TAXONOMIC REVISION OF THE *PACKERA CROCATA/DIMORPHOPHYLLA* (ASTERACEAE: SENECIONEAE) COMPLEX IN THE SOUTHERN ROCKY MOUNTAINS (U.S.A.)

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ABSTRACT

In the Southern Rocky Mountains, *Packera crocata* and *P. dimorphophylla* form a complex of intergrading forms leading to difficulty in distinguishing taxa. Here we review the morphological variation in the context of regional phylogenetic data from two independent datasets to recircumscribe the taxa. We show the complex consists of three taxa, *P. crocata, P. dimorphophylla* var. *dimorphophylla*, and **P. intermedia,** a new combination for a little-recognized taxon previously treated as a variety of *P. dimorphophylla*.

RESUMEN

En el sur de las Montañas Rocosas, *Packera crocata* y *P. dimorphophylla* forman un complejo de formas entremezcladas que dificultan la distinción de los taxones. Aquí revisamos la variación morfológica en el contexto de los datos filogenéticos regionales de dos conjuntos de datos independientes para recircunscribir los taxones. Mostramos que el complejo consta de tres taxones, *P. crocata, P. dimorphophylla* var. *dimorphophylla,* y **Packera intermedia,** una nueva combinación para un taxón poco reconocido y tradicionalmente tratado como una variedad de *P. dimorphophylla.*

INTRODUCTION

Packera Á. Löve & D. Löve (Asteraceae: Senecioneae) is a genus of some 64 species that occurs almost exclusively in North America and have been treated historically as the "Aureoid" complex of the genus *Senecio* L. (Trock 2006). The recognition at the level of genus was formalized by Löve and Löve (1976) based on gross morphology and chromosome number. While distinct at the genus level, species level taxonomy is complex due to geohistorical events during its evolution (Barkley 1988), including rampant hybridization and introgression (Fernald 1943; Barkley 1962; Chapman et al. 1971; Uttal 1982, 1984; Weakley et al. 2011), and a high incidence of polyploidy (Trock 2006).

Among the difficult to segregate species are *Packera crocata* (Rydb.) W.A. Weber & Á. Löve and *P. dimorphopylla* (Greene) W.A. Weber & Á. Löve. In central and western Colorado where they are most common, collections show a bewildering array of overlapping leaf shapes and flower colors, a fact that has suggested hybridization (Trock 2006) and led some authors to combine this variation under a single taxon (Ackerfield 2015).

Associated with both the typical *P. dimorphophylla* var. *dimorphophylla* and *P. crocata* is a third taxon described from subalpine meadows in the La Sal Mountains of eastern Utah, *P. dimorphophylla* var. *intermedia* (T.M. Barkley) Trock & T.M. Barkley (*Senecio dimorphophyllus* var. *intermedia* T.M. Barkley). This occasionally recognized variety is segregated from typical *P. dimorphophylla* by having a taller stature and leaves that are subcordate at the base as opposed to tapering and was believed to be the result of hybridization between the

J. Bot. Res. Inst. Texas 19(2): 77–88. 2025
https://doi.org/10.17348/jbrit.v19.i2.1399
Published online: 23 June 2025

typical *P. dimorphophylla* and *P. crocata* (Trock 2006) as the distinct leaf shape is not found in these two species.

Recent field work in northern New Mexico (Keller et al. 2017) has uncovered populations that are ascribable to var. *intermedia* and are consistent in the expression of defining traits at the level of populations. These occurrences led us to examine the distribution of this taxon across the Southern Rockies, and we have determined that it is more widespread and distinct than previously recognized. Its previously unrecognized occurrence across the region has contributed to the difficulty in segregating these taxa.

Here we provide multiple lines of evidence in support of recognition of Barkley's var. *intermedia* with a broader range across the Southern Rockies and propose its elevation to species rank as it represents a distinct evolutionary lineage sister to an intergrading complex of *P. crocata* and typical *P. dimorphophylla*. We additionally provide a key for segregation of these overlapping taxa across their range.

MATERIALS AND METHODS

Taxonomic history and recognition.—To understand the taxonomic concepts and variation associated with each of the members of the *P. crocata/dimorphophylla* complex in the Southern Rockies, we reviewed all pertinent published literature and type material pertaining to these taxa within our geographic region.

Morphological analysis of herbarium accessions.—To understand the distribution and variation in form of members of the *P. crocata/dimorphophylla* complex we examined morphological characters—height, leaf shape, ray flower color, elevation, and habitat—on specimens in the herbaria at COLO, FLD, JEMEZ, and UNM with additional specimens observed in digital format via SEINet (SEINet Portal Network 2023) from adjacent states.

Molecular phylogenetic analysis.—To provide an independent assessment of taxon segregation without direct interpretation of morphology we used two molecular analyses, a Sanger-sequencing-based approach utilizing the internal transcribed spacer (ITS) of nuclear ribosomal DNA nrITS and a next-generation sequencing (NGS) approach targeting known conserved gene sequences within the sunflower family.

For the generation of Sanger sequence data, we included 19 samples of taxa within the *P. crocata/dimorphophylla* complex with *P. neomexicana* (A. Gray) W.A. Weber & Á. Löve serving as an outgroup taxon (Table 1). DNA extraction, amplification, sequencing, and alignment followed the protocol presented in Fernández-Mazuecos et al. (2020). Phylogenetic analysis including model selection and maximum likelihood estimation was performed using IQ-TREE v. 2.2.0 (Nguyen et al. 2015) with branch support assessed using the ultrafast bootstrap with 1000 replications.

To produce NGS data, ten taxa within the *P. crocata/dimorphophylla* complex were included (Table 1). DNA extraction and sequencing methods followed steps outlined by Moore-Pollard and Mandel (2023). The resulting next-generation libraries were sequenced on an HiSeq X Five at Psomagen (Rockville, Maryland, USA). Two distantly related *Packera* taxa, *P. glabella* (Poir.) C. Jeffrey and *P. dubia* (Spreng.) Trock & Mabb., that were previously sequenced in Moore-Pollard and Mandel (2023), were included as outgroups and obtained from NCBI (Table 1). Adapters were trimmed from raw sequence reads of the twelve samples using the Sliding Window quality filter in Trimmomatic v. 0.36 (Bolger et al. 2014). Reads were then mapped to the Compositae-1061 probe set (Mandel et al. 2014, 2017) using the HybPiper v. 2.0.1 (Johnson et al. 2016) pipeline. Maximum likelihood gene trees were then built using RAxML v. 8.1.3 (Stamatakis 2014) with 1000 bootstrap replicates under the majority best fitting model, GTR+I+Γ, given results from PartitionFinder v. 2.1.1 (Lanfear et al. 2012). A final species tree was generated using the pseudo-coalescent tree building method, ASTRAL-III v. 5.7.3 (Zhang et al. 2018). Local posterior probability (LPP) values were generated at each node to indicate the probability that the resulting branch is the true branch given the set of input gene trees. Resultant ITS and NGS trees were drawn using the package *phytools* (Revell 2012) in R v. 4.0.5 (R Core Team 2016; RStudio 2020).

TABLE 1. Collection information and GenBank accession numbers for molecular phylogenetic analyses. Next-gen data can be found under BioProject PRJNA1046046.

Taxon	Voucher	Location	ITS	Next-gen
P. crocata	*McCauley 688* (FLD)	Lone Mesa State Park, CO	OM406207	SRR27089150
	Keller 4116 (JEMEZ)	Ice Lakes, CO	OR886793	
	Sivinski 9181 (UNM)	Goose Lake, NM	OR886801	SRR27089149
	Worthington 32626 (UNM)	Sangre de Cristo Mts, NM	OR886802	SRR27089148
	Sanderson 1379 (COLO)	Little Hohnholz Lake, CO	OR886799	
	Anderson 88-111 (COLO)	Uncompahgre Plateau, CO	OR886804	SRR27089147
P. crocata var. *dimorphophylla*	*Tabb 52* (FLD)	Stony Pass, CO	OM406213	
(=*P. dimorphophylla* var.	*Schneider 5095* (FLD)	La Plata Mts., CO	OM406209	SRR27089146
dimorphophylla)	*Keller 3206* (JEMEZ)	Williams Lake, NM	OR886794	SRR27089145
	Keller 2226 (JEMEZ)	Ridge above Williams Lake	OR886796	SRR27089144
	Fletcher 4690 (UNM)	Wheeler Peak Cirque, NM	OR886805	
	MacKay 5T-106 (UNM)	Rio Hondo, NM	OR886806	
P. dubia	*Fuller s.n.* (UNC)	Bell's Mill Park, NC		SAMN31976536
P. glabella	*DeSelm 06-04* (TENN)	Bradley County, TN		SAMN31976488
P. intermedia	*Keller 1987* (JEMEZ)	Valles Caldera, NM	OR886791	SRR27089143
	Keller 3049 (JEMEZ)	San Pedro Parks Wilderness, NM	OR886792	
	Keller 3805 (JEMEZ)	San Pedro Parks Wilderness, NM	OR886795	
	Keller 3164 (JEMEZ)	Bandelier National Monument, NM	OR886797	SRR27089142
	Michener 303 (COLO)	No-Name Basin, CO	OR886798	
	Siplivinsky 1522 (COLO)	Grand Mesa, CO	OR886800	SRR27089141
	Anderson 86-146 (COLO)	Uncompahgre Plateau, CO	OR886803	
P. neomexicana	*Tabb 32* (FLD)	Abajo Mountains, UT	OM406216	

RESULTS AND DISCUSSION

Taxonomic history and recognition.—The earliest description of a taxon in the *P. crocata/dimorphophylla* complex is what we now recognize as *P. crocata* made by Asa Gray. He placed two specimens with notably orangish-tinted ray flowers collected during C.C. Parry's second expedition to the mountains of Colorado in 1862 from Middle Park (Fig. 1) as a variety within his broad concept of the principally Eastern North American *S. aureus* L. (Gray 1863). Recognizing this as distinct, Rydberg elevated this taxon to species rank under the name *S. crocatus* and extended the range north along the Rocky Mountains to Montana (Rydberg 1897).

Packera dimorpophylla (as *Senecio dimorphophyllus*) was first proposed by E.L. Greene in 1900 as a plant occurring at high elevation from the southern Rockies in Colorado (Greene 1900) (Fig. 2). He remarked on the distinction between the rounded and obtuse basal leaves and the triangular and sessile to clasping cauline leaves as being diagnostic (Fig. 2). In a study of Rocky Mountain *Senecio* later the same year, Rydberg (1900) discussed both *Senecio crocatus* and *Senecio dimorphophyllus*. He included within his discussion of *S. crocatus* a reference to a specimen collected by Baker, Earle and Tracy (Num. 569) from the La Plata Mts. referencing this to a name proposed by E.L. Greene, *S. heterodoxa,* a taxon later seen as identical to *P. dimorphophylla*. In Rydberg's discussion of *P. dimorphylla*, he noted that the description of this species was very much like that of *P. crocata*, although he stated he had not seen any specimens ascribed to that species (Rydberg 1900).

The last member of the complex in the geographic region to be described was *Packera dimorphophylla* var. *intermedia* (as *Senecio dimorphophyllus* var. *intermedia*), recognized by T.M. Barkely as an endemic in the La Sal Mountains of eastern Utah (Fig. 3) (Barkley 1962). He segregated this from the typical form of *P. dimorphophylla* based on the basal leaf blades being orbicular/cordate to ovate or subreniform as opposed to ovate to oblong lanceolate and having a subcordate to contracted base above a narrow petiole. He remarked on the similarity of this taxon, however, to both *P. dimorphophylla* and *P. crocata* and choose the epithet "intermedia" to recognize this combination of characters. While recognizing this taxon as intermediate between *P. dimorphophylla* and *P. crocata*, he aligned var. *intermedia* with *P. dimorphophylla* due to the presence of a congested inflorescence as opposed to the more typical open inflorescence seen in *P. crocata*.

Since its description, *P. dimorphophylla* var. *intermedia* has been predominantly maintained as a restricted

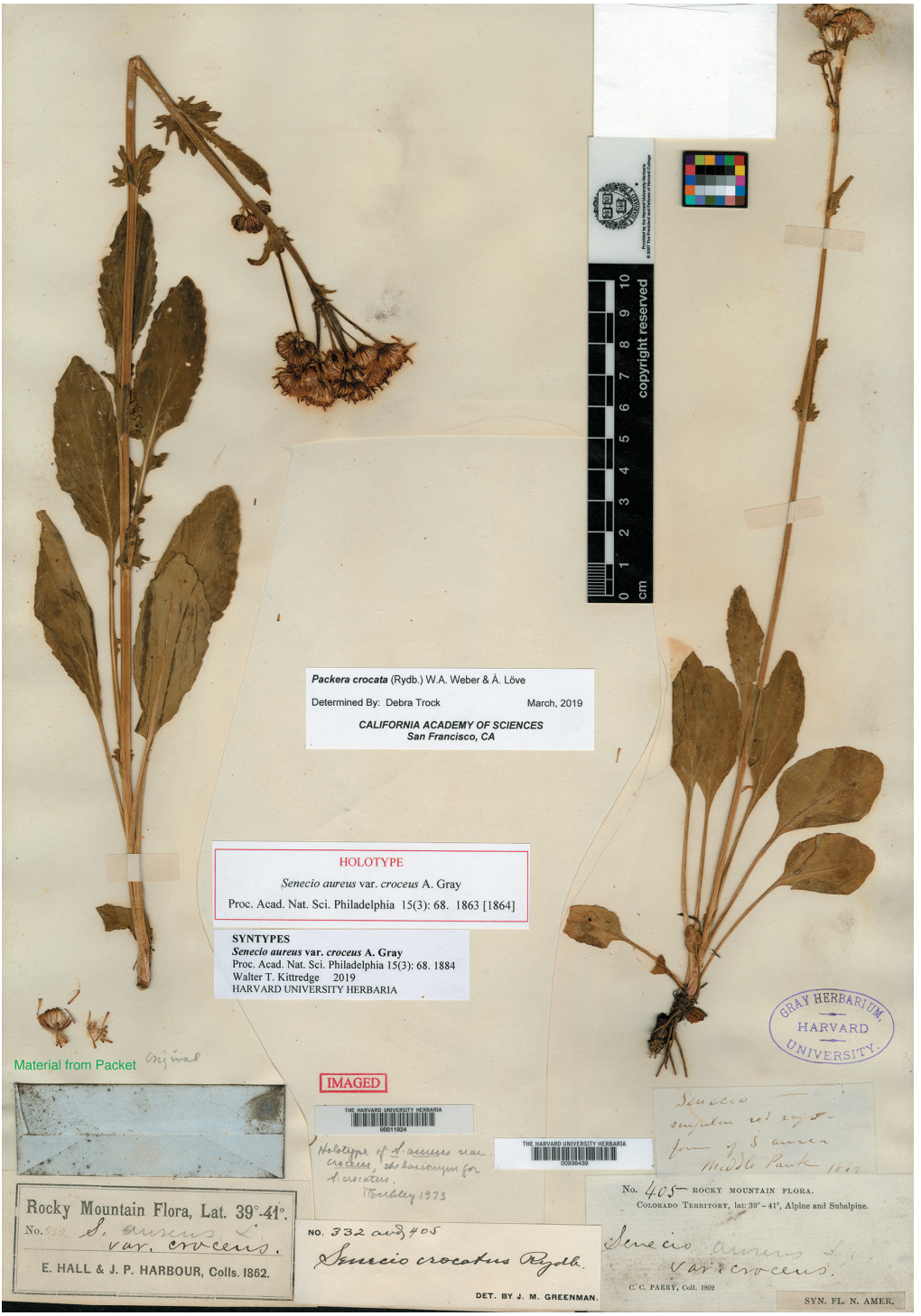

Fig. 1. Lectotype (*Hall and Harbour 332*) and Syntype (*C.C. Parry 405*) of *Packera crocata* (Barcode: GH00011924, GH00011925) from Middle Park, Colorado. Note large, lyrate, clasping, cauline leaves and tapered basal leaves. Courtesy of Gray Herbarium of Harvard University.

Fig. 2. Isotype of *Packera dimorphophylla* var. *dimorphophylla*, *Baker 705* (Barcode: MO-176762), near Pagosa Peak, Colorado. Note tapering basal leaves and clasping, deltate cauline leaves. Courtesy of Missouri Botanical Garden Herbarium.

Fig. 3. Holotype of *Packera dimorphophylla* var. *intermedia, Payson and Payson 4097* (Barcode: MO-176763), edge of swampy place at 10,500 ft elevation, Geyser Pass, La Sal Mts., Utah. Note subcordate to contracted leaf bases of basal leaves. Courtesy of Missouri Botanical Garden Herbarium.

endemic to the La Sal Mountains (Trock 2006; Welsh et al. 2008). With an increase of field work in southwestern Colorado associated with preparation of the Flora of the Four Corners, Trock (2013) recognized the taxon as occurring at intermediate elevations in both Montezuma and La Plata Counties. Keller et al. (2017) extended this occurrence southward into the Jemez Mountains of northern New Mexico where the form was identified from wet meadows (Fig. 4).

Morphological analysis.—While overlap among the taxa occurs, the differentiation of *P. dimorphophylla* var. *dimorphophylla*, *P. dimorphophylla* var. *intermedia*, and *P. crocata* is generally clear and based on a suite of morphological and ecological characters (Table 2).

Examination of specimens across the range of study showed plants with the diagnostic form of *P. dimorphophylla* var. *intermedia* with cordate/truncate basal leaves and yellow rays to be distributed in a line from the La Sal Mountains in Utah, south through western Colorado into the Tusas and Jemez Mountains in New Mexico.

Molecular phylogenetic analysis.—Both phylogenetic analyses show a similar pattern of taxon segregation with plants morphologically assigned to *P. dimorphophylla* var. *intermedia* occurring in a segregated clade (Fig. 5). Bootstrap support in the ITS dataset is relatively low; however, node support is generally higher in the next-generation tree, with five out of eight nodes indicating full support (1.0LPP). Plants ascribed to both *P. dimorphophylla* var. *dimorphophylla* and *P. crocata,* which are generally easily segregated based on morphology and ecological association, were found to be intermixed and indistinguishable in the ITS and next-generation sequence datasets but did show separation along a geographical gradient.

Our genetic evidence shows that plants ascribed to the morphological form of *P. dimorphophylla* var. *intermedia* represent a unique lineage. This pattern coupled with the consistent morphological expression of those forms across the range are strong evidence for us to propose recognition of this taxon at the rank of species as *P. intermedia*, recognizing a closely related yet genetically distinct form from that seen in *P. crocata* and *P. dimorphophylla* var. *dimorphophylla*.

The inclusion of *P. crocata* and *P. dimorphophylla* var. *dimorphophylla* in supported clades shows their sharing of a common lineage and thus support for inclusion within the same taxon as has been suggested by some recent authors (Ackerfield 2015). The generally clear morphological and ecological distinction between these taxa in the field, however, points to segregation of the lineage along ecological lines and thus warrants taxonomic recognition. Further study of this species pair would be warranted to understand the process of diversification occurring in this lineage.

TAXONOMIC TREATMENT

Packera crocata (Rydb.) W.A. Weber & Á. Löve, Phytologia 49:46. 1981. *Senecio aureus* var. *croceus* A. Gray, Proc. Acad. Nat. Sci. Philadelphia 15(1863):68. 1864. *Senecio crocatus* Rydb. Bull. Torrey Bot. Club 24:299. 1897. *Senecio pauciflorus* var. *croceus* (A. Gray) Jeps., Man. Fl. Pl. Calif. 1154. 1925. TYPE: U.S.A. COLORADO: Middle Park, *Hall and Harbour 332* (**LECTOTYPE, designated here:** GH).

Senecio pyrrhochrous Greene, Pl. Baker 3:24. 1901. TYPE: U.S.A. COLORADO: Jack's Cabin, Region of the Gunnison Watershed, *Baker 612* (ISOTYPES: GH, MIN, MO, NY, POM, RM, US, UTC, VT).

Senecio tracyi Rydb., Bull. Torrey Bot. Club 33:159. 1906. TYPE: U.S.A. COLORADO: Bob Creek, W of Mt. Hesperus, *Baker, Earle and Tracy 276* (HOLOTYPE: NY; ISOTYPE: RM).

Senecio crocatus var. *wolfii* Greenm., Ann. Missouri. Bot. Gard. 3:143. 1916. Type: U.S.A. COLORADO: South Park, *Wolf and Rothrock 582 and 586* (SYNTYPES: GH, US).

Packera crocata is a generally robust plant to 60 cm tall with deep yellow to orange-red ray flowers. It occurs principally in wet meadows and streamsides between 2100–3000 m.

Typification of this taxon has been unclear and has elicited much discussion in the literature. In his original description of this taxon Gray cited two specimens, *Hall and Harbour 332* and *C.C. Parry 405*. Most authors have referred to the Hall and Harbour specimen as the type although that designation has never been explicitly made (Greene 1900; Rydberg 1900; Greenman 1916, Barkley 1962). While both specimens cited by Gray represent this taxon, we designate the Hall and Harbour specimen at GH as the lectotype. The C.C. Parry specimen should be recognized as a syntype.

Fig. 4. *Packera intermedia*, *Jacobs 02483h* (JEMEZ), Sandoval Co., NM, Saddle between Pajarito and Cerro Grande.

TABLE 2. Diagnostic morphological characters for segregation of taxa in the *Packera crocata/dimorphophylla* complex in the Southern Rocky Mountains.

Taxon	Height (cm)	Leaves	Rays (color)	Habitat
P. crocata	30	Lyrate cauline lvs, tapered basal	Orange rarely golden yellow	Moist areas between 2100-3000 m
P. dimorphophylla var. *dimorphophylla*	20		Yellow rarely orange	Moist areas mostly above 3000 m
P. intermedia	30	Basal leaves cordate, cauline leaves greatly reduced upwards	Yellow	Moist areas between 2430-3200 m

Distribution.—Northern New Mexico north to Wyoming and Idaho and west to Nevada.

Representative specimens. **U.S.A. Colorado:** *Hazlett 12235* (GREE), 4 Aug 1991, *Jamieson s.n.* (FLD), *Lyon 7954, 9062* (FLD), *McCauley 586, 688* (FLD), *Rondeau 93-670* (COLO), Yeatts 4721 (KHD). **New Mexico:** *O'Kane 8282* (SJNM). **Utah:** *Goodrich 17802* (BYU), *Neese 10654* (BYU). **Wyoming:** *Nelson 2611, 16193* (RM).

Packera dimorphophylla var. **dimorphophylla** (Greene) W.A. Weber & Á. Löve, Phytologia 49:46. 1981.

Senecio dimorphophyllus Greene, Pittonia 4:109. 1900. TYPE: U.S.A. COLORADO: Pagosa Peak, *C.F. Baker 705* (HOLOTYPE: NDG; ISOTYPES: GH, MO, NMC, NY).

Senecio heterodoxus Greene ex Rydb., Bull. Torrey Bot. Club 27:178. 1900. TYPE: U.S.A. COLORADO: Little Kate Mine, La Plata Mts. *Baker, Earle and Tracy 569* (HOLOTYPE: MO; ISOTYPE: RM).

The typical form of *P. dimorphophylla* is recognized as a plant with a height generally less than 30 cm with yellow to orange ray flowers. It occurs in moist alpine and subalpine meadows at elevations greater than 3000 m.

Distribution.—North-central New Mexico through the mountains of Colorado north to Wyoming.

Representative specimens. **U.S.A. Colorado:** *Brummer 39* (CS), *Harrington 7700* (CS), *Holway 125* (CS), *Jamieson 0157* (FLD), *Kelso 11-215* (COCO), *Lyon 6282* (FLD), *McCauley 1654, 2070* (FLD), *Sanderson 92* (COCO). **New Mexico:** *Larson 8078* (RM). **Wyoming**: *Nelson 16283* (RM).

Packera intermedia (T.M. Barkley) C.F. Keller, **comb. & stat. nov.** *Packera dimorphophylla* (Greene) W.A. Weber & Á. Löve var. *intermedia* (T.M. Barkley) Trock & T.M. Barkley, Sida 18:386. 1998. *Senecio dimorphophyllus* Greene var. *intermedia* T.M. Barkley, Trans. Kansas Acad. Sci. 65:362. 1962. TYPE: U.S.A. UTAH: Geyser Pass, La Sal Mts., *Payson and Payson 4097* (HOLOTYPE: MO; ISOTYPES: GH, MO, MSC, RM, UC).

This species of *Packera* represents plants generally greater than 30 cm in height with yellow ray flowers, variable cordate to truncate basal leaves and cauline leaves greatly reduced upwards. It occurs between 2430–3200 m in seeps and marshy meadows often in large colonies.

Distribution.—Jemez Mountains of North-central New Mexico through southwestern Colorado to the La Sal Mts. of eastern Utah.

Representative specimens. **U.S.A. Colorado:** *Anderson 86-146* (COLO); *Heil 24346* (FLD, SJNM); *Michener 303* (COLO); *Siplivinsky 1406, 1522* (COLO). **New Mexico:** *Keller 3049* (JEMEZ), *McGrath 955* (UNM).

KEY TO THE *PACKERA DIMORPHOPHYLLA/CROCATA* COMPLEX IN THE SOUTHERN ROCKIES

1. Basal leaves tapered, cauline leaves lyrate, not much reduced; rays yellow to orange.
   2. Ray corolla laminae normally yellow; rarely orange; cauline leaves usually deltoid auriculate-clasping; heads 1–6 (sometimes more) on short peduncles, in congested clusters; elevation generally 3000 m (9,800 ft) or higher _____ **Packera dimorpophylla** var. **dimorphophylla**
   2. Ray corolla laminae orange to golden yellow; cauline leaves gradually reduced sessile, weakly clasping, lobed-lyrate; heads 5–7 on loose peduncles; elevation generally below 3000 m (9,800 ft) _____ **Packera crocata**

1 Basal leaves mostly truncate/cordate, cauline leaves normally greatly reduced; rays yellow._____ **Packera intermedia**

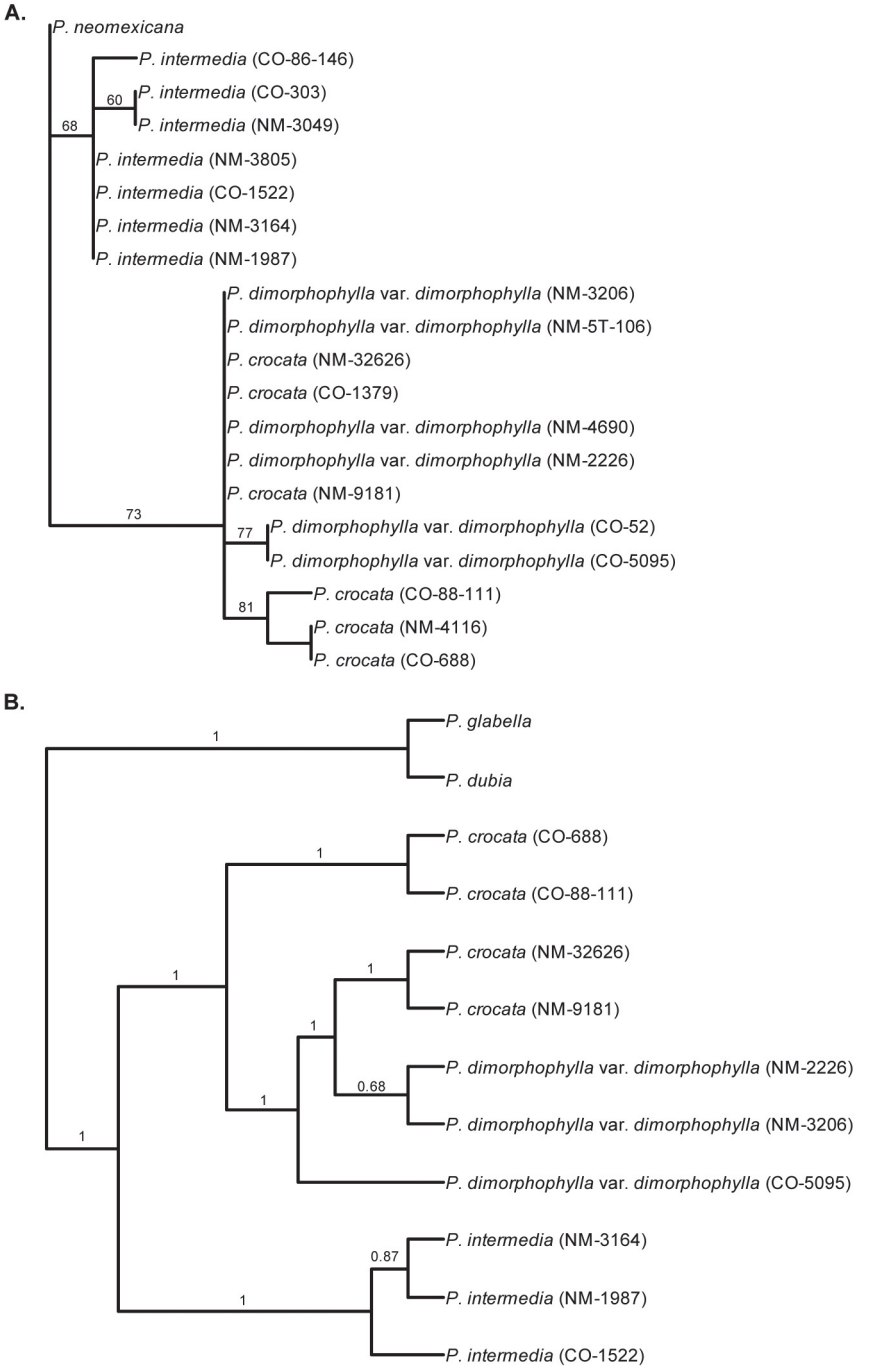

Fig. 5. Phylogenetic analyses of the *P. crocata/dimorphophylla* complex in the Southern Rocky Mountains. A. nrITS sequence data estimated using maximum likelihood. Bootstrap support is shown for clades having bootstrap values greater than 50. B. Next-gen generated data estimated using ASTRAL. Clade support shown through local posterior probability (LPP) for each node.

ACKNOWLEDGMENTS

We would like to thank Tim Hogan, Kelly Allred, Roger Peterson, Craig Martin, and anonymous informal reviewers for reading drafts and making valuable comments especially of terminology; Jim McGrath for showing us areas where these plants grow in New Mexico; curators of herbaria at Universities of Colorado Boulder and New Mexico for use of their collections, and the SEINet database for making digital copies of specimens available for study.

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