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Reinstatement of the Southern Andean Genus *Stenodraba* (Brassicaceae) Based on Molecular Data and Insights from its Environmental and Geographic Distribution

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Abstract*—Stenodraba* (Brassicaceae) included a group of eight species distributed along the Andes of South-Central Argentina and Chile. All of its species are currently treated in *Pennellia* (Tribe Halimolobeae) and *Weberbauera* (Tribe Thelypodieae). However, the phylogeny of *Stenodraba* and its tribal placement were never analyzed using molecular data. The lack of such studies, as well as the paucity of herbarium collections suggesting that some species are vulnerable and/or endangered, prompted us to address the molecular phylogeny of *Stenodraba*. For this purpose, we generated comprehensive molecular phylogenies using nuclear (ITS) and plastid (*trnL-F* and *trnH-psbA*) data and conducted different niche comparisons in the environmental and geographic spaces using climate data processed both by ordination and species distribution modelling (SDM) techniques. Results from phylogenetic analyses demonstrated that *Stenodraba* belongs to the South American tribe Eudemeae and is related to the genera *Aschersoniodoxa*, *Brayopsis*, *Dactylocardamum*, and *Eudema*. *Stenodraba* species formed two strongly supported clades, and although molecular data did not recover monophyly of the genus, this hypothesis could not be rejected with our data. The main clades were differentiated in their climatic niches (both in the environmental and geographical spaces), and niche overlap was greater within than between clades. Systematic implications, including a key distinguishing *Stenodraba* from the remaining genera of Eudemeae and a synopsis of its species, are also provided. The new combination ***S. lagunae*** is proposed.

***Keywords*—**Argentina, Chile, climatic niche, Cruciferae, Eudemeae, molecular phylogeny, *Pennellia*, *Weberbauera*.

Alpine ecosystems are considered highly sensitive to climate change because their distribution has been closely linked to temperature and precipitation patterns (Halloy and Mark 2003; Sklenář and Balslev 2005; Pauli et al. 2015; Cuesta et al. 2017). Moreover, the restricted altitudinal range that many species occupy within the alpine ecosystems has been suggested to enhance sensitivity to climate change (Sklenář and Jørgensen 1999). Because climate change and habitat loss can have an impact on different biodiversity components and biome integrity (Dawson et al. 2011; Bellard et al. 2012; Mantyka-Pringle et al. 2015; Urban 2015), one of the most crucial issues for any conservation initiative concerns the study of taxonomy and systematics of taxa, as well as the evolutionary and ecological patterns associated with their diversification (Mace 2004; Winter et al. 2013; Lean and Maclaurin 2016). Therefore, results from systematic, evolutionary, and ecological studies of different taxa can be incorporated, for example, as diverse measures of taxonomic, phylogenetic, and functional diversity (Tucker et al. 2017; Garnier et al. 2016).

One of the most important alpine ecosystems in the world extends along the Andes for some 9000 km in western South America, and it is characterized by significant vegetational diversity (Barthlott et al. 2005). These mountains are divided into three major geographical units: the northern Andes (Venezuela, Colombia, Ecuador, and northern Peru; ~11°N–8°S), the central Andes (central and southern Peru, Bolivia, and northern Argentina and Chile; ~8°S–29°S), and the southern Andes (South-central Argentina and Chile; ~29°S–55°S) (Weigend 2002). They provide highly diverse habitats for the evolution and diversification of numerous plant lineages of different families (Luebert and Weigend 2014). The Brassicaceae, with 52 tribes, 341 genera, and ca. 3973 species (including a basal tribe Aethionemeae and a core of three to five lineages) (Al-Shehbaz 2012a; German 2014; Huang et al. 2016; Özüdoğru et al. 2017; Guo et al. 2017; BrassiBase at: https://brassibase.cos.uni-heidelberg.de), are most abundant in the temperate regions of the Northern Hemisphere, especially the Irano–Turanian and Mediterranean regions and western North America (Appel and Al-Shehbaz 2003). However, they are well represented in South America by ca. 380 native species mainly distributed along the Andes (I. A. Al-Shehbaz, unpubl. data). Several phylogenetic studies on South American Brassicaceae were presented in the last five years, principally on the endemic tribes Cremolobeae, Eudemeae, and Schizopetaleae (e.g. Salariato et al. 2013a, 2015, 2016; Toro-Núñez et al. 2013, 2015). However, further phylogenetic analyses are still needed to clarify the systematics and evolution of the remaining South American crucifers. Such studies are crucial to understand the diversity of this family in particular and the Andean flora in general.

Schulz (1924) established the genus *Stenodraba* to include six species distributed along the Andes of South-central Argentina and Chile, from San Juan province (Argentina) and Region III (Chile) in the north, into Santa Cruz province and Region XII in the southernmost portion of this mountain range (Fig. 1). The group was morphologically characterized to include perennial herbs with a woody and several-branched caudex, rosettes of basal leaves, ebracteate inflorescences, and siliques (Fig. 2). Although Boelcke and Romanczuk (1984) maintained *Stenodraba* in their family treatment for the Patagonian Flora, Al-Shehbaz (1990b, 2004) included the eight accepted species in the Andean genus *Weberbauera* Gilg & Muschl, based on the similarities in habit, flowers, and fruits. Later, based on the presence of dendritic and malpighiaceous trichomes and cup-shaped flowers, Bailey and Al-Shehbaz (in Bailey et al. 2007) transferred two of these species to the genus *Pennellia* Nieuwl. [*P. lechleri* (E.Fourn.) Al-Shehbaz & C.D.Bailey and *P. parvifolia* (Phil.) Al-Shehbaz & C.D.Bailey] and maintained the remaining six species in *Weberbauera* [*W. chillanensis* (Phil.) Al-Shehbaz, *W. colchaguensis* (Barnéoud) Al-Shehbaz, *W. imbricatifolia* (Barnéoud) Al-Shehbaz, *W. lagunae* (O.E.Schulz) Al-Shehbaz, *W. stenophylla* (Leyb.) Al-Shehbaz, *W. suffruticosa* (Barnéoud) Al-Shehbaz] (Al-Shehbaz 2008, 2012b). However, the monophyly and phylogenetic placement of *Stenodraba* have never

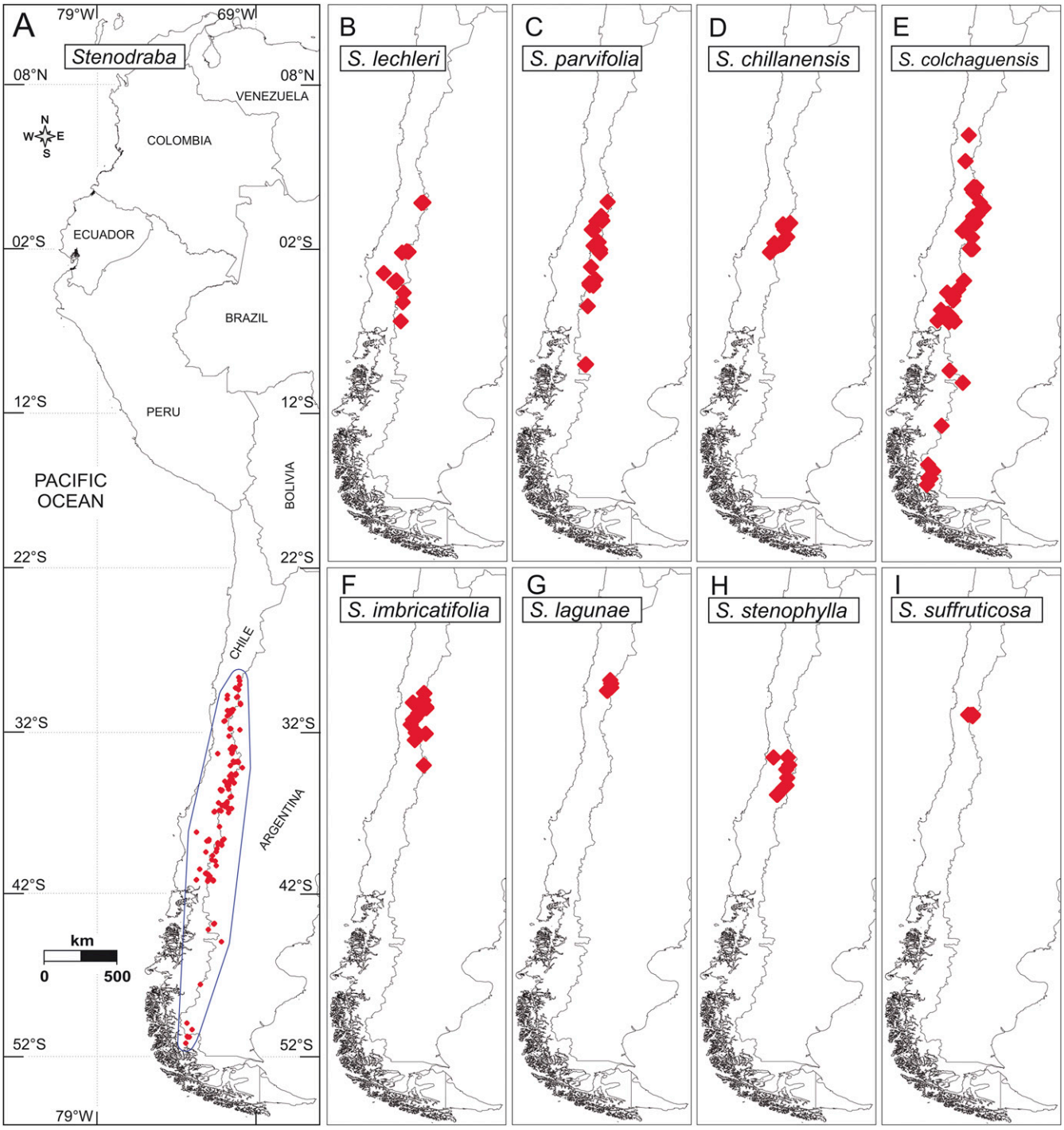

FIG. 1. Distribution maps of *Stenodraba* species. A. *Stenodraba*, delimited area corresponding to the 50 km-buffered minimum convex polygon used in the niche analyses. B. *S. lechleri*. C. *S. parvifolia*. D. *S. chillanensis*. E. *S. colchaguensis*. F. *S. imbricatifolia*. G. *S. lagunae*. H. S. *stenophylla*. I. *S. suffruticosa*. Dots represent specimen records for the different species.

been studied using molecular data. In order to avoid confusion, the above species of *Pennellia* and *Weberbauera* will be treated hereafter in *Stenodraba*.

Weberbauera, which was included in the tribe Thelypodieae and lineage II of Brassicaceae (Al-Shehbaz 2012a; Kiefer et al. 2014; BrassiBase), is a South American endemic genus with 24 species distributed primarily along the central Andes of Argentina, Bolivia, and Peru (Al-Shehbaz 1990b, 2004; Al-Shehbaz et al. 2015). However, its geographic distribution throughout the southern Andes of Argentina and Chile is represented exclusively by the six species previously recognized in *Stenodraba*. The genus *Pennellia* is placed in tribe Halimolobeae of lineage I (Al-Shehbaz 2012a; BrassiBase), and its ten species have a disjunct distribution in North America (western U. S. A. and Mexico), Central America (Costa Rica and Guatemala), and South America (Argentina, Bolivia, and Colombia). As in the geographic distribution of *Weberbauera*, the only species of *Pennellia* that inhabit the southern portion

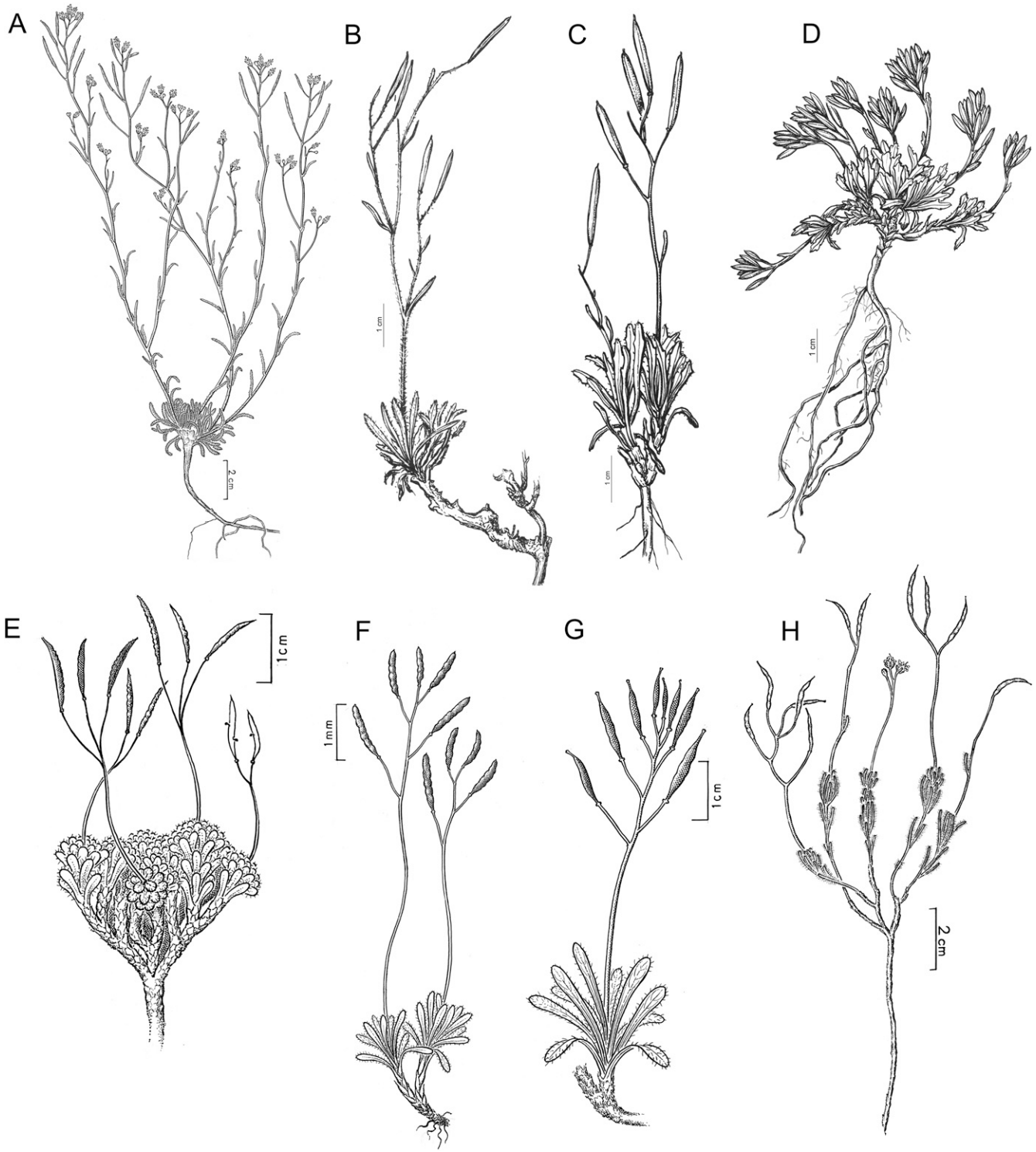

FIG. 2. Species of *Stenodraba*. A. *S. lechleri* (drawn from *Zuloaga 15141*, SI). B. *S. parvifolia* (*Boelcke 11565*, SI). C. *S. chillanensis* (*Boelcke 13946*, BAA). D. *S. colchaguensis* (*Boelcke 11370*, BAA). E. *S. imbricatifolia* (*Hunziker s.n.*, SI-167192). F. *S. lagunae* (*Johnston 6056*, CONC). G. *S. stenophylla* (*Montt 1671*, CONC). H. *S. suffruticosa* (*Jiles 3408*, CONC).

of the Argentinean-Chilean Andes are those assigned herein to *Stenodraba*.

Although species of *Stenodraba* grow along the southern Andes, predominantly in the Altoandina biogeographical province (sensu Cabrera and Willink 1973), they vary considerably in their geographical space. For example, *W. colchaguensis* and *P. parvifolia* are distributed at the southernmost portion of the Andes (~51°S) at 800–1500 m, while *W. imbricatifolia*, *W. lagunae*, and *W. suffruticosa* are found at 3000–4500 m along the Andes of central Argentina and Chile (~29°S) where aridity is higher. The lack of studies on *Stenodraba*, coupled with the poor representation of herbarium collections that suggest classifying some species in the vulnerable (UV) or endangered (EN) categories of the IUCN red

list (IUCN 2012), prompted us to investigate the monophyly, phylogenetic position, and tribal affinities of *Stenodraba*. In addition, we also investigated the ecological niche variation among these species and main lineages. To address these issues, we generated comprehensive molecular phylogenies using nuclear (ITS) and plastid (*trnL-F* and *trnH-psbA*) data and conducted different niche comparisons. Because it has been reported that tests of niche overlap using geographical projections derived from species-distribution modelling (SDM) techniques are likely to vary depending on the extent and distribution of environmental gradients in the study area (Broennimann et al. 2012), we used climate data processed both by ordination and SDM techniques that represent the environmental and geographical spaces, respectively. Results of these analyses would allow us to elucidate the molecular systematics of this group and the implications for its distribution and, therefore, contributing to understanding the evolutionary and ecological aspect of South American Brassicaceae and Andean flora.

Materials and Methods

Taxon Sampling—Twenty-five accessions representing eight species previously included in *Stenodraba* (see Al-Shehbaz 2008) were sampled from all major geographical areas and covering all morphological variation: *S. chillanensis* (four accessions), *S. colchaguensis* (six), *S. imbricatifolia* (two), *S. lagunae* (two), *S. lechleri* (two), *S. parvifolia* (five), *S. stenophylla* (three), *S. suffruticosa* (one) (see Appendix 1). To investigate their relationships within Brassicaceae, we generated ITS and *trnL-F* sequences for other members of *Pennellia* and *Weberbauera* and used an additional 143 (ITS) and 122 (*trnL-F*) accessions from GenBank (https://www.ncbi.nlm.nih.gov/genbank/) following the sampling strategy of Salariato et al. (2013b) and Salariato and Al-Shehbaz (2014), representing 45 and 34 tribes of Brassicaceae, respectively (GenBank numbers are in Appendix 2). Subsequent analyses within tribe Eudemeae (see results) were conducted using ITS, *trnL-F*, and *trnH-psbA* sequences for all *Stenodraba* accessions together with a dataset from Salariato et al. (2015), including all genera of the tribe and ca. 75% of its species.

Extraction, Amplification, and DNA Sequencing—Total DNA was isolated from leaves (collected in the field and dried in silica gel) using a modified (CTAB) protocol by Doyle and Doyle (1987), or from herbarium material using a DNeasy plant mini kit (Qiagen, Hilden, Germany). The nuclear ribosomal ITS region (ITS1–5.8S-ITS2) was amplified by PCR in one or two fragments using the ITS2, ITS3, ITS4, and ITS5 primers of Baldwin (1992); the chloroplast *trnL-F* region (*trnL* intron/*trnL-F* spacer) was amplified in one or two fragments using primers C, D, and E of Taberlet et al. (1991) and Fdw (Salariato et al. 2013b). Sequences for *trnH-psbA* spacer were amplified in one fragment using primers *trnH*(GUG)/*psbA* (Hamilton 1999). The PCR reactions were performed in 25 μL final volumes with 50–100 ng of template DNA, 0.2 μM of each primer, 25 μM dNTP, 5 mM $MgCl_2$, 1 × buffer, and 1.5 units of *Taq* polymerase provided by Invitrogen Life Technologies (São Paulo, Brazil). In addition, bovine serum albumin (BSA) 5% and dimethyl sulfoxide (DMSO) 5% (v/v) were used to increase the yield, specificity, and consistency of PCRs. The PCR amplifications were set at the following conditions for most species: (ITS) a first period of denaturation at 94°C for 5 min, followed by 35 cycles of denaturation at 94°C for 30 s, annealing at 50°C for 60 s, and extension at 72°C for 90 s, with a final extension at 72°C for 7 min; (*trnL-F*) a first period of denaturation at 94°C for 3 min, followed by 35 cycles of denaturation at 94°C for 30 s, annealing at 48°C for 60 s, and extension at 72°C for 90 s, with a final extension at 72°C for 10 min; (*trnH-psbA*) a first period of denaturation at 94°C for 3 min, followed by 35 cycles of denaturation at 94°C for 30 s, annealing at 55°C for 60 s, and extension at 72°C for 90 s, with a final extension at 72°C for 10 min. Cleaning of PCR products was done by Macrogen, Inc. (Seoul, South Korea) using the Montage PCR purification kit from Millipore and following the manufacturer's protocol. Sequencing reactions were also performed by Macrogen using the ABI PRISM BigDye Terminator cycle sequencing kits with AmpliTaq DNA polymerase (Applied Biosystems, Seoul, South Korea) following the protocols supplied by the manufacturer. Sequences were assembled and edited using the program Chromas Pro 1.7.7 (Technelysium Pty Ltd., Brisbane, Australia), which was also used for checking the presence of single peaks in the chromatograms, especially in the ITS sequences. Eighty-eight new sequences were obtained and submitted to GenBank (voucher information and GenBank accession numbers are provided in Appendix 1). Alignments were generated with Muscle 3.8.31 (Edgar 2004) using a first round of multiple alignments and posterior rounds of refinement under the default settings. The alignments obtained were then checked and improved manually where necessary using Bioedit 7.2.5 (Hall 1999). Aligned matrices, and all other supplemental data, including Tables S1–S4 and Figs. S1–S6, are available from the Dryad Digital Repository (Salariato et al. 2018).

Phylogenetic Studies in Brassicaceae—In order to assess the phylogenetic placement of *Stenodraba*, the Brassicaceae dataset from ITS and *trnL-F* sequences were analyzed separately using maximum likelihood (ML) and Bayesian inference (BI). In these analyses gaps were treated as missing data. The models of nucleotide substitution were selected by using the Akaike information criterion (AIC) implemented in jModeltest2 2.1.6 (Darriba et al. 2012): GTR + I + G (ITS) and TVM + G (*trnL-F*). The ML analyses were conducted in RAxML 8.2.4 (Stamatakis 2014) using nonparametric bootstrap (BS) analysis and searches for the best-scoring ML tree in a single run (Stamatakis et al. 2008). We performed 1000 rapid bootstrap inferences and, thereafter, a thorough ML search under the GTRGAMMAI (ITS) and the GTRGAMMA (*trnL-F*) models. Bayesian analyses were conducted using MrBayes 3.2.6 (Ronquist et al. 2012) using GTR + I + G (ITS) or GTR + G (*trnL-F*) models, and the priors on state frequencies, rates, and shape of the gamma distribution were estimated automatically from the data assuming no prior knowledge about their values (uniform Dirichlet prior). Two simultaneous analyses, starting from different random trees and with four Markov Monte Carlo chains, were run for 20 million generations, sampling every 10,000 generations to ensure independence of the successive samples. The convergence and effective sample size were checked with the average standard deviation of split frequencies (ASDSF) < 0.01, the potential scale reduction Factor (PSRF) ~ 1, and verifying with Tracer 1.6.0 (Rambaut et al. 2013) that effective sample size (ESS) for all parameters was over 400. The first 500 trees (25% of total trees) were discarded as burn-in, the remaining samples of each run were combined, and a 50% majority consensus tree was calculated. Trees obtained in ML and BI analyses are available from the Dryad Digital Repository (Salariato et al. 2018). Additionally, we tested the inclusion of *Stenodraba* species within the tribes associated to their current generic classification (*Pennellia* and *Weberbauera*) using the SH test (Shimodaira and Hasegawa 1999) and the approximately unbiased test (AU) (Shimodaira 2002). We selected tribes instead of genera to avoid assumptions of monophyly for *Pennellia* and *Weberbauera*. Searches of constrained topologies, where *Stenodraba* species were forced to be included in tribe Halimolobeae (for species under *Pennellia*), and tribe Thelypodieae (for species under *Weberbauera*) (sensu Al-Shehbaz 2012b) were conducted in RAxML with 1000 replicates and the models used above. Site-wise log-likelihoods of all hypotheses (Table 1) were first calculated with PAUP 4.0b10 (Swofford 2002), and then used in CONSEL 0.1j (Shimodaira and Hasegawa 2001) to estimate p values of the SH and AU tests, rejecting the hypothesis when $p < 0.05$.

Phylogenetic Studies in Eudemeae—Because results from the phylogenetic studies in Brassicaceae (see above) proved the inclusion of all *Stenodraba* species in the tribe Eudemeae, we conducted new phylogenetic analyses to study the monophyly and position of the genus in this tribe. For this, we used ITS, *trnL-F*, and *trnH-psbA* sequences from the *Stenodraba* accessions and the datasets of tribe Eudemeae obtained in Salariato et al. (2015). Alignments are available from the Dryad Digital Repository (Salariato et al. 2018). Data matrices were analyzed separately and combined using maximum likelihood and Bayesian inference, following the same methodology described above. However, in these analyses, we also assessed the inclusion of gaps coded as present or absent in accordance with the "simple indel coding" method implemented by Simmons and Ochoterena (2000) in the program FastGap 1.2 (Borchsenius 2009). Gaps derived from ambiguous alignment regions of mononucleotide repeat units (poly-N's) were discarded following recommendations of Kelchner (2000). Species of *Schizopetalon* Sims and *Menonvillea* DC. were included as outgroups following the phylogenetic relationships of the Cremolobeae-Eudemeae-Schizopetaleae clade in Salariato et al. (2016). Models selected by jModeltest for each region were: TVMef + G (ITS), TVM + G (*trnL-F*), and TPM1uf + G (*trnH-psbA*). Individual and concatenated datasets (cpDNA and ITS + cpDNA) were subjected to an ML search using RAxML under the GTRGAMMA model, 1000 replicates, and using two (cpDNA) or three (ITS + cpDNA) partitions for concatenated

TABLE 1. Comparisons of tree topology hypotheses by using SH and AU Tests. Hypotheses (H) in bold were rejected ($p < 0.05$). H1: inclusion of *S. chillanensis*, *S. colchaguensis*, *S. imbricatifolia*, *S. lagunae*, *S. stenophylla* and *S. suffruticosa* within tribe Thelypodieae; H2: inclusion of *S. lechleri* and *S. parvifolia* within tribe Halimolobeae; H3: inclusion of *S. chillanensis*, *S. colchaguensis*, *S. imbricatifolia*, *S. lagunae*, *S. stenophylla* and *S. suffruticosa* within tribe Thelypodieae and *S. lechleri* and *S. parvifolia* within tribe Halimolobeae; H4: monophyly of *Stenodraba* within tribe Eudemeae.

Dataset	Hypothesis (H)	ΔlnL (best tree vs H)	p (SH)	p (AU)
Brassicaceae: ITS	**H1**	158.50	$p < 0.001$	$p < 0.001$
Brassicaceae: ITS	**H2**	234.94	$p < 0.001$	$p < 0.001$
Brassicaceae: ITS	**H3**	296.04	$p < 0.001$	$p < 0.001$
Brassicaceae: *trnL-F*	**H1**	116.62	$p < 0.001$	$p < 0.001$
Brassicaceae: *trnL-F*	**H2**	165.92	$p < 0.001$	$p < 0.001$
Brassicaceae: *trnL-F*	**H3**	231.69	$p < 0.001$	$p < 0.001$
Eudemeae: ITS	H4	2.41	0.239	0.099
Eudemeae: cpDNA (*trnL-F* + *trnH-psbA*)	H4	4.74	0.139	0.054
Eudemeae: concatenated ITS + cpDNA	H4	5.20	0.102	0.059

analyses. Individual and concatenated BI analyses were set in MrBayes as nst = 6 and rates = gamma, with rate-matrix parameters, state frequencies, and gamma shape parameter unlinked across partitions for cpDNA and ITS + cpDNA datasets. All analyses were conducted using two run of four chains for 40 million generations, sampling every 10,000 generations and discarding the first 1000 trees (25% of total trees). Convergence and ESS of each replicate were verified checking for ASDSF < 0.01, PSRF ~1, and ESS >400 for all parameters.

To address levels of discordance among nuclear ribosomal (ITS) and plastid (*trnL-F*, *trnH-psbA*) trees and their influence on the concatenated analyses, congruence among partitions was assessed using a Bayesian concordance analysis (BCA) (Ané et al. 2007; Baum 2007) implemented in the software BUCKy 1.4.4 (Larget et al. 2010). The BUCKy analysis was conducted using the posterior distribution of the ITS and cpDNA gene trees produced with MrBayes, with 2 runs, 4 chains, and one million generations following a burn-in of 100,000. The discordance parameter (α), which represents the a priori expected level of discordance, was set to 1, 10, and 100. Alternatively, assuming that all topological discordance is caused by incomplete lineage sorting, we conducted species-tree analysis under the multispecies coalescent model (Xu and Yang 2016) implemented in *BEAST extension (Heled and Drummond 2010) of BEAST 2.4.4 (Bouckaert et al. 2014). All nucleotide substitution models were unlinked across loci, and an uncorrelated log-normal clock model (UCLN) was assigned to each sampled locus. We linked the tree model for the two chloroplast regions (*trnL-F* and *trnH-psbA*) because they are genetically linked, and we set separate tree models for the chloroplast dataset and the nuclear ribosomal ITS region. A Yule process was used for the species tree prior, and the piecewise linear with constant root was used for the population-size model. Four runs were conducted in BEAST using 100 million generations and sampling every 25,000. Effective sample size (ESS) > 200 was checked in Tracer 1.6, and the first 25% of each run was discarded as burn-in. Replicates were combined using LogCombiner 2.4.4, and the species maximum clade credibility tree (MCCT) was calculated using TreeAnnotator 2.4.4. In addition to the concatenated, concordance, and species tree analyses, incongruences between ITS and cpDNA data were also visualized in a filtered supernetwork calculated with SplitsTree 4.13.1 (Huson and Bryant 2006) using 1000 Bayesian posterior trees of each nuclear and plastid data set, and filtering the splits to show only those present in a minimum of 35% input trees.

Monophyly of *Stenodraba* within tribe Eudemeae under the ITS, cpDNA, and the concatenated ITS + cpDNA datasets was tested using the SH and AU tests implemented in CONSEL, constraining the monophyly of *Stenodraba,* and following the same strategy and settings as described above. Additionally, we also compared the hypothesis of monophyly using Bayes Factor (BF) analysis. For this, BF was calculated in MrBayes using marginal likelihood estimations (MLE) obtained via the stepping-stone sampling method (SS; Xie et al. 2011) and following the approach proposed in Bergsten et al. (2013), in which the marginal likelihoods are calculated from two alternative topology hypotheses after the specification of equally informed priors (constraints). We ran the stepping-stone sampling using two independent runs of four Markov chains, taking 50 steps for a total of 39,780,000 generations, sampling every 10,000 generations, and discarding the first 780,000 generations as burn-in (the same length as each step). The contribution to the marginal likelihood in each step was estimated from a sample size of 78. The 2lnBF was calculated from the MLE to compare the different hypotheses (monophyly vs. non-monophyly) following criteria of Kass and Raftery (1995): 2lnBF = 0–2 "not worth more than a bare mention," 2lnBF = 2–6 "positive" support, 2lnBF = 6–10 "strong" support and 2lnBF > 10 "decisive" support in distinguishing between competing hypotheses.

Niche Quantification in Environmental and Geographical Spaces—For studies of the geographical and environmental spaces of *Stenodraba,* we used species occurrences obtained from the examination of specimens deposited in different herbaria (BA, BAA, BAB, CONC, E, GH, K, LIL, LP, MERL, MO, P, SGO, SI, SRFA, UPS, and US; herbarium acronyms follow Thiers 2017) and material collected during field trips (vouchers at SI). All records were mapped using Diva-GIS 7.5 (Hijmans et al. 2012) for visual inspection. In cases of specimens with no GPS coordinates but exact locality names, records were georeferenced using Google Earth 7.1.8. After removing duplicates and occurrences closer to 30 arc-seconds (~1 km), we obtained a total of 170 occurrences, with an average of 21 data points per species (*Stenodraba chillanensis*: 22, *S. colchaguensis*: 67, *S. imbricatifolia*: 21, *S. lagunae*: seven, *S. lechleri*: 12, *S. parvifolia*: 27, *S. stenophylla*: 10, *S. suffruticosa*: four) (Table S1). Since we analyzed geographical and environmental variations in the two main lineages recovered from the molecular phylogenies (see Results, clades A and B), total occurrence number was 32 for clade "A" (*S. imbricatifolia*, *S. lagunae*, *S.suffruticosa*) and 138 for clade "B" (*S. chillanensis*, *S. colchaguensis*, *S. lechleri*, *S. parvifolia*, *S. stenophylla*). Information on the current climatic conditions within the study area was extracted from the WorldClim database 1.4 (Hijmans et al. 2005) with a resolution of 30 arc-seconds (~1 km). Values of all 19 bioclimatic variables were extracted from the area defined by a minimum convex polygon enclosing all species records with a 50-km buffer zone (ca. 28°31′–51°40′S, 69°11′–73°00′W, Fig. 1). Additionally, we also included data from the annual aridity index (IA) and potential evapotranspiration (PET) database (Trabucco and Zomer 2009) (http://www.cgiar-csi.org) at the same resolution. Data extraction and manipulation were done using the packages adehabitatHR (Calenge 2006), raster (Hijmans 2016), sp (Bivand et al. 2013), and maptools (Bivand and Lewin-Koh 2017), implemented in R 3.3.1 (R Core Team 2016).

Niche comparisons in the environmental (E)-space between main lineages and species of *Stenodraba* were estimated using the PCA-env approach of Broennimann et al. (2012), in which a principal component analysis is calibrated on the entire environmental space (in our case, 19 BIOCLIM variables + IA + PET) present in the study area (the 50 km-buffered minimum convex polygon enclosing all *Stenodraba* species occurrences for this work, Fig. 1). We considered the first two principal components (PC), and we divided this environmental space in a grid of 100 × 100 cells, in which each cell corresponds to a unique vector of the available environmental conditions in the study area. Because the number of species occurrences can be biased, resulting in an under- or over-estimation of the species density, a kernel-density function is applied for smoothing the density of occurrences for each of the cells in the environmental space (for details, see Broennimann et al. 2012). The density grids for each species (or lineage) were used subsequently to compute the niche overlap by means of the Schoener's D statistic (Schoener 1970; reviewed in Warren et al. 2008). Schoener's D ranges from 0 (no overlap) to 1 (complete overlap). The PCA-env approach and niche-overlap estimation in the (E)-space was conducted using the ecospat package (Broennimann et al. 2016; Di Cola at al. 2017). When analyzing niche affinities between main lineages of *Stenodraba* (clades A and B) along the (E)-space, we used the niche equivalency test implemented in ecospat with 1000 replications to assess whether the ecological niches of these clades are significantly different from each other and if two niche spaces are interchangeable. The null hypothesis (niches are equivalent) was rejected when the measured overlap was significantly lower than the 95% of null distribution. Alternatively, we

also performed the niche similarity test (Warren et al. 2008) to assess whether the climatic niches of *Stenodraba* clades are dissimilar or more similar than expected by chance, accounting for the differences in the surrounding environmental conditions. For this test, we used 1000 repetitions, and the null hypothesis was rejected if niche overlap of the observed value was lower or greater than 95% of simulated values. Furthermore, comparisons of environmental niche overlaps among main clades were also visualized using density profiles computed for each bioclimatic niche axis in the sm package (Bowman and Azzalini 2014), and performing the Mann-Whitney *U* test on the PC 1–2 values for clades A and B. Later, we studied niche affinities among species, and because at least five relocations per species in the (E)-space are needed for PCA-env analyses, we generated one additional point for *S. suffruticosa* using the mean values of its four occurrences for PC1 and PC2. We calculated the Schoener's D metric for each pair of species, and then used the R package cluster (Maechler et al. 2016) to conduct agglomerative hierarchical clustering with the unweighted pair-group average (UPGMA) algorithm and a distance matrix composed by the niche-overlap estimation among all species. We also used this matrix to conduct K-means clustering under k = 2 to compare the species composition of the clusters obtained vs. the two main clades recovered in the phylogenetic analyses.

For niche comparisons in the geographical (G) space, we applied species distribution modelling (SDM) to model distribution of clades A and B using the maximum entropy algorithm implemented in Maxent 3.3.3k (Phillips et al. 2006). Because inclusion of the 21 bioclimatic variables (19 BIOCLIM + IA + PET) in the SDM can be problematic due to high degrees of colinearity among predictors (Heikkinen et al. 2006), we performed initial analyses on all 21 variables and then chose climatic variables that contribute most in the Maxent models using jackknife test, and with a Spearman's rank correlation coefficient (ρ) < 0.7. Five variables were selected for the SDM analyses: BIO3 (isothermality), BIO4 (temperature seasonality), BIO8 (mean temperature of wettest quarter), BIO12 (annual precipitation), and BIO15 (precipitation seasonality). Each Maxent analysis was performed using 10 cross validation runs with a maximum iterations of 1000, and all other options were left as default (logistic output, convergence threshold of 1.10^{-5}, 1.10^{4} background points, regularization multiplier of 1, default prevalence of 0.5, and autofeatures). The area under the receiver operating characteristic curve (AUC) was used as a measure of model performance, and variable contribution to SDM was evaluated through permutation importance test. We used two complementary approaches to explore niche comparison among clades A and B based on the SDM predictions. Firstly, to quantify the niche breadth, we generated the predicted niche occupancy (PNO) profiles using the phyloclim package (Heibl and Calenge 2013), following the methodology proposed by Evans et al. (2005). In order to obtain a PNO profile per variable, median suitability projections obtained for each clade in the SDM were integrated with each of the five variables and binned into 100 evenly spaced categories. From each PNO profile, we extracted 1000 random values associated with its probability distribution, and significant differences of these variables between the main lineages were tested using the non-parametric Mann-Whitney *U* test. Secondly, we conducted the niche equivalency and similarity tests in phyloclim using the ecological niche models obtained for each clade, the Schoener's D index, and 1000 permutations. The null hypothesis of niche equivalency and niche similarity was rejected when observed values for D index were significantly different ($p < 0.05$) from the pseudoreplicated data sets. Finally, to calculate the percentage of distribution area shared by each clade, we used binary presence/absence maps of clades A and B derived from the SDM predictions. Because the choice of a threshold is a topic of ongoing debate, we used the threshold indicating maximum training sensitivity plus specificity, which is considered as a more robust approach (Liu et al. 2005, 2013).

Results

Phylogenetic Studies in Brassicaceae—The ITS alignment for the Brassicaceae dataset included 154 sequences and was 719 bp long, of which 325 (45%) were parsimony informative. The *trnL-F* alignment included 144 sequences and was 1316 bp long, of which 323 (24%) were parsimony-informative. All ML and BI analyses of both regions placed the *Stenodraba* species within the tribe Eudemeae, specifically in a clade together with the genera *Aschersoniodoxa* Gilg & Muschl., *Brayopsis* Gilg & Muschl., *Eudema* Bonpl., and *Dactylocardamun* Al-Shehbaz (the "Northern-Central Andes" clade presented in Salariato et al. 2015) BS: 99%, PP: 0.99 (ITS); BS: 89%, PP: 1 (*trnL-F*) (Fig. 3, Fig. S1). Other species of *Pennellia* and *Weberbauera* were included in tribes Halimolobeae and Thelypodieae, respectively. Furthermore, the inclusion of *Stenodraba* species in their current generic placement was rejected under the SH and AU tests for both ITS and *trnL-F* datasets ($p < 0.01$ for all hypotheses, see Table 1).

Phylogenetic Studies in Eudemeae—Features of ITS, *trnL-F*, and *trnH-psbA* alignments are summarized in Table S2. The ML and BI analyses of the ITS and cpDNA data recovered similar topologies, showing the same strongly supported clades (Fig. 4A–B). Results from analyses of the individual cpDNA regions are available from the Dryad Digital Repository (Salariato et al. 2018). Both ITS and cpDNA data, as well as the concatenated ITS + cpDNA dataset (Fig. 4C), recovered *Stenodraba* species within a clade along with the North-central Andean genera (hereafter called NCA* clade to differentiate it from the NCA "North-central Andes" clade of Salariato et al. 2015 which did not include *Stenodraba*) (BS: 99% and PP: 1 with concatenated dataset), but split in two strongly supported subclades: clade A (*S. imbricatifolia*, *S. lagunae*, and *S. suffruticosa*) and clade B (*S. lechleri*, *S. parvifolia*, *S. chillanensis*, *S. colchaguensis*, and *S. stenophylla*) (BS: 100% and PP: 1 for both clades). However, monophyly of *Stenodraba* was never obtained in any dataset. Finally, all North-central Andean species, except *Aschersoniodoxa peruviana* Al-Shehbaz et al. were grouped in a third strongly supported subclade (BS: 98%, PP: 1). Similar results were also recovered when analyses also included indel data (Fig. S2). Results from concordance analyses varying the discordance prior (α) had no effect on topology or concordance. The primary concordance tree produced by BUCKy (Fig. 4D) was topologically congruent with the concatenated phylogeny, and main clades, including *Stenodraba* species, also presented high concordance factor (CF) values. Species trees obtained under the multispecies coalescent model also were congruent with the concatenated and concordance trees, showing high support for the NCA*, A, and B clades (pp: 1) (Fig. S3A). Additionally, differences between the cpDNA and ITS trees were represented graphically by a filtered supernetwork (Fig. S3B), in which cycles in the network represent conflicting phylogenetic signals. Evidence of incongruences was mainly located within the clade B and the "*Aschersoniodoxa-Brayopsis-Eudema-Dactylocardamum*" clade, but supported clades obtained in the phylogenetic analyses were also present in the supernetwork. Finally, although the monophyly of *Stenodraba* was not obtained by any analyses, the SH and AU tests failed to reject this hypothesis with all datasets ($p > 0.05$, Table 1). Bayes Factor analyses only slightly favored the non-monophyly of the genus ($2\ln BF_{\text{non-monophyly/monophyly}} = 0.58$, 2.74, and 1.96 for ITS, cpDNA, and concatenated ITS + cpDNA datasets, respectively).

Niche Quantification in Environmental Space—Eigenvalues and variable loadings for the PCA-env approach are shown in Table S3. The first two PCs accounted for 78.57% of the niche variation (42.60% and 35.97%, respectively). Variable loadings (Table S3, Fig. S4) showed that the first component was primarily influenced by variables associated with humidity and precipitation, such as the PET (ability of the atmosphere to remove water through evapotranspiration processes), the precipitation of the warmest /driest quarters (BIO18 and BIO17), and the precipitation availability over atmospheric water demand defined by the index aridity (IA); and

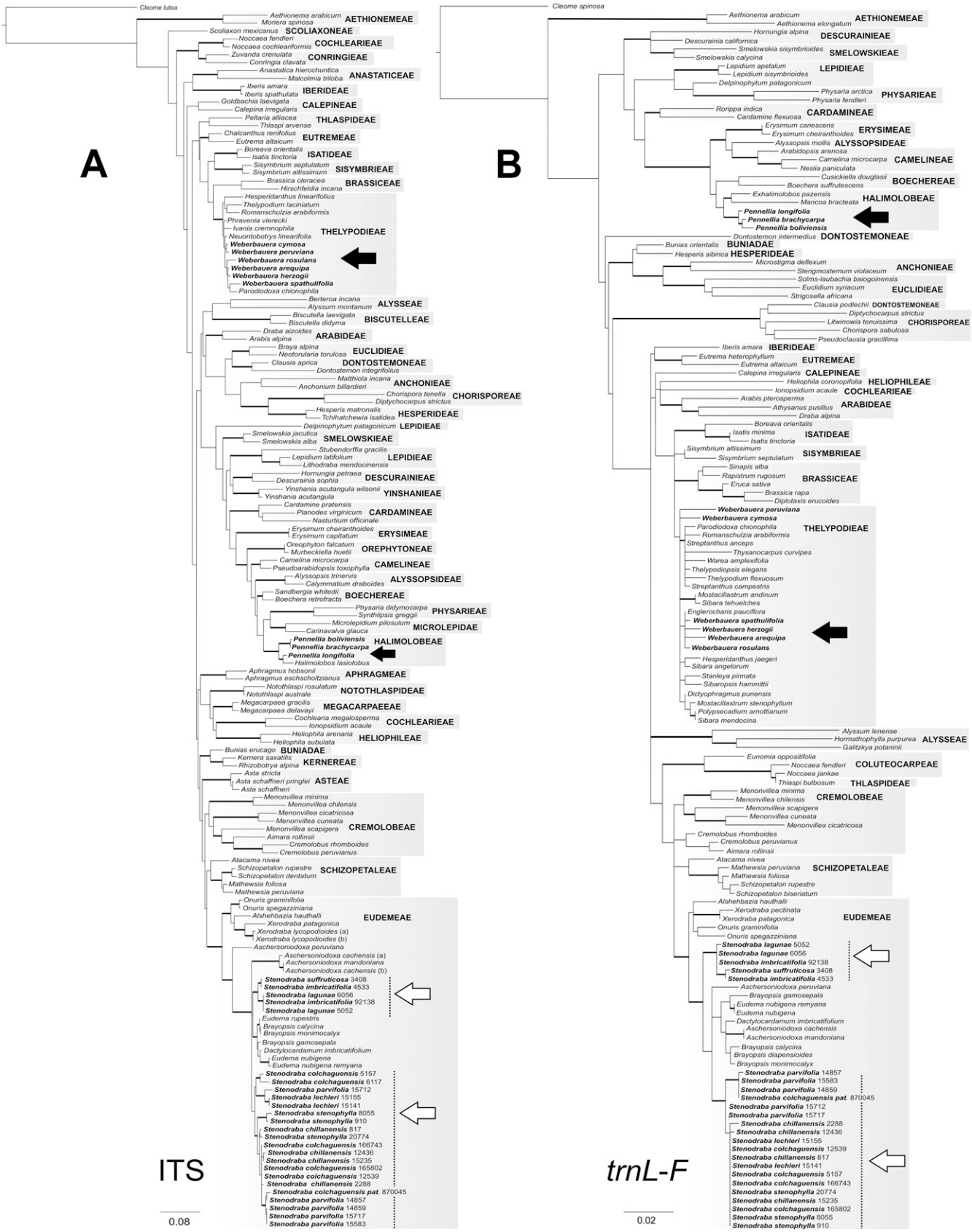

FIG. 3. Maximum likelihood trees for Brassicaceae generated with RAxML. A. ITS dataset. B. *trnL-F* dataset. Tribes are indicated to the right of the boxes. Thick branches indicate bootstrap support values > 80%. The white arrows indicate phylogenetic position of *Stenodraba*, while black arrows show the position of species of *Pennellia* (tribe Halimolobeae) and *Weberbauera* (tribe Thelypodieae).

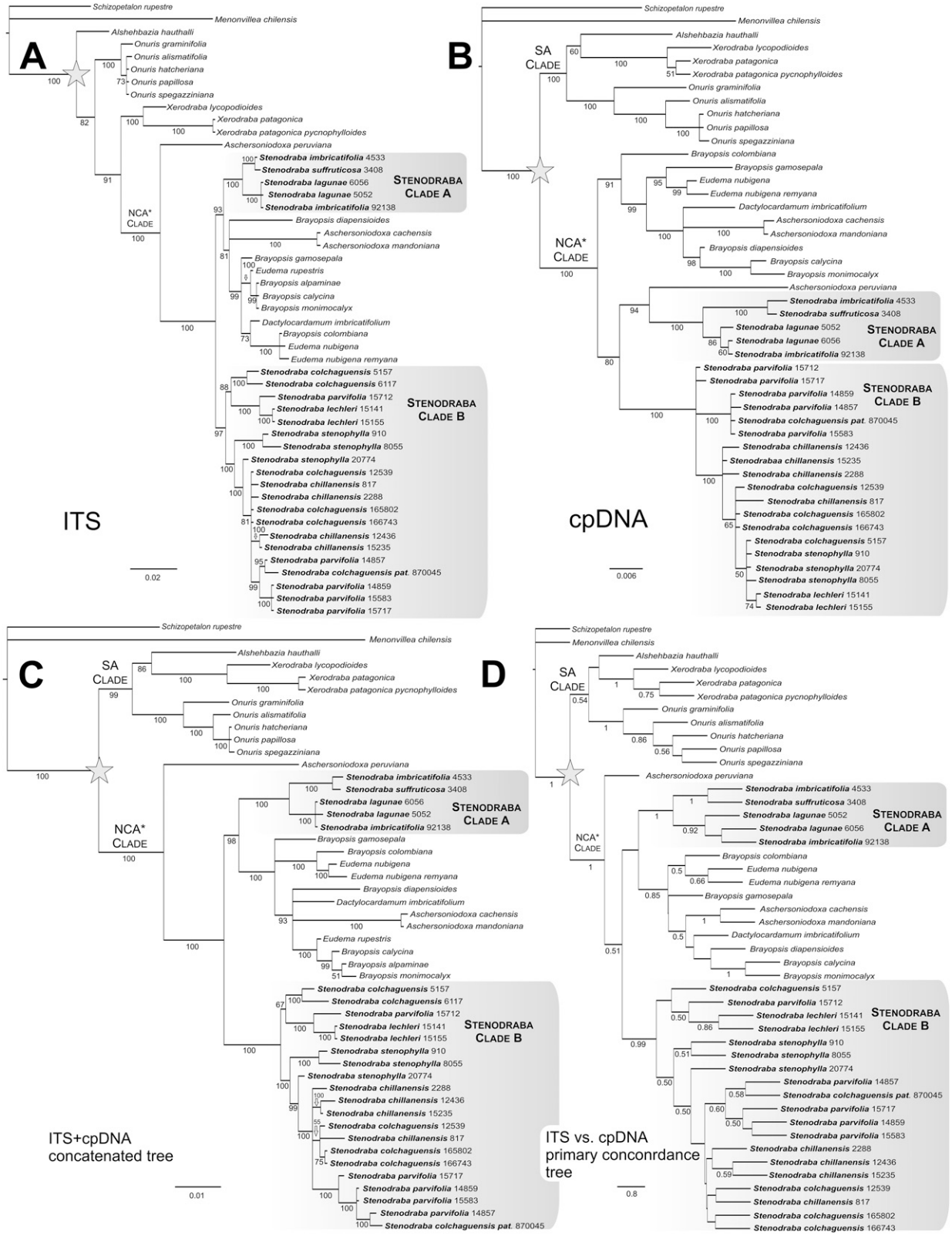

FIG. 4. Phylogenetic placement of species of *Stenodraba* within tribe Eudemeae. A– C. Bayesian 50% majority-rule consensus trees from 6002 trees generated by Bayesian inference with MrBayes. A. nrITS dataset. B. cpDNA dataset (*trnL-F/trnH-psbA*). C. Concatenated cpDNA + nrITS dataset. Values on branches correspond to Bayesian posterior probability (%). D. Primary concordance tree from the BUCKy analyses using the 6002 trees from the ITS and the cpDNA datasets obtained in the MrBayes analyses. Concordance factor values (CF) ≥ 0.5 are shown on branches. The start on the nodes indicates the crown node of tribe Eudemeae. Units of branch length are proportional to nucleotide substitutions per site for A–C and to the concordance factor obtained in the concordance analyses for D.

secondarily by variables related to the temperature annual range (BIO7) and the max temperature of warmest month (BIO5). The second PC showed higher correlation with the min temperature of coldest month/quarter (BIO6/BIO 11), and with variables related to precipitation of the coldest/wettest quarters (BIO16 and BIO 19). Thus, in the (E)-space, environments with higher aridity, lower precipitation, and higher temperatures in the summer load negatively in the first PC, while in the second PC higher minimum temperatures and winter precipitation load negatively (Fig. S4). Climatic niches occupied by clades A and B in the (E)-space are shown in Fig. 5A–B. The niche equivalency test recovered significant differences (non-equivalency) for clades A and B (Schoener's D = 0.081, $p = 0.037$, Table 2), while the niche-similarity test did not recover significant similarity between these clades (clade A→ clade B $p = 0.128$; clade B→ clade A $p = 0.288$). Additionally, the Mann-Whitney *U* test supported significant differences among clades A and B for values of the PCs 1 and 2 ($p = 0.004$ and $p < 0.001$, respectively), while density plots (Fig. 5C–D) show that niche differentiation in clades A and B was greater along PC2. Climatic niches in the (E)-space for species of clades A and B also exhibited greater differentiation along the PC2 (Fig. S5), while cluster analyses using the niche overlap measures (Schoener's D) show two main clusters (Fig. 5 E–G), including the same species of clades A and B. This result was also confirmed by the K-means clustering under k = 2.

Niche Quantification in Geographical Space—Values of the AUC obtained in the SDM for clade A and B resulted in 0.982 (SD = ± 0.012) and 0.931 (± 0.019) indicating a good model performance (Fig. 6A–B, Table S4). The isothermality (BIO3) and mean temperature of wettest quarter (BIO8) were the variables that contributed most to the SDM of clade A, while for clade B it was BIO8 and annual precipitation (BIO12) (Table S4). Mann-Whitney *U* test recovered significant differences between clades A and B for the five variables used (BIO8-BIO12: $p < 0.001$, BIO15: $p = 0.003$), however, the mean temperature of wettest quarter (BIO8) and the precipitation seasonality (BIO15) showed the larger overlap between clades (Figs. 7 and S6). Niche equivalency test using the distribution models for clades A and B rejected the equivalency of both niches in the (G)-space (Schoener's D = 0.169, $p < 0.01$), and the similarity test did not recover significant similarity between clades, but it did show significant differentiation for niche of clade B vs clade A ($p < 0.01$) (Table 2). Finally, percentage of distribution area shared by each clade and estimated using the binary presence/absence maps derived from the SDM predictions (Fig. 6C) resulted in 6.68% for clade A and 1.49% for clade B, with the sympatric area mainly located in the Andes of Southern Region IV (Chile) and San Juan province (Argentina) (~30°55′S – 32°15′S, 70°53′W – 70°20′W).

Discussion

The results presented here strongly support the inclusion of *Stenodraba* in tribe Eudemeae and, therefore, its belonging to the Cremolobeae-Eudemeae-Schizopetaleae clade (CES clade, Salariato et al. 2016) of the expanded lineage II. Previous treatments of these species in *Weberbauera* and *Pennellia* were based exclusively on morphology (Al-Shehbaz 1990b, 2004; Bailey et al. 2007) and thus revealing the substantial homoplasy of morphological characters that are well documented in Brassicaceae (e.g. Franzke et al. 2011; Hall et al. 2011; Huang et al. 2016). The tribe Eudemeae, which is closely related to the South American Cremolobeae and Schizopetaleae (Salariato et al. 2016), is represented by seven South American endemic genera distributed along the Andes and Argentinean Patagonia: *Alshebazia* Salariato & Zuloaga (one species), *Aschersoniodoxa* (four species), *Brayopsis* (seven species), *Dactylocardamum* (two species), *Eudema* (four species), *Onuris* Phil. (five species), and *Xerodraba* Skottsb. (five species) (Al-Shehbaz 2012a; Salariato and Zuloaga 2015). Although the tribe comprises only perennial species, it exhibits a wide variation in vegetative and reproductive characters, including growth forms (rosettes or cushions), presence or absence of bracts, production of solitary flowers vs. racemes, and diverse fruit morphology (silicles or siliques; latiseptate, terete, or angustiseptate) (Salariato et al. 2015). Molecular studies on this tribe have recovered two main lineages represented by the North-central Andean clade (*Aschersoniodoxa*, *Brayopsis*, *Dactylocardamum,* and *Eudema*) and the South Andean clade (*Alshebazia*, *Onuris*, and *Xerodraba*), and estimated its divergence (crown node age) in the mid-Miocene (12.95 MYA, 95% highest posterior density "HPD" 9.29–16.57 MYA), with the central and southern Andes as ancestral areas of its diversification and subsequent colonizations of the northern Andes in the Pliocene (Salariato et al. 2015, 2016). Specifically, *Stenodraba* is related to the genera of the NCA clade, from which it is clearly differentiated by its morphology and distribution (see below and Key to Genera). The geographical distribution of *Stenodraba* is differentiated from other members of the NCA clade because it extends from the southern limit of the central Andes (San Juan Province and Region III in Argentina and Chile, respectively) in the North, into the Austral portion of southern Andes (Santa Cruz province and Region XII) (~28.6°S – 51.2°S) in the South. By contrast, genera of the NCA clade are distributed along the Andean highlands from Colombia into northern Argentina and do not reach the southern portions of the Central Andes (Salariato et al. 2015).

Although the phylogenetic placement of *Stenodraba* in Eudemeae, and more specifically with genera of the NCA clade, was strongly supported by the molecular data, its monophyly was not recovered. Two strongly supported clades (clades A and B) which are morphologically and geographically defined, were obtained, but the analyses failed to retrieve relationships among them. Nevertheless, SH - AU tests and Bayes factor analyses did not unambiguously reject the monophyly of the genus. Furthermore, monophyly of *Stenodraba* in the cpDNA phylogenies was interrupted only by the placement of *A. peruviana*. *Aschersoniodoxa* is a genus of four species distributed along the Central Andes of Northern Argentina, Bolivia, and Peru, and it is clearly distinguished from the remaining genera of Eudemeae (including *Stenodraba*) by having leaflike, strongly latiseptate, and basipetally dehiscent siliques with valves remaining adnate to the replum base (Al-Shehbaz 1990a; Al-Shehbaz et al. 2012). In particular, *A. peruviana* is endemic to Peru, and though it was separated from the remaining *Aschersoniodoxa* species in the analyses of Salariato et al. (2015) and here, new phylogenetic studies including more accessions and loci should be conducted to corroborate its placement. The above sources of evidence, together with the morphological similarities among *Stenodraba* species, lead us not to split the genus but to retain species of clades A and B under the same generic name.

Stenodraba is readily distinguished from the remaining genera of Eudemeae by producing rosettes, elongated racemes, and linear siliques. Within the genus, there are few

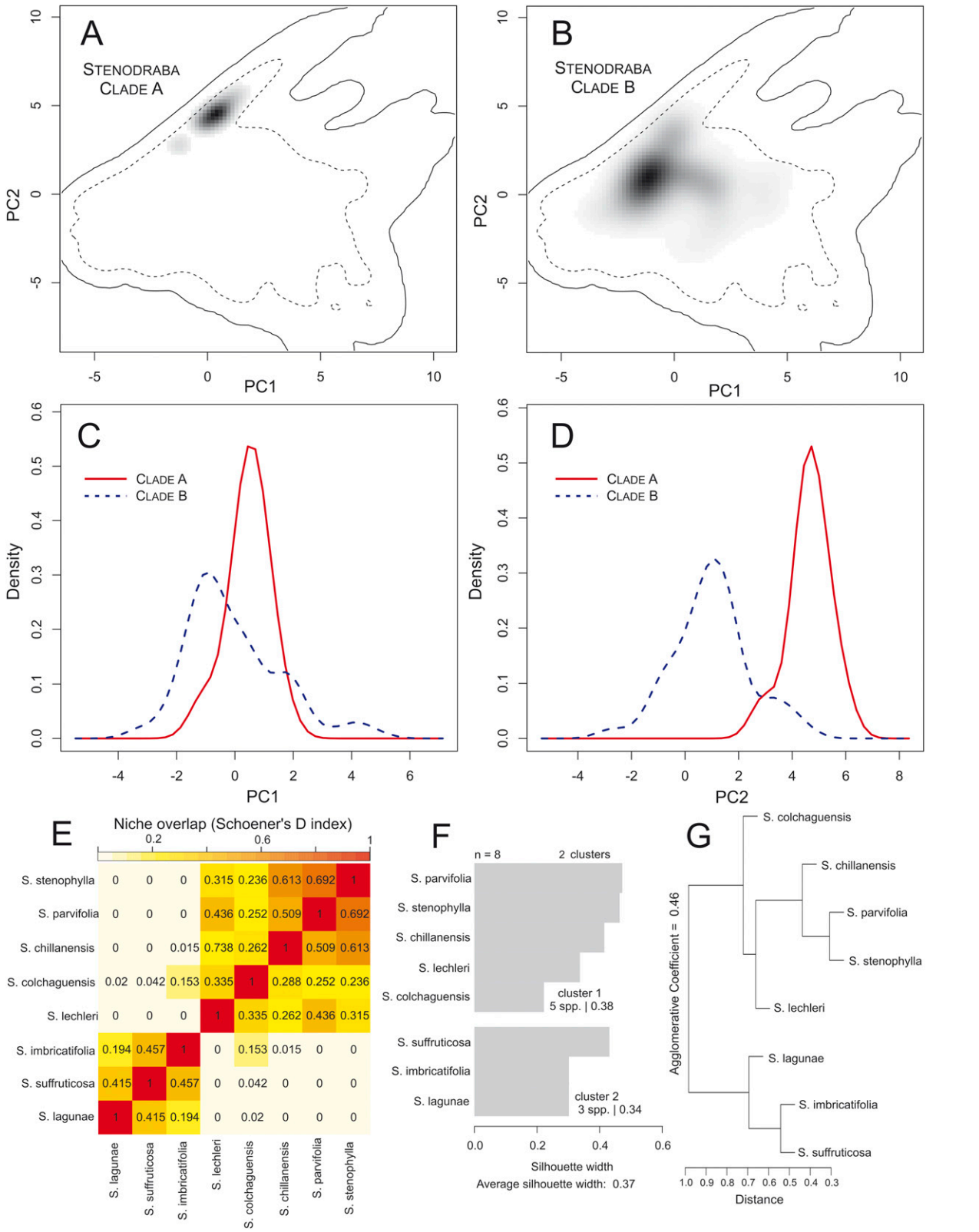

FIG. 5. Results from the niche comparisons in the environmental (E) space. A–B. Climatic niches for clades A and B of *Stenodraba* produced by the two main axes of the PCA-env. For each clade, the gray to black shading represents the grid cell density of the clade occurrence (black being the highest density). The dashed line represents 50% of the available environment and the solid line represents 100%. A. Clade A. B. Clade B. C–D. Density plots computed for clades A and B of *Stenodraba* using the PC1 (C) and PC2 (D); solid red line corresponds to clade A, blue dashed line to clade B. E–G. Niche overlap estimations among *Stenodraba* species. E. Pairwise niche overlap between each *Stenodraba* species quantified using the Schoener's D index. F. K-means clustering (k = 2). G. Agglomerative hierarchical clustering UPGMA algorithm using niche overlap estimations.

TABLE 2. Niche comparisons between clades A and B of *Stenodraba* in the environmental (E) and geographical (G) space. Comparisons with $p < 0.05$ (in bold) indicate that niches of clades A and B are not identical/equivalent (equivalency test), or that niches are more dissimilar or similar (similarity test) than expected by chance. [a] More dissimilar than expected by chance.

	Niche overlap	Niche equivalency	Niche similarity *p* value	
	(Schoener's D)	*p* value	clade A → clade B	clade B → clade A
(E)-space	0.081	**0.037**	0.128	0.132
(G)-space	0.161	**< 0.01**	0.288	**< 0.01**[a]

characters that differentiate the main clades. Species of clade A (*S. imbricatifolia*, *S. lagunae*, and *S. suffruticosa*) are scapose perennial herbs with few-flowered racemes (Fig. 2). They are distributed in the Andes of Central Argentina and Chile at elevations between 2900–4400 m, and are the only taxa of Eudemeae occupying this geographical range (Salariato et al. 2015). Species of clade B (*S. lechlerii*, *S. parvifolia*, *S. colchaguensis*, *S. chillanensis*, and *S. stenophylla*) are cespitose perennial herbs usually with cauline leaves and many-flowered racemes. They inhabit an area from the central Andes of Argentina and Chile to their southern portion (~51.2S°) in Santa Cruz province and Region XII of Argentina and Chile, respectively (Fig. 1), at elevations between 700–3700 m. Of these, S. *colchaguensis* exhibits the largest distribution range and overlaps in the north with the range of clade A. In this work, we followed the species circumscription presented by Al-Shehbaz (2008, 2012b), and species descriptions and discussions of their delimitation is beyond the scope of the study. This is because specimen sampling and analyses used here are inadequate for testing and inferring species limits (methods reviewed in Fujita et al. 2012). However, molecular species delimitation within each clade should be conducted in the future to test the validity of the different species and their associated morphological variation, particularly for the widespread *S. colchaguensis*.

In contrast to morphology, climatic niches both on environmental (E) and geographic (G) spaces were clearly differentiated between the two lineages of *Stenodraba*. Species of lineage A grow at high elevations of central Argentina and Chile and are exposed to lower annual precipitation, lower winter temperatures, and higher day-to-night temperature oscillation when comparing them with niches of lineage B. This differentiation is also reflected in their geographical distribution by the lower sympatric area predicted for the two clades (lower than 10% in the SDM analyses). Our results suggest that each *Stenodraba* clade is constrained by a unique set of environmental conditions, and conservation for each clade should reflect its unique environmental requirements, especially for clade A, which shows narrow environmental and geographical ranges. Conversely, species clustering using niche-overlap distances suggests that niche space within *Stenodraba* clades seems to present a certain degree of conservatism, revealing that diversification in these clades could have occurred predominantly under sympatry and niche conservatism. Similar patterns of niche divergence among clades and similarity within clades, with the species retaining their fundamental niches over time, were found in the Andean genus *Menonvillea* DC. (Salariato and Zuloaga 2017). Future studies on niche evolution across the entire tribe and other Andean Brassicaceae might indicate whether or not this is a general pattern of the southern-central Andean lineages.

Based on the present results, the genus *Stenodraba* is reinstated and included in tribe Eudemeae. A key to the genera of Eudemeae, a key to the species of *Stenodraba*, and a synopsis of its eight species are presented.

TAXONOMIC TREATMENT

KEY TO THE GENERA OF THE TRIBE EUDEMEAE

1. Fruit a silique; valves 4–11 mm broad, leaflike, prominently veined; Argentina, Bolivia, Peru ..... *Aschersoniodoxa*
1. Fruit a silique or silicle, valves < 3 mm broad, not leaflike, obscurely veined 2
2. Cushion plants with solitary pseudoterminal flowers, rarely racemes 2- or 3-flowered 3
2. Herbs not forming cushions, with 3–many-flowered racemes 4
3. Leaves thin, silicles terete; Peru ..... *Dactylocardamum*
3. Leaves thick, rather fleshy; silicles latiseptate; Argentina and Chile ..... *Xerodraba*
4. Racemes elongated in fruit 5
4. Racemes not elongated in fruit or flowers on long solitary pedicels arising from basal rosette 6
5. Fruit silicles; racemes bracteate throughout ..... *Onuris*
5. Fruit siliques; racemes ebracteate ..... ***Stenodraba***
6. Fruit terete siliques ..... *Brayopsis*
6. Fruit flattened silicles 7
7. Fruit angustiseptate, oblong; seed coat coarsely reticulate; Ecuador and Peru ..... *Eudema*
7. Fruit latiseptate, pyriform; seed coat smooth; Argentina and Chile ..... *Alshehbazia*

STENODRABA O.E.Schulz in Engler, Pflanzenreich. IV. 105(Heft 86): 186. 1924. TYPE: *S. chillanensis* (Phil.) O.E.Schulz.

Eight species distributed along central-southern Andes of Argentina and Chile.

KEY TO THE SPECIES OF *STENODRABA*

1. Flowers cup-shaped; petals subequaling sepals 2
1. Flowers bell-shaped or tubular; petals distinctly longer than sepals 3
2. Basal leaves with malpighiaceous (sessile, medifixed, 2-rayed) trichomes ..... *S. lechleri*
2. Basal leaves with simple and stalked branched trichomes ..... *S. parvifolia*
3. Basal leaves semiterete, thick, linear ..... *S. suffruticosa*
3. Basal leaves flat, thin, oblong to oblanceolate or spatulate, rarely linear-lanceolate 4
4. Style obsolete or rarely to 0.6 mm long in fruit 5

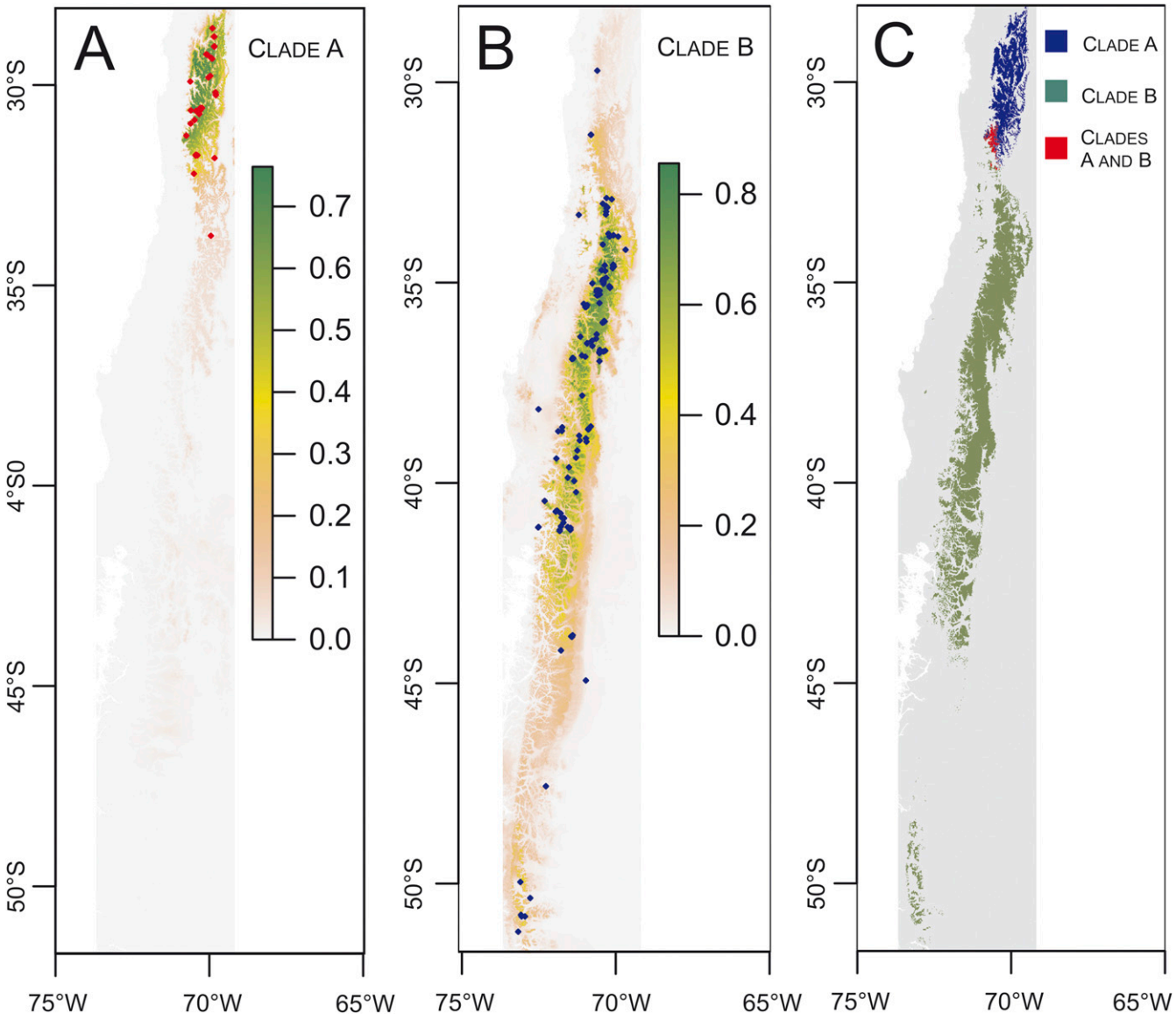

FIG. 6. Results from the species distribution modelling (SDM) for clades A and B of *Stenodraba*. A–B. Predicted suitable climatic conditions (logistic output) from the MaxEnt model for clades A and B of *Stenodraba* using BIO3, BIO4, BIO8, BIO12, and BIO15 as climatic variables. Dots represent specimen occurrences used for the SDM analyses. C. Binary (presence/absence) distributions maps for clades A and B derived from the SDM outputs using the maximum training sensitivity plus specificity as threshold. Blue cells indicate presence of clade A, green cells presence of clade B, and red cells indicate presence of both clades A and B.

4. Style 1−3 mm long in fruit, if shorter then fruits conspicuously flattened 6
5. Fruit torulose; infructescence lax racemes; fruiting pedicel slender, divaricate, 4−8(−12) mm long; basal leaves entire, to 1.5 mm wide . . . . . *S. lagunae*
5. Fruit smooth; infructescence usually dense, subumbellate; fruiting pedicels stout, subappressed, 1.5−4.5(−7) mm long; basal leaves usually dentate, 2−4.5(−6) mm wide . . . . . *S. colchaguensis*
6. Leaves abaxially with trichomes shorter than those adaxially or along margin; fruit torulose; stems usually leafless; petioles of basal leaves stout, swollen . . . . . *S. imbricatifolia*
6. Leaves abaxially glabrous; fruit smooth; stems few leaved; petioles of basal leaves slender, not swollen 7
7. Basal leaves entire; petals (3.5−)4−5 mm long; style (0.8−)1.5−2 mm long in fruit . . . . . *S. stenophylla*
7. Basal leaves dentate; petals 2.5−3.5 mm long; style 0.5−0.9(−1.1) mm long in fruit . . . . . *S. chillanensis*

STENODRABA CHILLANENSIS (Phil.) O.E.Schulz in Engler, Pflanzenreich IV. 105(Heft 86): 188. 1924. *Draba chillanensis* Phil., Anal. Univ. Chile 2: 377. 1862; *Weberbauera chillanensis* (Phil.) Al-Shehbaz, J. Arnold Arbor. 71: 244. 1990. TYPE: CHILE. [Region VIII Biobio], Termas de Chillán, *R. A. Philippi s.n.* (holotype: SGO-49187!).

STENODRABA COLCHAGUENSIS (Barnéoud) O.E.Schulz, Notizbl. Bot. Gart. Berlin-Dahlem 11: 644. 1932. *Cardamine colchaguensis* Barnéoud in C.Gay, Fl. Chile 1: 115. 1846; *Arabis colchaguensis* (Barnéoud) Turcz., Bull. Soc. Imp. Naturalistes Moscou 27(2): 293. 1854; *Sisymbrium colchaguensis* (Barnéoud) Wedd. ex E.Fournier, Rech. Anat. Tax. Fam. Crucif. 135. 1865; *Hesperis colchaguensis* (Barnéoud) Kuntze, Rev. Gen. Pl. 2: 934. 1891; *Weberbauera colchaguensis* (Barnéoud) Al-Shehbaz, J. Arnold. Arbor. 71: 241. 1990. TYPE: CHILE. [Region VI O'Higgins], Colchagua, cordillera del Cajón

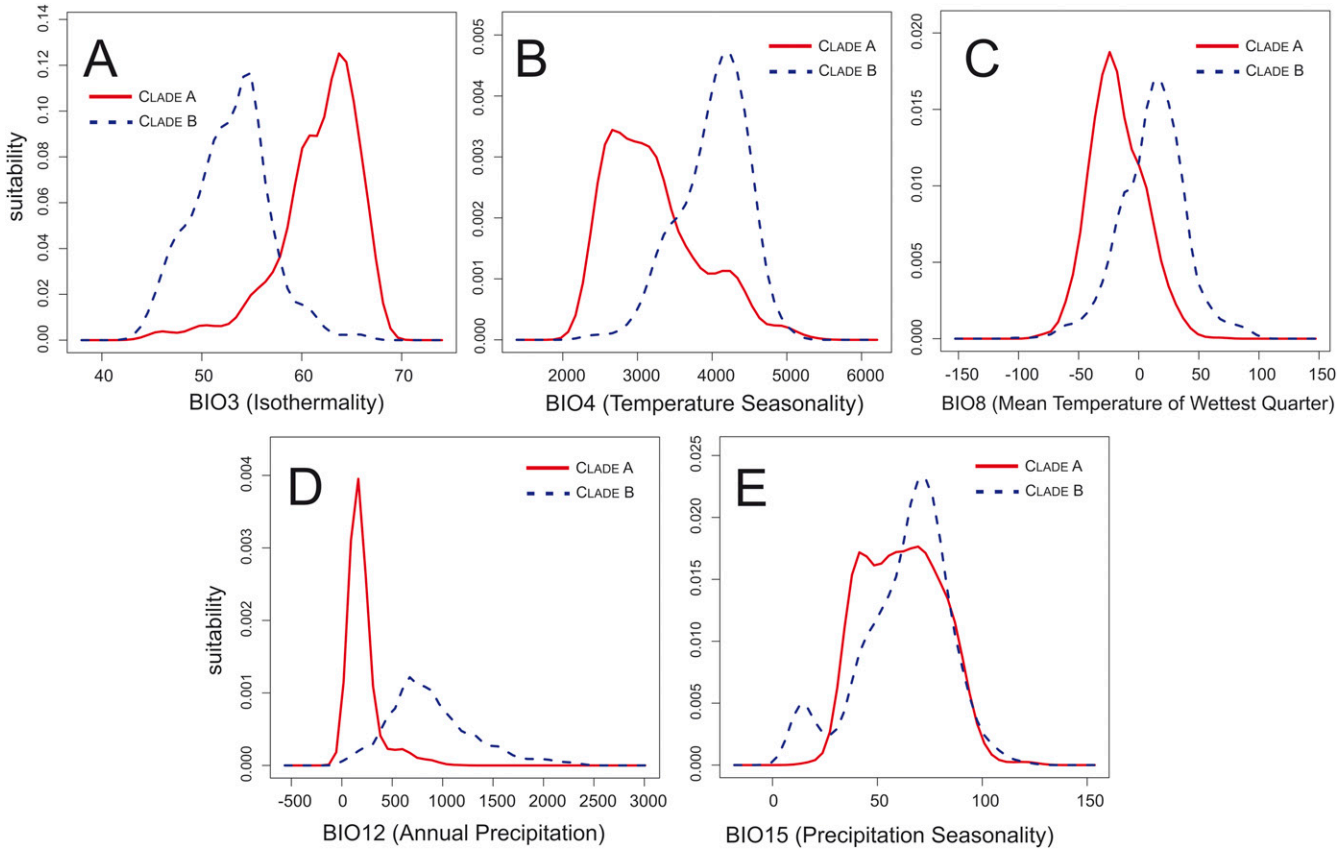

FIG. 7. Results from the niche comparisons in the geographical (G) space. Density plots computed for clades A and B of *Stenodraba* using the predicted niche occupancy (PNO) profiles of each variable used in the SDM analyses. A. BIO3 (Isothermality). B. BIO4 (Temperature Seasonality). C. BIO8 (Mean Temperature of Wettest Quarter). D. BIO12 (Annual Precipitation). E. BIO15 (Precipitation Seasonality). Solid red line corresponds to clade A while blue dashed line indicates clade B.

del Azufre, cerca de volcán de Talcarégue, 8000 - 9000 ft. [2438 - 2743 m], *C. Gay 171* (holotype: P!, isotypes: BAA!, G!).

Erysimum pusillum Gillies ex Hook. & Arn., Bot. Misc. 3: 140. 1833, not *E. pusillum* Bory & Chaub. in Bory, Exp. Sci. Morée, Bot. 3(2): 190. 1832; *Braya pusilla* A.Gray, U.S. Expl. Exped. Phan. 15(1): 57. 1854; *Sisymbrium pusillum* (A.Gray) Wedd. ex E.Fournier, Rech. Anat. Tax. Fam. Crucif. 131. 1865, not *S. pusillum* Villars, Fl. Delph in Gilibert, Syst. Pl. Europ. 1: 69. 1785; *Hesperis pusilla* (A.Gray) Kuntze, Rev. Gen. Pl. 2: 935. 1891; *Weberbauera pusilla* (A.Gray) O.E.Schulz in Engler, Pflanzenreich IV. 105(Heft 86): 194. 1924; *Stenodraba pusilla* (A.Gray) Boelcke, Dansk. Bot. Ark. 22: 143. 1968. TYPE: CHILE. El Cerro de la Porcura and la Cumbre de los Andes, 12,000 f [3656 m], *Gillies 8* (holotype: E!).

Draba andina Phil., Linnaea 28: 669. 1856; *Stenodraba andina* (Phil.) O.E.Schulz in Engler, Pflanzenreich IV. 105(Heft 86): 187. 1924. TYPE: CHILE. "in andibus prope oppidum Linares", *P. Germain s.n.* (holotype: SGO-63987!).

Draba patagonica Phil., Linnaea 28: 669. 1856; *Stenodraba andina* var. *patagonica* (Phil.) O.E.Schulz in Engler, Pflanzenreich IV. 105(Heft 86): 188. 1924; *S. patagonica* (Phil.) Ravenna, Nord. J. Bot. 1: 141. 1981; *S. pusilla* (A. Gray) Boelcke var. *patagonica* (Phil.) Boelcke, Fl. Patagonica 4a: 530. 1984. TYPE: CHILE. [Region X Los Lagos], Volcani de Osorno, Mar 1852, *R. A. Philippi s.n.* (holotype: SGO-63955!).

Arabis drabaeformis Schltdl., Flora 39: 410. 1856. TYPE: CHILE. [XIV Los Ríos], Cordillera de Ranco, *W. Lechler 2958* (holotype: HAL!, isotypes: G!, P!).

Stenodraba andina var. *hirticaulis* O.E.Schulz in Engler, Pflanzenreich IV. 105(Heft 86): 188. 1924. TYPE: CHILE. "Gipfel des Berges Pichiguan", *R. A. Philippi 67* (holotype: B!).

Stenodraba andina var. *stylosa* O.E.Schulz in Engler, Pflanzenreich IV. 105(Heft 86): 188. 1924. TYPE: CHILE. Volcán Lanín, 1800 m, Apr 1897, *F. Neger s.n.* (holotype: B!, isotype: M!).

STENODRABA IMBRICATIFOLIA (Barnéoud) O.E.Schulz in Engler, Pflanzenreich IV. 105(Heft 86): 190. 1924. *Draba imbricatifolia* Barnéoud in C.Gay, Fl. Chile 1: 158. 1846; *Braya imbricatifolia* (Barnéoud) A.Gray, U.S. Expl. Exped. Phan. 15(1): 58. 1854; *Sisymbrium imbricatifolium* (Barnéoud) Wedd., Chloris Andina 2: t. 58B. 1857; *Hesperis imbricatifolia* (Barnéoud) Kuntze, Rev. Gen. Pl. 2: 934. 1891; *Weberbauera imbricatifolia* (Barnéoud) Al-Shehbaz, J. Arnold Arbor. 71: 247. 1990. TYPE: CHILE. [Region IV Coquimbo], Cordillera de Coquimbo, 12,000 ft. [3658 m], *C. Gay s.n.* (holotype: P, isotype: B!).

Stenodraba imbricatifolia var. *glabrata* O.E.Schulz in Engler, Pflanzenreich IV. 105(Heft 86): 190. 1924. TYPE: CHILE. Without locality, *F. Leybold 2974* (holotype: B!, isotype: W!).

Stenodraba lagunae (O.E.Schulz) Salariato & Al-Shehbaz, comb. nov. Basionym: *Stenodraba suffruticosa* (Barnéoud) O.E.Schulz var. *lagunae* O.E.Schulz, Notizibl. Bot. Gart. Berlin-Dahlem 10: 469. 1928; *Weberbauera lagunae* (O.E. Schulz) Al-Shehbaz, J. Arnold Arbor. 71: 246. 1990. TYPE: CHILE. [Region III Atacama]. Vallenar, Cordillera Laguna Chica, ca. 4000 m, Jan 1924, *E. Werdermann 262* (holotype: B!, isotypes: BM!, CONC!, GH!, UC!).

STENODRABA LECHLERI (E.Fournier) Ravenna, Nord. J. Bot. 1: 141. 1981. *Sisymbrium lechleri* E.Fournier, Rech. Crucif. 129. 1865; *Hesperis lechleri* (E.Fournier) Kuntze, Rev. Gen. Pl. 2: 934. 1891; *Weberbauera lechleri* (E.Fournier) Al-Shehbaz, Novon 14: 263. 2004; *Pennellia lechleri* (E.Fournier) Al-Shehbaz & C.D.Bailey, Syst. Bot. 32: 153. 2007; *Sisymbrium stenophyllum* Schltdl., Linnaea 28: 475. 1856, non *S. stenophyllum* Gillies ex Hook. & Arn., Bot. Misc. 3: 139. 1833. TYPE: CHILE. Terra Pehuenchorum, Dec 1854, *W. Lechler 3080* (holotype: P!, isotypes: BAA!, G!, K!, P!).

Sisymbrium petraeum Phil., Linnaea 28: 668. 1856, non (L.) Delarbre, Fl. Auv. ed. 2: 349. 1800; *Hesperis petraea* Kuntze, Rev. Gen. Pl. 2: 935. 1891; *Heterothrix petraea* (Kuntze) O.E. Schulz in Engler, Pflanzenreich IV. 105(Heft 86): 298. 1924; *Pennellia petraea* (Kuntze) O.E.Schulz in Engler and Prantl, Nat. Pflanzenfam. 17B: 644. 1936; *Stenodraba glareosa* Ravenna, Nord. J. Bot. 1: 141. 1981. TYPE: CHILE. [Region VIII BioBio], "in Andibus prope oppidum Chillán," *R. A. Philippi s.n.* (holotype: SGO-49254!).

Sisymbrium fastigiatum Phil., Anal. Univ. Chile 41: 670. 1872; *Stenodraba fastigiata* (Phil.) Ravenna, Nord. J. Bot. 1: 140. 1981. TYPE: CHILE. [Prov. Santiago], Mina Cristo, valley of Maipo, *B. Dávilla s.n.* (lectotype: SGO 45138!, designated by Muñoz-Schick, An. Univ. Chile 128: 30. 1973).

Sisymbrium caespitosum Phil., Anal. Univ. Chile 81: 184. 1892. TYPE: CHILE. En la Araucanía, entre Ercilla & Victoria, Nov. 1887, *R. A. Philippi s.n.* (holotype: SGO-71496!).

STENODRABA PARVIFOLIA (Phil.) O.E.Schulz in Engler, Pflanzenreich IV. 105(Heft 86): 187. 1924. *Sisymbrium parvifolium* Phil., Linnaea 28: 667. 1856; *Weberbauera parvifolia* (Phil.) Al-Shehbaz, J. Arnold Arbor. 71: 248. 1990; *Pennellia parvifolia* (Phil.) Al-Shehbaz & C.D.Bailey, Syst. Bot. 32: 153. 2007. TYPE: CHILE. [Region VII Maule], Cordillera de Linares, *P. Germain s.n.* (holotype: SGO!).

Sisymbrium hispidum Phil., Anal. Univ. Chile 41: 670. 1870, non Vahl, Symbl. Bot. 2: 77. 1791, nec Poiret Encycl. Suppl. 5: 161. 1817; *Stenodraba vestita* Ravenna, Nord. J. Bot. 1: 141. 1981; *Sisymbrium vestitum* (Ravenna) Al-Shehbaz, Harvard Pap. Bot. 2: 16. 1990. TYPE: CHILE. Cordillera de Talcaregue, 1869–1870, *R. A. Philippi s.n.* (holotype: SGO-63213!).

STENODRABA STENOPHYLLA (Leybold) O.E.Schulz in Engler, Pflanzenreich IV. 105(Heft 86): 189. 1924. *Draba stenophylla* Leybold, Anal. Univ. Chile 16: 679. 1859; *Weberbauera stenophylla* (Leybold) Al-Shehbaz, J. Arnold Arbor. 71: 245. 1990. TYPE: CHILE. [Region Metropolitana de Santiago], Cord. Santiago, Cerro Colorado, Mapocho Valley, 6000–7000 ft. [1829–2134 m], *F. Leybold s.n.* (lectotype: illustration in the original description, designated by I.A Al-Shehbaz, Novon 14: 266. 2004).

Draba leyboldii Phil., Linnaea 33: 10. 1864; *Stenodraba stenophylla* var. *leyboldii* (Phil.) O.E.Schulz in Engler, Pflanzenreich IV. 105(Heft 86): 189. 1924. TYPE: Chile. [Region IV Coquimbo], Cordillera Doña Rosa, *H. Volckmann s.n.* (holotype: SGO!)

Draba cauquenensis Phil., Anal. Univ. Chile 81: 330. 1893. TYPE: CHILE. "In praedii Cauquenes Andibus, locis dictis la Chapa verde et Cajon del Arriero", *H. von Dessauer s.n.* (lectotype: SGO designated by Al-Shehbaz (1990b: 245), isolectotypes: B!, M!).

STENODRABA SUFFRUTICOSA (Barnéoud) O.E.Schulz in Engler, Pflanzenreich IV. 105(Heft 86): 190. 1924. *Draba suffruticosa* Barnéoud in C.Gay, Fl. Chile 1: 157. 1846; *Sisymbrium suffruticosum* (Barnéoud) E.Fournier, Rech. Anat. Tax. Fam. Crucif. 132. 1865; *Draba imbricatifolia* Barnéoud var. *suffruticosa* (Barnéoud) Reiche, Fl. Chile 1: 116. 1896; *Hesperis suffruticosa* (Barnéoud) Kuntze, Rev. Gen. Pl. 2: 935. 1891; *Weberbauera suffruticosa* (Barnéoud) Al-Shehbaz, J. Arnold Arbor. 71: 247. 1990. TYPE: CHILE. [Region IV Coquimbo], Cordillera Ovalle, 12,000 ft. [3658 m], *C. Gay s.n.* (holotype: P!, isotype: B!).

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Appendix 1. New sequences generated for this study. Species, specimen voucher, and GenBank accession numbers (ITS, trnL-F, trnH-psbA). For sequences downloaded from the GenBank, see Appendix 2.

Pennellia boliviensis (Muschl.) Al-Shehbaz: *Zuloaga F. O. 13096* (SI) Argentina: Jujuy, MF806408 MF806439, -. ***Pennellia brachycarpa*** Beilstein & Al-Shehbaz: *Zuloaga F. O. 13145* (SI) Argentina: Salta, MF806409, MF806440, -. ***Stenodraba chillanensis*** (Phil.) O.E. Schulz: *Zuloaga F. O. 12436* (SI) Argentina: Mendoza, MF806382, MF806415, MF806446; *Zuloaga F. O. 15235* (SI) Argentina: Mendoza, MF806386, MF806419, MF806448; *Al-Shehbaz I. A. 817* (SI) Argentina: Mendoza, MF806392, MF806424, MF806450; *Luebert F. 2288* (CONC) Chile: VII Maule, MF806399, MF806431, MF806457. ***Stenodraba colchaguensis*** (Barn.) O.E. Schulz: *Zuloaga F. O. 12539* (SI) Argentina: Neuquén, MF806383, MF806416, MF806447; *Teillier S. 5157* (CONC) Chile: Metropolitana de Santiago, MF806398, MF806430, MF806456; *Jiles C. 6117* (CONC) Chile: IV Coquimbo, MF806405, -, -; *Mieres G. s.n.* (CONC-165802) (CONC) Chile: V Valparaíso, MF806406, MF806437, MF806463; *Mieres G. s.n.* (CONC-166743) (CONC) Chile: V Valparaíso, MF806407, MF806438, MF806464. ***Stenodraba colchaguensis*** var. **patagonica** (Phil.) Boelcke: *Arroyo M.T.K. 870045* (CONC) Chile: XII Magallanes y Antártica Chilena, MF806404, MF806436, MF806462. ***Stenodraba imbricatifolia*** (Barn.) O.E. Schulz: *Arancio G. 92138* (CONC) Chile: IV Coquimbo, MF806396, MF806428, MF806454; *Rosas M. 4533* (CONC) Chile: IV Coquimbo, MF806397, MF806429, MF806455. ***Stenodraba lagunae*** (O.E. Schulz) Salariato & Al-Shehbaz: *Johnston I.M.* 6056 (CONC) Chile: III Atacama, MF806394, MF806426, MF806452; *Teillier S. 5052* (CONC) Chile: III Atacama, MF806395, MF806427, MF806453. ***Stenodraba lechleri*** (E. Fourn.) Ravenna: *Zuloaga F. O. 15141* (SI) Argentina: Neuquén, MF806410, MF806441,

MF806465; *Zuloaga F. O. 15155* (SI) Argentina: Neuquén, MF806411, MF806442, MF806466. ***Stenodraba parvifolia*** (Phil.) O.E. Schulz: *Zuloaga F. O. 14859* (SI) Argentina: Chubut, MF806387, MF806420, MF806449; *Zuloaga F. O. 14857* (SI) Argentina: Chubut, MF806393, MF806425, MF806451; *Zuloaga F. O. 15583* (SI) Argentina: Chubut, MF806412, MF806443, MF806467; *Zuloaga F. O. 15712* (SI) Argentina: Neuquén, MF806413, MF806444, MF806468; *Zuloaga F. O. 15717* (SI) Argentina: Neuquén, MF806414, MF806445, MF806469. ***Stenodraba stenophylla*** (Leybold) O. E. Schulz: *Marticorena C. 910* (CONC) Chile: VII Maule, MF806401, MF806433, MF806459; *Gunckel H. 20774* (CONC) Chile: Metropolitana de Santiago, MF806402, MF806434, MF806460; *Garaventa A. 8055* (CONC) Chile: VII Maule, MF806403, MF806435, MF806461. ***Stenodraba suffruticosa*** (Barnéoud) O.E.Schulz: *Jiles C. 3408* (CONC) Chile: IV Coquimbo, MF806400, MF806432, MF806458. ***Weberbauera arequipa*** Al-Shehbaz & Montesinos: *Montesinos D. 3842* (MO) Peru: Moquegua, MF806388, MF806421, **-**. ***Weberbauera cymosa*** Al-Shehbaz: *Trinidad H. 1911* (MO) Peru: Junin, MF806389, MF806422, **-**. ***Weberbauera herzogii*** (O.E. Schulz) Al-Shehbaz: Zuloaga F. O. 13553 (SI) Argentina: Jujuy, MF806384, MF806417, -. ***Weberbauera peruviana*** (DC.) Al-Shehbaz: *Zuloaga F. O. 13553* (SI) Argentina: Jujuy, MF806385, MF806418, **-**. ***Weberbauera rosulans*** (O.E. Schulz) Al-Shehbaz*: Latorre 4159 (MO)* Peru: Ancash, MF806390, **-**, **-**. ***Weberbauera spathulifolia*** (A. Gray) O.E. Schulz: *Donadio S. 122* (SI) Argentina: La Rioja, MF806391, MF806423, **-**.

APPENDIX 2. Taxa and GenBank accession numbers for the ITS, trnL-F, and trnH-psbA sequences downloaded from GenBank and used in the phylogenetic analyses. New sequences generated for this study are shown in Appendix 1.

CLEOMACEAE. *Cleome lutea* Hook. (AF137588, -, -); *Cleome spinosa* Jacq. (-, DQ649093, -). BRASSICACEAE. **Tribe Aethionemeae**. *Aethionema arabicum* Andrz. ex DC. (AY254539, DQ180218, -); *Aethionema elongatum* Boiss. (-, DQ180216, -); *Moriera spinosa* Boiss. (GQ424545, -, -). **Tribe Alysseae**. *Alyssum lenense* Adams (-, FN677633, -); *Alyssum montanum* L. (AY237938, -, -); *Berteroa incana* (L.) DC. (EF514632, -, -); *Galitzkya potaninii* (Maxim.) V. V. Botschantz. (-, FN677635, -); *Hormathophylla purpurea* (Lag. & Rodr.) P.Küpfer (-, FN677738, -). **Tribe Alyssopsideae**. *Alyssopsis mollis* O.E.Schulz (-, FJ188227, -); *Alyssopsis trinervis* Botsch. & Seifulin (GQ497846, -, -); *Calymmatium draboides* O.E.Schulz (GQ497854, -, -). **Tribe Anastaticeae**. *Anastatica hierochuntica* L. (GQ424524, -, -); *Malcolmia triloba* Spreng. (DQ357561, -, -). **Tribe Anchonieae**. *Anchonium billardieri* DC. (DQ357512, -, -); *Matthiola incana* (L.) W.T.Aiton (AJ628339, -, -); *Microstigma deflexum* Juz. (-, FN677641, -); *Sterigmostemum violaceum* (Botsch.) H. L.Yang (-, FN677640, -). **Tribe Aphragmeae**. *Aphragmus eschscholtzianus* Andrz. ex DC. (DQ165334, -, -); *Aphragmus hobsonii* (H.Pearson) Al-Shehbaz & Warwick (DQ165357, -, -); *Aphragmus oxycarpus* (Hook.f. & Thomson) Jafri (-, DQ518350, -). **Tribe Arabideae**. *Arabis alpina* L. (AF137559, EF449508, -); *Athysanus pusillus* (Hook.) Greene (-, GU246241, -); *Draba aizoides* L. (AF146512, -, -); *Draba alpina* L. (-, DQ467004, -). **Tribe Asteae**. *Asta schaffneri* (S.Watson) O.E.Schulz (HQ541168, -, -); *Asta schaffneri* (S.Watson) var. *pringlei* (O.E.Schulz) Rollins (HQ541170, -, -); *Asta stricta* Rollins (HQ541171, -, -). **Tribe Biscutelleae**. *Biscutella didynima* L. (DQ452058, -, -); *Biscutella laevigata* L. (DQ452056, -, -). **Tribe Boechereae**. *Anelsonia eurycarpa* (A. Gray) J.F.Macbr. & Payson; *Boechera retrofacta* (Graham) Á.Löve & D.Löve (AF183105, -, -); *Boechera suffrutescens* (S. Watson) Dorn (-, DQ013046, -); *Cusickiella douglasii* (A.Gray) Rollins (-, AF307557, -); *Sandbergia whitedii* (Piper) Greene (AJ628295, -, -). **Tribe Brassiceae**. *Brassica oleracea* L. (AY722423, -, -); *Brassica rapa* L. (JN564039, GQ268033, -); *Diplotaxis erucoides* (L.) DC. (-, AY751763, -); *Eruca sativa* Mill. (-, AY751765, -); *Hirschfeldia incana* (L.) Lagr.-Fossat (AY722470, EU620407, -); *Rapistrum rugosum* (L.) All. (-, AY751769, -); Sinapsis alba L. (-, JQ041854, -). **Tribe Buniadae**. *Bunias erucago* L. (GQ497885, -, -); *Bunias orientalis* L. (-, FN677645, -). **Tribe Calepineae**. *Calepina irregularis* (Asso) Thell. (DQ249822, AY751760, -); *Goldbachia laevigata* (M.Bieb.) DC. (DQ357545, -, -). **Tribe Camelineae**. *Arabidopsis arenosa* (L.) Lawalrée (-, GQ386472, -); *Camelina microcarpa* DC. (AF137574, DQ821412, -); *Neslia paniculata* (L.) Desv. (-, DQ310518, -); *Pseudoarabidopsis toxophylla* (M.Bieb.) Al-Shehbaz, O'Kane & R.A.Price (AF137558, -, -). **Tribe Cardamineae**. *Cardamine flexuosa* With. (-, AB247985, -); *Cardamine pratensis* L. (AY245995 and AY246025, -, -); *Nasturtium officinale* W.T.Aiton (AY254531, -, -); *Planodes virginicum* (L.) Greene (GQ424554, -, -); *Rorippa indica* (L.) Hiern (-, EF426788, -). **Tribe Chorisporeae**. *Chorispora sabulosa* Cambess. (-, FN677724, -); *Chorispora tenella* (Pall.) DC. (DQ357526, -, -); *Diptychocarpus strictus* (Fisch. ex M.Bieb.) Trautv. (DQ357534, FN677717, -); *Litwinowia tenuissima* (Pall.) Woronow ex Pavlov (-, FN677714, -); *Pseudoclausia gracillima* A.N.Vassiljeva (-, FN677652, -). **Tribe Cochlearieae**. *Cochlearia megalosperma* Vogt (AF336208, -, -); *Ionopsidium acaule* (Desf.) DC. ex Rchb. (AF336210 and AF336211, HQ268714, -). **Tribe Coluteocarpeae**. *Eunomia oppositifolia* DC. (-, AY122456, -); *Noccaea cochleariformis* (DC.) Á.Löve & D. Löve (DQ249838, -, -); *Noccaea fendleri* (A.Gray) Holub (AY154824, AY154786, -); *Noccaea jankae* (A.Kern.) F.K.Mey. (-, AY154796, -). **Tribe Conringieae**. *Conringia clavata* Boiss. (AY722505, -, -); *Zuvanda crenulata* Askerova (DQ357606, -, -). **Tribe Cremolobeae**. *Aimara rollinsii* (Al-Shehbaz & Martic.) Salariato & Al-Shehbaz (KF662736, KF662775, -); *Cremolobus peruvianus* (Lam.) DC. (KF662763, KF662808, -); *Cremolobus rhomboideus* Hook. (KF662762, KF662807, -); *Menonvillea chilensis* (Turcz.) B. D.Jacks. (KF662739, KF662777, KU764631); *Menonvillea cicatricosa* (Phil.) Rollins (KF662747, KF662801, -); *Menonvillea cuneata* (Gillies & Hook.) Rollins (KF662746, KF662784, -); *Menonvillea minima* Rollins (KF662735, KF662773, -); *Menonvillea scapigera* Rollins subsp. *scapigera* (JX470564, KF662804, -); **Tribe Descurainieae**. *Descurania californica* (A.Gray) O.E. Schulz (-, GU246239, -); *Descurania sophia* (L.) Webb ex Prantl (DQ418727, -, -); *Hornungia alpina* (Sievers) O.Appel (-, DQ310515, -); *Hornungia petraea* Rchb. (AJ628293 and AJ628294, -, -). **Tribe Dontostemoneae**. *Clausia aprica* (Stephan) Korn.-Trotzky (DQ357529, -, -); *Clausia podlechii* Dvořák (-, FN677719, -); *Dontostemon integrifolius* (L.) C.A.Mey. (DQ357536, -, -); *Dontostemon intermedius* Vorosch. (-, FN677644, -). **Tribe Erysimeae**. *Erysimum canescens* Roth (-, EU170623, -); *Erysimum capitatum* (Douglas ex Hook.) Greene (DQ357540, -, -); *Erysimum cheiranthoides* L. (DQ005989, EU170622, -). **Tribe Euclidieae**. *Braya alpina* Sternb. & Hoppe (AY353095, -, -); **Euclidium syriacum** (L.) W. Aiton (-, EF426780, -); *Neotorularia torulosa* (Desf.) Hedge & J.Léonard (AY353164, -, -); *Solms-laubachia baiogoinensis* (K. C.Kuan & C.H.An) J.P.Yue, Al-Shehbaz & H.Sun (-, DQ523315, -); *Strigosella africana* (L.) Botsch. (-, EU170625, -). **Tribe Eudemeae.** *Aschersoniodoxa cachensis* (Speg.) Al-Shehbaz **(**KM376250, KM376288, KM376360); *Aschersoniodoxa mandoniana* (Wedd.) Gilg & Muschl. (KM376252, KM376290, KM376362); *Aschersoniodoxa peruviana* Al-Shehbaz, Navarro & A. Cano (KM376253, KM376291, KM376363); *Brayopsis alpaminae* Gilg & Muschl. (KM376242, -, -); *Brayopsis calycina* (Desv.) Gilg & Muschl. (KM376247, KM376285, KM376357); *Brayopsis colombiana* Al-Shehbaz (KM376244, -, -); *Brayopsis diapensioides* (Wedd.) Gilg & Muschl. (KM376243, KM376282, KM376356); *Brayopsis gamosepala* Al-Shehbaz (KM376245, KM376283, -); *Brayopsis monimocalyx* O.E. Schulz (KM376240, KM376280, KM376354); *Dactylocardamum imbricatifolium* Al-Shehbaz (KM376257, KM376295, KM376367); *Eudema nubigena* Bonpl. subsp. *nubigena* (KM376255, KM376292, KM376364); *Eudema nubigena* Bonpl. subsp. *remyana* (Wedd.) Al-Shehbaz (KM376256, KM376293, KM376365); *Eudema rupestris* Bonpl. (KM376254, -, -); *Onuris alismatifolia* Gilg ex Skottsb. (KM376232, KM376272, KM376346); *Onuris graminifolia* Phil. (KM376227, KM376267, KM376341); *Onuris hatcheriana* (Gilg ex Macloskie) Gilg & Muschl. (KM376237, KM376277, KM376351); *Alshehbazia hauthalii* (Gilg & Muschl.) Salariato & Zuloaga (KM376235, KM376275, KM376349); *Onuris papillosa* O.E. Schulz (KM376229, KM376269, KM376343); *Onuris spegazziniana* Gilg & Muschler (KM376230, KM376270, KM376344); *Xerodraba patagonica* (Speg.) Skottsb. (KM376224, KM376264, KM376338); *Xerodraba patagonica* (Speg.) Skottsb. subsp. *pycnophylloides* (Speg.) Salariato & Al-Shehbaz (KM376222, KM376262, KM376336). **Tribe Eutremeae**. *Chalcanthus renifolius* (Boiss.) Boiss. (GQ424528, -, -); *Eutrema altaicum* (C.A.Mey.) Al-Shehbaz & Warwick (DQ165364, DQ649087, -); *Eutrema heterophyllum* (W.W.Sm.) H.Hara (-, DQ649086, -, -). **Tribe Halimolobeae**. *Exhalimolobos pazensis* (Rusby) Al-Shehbaz & CD.Bailey (-, AF307547, -); *Halimolobos lasiolobus* O. .Schulz (-, AF307647, -); *Mancoa bracteata* (S. Watson) Rollins (-, AF307556, -); *Pennellia longifolia* (Benth.) Rollins (AF307627, AF307549, -). **Tribe Heliophileae**. *Heliophila arenaria* Sond. (AJ863600, -, -); *Heliophila coronopifolia* L. (-, DQ518369, -); *Heliophila subulata* Burch. & DC. (AJ863580 and AJ864835, -, -). **Tribe Hesperideae**. *Hesperis matronalis* L. (DQ357547, -, -); *Hesperis sibirica* L. (-, FN677642, -); *Tchihatchewia isatidea* Boiss. (GQ497882, -, -). **Tribe Iberideae**. *Iberis amara* L. (AJ440311, AY122455, -); *Iberis spathulata* Bergeret (AJ440312, -, -). **Tribe Isatideae**. *Boreava orientalis* Jaub. & Spach (DQ249859, DQ518353, -); *Isatis minima* Bunge (GQ131320, DQ821409, -); *Isatis tinctoria* L. (DQ249851, DQ518370, -). **Tribe Kernereae**. *Kernera saxatilis* (L.) Rchb. (AF401118 and AF401119, -, -); *Rhizobotrya alpina* Tausch (AJ440315, -, -). **Tribe Lepidieae**. *Lepidium angustissimum* Phil. (KC174369, -, KC174447, KC174484, -); *Lepidium apetalum* Willd. (FJ980405, DQ821406, JN045141, -, -); *Lepidium latifolium* L. (AJ582447 and AJ582521, -, -); *Lepidium sisymbrioides* Hook.f. (-, DQ997056, -); *Lithodraba mendocinensis* (Hauman) Boelcke (GQ497890, -, -); *Stubendorffia gracilis* Botsch. & Vved. (DQ780944 and DQ780945, -, -). **Tribe Megacarpareae**. *Megacarpaea delavayi* Franch. (AJ628325 and AJ628326, -, -); *Megacarpaea gracilis* Lipsky (AJ628327 and AJ628328, -, -). **Tribe Microlepidae**. *Carinavalva glauca* Ising (GQ424527, -, -); *Microlepidium pilosulum* F. Mull. (GQ497869, -, -). **Tribe Notothlaspideae**. *Notothlaspi australe* Hook.f.

(AF100689, -, -); *Notothlaspi rosulatum* Hook.f. (AF100690, -, -). **Tribe Oreophytonea**e. *Murbeckiella huetii* Rothm. (GQ424546, -, -); *Oreophyton falcatum* O.E.Schulz (GQ424549, -, -). **Tribe Physarieae**. *Physaria arctica* (Wormsk. ex Hornem.) O'Kane & Al-Shehbaz (-, GQ245072, -); *Physaria didymocarpa* (Hook.) A. Gray (AF137583, -, -); *Physaria fendleri* (A.Gray) O'Kane & Al-Shehbaz (-, AF055266, -); *Synthlipsis greggii* A.Gray (AF137590, -, -). **Tribe Schizopetaleae**. *Atacama nivea* (Phil.) O.E.Schulz (KC174380, KM575848, -); *Mathewsia foliosa* Hook. & Arn. (KC174388, EU620360, -); *Mathewsia peruviana* O.E. Schulz (EU620303, EU620362, -); *Schizopetalon biseriatum* Phil. (-, EU620375, -); *Schizopetalon dentatum* (Barnéoud) Gilg & Muschl. (KC174396, -, -); *Schizopetalon rupestre* (Barnéoud) Reiche (KC174402, EU620376, KC174478). **Tribe Scoliaxoneae**. *Scoliaxon mexicanum* (S.Watson) Payson (HQ541174, -, -). **Tribe Sisymbrieae**. *Sisymbrium altissimum* L. (AF531560, AY958545, -); *Sisymbrium septulatum* DC. (AF531600, AY958565, -). **Tribe Smelowskieae**. *Smelowskia alba* (Pall.) Regel (AY230562, -, -); *Smelowskia calycina* (Stephan) C.A.Mey. (AY230581, DQ180249, FJ972349, FJ972329, -); *Smelowskia jacutica* (Botsch. & Karav.) Al-Shehbaz & Warwick (AY230646, -, -); *Smelowskia sisymbrioides* (Regel & Herder) Lipsky ex Paulsen (-, JF298539, -). **Tribe Thelypodieae**. *Dictyophragmus punensis* (Romanczuk) Al-Shehbaz (EU620294, EU620349, -); *Englerocharis pauciflora* Al-Shehbaz (EU620295, EU620351, -); *Hesperidanthus jaegeri* (Rollins) Al-Shehbaz (GQ424569, EU620357, -); *Hesperidanthus linearifolius* (A.Gray) Rydb. (AF531612, EU620358, -); *Ivania cremnophila* (I. M. Johnst.) O.E.Schulz (HQ541176, -, -); *Mostacillastrum andinum* (Phil.) Al-Shehbaz (AF531649, EU620363, -); *Mostacillastrum stenophyllum* (Gilles ex Hook. & Arn.) O. E. Schulz (EU620305, EU620364, -); *Neuontobotrys linearifolia* (Kuntze) Al-Shehbaz (EU620306, EU620367, -); *Parodiodoxa chionophila* (Speg.) O.E.Schulz (JX971121, JX971122, -); *Phravenia viereckii* (O.E.Schulz) Al-Shehbaz & S.I. Warwick (HQ541181, -, -); *Polypsecadium arnottianum* (Gillies ex Hook. & Arn.) Al-Shehbaz (AF531629, EU620369, -); *Romanschulzia arabiformis* (DC.) Rollins (AF531635, AY958538, -); *Sibara angelorum* (S.Watson) Greene (EU620317, EU620379, -); *Sibara mendocina* (Boelcke) Al-Shehbaz (EU620338, EU620404, -); *Sibara tehuelches* (Speg.) Al-Shehbaz (EU620311, EU620374, -); *Sibaropsis hammittii* S.Boyd & T.S.Ross (EU620318, EU620380, -); *Stanleya pinnata* (Pursh) Britton (EU620319, EU620381, -); *Streptanthus anceps* (Payson) Hoover (-, JF827264, -); *Streptanthus campestris* S.Watson (EU620321, AY958571, -); *Thelypodiopsis elegans* (M.E.Jones) Rydb. (-, EU620391, -); *Thelypodium flexuosum* B.L.Rob. (-, AY958582, -); *Thelypodium laciniatum* (Hook.) Endl. (EU620328, EU620392, -); *Warea amplexifolia* (Nutt.) Nutt. (EU620280 and EU620265, EU620397, -); *Weberbaurea herzogii* (O.E.Schulz) Al-Shehbaz (EU620334, EU620400, -); *Weberbauera rosulans* (O.E.Schulz) Al-Shehbaz (EU620284, EU620340, -). **Tribe Thlaspideae**. *Peltaria alliacea* Jacq. (DQ249855, -, -); *Thlaspi arvense* L. (AF336152S1 and AF336152S2, -, -); *Thlaspi bulbosum* Boiss. (-, AY154798, -,-, -). **Tribe Yinshanieae**. *Yinshania acutangula* (O.E.Schulz) Y.H.Zhang (AH007969, -, -); *Yinshania acutangula* subsp. *wilsonii* (O.E. Schulz) Al-Shehbaz, G.Yang, L.L.Lu & T.Y.Cheo (AH007968, -, -).