligan & Mulligan 3489* (DAO), AY047685 (Mulligan, 1971b). ***Draba verna*** L.: U.S.A., Utah, Salt Lake Co., W base of Wasatch Mountains *Windham et al. 90-80* (UT), AY047686.

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