TAXONOMY AND PHYLOGENY OF THE GENUS *LAPPULA* MOENCH (BORAGINACEAE) IN NORTH AMERICA

by

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B.A., University of Montana, 1997
M.S., University of Nebraska, Lincoln, 2000

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Division of Biology
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KANSAS STATE UNIVERSITY
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Abstract

The genus *Lappula* Moench is a diverse group of herbaceous plants in the large, cosmopolitan family Boraginaceae. Over sixty species are recognized in Eurasia; many are found in cold deserts, steppes, and semi-deserts of Central Asia. Fewer species were described from western North America, and compared with the Asian species they are poorly known. Various North American taxa have been placed into synonomy under Eurasian species, and complex patterns of variation have made species circumscription challenging. The goal of this dissertation was to explore phylogenetic relationships between North American and Eurasian species and to revise the taxonomy of the North American species.

A molecular phylogenetic study was initiated in order to infer patterns of relationships among the North American species relative to Eurasian diversity. Samples were collected from throughout the western United States and from Siberia. Additional samples of Eurasian species were taken from herbarium specimens. Sequences were generated for three DNA regions (the ITS region of the nuclear ribosomal DNA, and chloroplast intergenic spacers *trnS-trnG* and *rpl32-trnL*) and phylogenies were generated using parsimony and Bayesian analyses. Results were in general agreement among all analyses. The genus *Lappula* was recovered as a monophyletic group, with the exception of the morphologically anomalous *L. sessiliflora* (Boiss.) Gürke, which was sister to the genus *Rochelia* Rchb. The native North American species of *Lappula* and *L. redowskii* (Hornem.) Greene formed a clade. Samples of *L. squarrosa* (Retz.) Dumort., a Eurasian steppe plant with a wide introduced range in North America, grouped with samples from Eurasia. Sampled species of *Hackelia* Opiz, a genus sometimes treated as part of *Lappula*, formed a clade separate from the *Lappula* species sampled here.

Herbarium and field studies resulted in a revised taxonomy for the North American *Lappula*. Nomenclatural problems were resolved; nine native species and four varieties were recognized along with the introduced Eurasian species *L. squarrosa*.

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Dedication

There are many people whose kindness and assistance have helped this work come to fruition. However, my family cannot be thanked enough for their love and encouragement over the years. It is with great affection that I dedicate this dissertation to them, in particular, to my husband Steven B. Rolfsmeier, our beloved son Christoph F. Rolfsmeier, and to my parents Joseph W. Stout and Hilde W. Stout (in memory of).

Chapter 1 - A molecular phylogenetic study of the genus *Lappula* Moench

Introduction

The genus *Lappula* Moench comprises a group of annual, biennial, and occasionally perennial herbs in the large and cosmopolitan family Boraginaceae. The genus is generally distributed throughout the Holarctic Kingdom though much of the diversity is concentrated in the Circumboreal and Irano-Turanian Regions of Siberia and Central Asia (following Takhtajan 1986). Habitats where *Lappula* species can be found include steppes, deserts and semi-deserts, and barren substrates (Popov 1953; Ovczinnikova 2006a). Over 60 species have been recognized for Eurasia (Ovczinnikova 2009b). *Lappula squarrosa* (Retz.) Dumort. is widely introduced throughout the northern hemisphere and this species has given the genus in general the reputation as being weedy (at least in North America). *Lappula squarrosa* is considered native to the Eurasian steppes and is thought to have spread westward into Europe and to North America and elsewhere (Popov 1953). In contrast, many species of *Lappula* have much narrower ranges; a number are narrow endemics found only in the Siberian and Mongolian Altai, Kazakhstan, and in Tian Shan Mountains of China, and are not invasive (Popov 1953; Zhu et al. 1995; Ovczinnikova 2009). Whereas Asian *Lappula* species have been studied in terms of cytology (Lugue 1992; Coppi et al 2006), developmental anatomy (Hilger 1985), palynology (Diez and Valdez 1991; Ovczinnikova 2006c), micromorphology (Ovczinnikova 2006b) and ecology (Ma et al. 2010), comparatively little is known about the North American species.

In North America, estimates of diversity have varied from two polymorphic species, including the introduced species *L. squarrosa* (Al-Shehbaz 1991) to five species with eight varities (Johnston 1924). No less than 26 varietal combinations and species names have been applied by various authors to North America taxa (The International Plant Names Index [IPNI],

2012), but the taxonomic identity of North American species has been confounded by complicated patterns of variation, and nomenclatural confusion. Similarities among North American and Eurasian taxa have resulted in unresolved questions regarding the distinctiveness of North American *Lappula* species.

Lappula species are typically pubescent, covered variously in simple hairs and have funnel shaped or campanulate corollas in shades of blue or white (Popov 1953; Edmonson 1978; Ovczinnikova 2006a). The inflorescence is a scorpoid cyme (Buys 2003). Species are distinguished by a suite of characters, but fruit characters are most important for identification. The fruits in *Lappula* are schizocarps of four mericarps (also called nutlets). Each mericarp has an abaxial (outward facing) disk that can be narrowly linear to broadly ovate, and is bordered by one or more rows of marginal spines which can be free or variously connate (Al-Shebaz 1991; Edmonson 1978). Heterocarpy (multiple fruits types on a single plant or among plants in the same species) and heteromericarpy (multiple nutlet types in a single fruit) are not uncommon in *Lappula* (see for example Popov 1953; Zhu et al. 1995; Ma et al. 1992). Heteromorphic fruit characters can include differences in the degree of connation or inflation of marginal spines, and degree of attachment to the gynobase.

The taxonomy of North American *Lappula* species has been complicated by multiple factors. While Greene described seven species (IPNI 2012), specimens with his determinations were not widely distributed, and it would seem that his nomenclatural types were not seen by revisionary workers (as observed in Nelson and Macbride [1916]; and Johnston [1924] who omitted names in synonymy, recorded questions marks, or by disregarded specific epithets with nomenclatural priority), and this resulted in unclear concepts of species identities. Variation relative to heteromorphic fruits and the connate spines and swollen margins has also been a

cause of taxonomic confusion. Specimens with fruits having thin margins on their nutlets had been described as distinct species: *L. desertorum* Greene , *L. foliosa* A. Nels. [based upon *L. desertorum* Greene var. *foliosa* A. Nelson], *L. infelix* Greene, *L. columbiana* A. Nelson, and *L. leucotricha* Rydberg. *Lappula desertorum* (including *L. foliosa*) is distinguished from the others by its low branching growth form and fruits shorter than the style. However the other taxa with thin variously connate nutlet margins are distinct in part of their ranges but where their ranges overlap it is challenging if impossible to assign specimens to a particular species. These were assigned to infraspecific ranks under *L. cupulata* Rydberg (Nelson and Macbride 1916) and under *L. texana* by Johnston (1924), but the relationship of these heteromorphic forms to the species under which they were placed is unknown and the classification was largely superficial. For example, Johnston's 1924 treatment had placed all taxa with heteromorphic fruits as varieties of *L. texana* (Scheele) Britton regardless of other morphological traits. This was a change from Nelson and Macbride's treatment (1916) where the fruits with thin wings were considered a species separate from *L. texana*. Johnston (1935) later changed his taxonomy, noting differences between the fruits where the marginal spines arise from a swollen margin versus those where the spines arise from an obscure or thin margin and become variously connate at maturity. He placed taxa with swollen nutlet margins into synonomy under *L. texana* and those with a thin margin or "wing" under *L. redowskii* as *Lappula redowskii* var. *desertorum* (Greene) I.M. Johnst. (1935).

Relationships to Asian species have been proposed for some North American *Lappula* taxa on the basis of fruit morphology, and are reflected in various taxonomic treatments of these species. One example is the treatment of North American *L. occidentalis* (S. Watson) Greene,

described originally as a variety of a primarily Siberian species *L. redowskii* (Hornem.) Greene (originally *Echinospermum redowskii* (S. Wats.) Greene var. *occidentale*).

Authors have differed in their treatment of this taxon. However, the identity of *Lappula redowskii* is not as straightforward as it would seem. Hornemann's description of *Myosotis redowskii* Hornem., the basionym of *E. redowskii,* served only to distinguish the species from others in the garden at Copenhagen, It does not clearly distinguish the species from other species of *Lappula*, referring only to vegetative and floral characters (shared by many species in the genus), and noting that the collection in the garden was from imperial Russia. Watson based his description upon comparisons of North American material collected from various localities in Nevada with representative Asian species from the Gray Herbarium (Watson 1871). He concluded that the North American material was distinct, and included in the description of his new variety illustrations of the Asian species *E. redowskii* and *E. patula* Lehm. for comparison (Watson 1871). Watson cited de Candolle (1846) who followed Lehmann's (1818) characterization of *E. redowskii* which was based upon material from the vicinity of Lake Baikal in eastern Russia. In our study, we follow Ovczinnikova's (2005) concept of *L. redowskii* as an eastern Asian species, also in line with Lehman's and Watson's concept of the species.

Lappula squarrosa appears fairly early in the collection history of North America and was reported for Maryland as early as 1698 (Johnston 1935). *Lappula squarrosa* is now found in every Canadian province, especially in the prairie provinces, and it was such a problem in crop fields that by 1904 the species was declared a noxious weed in Canada (Frick 1984). Though not federally listed in the United States, it is state listed in Alaska (http://aknhp.uaa.alaska.edu) where that state's Natural Heritage Program gives *L. squarrosa* an invasiveness rank of forty-

four (out of one hundred). Hultén noted that it was common along roadsides and was "apparently introduced into our area [Alaska] recently" (Hultén 1949).

Three species similar to *L. squarrosa* in having multiple rows of spines on their nutlets were described from the western United States: *L. fremontii* (Torr.) Greene, *L. cenchrusoides* A. Nelson, and *L. erecta* A. Nelson. In the two revisionary works focused on North American species (Nelson and Macbride 1916; Johnston 1924), these were considered distinct North American species. *Lappula fremontii* was hypothesized to be close to the Central Asian *L. semiglabra* (Ledeb.) Gürke (Nelson and Macbride 1916). Brand retained one species from Wyoming, *L. cenchrusoides* A. Nelson, as distinct, but placed *L. erecta* as a variety under *L. squarrosa* (as *L. echinata* Gilib.). Subsequent floristic works have followed this to a certain degree, though *L. cenchrusoides* has been treated variously as a distinct species, or as synonymous with *L. squarrosa*. The varying treatments reflect confusion not only about the taxonomic identity of *L. fremontii* relative to *L. cenchrusoides* and *L. erecta*, but about the identity of each of these relative to the introduced *L. squarrosa*. Determining how the North American taxa relate to the diversity in Eurasia has implications for the taxonomy of the group.

Historically, *Lappula* has been considered part of tribe Eritrichieae Benth. et Hook, a tribe characterized by corollas with a short tube, a distinct limb with rounded-obtuse floral lobes, and a pyramidal to subulate gynobase (Popov 1953), and by its fruits, which attach to a subulate or pyramidal gynobase along the middle or lower adaxial side (Ovczinnikova 2009a). Gray disagreed with the splitting Eritrichieae and Cynoglossaeae into two tribes, noting that there were too many overlapping characters between the genera of these tribes to justify separating them and followed DeCandolle in including them in the single tribe Cynogossaeae (Gray 1884). Phylogenetic investigations into relationships in Boraginaceae using data from nuclear and

chloroplast DNA support a broader Cynoglosseae including the former Eritrichieae (Långström and Chase 2002; Weigend 2010; Cohen and Davis 2012; Nazaire and Hufford 2012). Pollen shape is the known morphological synapomorphy supporting this circumscription of Cynoglosseae (Hargrove and Simpson 2003; Långström and Chase 2002).

Relationships between *Lappula* and other genera have been proposed based on morphological similarities. *Hackelia* Opiz., *Rochelia* Rchb., and *Lepechiniella* Popov have each been suggested as potential close relatives to *Lappula*. Several species of *Hackelia* from the western United States were treated as part of *Lappula* in Nelson and Macbride's revision of the North American *Lappula* (1916). In distinguishing *Hackelia* from *Lappula*, Johnston (1923) reasoned the two genera were clearly morphologically distinct, basing this separation upon inferences from a number characters including gynobase morphology, shape of the fruit attachment scar, life history traits and vegetative characters. Furthermore, he asserted that *Hackelia* shared more characteristics with *Eritrichium*, in particular section Coloboma D.C. (Johnston 1923). This similarity has resulted varying treatments for some species. For example the plant treated as *Hackelia thymifolia* (A. DC.) I. M. Johnst. by Johnston (1940), Popov (1953), and Ovczinnikova (2007) is alternately treated as *Eritrichium thymifolium* (A. DC.) Y.S. Lian & J.Q. Wang in the *Flora of China* (Zhu et al. 1995). *Amblynotus rupestris* (Pall. ex Georgi) Popov ex Serg., separated as a monospecific genus because of its unique smooth fruits, was shown to be nested within a clade of *Eritrichium* species (Nazaire and Hufford 2012). Reflecting disagreement on taxonomic affinities of the species, some authors continue to treat *H. deflexa* Opiz as part of *Lappula* (e.g. *Flora Europea* [Chater 1972] Mansion et al. 2009). Popov (1953) considered the narrow endemic Central Asian genus *Lepechiniella* Popov and not *Hackelia* to be the closest relative of *Lappula*. While he noted similarities between *Rochelia* and the

morphologically anomalous *L. sessiliflora,* Popov (1953) treated the genus *Rochelia* as part of its own tribe. Ovczinnikova's subtribal classification of the former Eritrichieae grouped *Lappula* and *Lepechiniella* into their own sub-tribe Echinosperminae.

Molecular phylogenetic studies that have sampled from *Lappula* have confirmed its taxonomic placement in Cynoglosseae s.l. (Långström and Chase 2002). A study of the Trigonotideae showed a sister relationship between *Lappula* and *Mertensia*, but sampling of Cynoglosseae was limited (Weigend et al. 2010). Khoshsokhan et al. (2010), studying interspecific relationships in *Rochelia*, included *L. sessiliflora* and *L. barbata* as outgroup taxa based on their earlier unpublished work indicating a sister relationship between the two genera (they did not share if *Lepechiniella* or *Hackelia* had been included in those studies). Nazaire and Hufford (2012), with the most comprehensive sampling in Cynoglosseae s.l. to date, included four *Lappula* species, three *Rochelia* species, and three *Hackelia* species. In their study, these three genera formed a strongly supported clade, consistent with morphological hypotheses of relationship. We are aware of no published phylogenetic studies that have included species of *Lepechiniella*.

This work represents the first molecular phylogenic study focused on the genus *Lappula*. The aims of this research were to investigate relationships of North American taxa and to place these findings within the broader context of relationships of the genus, relating North American members to Eurasian diversity. Additionally, we test the alternate taxonomic hypotheses of *L. fremontii* as distinct and native, or part of the introduced *L. squarrosa*.

Materials and Methods

Taxon sampling

Sampling within *Lappula* aimed to include diversity from throughout western North America as well as species from Asia that have been hypothesized to be synonymous with or closely related to the North American species (Nelson and Macbride 1916; Macbride 1916; Johnston 1929; Brand, 1931Popov 1953, Ovczinnikova 2005, 2006d). Eurasian species with similar morphology to *L. occidentalis* and *L. redowskii* were included to compare relationships among morphologically similar species; samples were included from the Eurasian species *Lappula patula* Asch. ex Gürke, *Lappula stricta* (Ledeb.) Gürke, and *L. brachycentroides* Popov. Samples of *L. squarrosa* from North America and Siberia were included. Samples of *Hackelia* (North American and Siberian), *Eritrichium*, and *Amblynotus*, were included among the ingroup taxa. *Mertensia* was selected as the outgroup taxon for the phylogenetic analyses as it is consistently placed outside *Lappula* (Weigend 2010; Gertsen and Olmstead 2008).

In sampling the North American taxa, the present study follows the taxonomic revision of Johnston (1924), but in some cases not all varieties were sampled. Samples were compared with type specimens during preparation of the taxonomic revision (Chapter 2) and nomenclatural adjustments were made to reflect this. The taxonomy of the Eurasian species follows that of Ovczinnikova (2010), who recognized eight subsections and fourteen series (Table 1.1). Efforts were made to sample diversity throughout the genus, though much of the material obtained from field collections and herbarium specimens came from Section *Lappula*. It was not possible to sample from sections *Rupestres* and *Lipshitzia* as these include narrow endemics and collections were unavailable. Samples of Siberian *L. redowskii*, as well as species with superficially similar

morphology including *L. patula*, *L. tenuis*, *L. stricta* (species in Section *Lappula* that have a single row of marginal spines) were included. Samples were also included from species with multiple rows of spines that have been hypothesized to be related to *L. fremontii* (including *L. cenchrusoides* and *L. erecta*).

A total of 30 accessions of *Lappula* were included (Table 1.2), with material from North America (18 samples), Siberia (7 samples), Kazakhstan (3 samples), and China (2 samples). We sampled thoroughly in section Lappula and sampled four of the remaining seven sections of the genus. Field collected samples were dried in silica gel and stored at room temperature until extraction. Material obtained from herbarium specimens, is indicated in Table 1.2. with an asterisk.

Table 1.1 Subgeneric Classification of Eurasian *Lappula* species following Ovczinnikova (2009).

Section	Series	No. species
Lappula DC, 1846		20
	Lappula Ovczinnikova, 2005	7
	Redowskianae Ovzinnikova, 2005	1
	Anisacanthae Ovzinnikova, 2005	3
	Strictae M. Popov ex Ovczinnikova, 2005	8
	Patulae Ovczinnikova, 2005	1
Omphalolappula (Brand) Ovczinnikova, 2005		6
	Omphalolappula (Brand) Ovczinnikova, 2005	4
	Macrae M. Popov ex Ovczinnikova, 2005	1
	Anomalolappula M. Popov ex Ovczinnikova, 2005	1
Lipschitzia Ovczinnikova, 2005		2
Sclerocaryum DC. et A. DC., 1846		2
Sinaicaeae (Riedl) Ovczinnikova, 2005		3
Macranthae (Riedl) Ovczinnikova, 2005		8
	Macrantheae (Riedl) Ovczinnikova, 2005	2
	Semiglabrae Ovczinnikova 2005	5
	Lipskyanae Ovczinnikova 2005	1
Rupestres Ovczinnikova, 2005		2
Microcarpae (M. Pop.) Ovczinnikova, 2005		19
	Microcarpae M. Pop. 1953	7
	Tianschanicae M. Pop. ex Ovczinnikova 2005	8
	Popovianae Ovczinnikova, 2005	4

Table 1.2 Sampling. Summary of DNA samples tied to field collection numbers and locality data with indication of DNA regions sequenced for each one. Classification of Eurasian samples follows Ovczinnikova (2006d, 2009). Samples indicated with an asterisk (*) were extracted from herbarium material. In cases where the species name used here for North American taxa differs from Johnston's 1924 treatment, Johnston's taxon recognition is indicated in brackets.

DNA number	Collector number	Species name [Name used by Johnston 1924 if different (North American species only)]	Fruit morphology	Locality data	DNA region(s) sequenced
2455	SJR 1217b	*L. anisacantha* (Turcz. ex Bunge) Gürke Sect. *Lappula*, Ser. *Anisacanthae*	Fruits with two rows of spines	Irkutsk Oblast, Siberia, Russian Federation	ITS, cpDNA
2474	OVC s.n.	*L. brachycentra* (Ledeb.) Gürke Sect. *Microcarpae*, Ser. *Microcarpae*	Fruits with a single row of spines	Vostochno-Kazahkstanskaya Oblast, Kazakhstan	ITS, cpDNA
2458*	AUK 27.06.05	*L. brachycentroides* Popov Sect. *Lappula,* Ser. *Lappula*	Fruits with a single row of spines	Kazakhstan	ITS, cpDNA
2485*	M. Nazaire 1912	*L. consanguinea* (Fisch. & C.A. Mey.) Gürke Sect. *Lappula,* Ser. *Lappula*	Fruits with two rows of spines	China, Xinjiang	ITS, cpDNA
2454	SJR 1216a	*L. consanguinea* Gürke Sect. *Lappula,* Ser. *Lappula*	See above	Irkutsk Oblast, Siberia, Russian Federation	ITS, cpDNA

DNA number	Collector number	Species name [Name used by Johnston 1924 if different (North American species only)]	Fruit morphology	Locality data	DNA region(s) sequenced
2440*	SJR 757A	*L. cucullata* A. Nels. [*L. texana* (Scheele) Britt. var. *heterosperma* (Greene) A. Nelson & J.F. Macbr.]	Fruits with a single row of spines, plants have heteromorphic fruits. Fruits have homomorphic and heteromorphic nutlets. Some nutlets with connate spines and inflated margins.	Wyoming, Carbon Co.	ITS, cpDNA
2423	SJR 1102B	*L. cucullata* A. Nelson [*L. texana* (Scheele) Britt. var. *heterosperma* (Greene) A. Nelson & J.F. Macbr.]	See above	North Dakota Bowman Co.	ITS, cpDNA
2488	SJR 1124	*L. desertorum* Greene [Greene,1924 treats as *L. texana* (Scheele) Britt. var. *heterosperma* (A. Nelson) J.F. Macbr. later as *L. occidentalis* var. *desertorum* (Greene) I.M. Johnst.	Nutlets with a single row of spines, frequently connate at their bases forming a wing in the lower part.	Elko, Nevada	cpDNA
2327	SJR 1081	*L. fremontii* (Torr.) Greene var. *fremontii*	Nutlets with two rows of spines.	Wyoming, Albany Co.	ITS, cpDNA
2422	SJR 1101b	*L. fremontii* (Torr.) Greene var. *fremontii*	See above	North Dakota, Bowman Co.	ITS, cpDNA

DNA number	Collector number	Species name [Name used by Johnston 1924 if different (North American species only)]	Fruit morphology	Locality data	DNA region(s) sequenced
2330	SJR 1080	*L. fremontii* (Torr.) Greene var. *nelsonii* var. novem [*L. fremontii* (Torr.) Greene]	See above	Wyoming, Albany Co.	ITS, cpDNA
2325	SJR 1071	*L. heterosperma* Greene [*L. texana* (Scheele) Britt. var. *heterosperma* (Greene) A. Nelson & J.F. Macbr.]	Nutlets with a single row of spines. Fruits heteromericarpic with three or more nutlets with a swollen nutlets margin.	Wyoming, Sweetwater Co.	ITS
2326	CJF 812	*L. heterosperma* Greene [*L. texana* (Scheele) Britt. var. *heterosperma* (Greene) A. Nelson & J.F. Macbr.]	See above	Wyoming, Fremont Co.	ITS, cpDNA
2428	SJR 1062A	*L. heterosperma* Greene [*L. texana* (Scheele) Britt. var. *heterosperma* (Greene) A. Nelson & J.F. Macbr.]	See above	Colorado, San Miguel Co.	ITS, cpDNA
2438	SJR 670A	*L. heterosperma Greene* (homomorphic) *[L. texana* var. *homosperma* (A. Nelson) A. Nelson and J.F. Macbr.]	Plants from this population had homomorphic fruits and nutlets with swollen margins.	Montana, Prairie Co.	ITS

DNA number	Collector number	Species name [Name used by Johnston 1924 if different (North American species only)]	Fruit morphology	Locality data	DNA region(s) sequenced
2425	SJR 1122	*L. longispinus sp. novem* [Not clear that Johnston saw this.]	Fruits with a single row of spines homomorphic.	Washington, Adams Co.	ITS, cpDNA
2420	SJR 1082	*L. occidentalis* (S. Watson) Green [*L. redowskii* (Hornem.) Greene var. *occidentalis* (S. Wats) Rydb].	Fruits with a single row of spines, homomorphic	Nebraska, Kimball Co.	ITS, cpDNA
2331	SJR 1054	*L. occidentalis* (S. Watson) Greene [*L. redowskii* (Hornem.) Greene var. *occidentalis* (S. Wats) Rydb.] Sect. *Lappula,* Ser. *Redowskianae*	See above	Colorado, Montezuma Co.	ITS
2429	SJR 1073	*L. occidentalis* (S. Watson) Greene *[L. redowskii* (Hornem.) Greene var. *occidentalis* S. Wats.] Sect. *Lappula,* Ser. *Redowskianae*	See above	Wyoming, Uinta Co.	ITS

DNA number	Collector number	Species name [Name used by Johnston 1924 if different (North American species only)]	Fruit morphology	Locality data	DNA region(s) sequenced
2431	SJR 1084	*L. occidentalis* (S. Watson) Greene *[L. redowskii* (Hornem.) Greene var*. occidentalis* S. Wats.] Sect. *Lappula,* Ser. *Redowskianae*	See above	Nebraska, Keith Co.	ITS
2475	Fehlberg 50208-3	*L. occidentalis* (S. Watson) Greene var. *stricta* (S. Wats) comb. nov. [L. redowskii (Hornem.) Greene var. desertorum (Greene) I.M. Johnst. Sect. *Lappula,* Ser. *Redowskianae*	Fruits with a single row of spines, heteromorphic or homomorphic. This sample had all nutlets the same. Some plants assigned to this variety are heteromericarpic.	Arizona, Yavapai Co.	ITS, cpDNA
2461*	AUK s.n.	*L. patula* Asch. ex Gürke Sect. *Lappula,* Ser. *Patulae*	Fruits with a single row of spines, homomorphic.	Alma-Ataysky Oblast, Kazakhstan	ITS, cpDNA
2453	SJR 1203a	*L. redowskii* (S. Watson) Greene Sect. *Lappula,* Ser. *Redowskianae*	Fruits with a single row of spines, homomorphic.	Irkutsk Oblast, Siberia Russian Federation	ITS, cpDNA
2480*	AUK 28.05.2003	*L. semiglabra* (Ledeb.) Gürke Sect. *Macranthae,* Ser. *Semiglabrae*	Fruits with more than one row of spines, heteromorphic.	Kazakhstan	ITS, cpDNA

DNA number	Collector number	Species name [Name used by Johnston 1924 if different (North American species only)]	Fruit morphology	Locality data	DNA region(s) sequenced
2436	SJR 447D	*L. squarrosa* (Retz.) Dumort. Sect. *Lappula,* Ser. *Lappula*	Fruits with two rows of spines, homomorphic.	North Dakota, McKenzie	ITS, cpDNA
2476	SJR 1200	*L. stricta* (Ledeb.) Gürke Sect. *Lappula,* Ser. *Strictae*	Fruits with a single row of spines, homomorphic.	Irkutsk Oblast, Siberia, Russian Federation	ITS, cpDNA
2486*	M. Nazaire 1899	*L. tenuis* (Ledeb.) Gürke Sect. *Lappula,* Ser. *Lappula*	Fruits with a single row of spines, homomorphic.	China, Xinjiang,	ITS
2421	SJR 1100	*L. texana* var. *septemptrionalis=var. novem* [*L. texana* (Scheele) Britt. var. *texana]*	Fruits with a single row of spines, fruits heteromericarpic, with three nutlets having inflated margins.	Nebraska, Dawes Co.	ITS
2333	SJR 1083	*L. texana* var. *septemptrionalis*=var. *novem* [*L. texana* (Scheele) Britt. var. *texana]*	See above.	Nebraska, Keith Co.	ITS, cpDNA
2459*	OVC 2004	*L. tuvinica* Ovczinnikova Sect. *Lappula,* Ser. *Lappula*	Fruits with two rows of spines, homomorphic.	Siberia, Russian Federation	ITS, cpDNA
2463	SJR 1204	*Amblynotus rupestris* (Pall.) Popov	NA	Irkutsk Oblast, Siberia Russian Federation	ITS, cpDNA

DNA number	Collector number	Species name [Name used by Johnston 1924 if different (North American species only)]	Fruit morphology	Locality data	DNA region(s) sequenced
2464	SJR 1211	*Eritrichium thymifolium* (DC.) Y.S. Lian & J.Q. Wang [Ovchinnkova follows *Hackelia thymifolia* (A. DC.) I.M. Johnst.]	NA	Irkutsk Oblast, Siberia, Russian Federation	ITS, cpDNA
2472*	SJR 428	*Hackelia deflexa* Opiz	NA	Dawson Co, Montana	ITS, cpDNA
2465	SJR 1224	*H. deflexa* Opiz	NA	Buryatia, Siberia, Russian Federation	ITS, cpDNA
2358*	SJR 805	*H. floribunda* (Lehm.) I.M. Johnst.	NA	Utah, Summit Co.	ITS, cpDNA
2483	SJR 1205	*Mertensia dahurica* G. Don	NA	Irkutsk Oblast, Siberia, Russian Federation	ITS, cpDNA

DNA extraction, PCR, and sequencing

Total genomic DNA was extracted using the CTAB (hexadecyltrimethylammonium bromide) method (Doyle and Doyle, 1987) as modified by Lookerman and Jansen (1996). Generally, undiluted total genomic DNA was used in PCR reactions except for a few samples where the template was diluted with ddH_20 to a one-tenth, or one-one hundredth concentration.

The internal transcribed spacer region (ITS) region of nuclear ribosomal DNA was amplified using the primers ITS4 of White et al. (1990) and modified ITS5 of Downie and Katz-Downie (1996). PCR reactions of 50 µl were prepared using 5 ul of 2 µM primer, 10 µl of 5X PCR buffer, 5 µl of 25 mM $MgCl_2$, 4 ml of 10mM dNTP, 1.25-2.50 µl of Gotaq *Taq* polymerase (Promega) and 1-2 µl of DNA template. Amplifications were run in a PTC-200 thermal cycler (MJ Research, Inc.), in most cases with a 5 minute "hot start" at 94ºC and one minute at 72ºC when *Taq* was added to each tube. This was followed by 28-35 cycles consisting of a one minute denaturing step at 94ºC, a one minute annealing step at 50ºC or 52ºC, and a one minute extension at 72ºC; followed by a final extension at 72ºC for five minutes.

The chloroplast intergenic spacer regions *rpl*32-*trnL*, and *trn*S-*trn*G were amplified using the primers *rpl* 32 (Shaw et al 2007) and $trnL^{UAG}$ (Shaw et al 2007) and trnG (GCU) and trnS (UCC) (Hamilton 1999). For both regions, PCR reactions of 50 µl were prepared using 5µl of each primer, 10 µl of 5X PCR buffer, 5 µl of 25mM $MgCl_2$, 4 µl of 10mM dNTP, 1.25-2.5 units of Gotaq *Taq* polymerase (Promega), and 1-2 µl of DNA, with the following exception: for 18 samples, 4µl of 25 m $MgCl_2$ was used to amplify the *trnS-trnG* region, this modification enabled sufficient amplification and improved sequence data quality in these samples. Amplifications for *rpl32-trnL* began with a 2 minute denaturing step at 94ºC, followed by 30 cycles consisting of a one minute denaturing step at 94ºC, a one minute annealing step at 56ºC, and a one minute

extension step at 72ºC, followed by a final extension at 72ºC for five minutes. Templates that did not amplify were subjected to a "hot start" PCR at 94ºC for 5 minutes followed by the steps summarized above. For *trn*S-*trn*G, samples were run using two different PCR programs (both with a hot start 5 minutes at 94ºC) followed by 28 or 30 cycles of a one minute denaturing temp of 94ºC, a one minute annealing step at 52ºC or 54.5ºC, and a five minute extension step at 72ºC.

PCR results were visualized on a 2% agarose gel stained with ethidium bromide solution. Samples were compared against a standard 1 kilobase DNA ladder (Invitrogen). PCR products were purified using a QiaQuick purification kit (Qiagen Corp.) following manufacturer's instructions. Purified PCR products were visualized on a 2% agarose gel stained with ethidium bromide. Concentrations for sequencing reactions were estimated by visual comparison with a low DNA mass ladder (Invitrogen). Purified PCR reactions were sequenced in both directions using the same primers as for PCR, and sequencing reactions were performed with a BigDye v3.1 kit (Applied Biosystems Inc.) following manufacturer's instructions except that quarter reactions were used. Sequencing reactions were run for 2 minutes at 96ºC followed by 25 cycles of 96ºC for 15 seconds, 50ºC for 5 seconds, and 60ºC for four minutes as per manufacturer's instructions. Samples were purified using columns filled hydrated Sephadex G-50® (Sigma Life Sciences) and dehydrated in a vacuum centrifuge for 20 minutes. Samples were run on an ABI sequencer either at the DNA facility at the Iowa State University Office of Biotechnology or at the Kansas State University DNA Sequencing and Genotyping Facility in the Plant Pathology Department.

Sequence Editing and Alignment

Sequence data were edited in Sequencher ver. 4.9 (Gene Codes Corp., Ann Arbor, MI), and manually aligned in SeAl ver. 2.0a11 (Rambaut, 2002). The ITS sequence data did not include extensive polymorphisms. However, in a few sequences there were single basepair (bp)

polymorphisms, and these were treated as ambiguous data. Five sequences were downloaded from GenBank and added to the ITS alignment: *L. barbata* (AB564703.1), *Rochelia cancellata* (AB564702.1), *R. cardiosepala* (AB564711.1), and *Eritrichium nanum* (AY092901.1). Some areas of ambiguity were observed in the ITS (4 bp), and *trnS-G* (5 bp) alignments and were excluded in the phylogenetic analyses (Table 1.4).

Three datasets were analyzed in this study, one nuclear region (ITS), one dataset comprising the two chloroplast regions, and one concatenated data set including the chloroplast plus ITS regions (combined).

Gaps in sequence alignments (also referred to as indels) of varying lengths have been hypothesized to be phylogenetically informative when coded as binary presence absence characters (reviewed by Simmons and Ochoterena 2000). Comparative analyses of simulated datasets suggest that both simple and modified complex indel coding can increase support values and improve resolution in those datasets that have low sequence variation but numerous gapped positions (Simmons et al. 2007). Alignments for the ITS, chloroplast and combined datasets were coded following the simple indel coding (SIC) and modified complex indel coding (MCIC) schemes in the program SeqState (Mueller 2005). Prior to loading the files, the alignments were exported from Se-Al as nexus files, and checked and edited in a text editor to ensure that the formatting was compatible with SeqState. Edited nexus files were loaded into SeqState and the SIC and MCIC options were selected.

Phylogenetic Analyses

Maximum parsimony (MP) analyses were performed in PAUP* ver. 4.0b10 (Swofford, 2003) for the ITS, chloroplast, and combined datasets, with various approaches to coding indels in order to compare how coding gaps (using both SIC and MCIC) versus treating gaps as missing data would affect tree resolution and branch support (Table 1.3). For all analyses, the ambiguous

regions in the alignments (9 bp total) were excluded, and polymorphisms were treated as ambiguous data. When heuristic searches could not run to completion, 20,000 maximum trees were selected. Statistical support for relationships was assessed using bootstrap analyses (Felsenstein 1985). Bootstrap support was assessed using a heuristic search with simple taxon addition and tree bisection reconnection (TBR) swapping. The number of bootstrap replicates and maximum trees held per bootstrap pseudoreplicates are summarized in Table 1.3. Visual inspection of the trees did not reveal strongly supported incongruence. The partition homogeneity test (Farris 1994) was implemented in PAUP* (as the ILD test) to check for incongruence of the nuclear and plastid data partitions (1000 repetitions). The result was insignificant (p=0.350), and the concatenated ITS and chloroplast datasets were analyzed as a combined dataset.

Table 1.3 Summary of parsimony analyses.

Dataset	Maximum trees set for Heuristic tree search	Bootstrap Pseudoreplicates	Maximum trees held per bootstrap pseudoreplicate
ITS gaps excluded/SIC/MCIC	Maximum trees allowed to increase in in all analyses	1000/500/1000	500/100 (but allowed to increase)/500
Plastid gaps excluded/SIC/MCIC	Maximum trees held at 20,000 for all analyses	10000/500/500	1/100/100
Combined gaps excluded/SIC/MCIC	Maximum trees allowed to increase in all analyses	500/500/500	500/100/100

For the Bayesian analyses, models of evolution were chosen using MrModeltest v.2 (Nylander 2004). The selected models are summarized in table 1.4 (below). Bayesian analyses were performed in the program Mr. Bayes v. 3 (Huelsenbeck 2001; Ronquist 2003) on the ITS, plastid and combined datasets using the selected model selected (Table 1.4), and model parameters were estimated directly in Mr. Bayes in all analyses. Both the chloroplast and combined datasets were partitioned by gene region. The partitions were unlinked and rates were set to variable. Two million generations were run for each analysis, sampling one tree every 500 generations. Twenty-five percent of the total trees were discarded as burn in.

Table 1.4 Models selected for Bayesian analyses.

DNA region	Model selected Mr. Modeltest
ITS	GTR+G GTR+R
rpl32	HKY, F81
trnS-trnG	F81

Results

Alignments

The ITS alignment had the shortest length but had 73 more parsimony informative nucleotide characters than the chloroplast data matrix (Table 1.5). The combined dataset was 2131 basepairs (bp) long and included 99 parsimony informative characters (with gaps coded as missing data Table 1.5). *Trn*S-*trn*G had more indels than *rpl*32-*trn*l. For all the data sets, simple indel coding (SIC) contributed more parsimony informative characters than did modified complex indel coding (MCIC, Table 1.5).

Table 1.5. Summary of characters and tree statistics for each indel coding scheme for each dataset.

	ITS (nuclear)	Chloroplast	Combined
Aligned matrix length	637	total: 1494 *rpl*32-*trnL*: 738 *trn*S-*trn*G: 756	2131
Number of ambiguous characters excluded from analyses	4	total: 5 *rpl*32-*trnL*: 0 *trn*S-*trn*G: 5	9
Total number of characters (included)	633/682/670	1489/1574/1527	2119/2250/2192
Number of coded indel characters (SIC/MCIC)	49/37*	85/38**	131/73
Number of parsimony informative characters (excl. indels/SIC/MCIC)	95/120/114	22/64/40	99/160/133
Number of equally parsimonious trees (excl./SIC/MCIC)	192/1407/1407	20,000[§]/20,000[§]/20,000[§]	576/6/576
Tree length (excl./SIC/MCIC)	272/340/339	122/221/216	331/484
CI ex (excl./SIC/MCIC)	0.64/0.62/0.63	0.98/0.79/0.89	0.72/0.72/.72
HI ex (excl./SIC/MCIC)	0.33/0.37/0.37	0.02/0.21/0.11	0.28/0.28/.28
RC (excl./SIC/MCIC)	0.63/0.63/0.63	0.92/0.83/0.88	0.76/0.75/.76

*30 unordered 7 step matrices
**23 unordered 15 step matrices
***51 unordered 22 step matrices
[§]Maxtrees set at 20,000

ITS trees

In the analysis of the ITS data where indels were scored as missing data, the strict consensus of 192 trees resolved all samples of the genus *Lappula* except *L. sessiliflora* as a strongly supported clade with 100% maximum parsimony bootstrap (MPBS) support (Figure 1.1). Within this clade, the North American *Lappula* species plus Siberian *L. redowskii* formed a clade with 100% MPBS and the Eurasian *Lappula* (including the North American accession of introduced *L. squarrosa*) formed a moderately supported clade with 74% MPBS support. In the Bayesian ITS tree, where a Genbank sequence of *L. barbata* was available, it formed a clade of *L. brachycentra* (Section Microcarpeae) though with very little PP support. *Lappula sessiliflora* (an anomalous species in the genus) grouped with the accessions of *Rochelia*. *Amblynotus rupestris* and *E. nanum* formed a clade, but the position of *E. thymifolium* relative to that clade and to the rest of *Lappula* was not resolved. Analyses of the ITS data with SIC and MCIC indel coding did not change the tree topology and had minimal impact on bootstrap support values (Figure 1.2 and Figure 1.3). The Bayesian analysis of the ITS data recovered a very similar tree topology as the parsimony analyses and had similar support values (Figure 1.4).

Chloroplast trees

The chloroplast dataset was reduced relative to the ITS dataset and did not include Genbank sequences. The plastid dataset resulted in a less resolved tree topology, but no strongly supported contradictions with the ITS dataset. When gaps were treated as missing data, *Lappula* forms a group with little internal resolution with 75% MPBS support (Figure 1.5). *Lappula redowskii* and several North American taxa formed a clade with 85% MPBS. Accessions of *Hackelia* were resolved as a clade with 97% MPBS. Bayesian analysis of the plastid data resulted in the same tree topology as the parsimony analysis but with very strong support for the clades that were recovered (Figure 1.8). Coding indels as informative characters in the plastid

dataset resulted in increased resolution within the tree as well as higher support values. When the gaps were coded followed SIC, four clades were recovered within the genus and the placement of four species was unresolved (Figure 1.6). *Hackelia* formed a strongly supported clade that did not include either *E. thymifolium* or *A. rupestris*. MCIC coding of the plastid tree changed the tree topology only slightly (for example, the clade including *L. fremontii* accessions was not recovered in the consensus tree (Figure 1.7)).

The combined analysis with gaps treated as missing data resolved *Lappula* with 100% MPBS, a clade of North American species plus *L. redowskii*, and a clade of *Hackelia* species (Figure 1.9). The MCIC tree was identical to the tree where gaps were treated as missing data, though with slightly higher bootstrap support for some relationships within the genus (Figure 1.11). Relationships within *Lappula* were better resolved in the SIC consensus tree, though with weak to moderate support (Figure 1.10). The Bayesian tree showed the same general patterns of relationships as those recovered from the parsimony analyses, and with similar support values. However, in the Bayesian analysis, some clades within the North American/*L. redowskii* clade were resolved with higher support than in the parsimony analyses (Figure 1.12).

With the exception of L. sessiliflora, Lappula samples form a clade

In all analyses of the plastid, and combined datasets, *Lappula* was recovered as a monophyletic group. However, in the ITS dataset, when the Genbank accession of *L. sessiliflora* were included, *L. sessiliflora* did not group with the remaining *Lappula* species and was consistently strongly supported as sister to a clade of *Rochelia* accessions (Figure 1.13). In a parsimony analysis including all available Genbank accessions of *Rochelia* species as part of the ingroup, *L. sessiliflora* resolved as sister to that genus.

North American Lappula plus L. redowskii form a clade

The North American *Lappula* and *L. redowskii* formed a strongly supported clade in all parsimony (regardless of indel coding schemes) and Bayesian analyses of the ITS and combined datasets (Figure 1.13, Figure 1.14). While relationships among the North American taxa were poorly resolved by the chloroplast data, *L. redowskii* was part of a clade that included all the North American taxa that had a single row of spines, including heteromorphic and heteromericarpic taxa. *L. redowskii* was the only Eurasian species sampled that grouped with the North American species.

Within this clade, *L. heterosperma* and similar taxa were recovered as a clade in all analyses of the ITS and combined data matrices. This relationship is most strongly supported by the ITS dataset with 95% MPBS values, and a high posterior probability value (1 PP) in the Bayesian analysis (Figure 1.13). Two accessions of *L. heterosperma* form a weakly supported clade in the parsimony analyses of the plastid datasets where gaps were coded as parsimony informatics characters: SIC (67% MPBS), MCIC (60% MPBS), otherwise there was little resolution in the plastid dataset. *Lappula texana* was not part of the *L. heterosperma* sub-clade of North American species in any of the analyses where that sub-clade was resolved.

In all analyses of the ITS and combined datasets, *L. fremontii* grouped with the North American species and not with *L. squarrosa*, *L. anisacantha*, or *L. semiglabra*. *Lappula fremontii* was part of an unresolved polytomy in both parsimony and Bayesian analyses of the plastid dataset, except in the analysis of the SIC plastid dataset where the three accessions formed a moderately supported clade. The plains form of *L. fremontii* var. *fremontii* was resolved as part of a clade of *L. fremontii* accessions (76% MPBS) in the parsimony analyses of both the SIC plastid and SIC combined datasets, but not in the other analyses.

Lappula squarrosa samples group with Eurasian species

Both North American and Siberian samples of *L. squarrosa* were consistently resolved as part of a clade of Eurasian species; though relationships of *L. squarrosa* to *L. consanguinea*, *L. tuvinica*, *L. tenuis* and *L. brachycentroides* was not resolved (Figure 1.7). Coding the indels (both methods) recovered trees where *L. squarrosa* formed a clade (though weakly supported) with other Eurasian species with similar morphology (Figure 1.6, Figure 1.7).

Placement of other genera related to Lappula

In none of the analyses did *Hackelia* species nest within accessions of *Lappula*. *Hackelia deflexa* and *H. floribunda* consistently formed a strongly supported clade and this relationship was supported by both ITS and plastid data. *Eritrichium thymifolium* did not group with the remaining *Hackelia* species, but it did form a clade with *Amblynotus rupestris* in analyses of SIC plastid and SIC combined datasets.

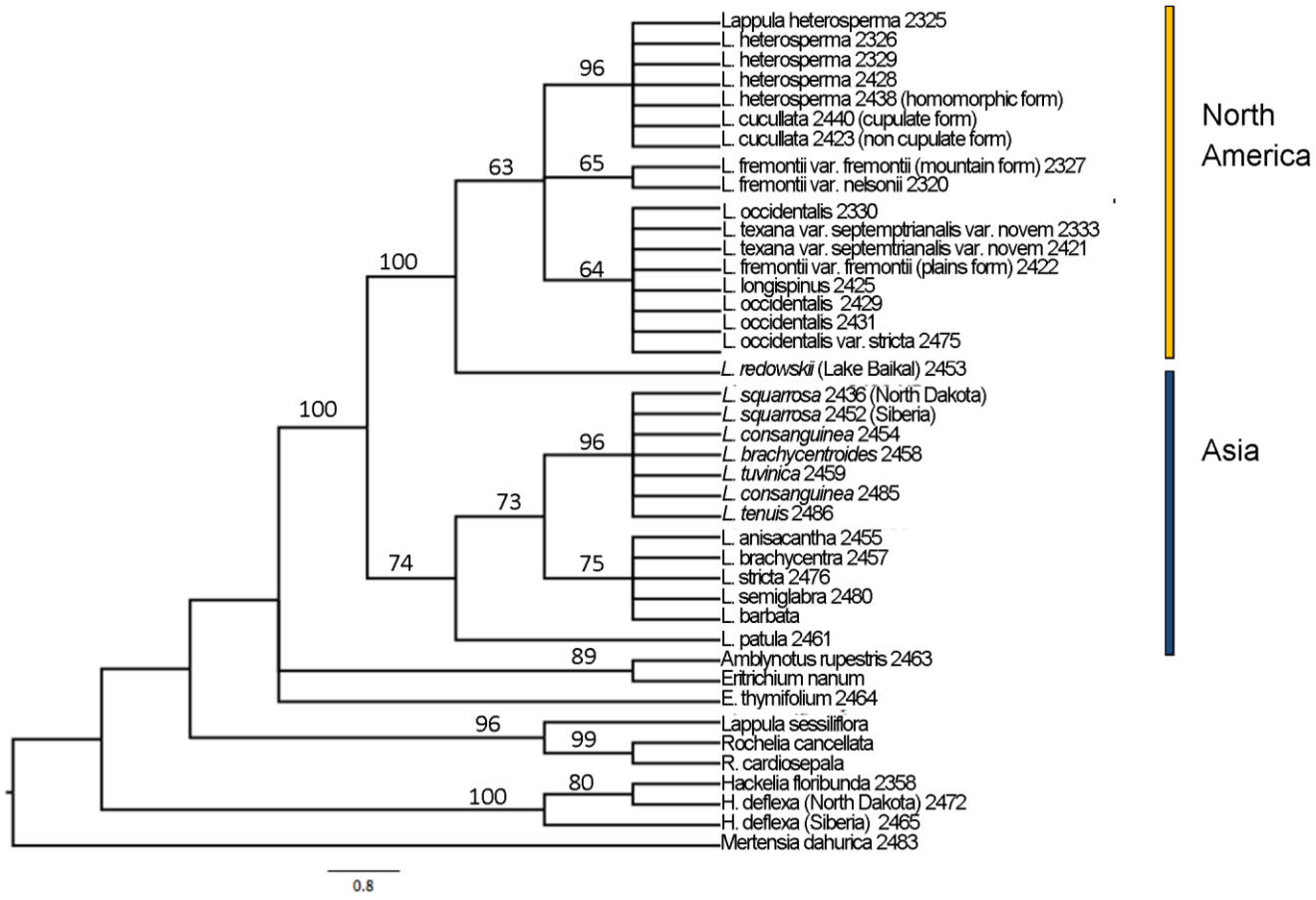

Figure 1.1 ITS parsimony strict consensus tree. In this analysis, gaps were treated as missing data. Parsimony bootstrap values are shown above the branches.

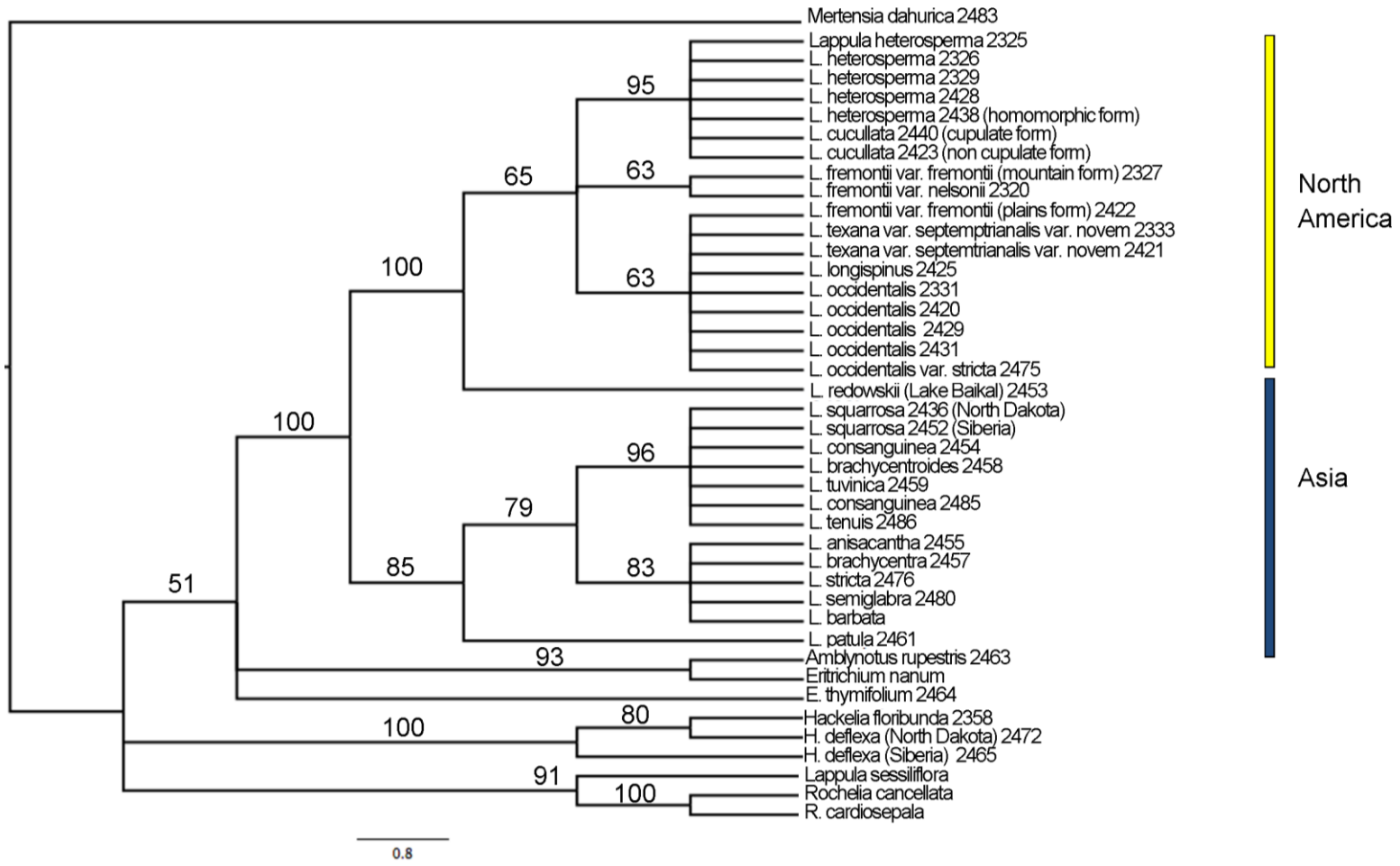

Figure 1.2 ITS parsimony consensus tree (SIC). In this analysis gaps were coded using simple indel coding. Parsimony bootstrap values are shown above the branches.

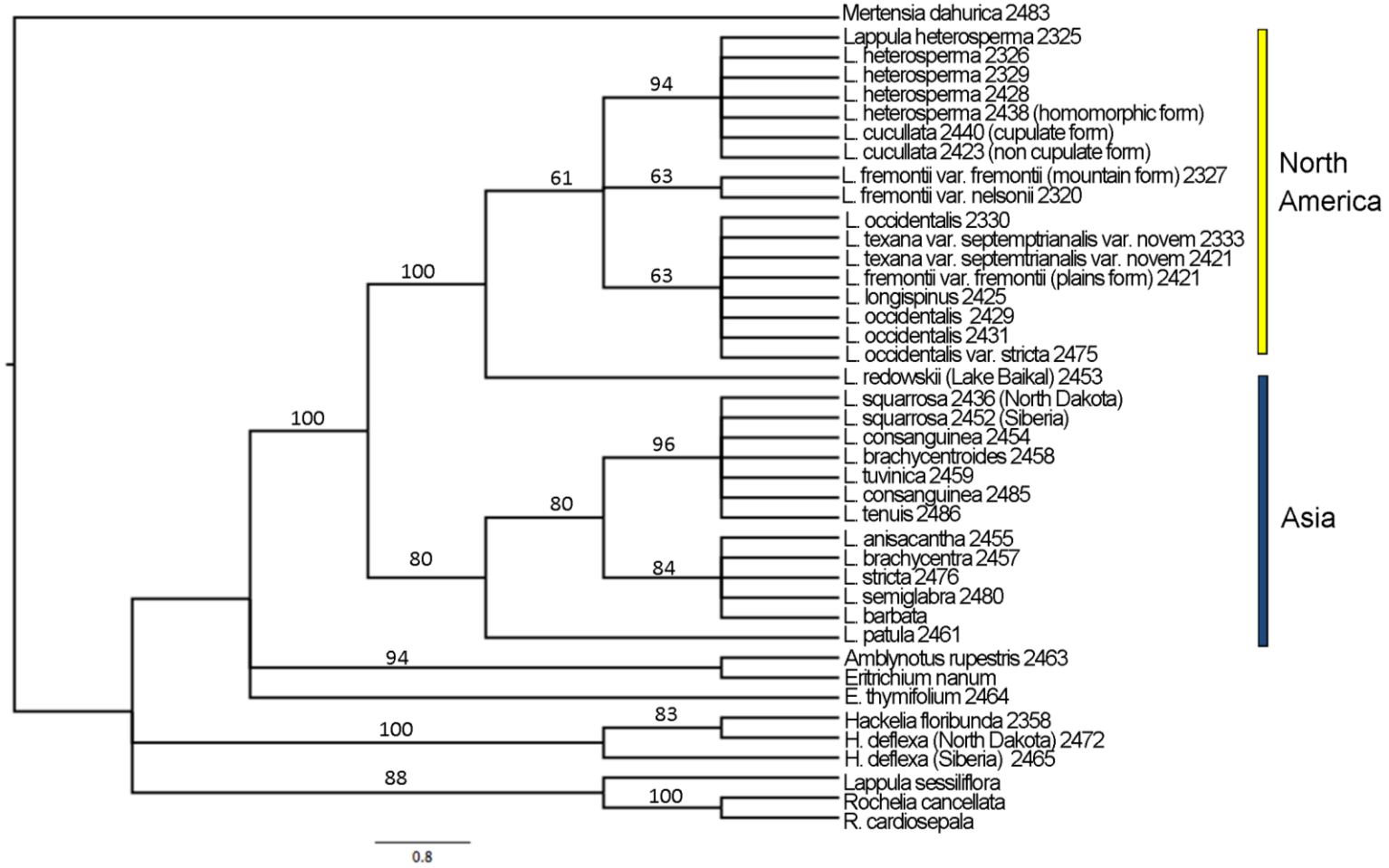

Figure 1.3 ITS strict parsimony consensus tree (MCIC). This tree was generated from data coded using modified complex indel coding.

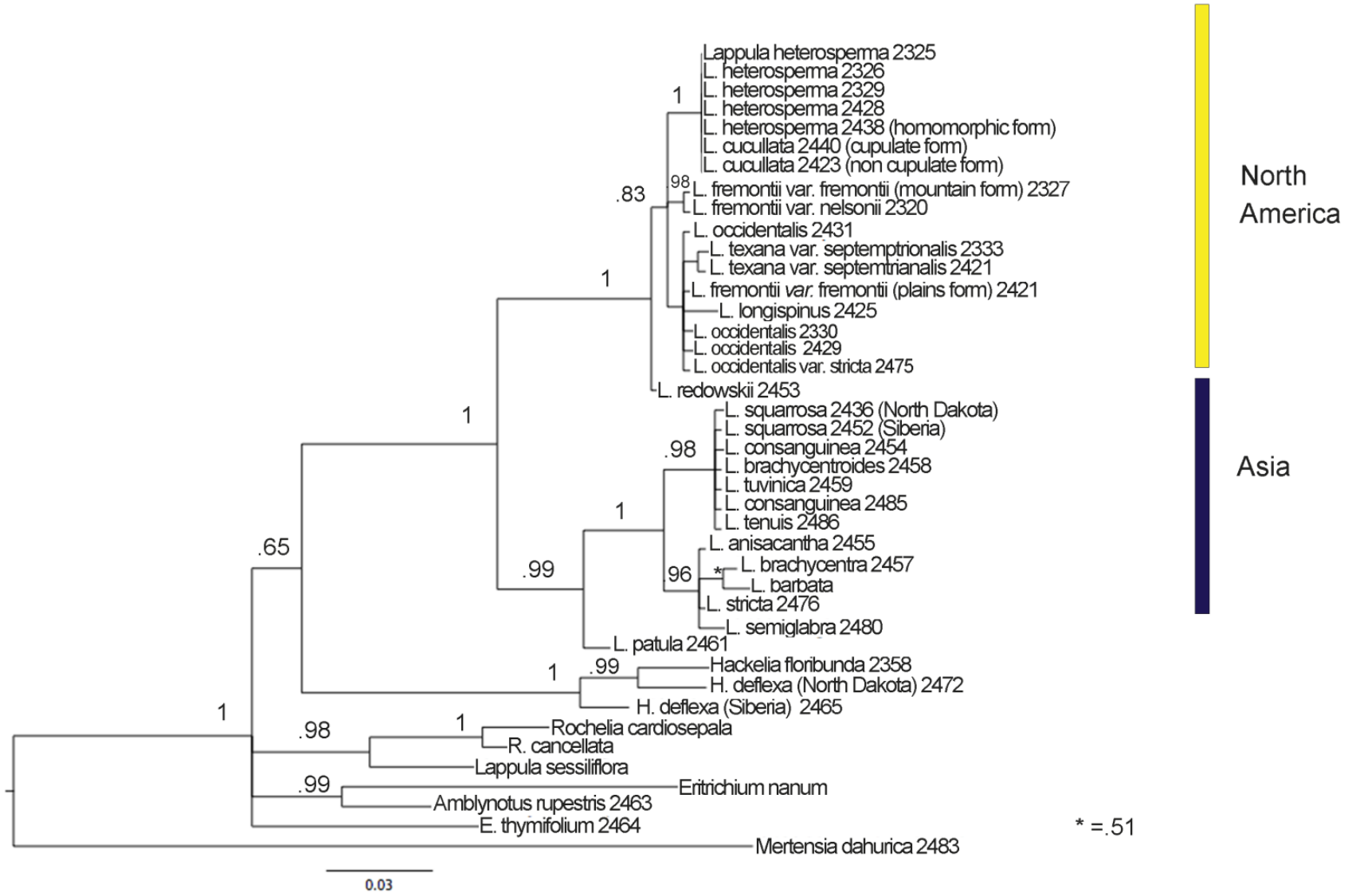

Figure 1.4 Bayesian ITS tree. Fifty percent majority rule tree from MCMC analysis of data. Bayesian posterior probability support values are shown above the branches. Branch marked with an asterisk has a support value of .51.

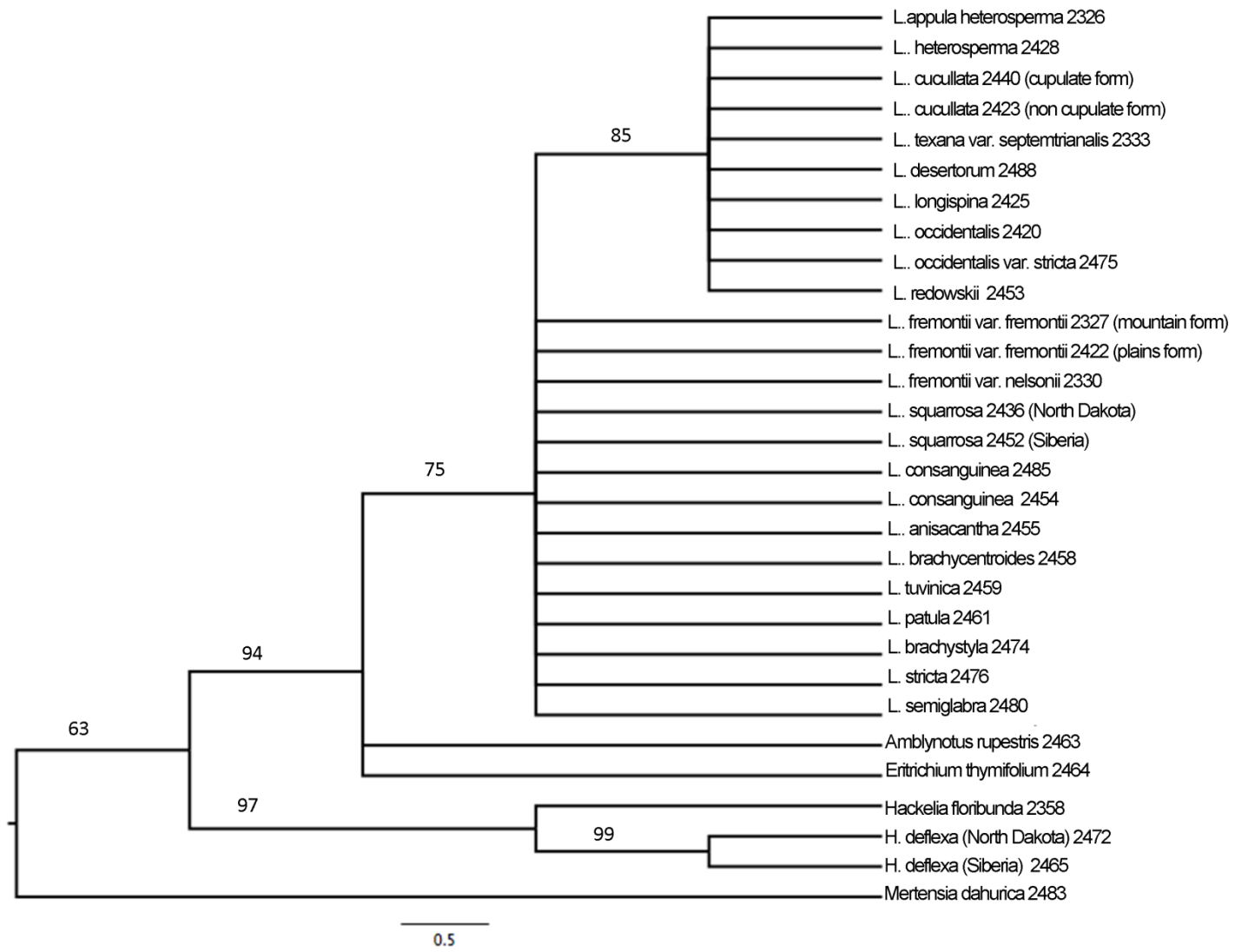

Figure 1.5 Chloroplast (CpDNA) parsimony strict consensus tree. Gaps are treated as missing data in this analysis.

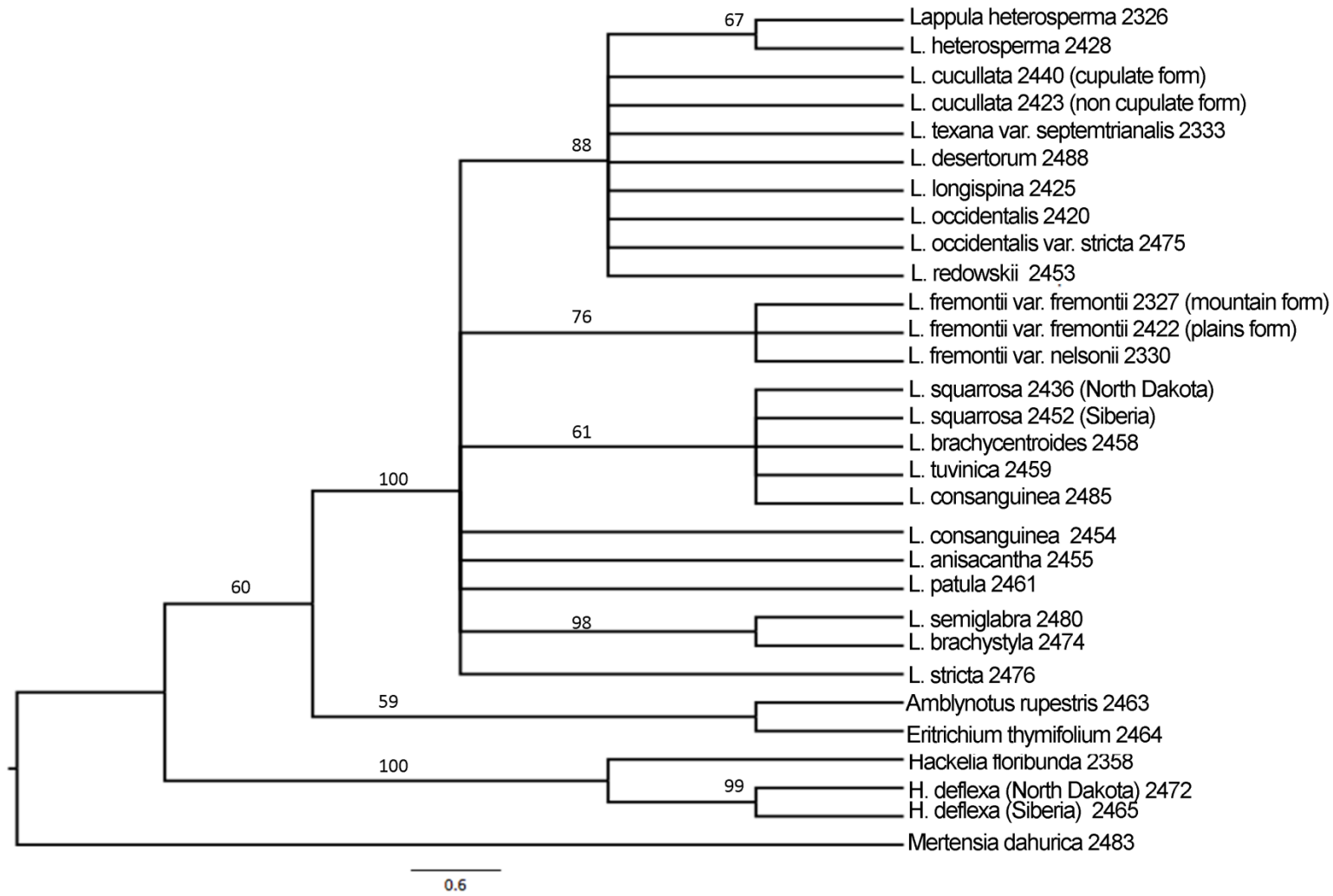

Figure 1.6. CpDNA parsimony strict consensus tree (SIC). Data in this analysis were coded using simple indel coding.

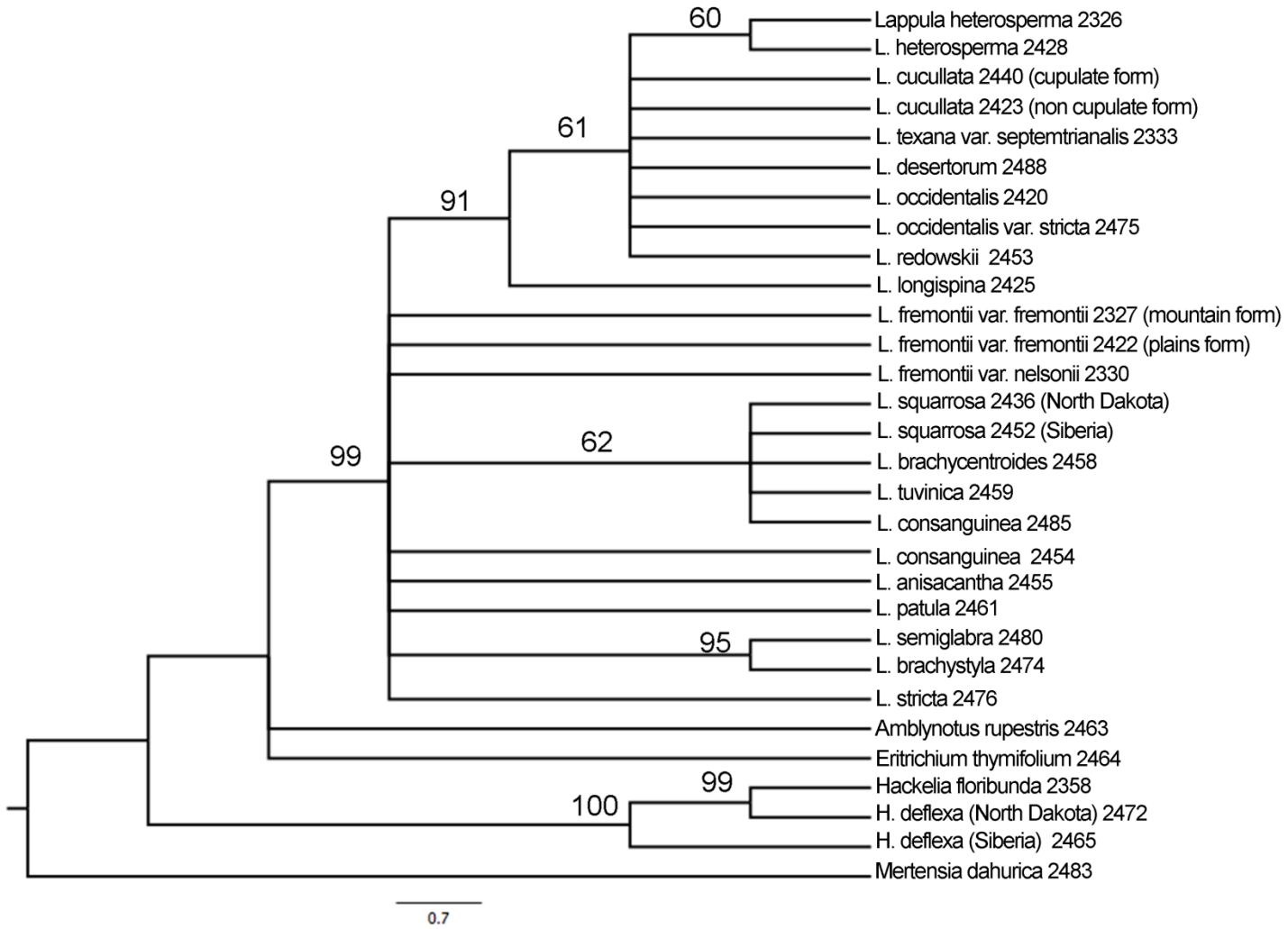

Figure 1.7 CpDNA strict parsimony consensus tree (MCIC). Data were in this analysis were coded using MCIC.

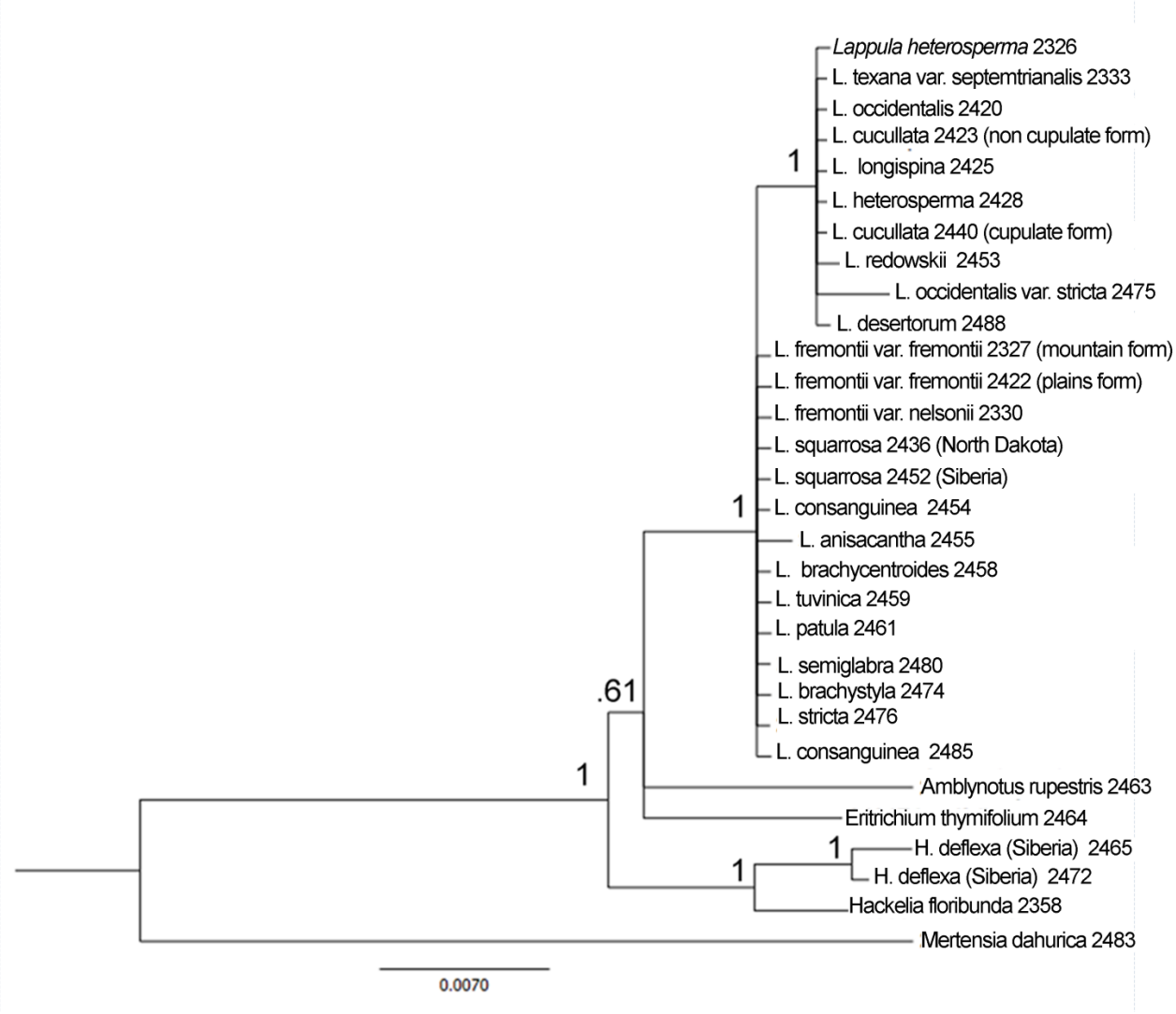

Figure 1.8 Bayesian CpDNA tree. Fifty percent majority rule tree generated from MCMC analysis of cpDNA data. Bayesian posterior probability values are shown above the branches.

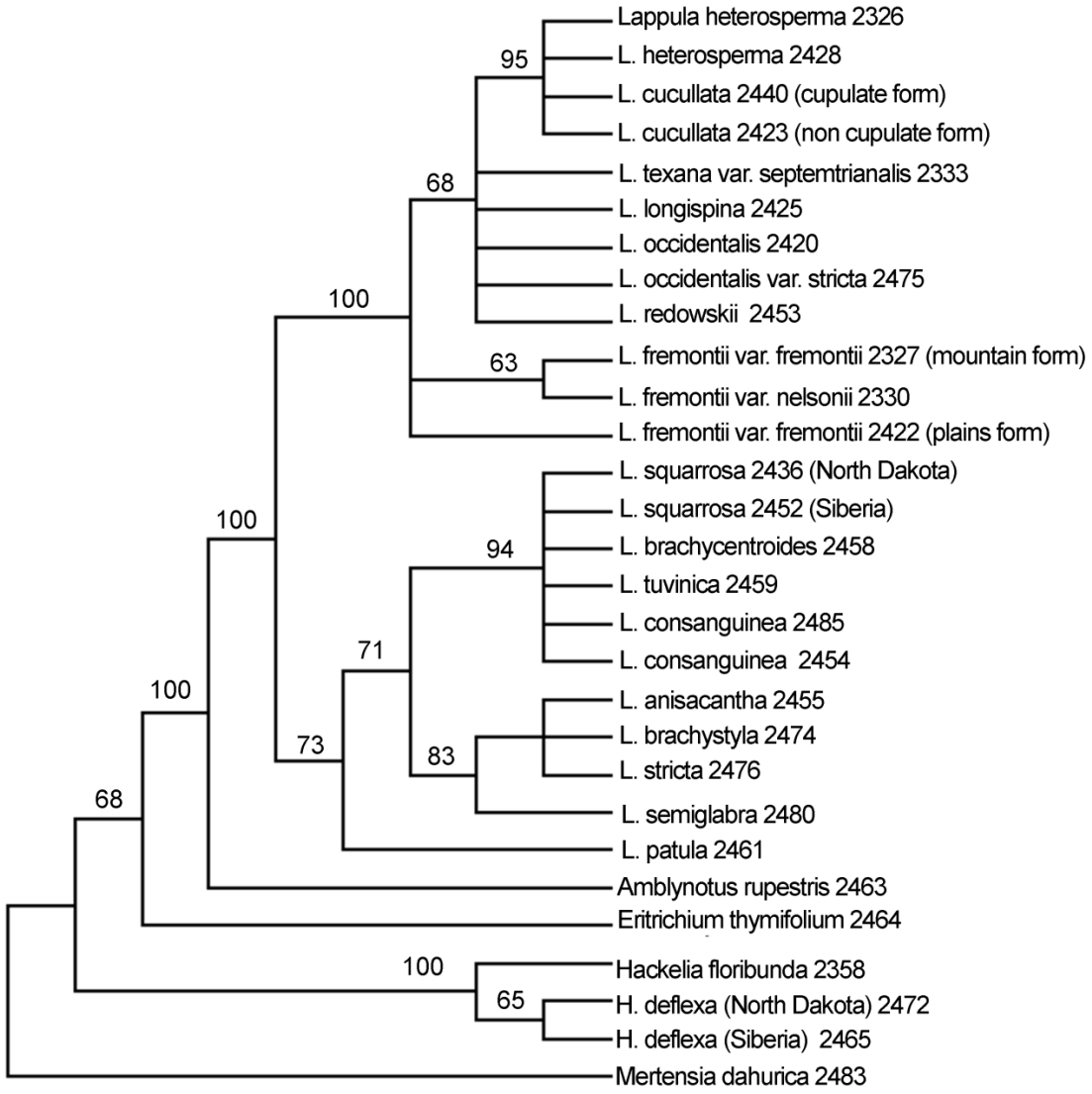

Figure 1.9 Combined dataset strict consensus tree. In this analysis gaps were treated as missing data.

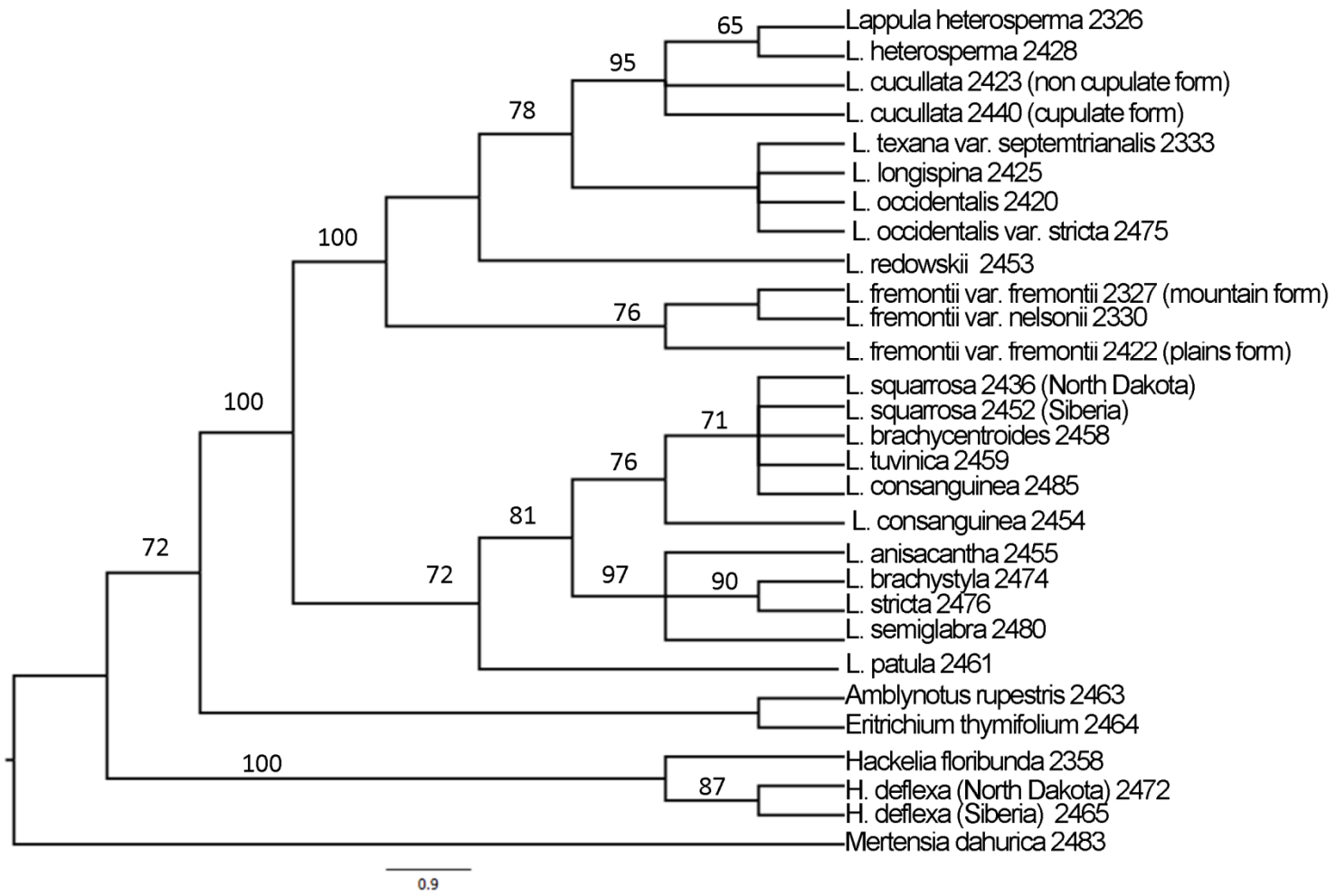

Figure 1.10 Combined dataset parsimony strict consensus tree (SIC). The data in this analysis were coded using simple indel coding

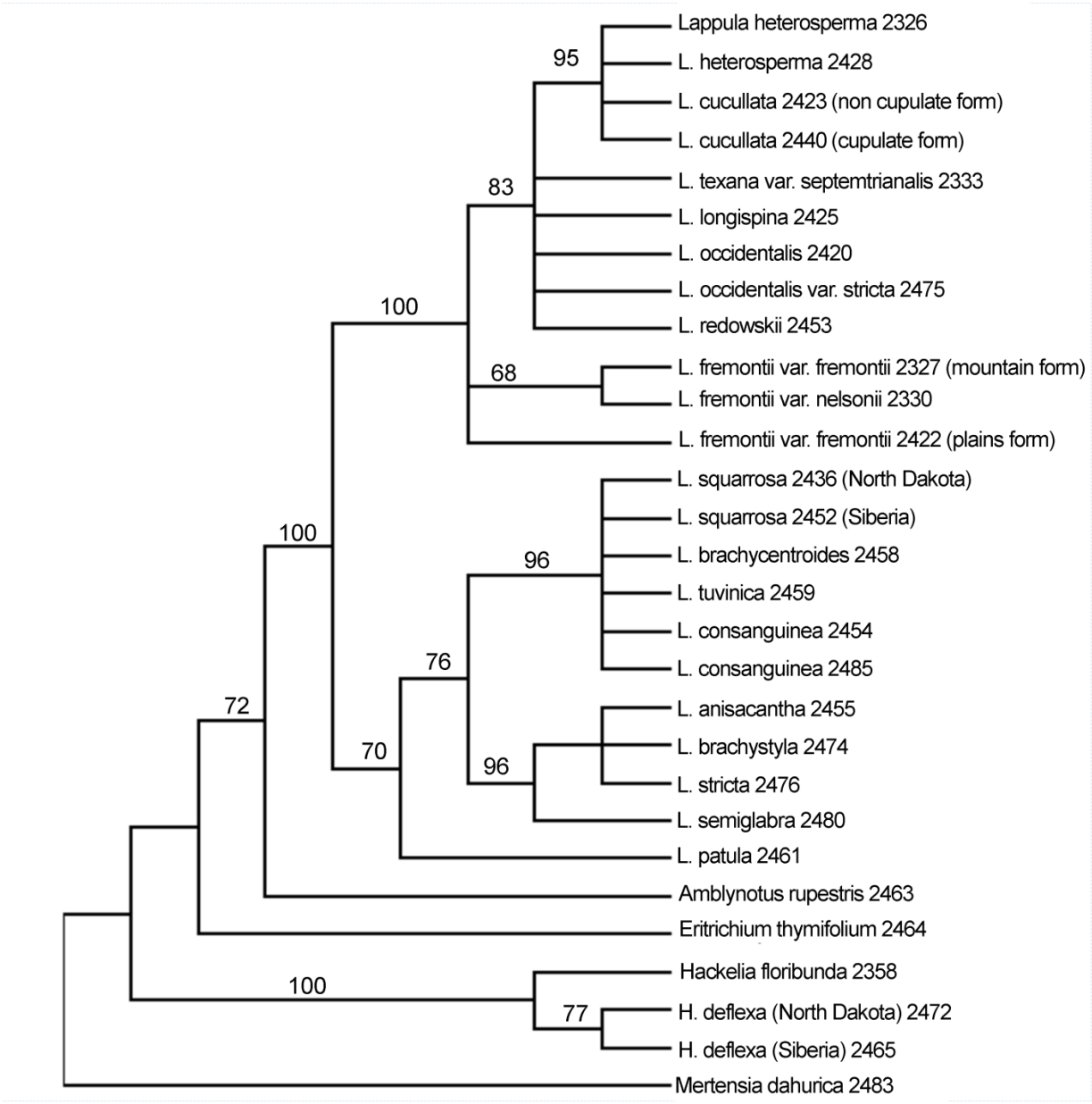

Figure 1.11 Combined parsimony strict consensus tree (MCIC). The data for this analysis were coded using modified complex indel coding.

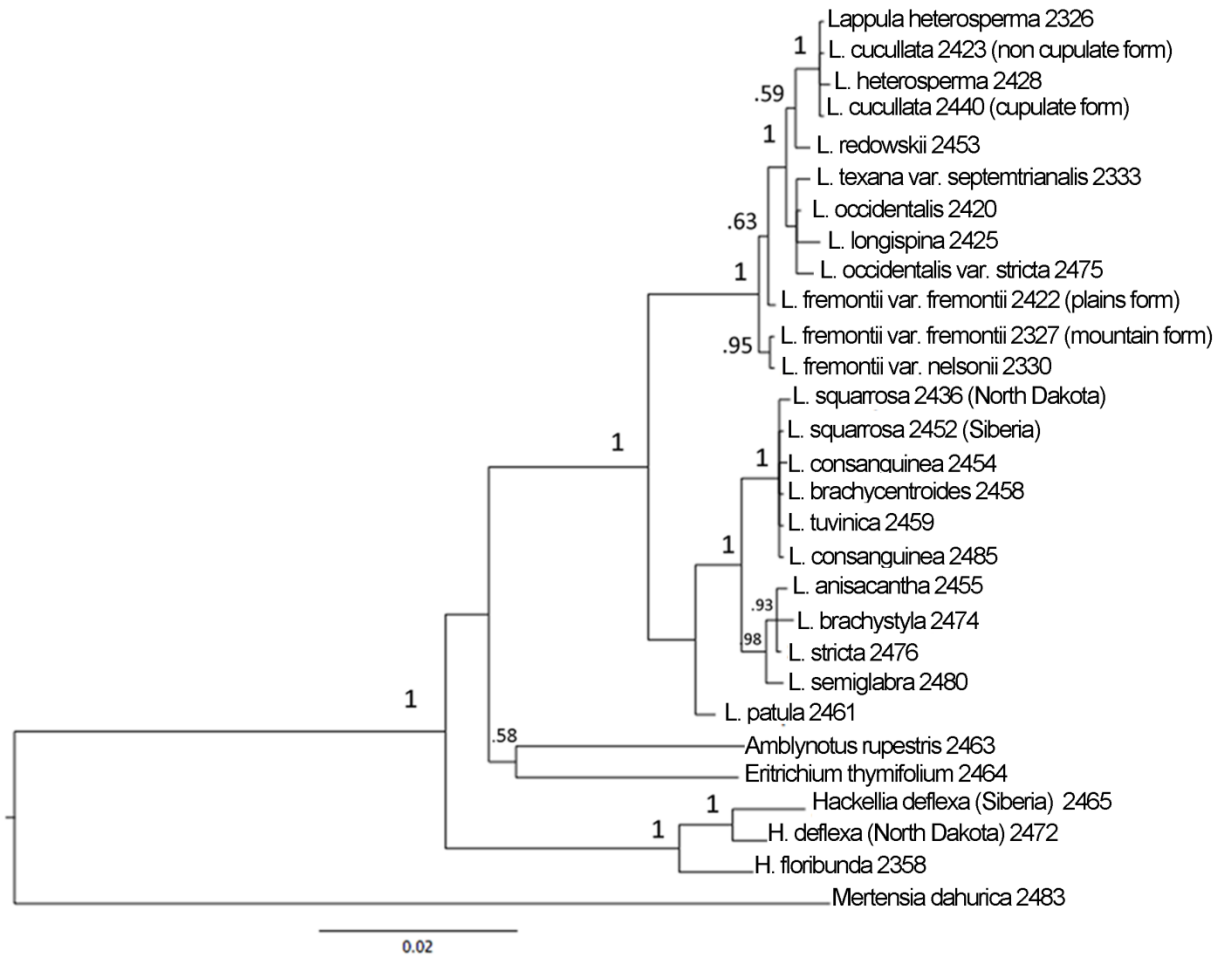

Figure 1.12 Combined Bayesian analysis. Fifty percent majority rule tree from MCIC analysis. Posterior probability values are shown above the branches.

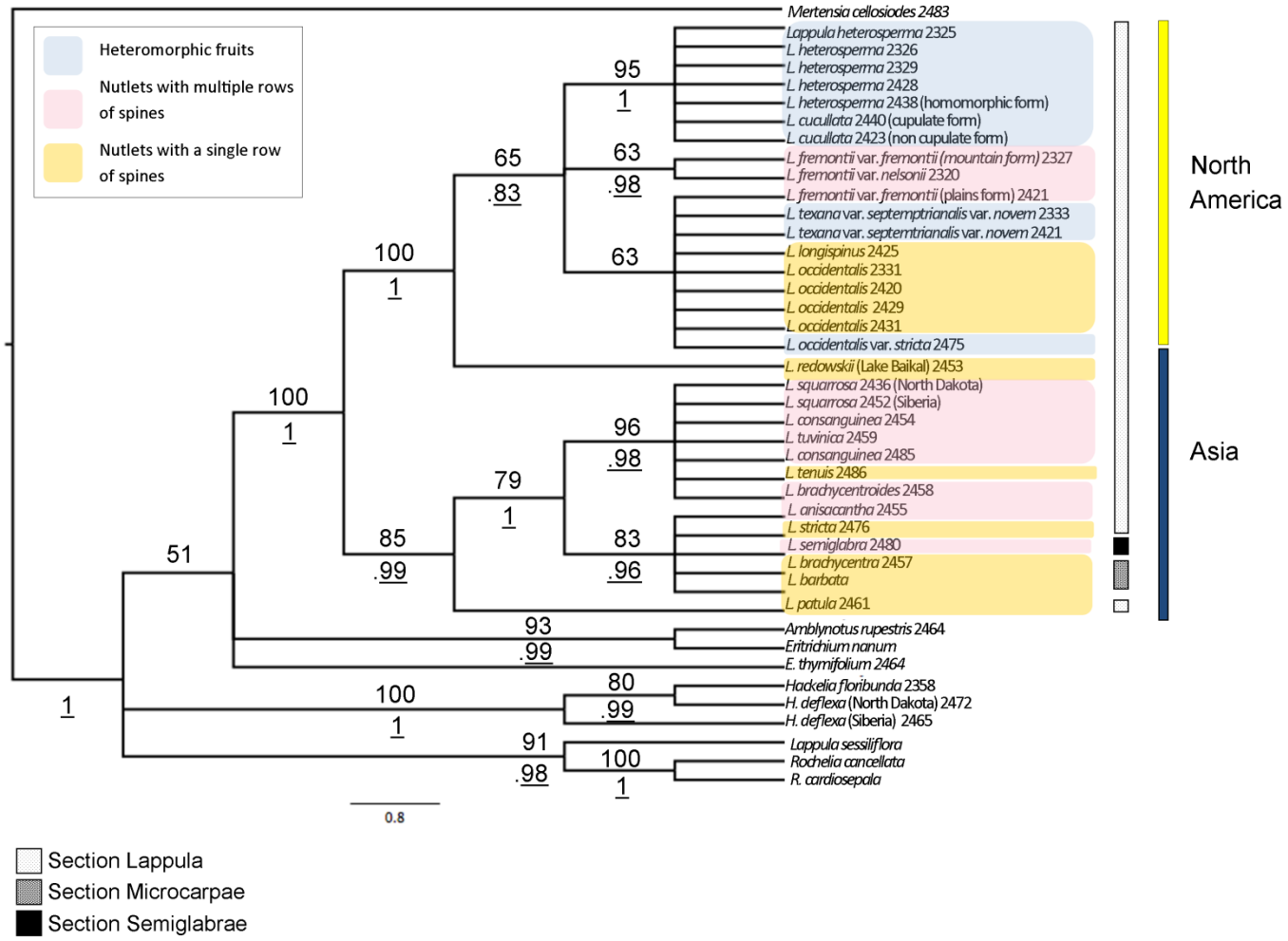

Figure 1.13. Overall ITS tree. Strict consensus tree from MP analysis where gaps where coded using SIC. Parsimony bootstrap support values are shown above the branches and Bayesian posterior probabilities below. The fruit morphology is indicated in color and sectional classification is indicated next to the tree (legends for both in figure).

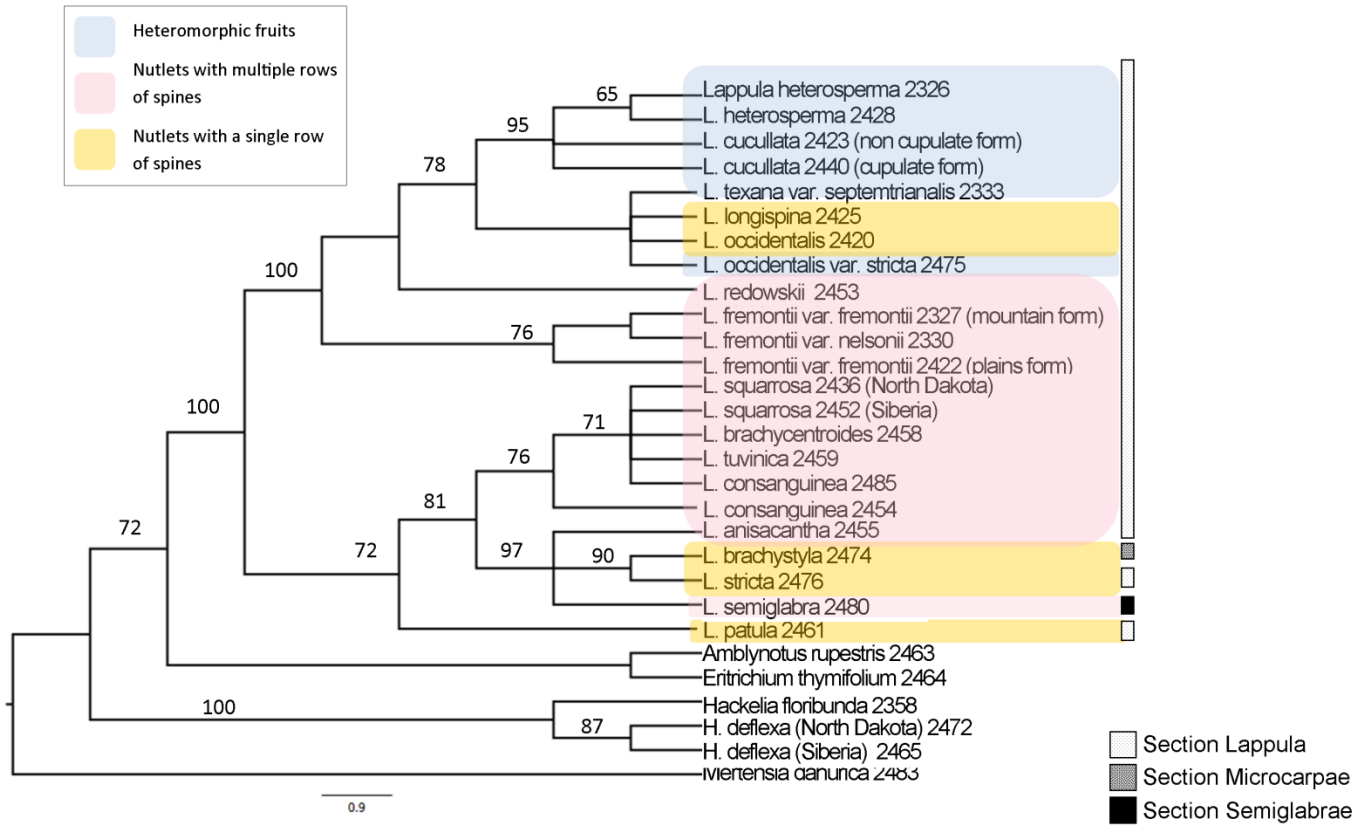

Figure 1.14 Strict consensus tree based on parsimony analysis of combined dataset (simple indel coding). Maximum parsimony bootstrap values are shown above the branches and Bayesian posterior probability values are underlined below. Fruit characters are highlighted on the tree, and sectional classification is indicated by bars next to the tree.

Discussion

The phylogenetic analyses are in general agreement across the DNA regions sampled and were little affected by various indel coding schemes. *Lappula* samples consistently formed a monophyletic group (with the exception of *L. sessiliflora*) Siberian *L. redowskii* consistently groups with the North American species. The trees illustrated in Figure 1.13 and Figure 1.14 illustrate general patterns of relationships for the ITS and combined datasets.

Lappula s. str. is strongly supported

In all analyses, *Lappula* s. str. formed a strongly supported clade. The Eurasian species of Section *Lappula*, series *Lappula* formed a monophyletic group, the remaining Eurasian and North American species sampled from that section did not. *Lappula patula* (Series Patula) was sister to all Eurasian *Lappula* samples except for *L. redowskii* and *L. sessiliflora* in all analyses. *Lappula anisacantha* (Series Anisacanthae) and *L. stricta* (Series Stricta) formed a clade with *L. brachycentra* (Section Microcarpae) and *L. semiglabra* (Section Macranthae). Though samples from herbarium specimens were taken from species representing each section (except the endemic Section Rupestres), extractions from these samples yielded highly fragmented DNA that did not amplify despite repeated attempts. Sampling in the genus is not complete enough to support or refute the current sub-generic classification in the genus overall. However, this study does not support the separation of *L. semiglabra* and *L. brachycentra* into sections outside of section *Lappula*, as these species are grouped in the phylogeny with species from Section *Lappula*.

Phylogenetic analyses consistently placed GenBank accession of the ITS region of *L. sessiliflora* as sister to *Rochelia* and not as part of the *Lappula* clade (Figure 1.13). The position of *L. sessiliflora* as sister to *Rochelia* is not surprising given the anomalous morphology of the

species. *Lappula sessiliflora* has fruits that are sessile on the stems and flowers that occur in sessile heads (Nasir 1989). Lists of synonyms show that it has been treated as *Heterocaryum divaricatum* Stocks ex Boiss., but more recent treatments include it in *Lappula* (Popov 1953; Nasir 1989; Ovczinnikova 2010). Popov placed the species in Series Anomalolappula reflecting his uncertainty regarding its classification. *L. sessiliflora* is similar to *Rochelia* in floral morphology, but in the later genus, only two ovules develop whereas in *L. sessiliflora* as in other species of *Lappula* four of the nutlets develop (Popov 1953). Cytological data would seem to suggest a closer relationship with *Lappula*. Whereas *Rochelia cardiosepala* has a reported diploid count of 2n=20, the mitotic count for *L. sessiliflora* was 2n=48, in line with other tetraploid *Lappula* species (Coppi et al. 2006).

There are other species currently placed in *Lappula* that may be misplaced. For example, Brand (1932) treated *L. spinocarpos* as part of a separate genus, *Sclerocaryopsis* Brand as did Hilger (1985) , who observed different fruit developmental patterns for this species relative to other species of *Lappula*. The fruiting gynobase in *L. spinocarpos* is taller than the fruit, and at maturity the fruits do not dehisce (Edmondson 1978; Federov 1999). While *L. occultata* and *L. sinaica* are more similar to *Lappula* in their nutlet morphology than the aforementioned species, the gynobase extends above the fruits as in *L. spinocarpos* (see treatments of these species in Popov 1953; Riedl 1967; Edmondson 1978; Nasir 1989; Zhu et al. 1995).

North American Lappula including L. redowskii is strongly supported

A clade that includes taxa from North America and Siberian *L. redowskii* is strongly supported in the analyses. Analyses of the ITS dataset support *L. redowskii* as sister to the North American species, but analyses of the plastid and combined datasets returned a clade that included *Lappula redowskii* nested within the North American taxa. The close relationship

between *L. redowskii*, a species from the Baikal region of Siberia, and the North American species supports the close relationship implicit in Ovczinnikova's classification of *L. occidentalis* and *L. redowskii* as part of Series Redowskianae; however, all the North American species regardless of morphology are in the same clade, rendering the sub-sectional classification artificial.

Relationships among the species in this clade were not well resolved, particularly based on analyses of the plastid data. However, some consistent topological patterns were observed. The two accessions of *L. heterosperma* along with the cupulate and non-cupulate form of *L. cucullata* grouped together in a strongly supported sub-clade. This clade is supported by a suite of morphological characters. *L. cucullata* tends produces heteromorphic plants with homomorphic or only weakly heteromorphic fruits, but *L. heterosperma* can produce either "variously" heteromorphic or monomorphic fruits (usually cupulate only). The species in this sub-clade generally produce fruiting branches that arise from the base of the plant (there are some variant forms of *L. heterosperma* that do not) and plants generally have a bright green cast. In contrast, specimens of *L. texana* tend to be canescent, with fruiting branches arising in the top half of the plant, and have white or blue flowers (small, white flowers are consistently observed in the northern variety of *L. texana*).

Without sampling *L. diploma* or *L. balchaschensis*, it is not possible to support or refute the hypothesized relationship of the North American heteromorphic species with those in Section *Omphalolappula* (Ovczinnikova 2006d). On the other hand, *L. heterosperma* and related species with connate marginal spines and heteromorphic fruits are derived within the strongly supported North American *Lappula* plus *L. redowskii* clade (though the position of *L. texana* is unresolved relative to *L. occidentalis* and other species with a single row of spines), lending support to the

assignment of the North American species to Section *Lappula* (Ovczinnikova personal communication 2010). Given the prevalence of heteromorphic and winged nutlets in species of *Lappula*, *Lepechiniella*, *Heterocaryum* and other species in Cynoglosseae s.l. it is possible that similarities between the Central Asian and North American species represents convergent adaptations to arid habitats. Further sampling of Central Asian species would be necessary to test this, but for now it is appropriate to maintain the North American species as part of Section *Lappula*, as this is supported by the phylogenetic data.

In all of our analyses *L. occidentalis* is part of a clade that includes North American species. The sample of *L. redowskii* from Lake Baikal is sister to this clade in the analysis of the ITS data, and part of it in all other analyses. Regardless of the taxonomic interpretation of *L. redowskii*, our data suggest a relationship between *L. occidentalis* and *L. redowskii* as circumscribed by Ovczinnikova (2005, 2006d). Morphological data point to the distinctiveness of *L. occidentalis*, and the phylogenetic data lend support to the taxonomic interpretation of *L. occidentalis* as a species distinct from *L. redowskii* (Ovczinnikova 2005). This interpretation is supported by micromorphology of the fruit ultrastructure (Ovczinnikova 2005) and by cytological data (Probatova et. al 2011, Probatova et al. 2012). Species with fruits that have a single row of spines resolved in various places throughout the phylogeny suggesting that morphological character is not indicative of relationship (Figure 1.13, Figure 1.14). Observations in the North American species suggest that while the number of rows of nutlet marginal spines is likely not a useful character by itself for identification, it can be useful in combination with other characters.

Introduced L. squarrosa is Eurasian and not closely related to L. fremontii

The North American accession of *L. squarrosa* was not part of the North American plus *L. redowskii* clade. Rather, both accessions were part of a clade of Eurasian species. These results support the hypothesis that *L. squarrosa* is a Eurasian species introduced to North America.

The phylogenetic data did not support hypotheses of a close relationship between *L. fremontii* and *L. squarrosa* or *L. semiglabra.* Likewise *L. fremontii* accessions did not resolve as sister *to L. anisacantha*. These were unexpected results as *L. fremontii* and *L. anisacantha* are remarkably similar in terms of habit, flowers, and nutlet morphology.

In this study *L. cenchrusoides* A. Nelson and *L .erecta* A. Nelson (in part) were treated as synonymous with *L. fremontii* (Torr) Greene var. *fremontii* (see Chapter 2 for discussion). *Lappula fremontii* var. *nelsonii* was described as a new variety in Chapter 2. A close relationship between the biennial/winter annual Rocky Mountain form of *L. fremontii* var. *fremontii* and the morphologically distinct *L. fremontii* var. *nelsonii* is strongly supported by the ITS data, while the annual form of *L. fremontii* var. *fremontii* is in the unresolved polytomy with *L. occidentalis* and other species with a single row of spines (Figure 1. 13). This relationship was also recovered in the combined analysis.

Hackelia is not supported as part of Lappula

Hackelia deflexa has been treated as part of *Lappula* (see treatments by Chater 1972, and Nelson and Macbride 1916) though the North American *Hackelia* species have been treated as a distinct genus since Johnston resurrected the genus (1923). Like the majority of *Lappula* species, some species of *Hackelia* have blue myosotis-like corollas and produce four parted spiny fruits, though the fruit walls in the latter tend to be thinner (Popov, 1953). Some authors

have maintained that there is little difference between the two genera (Carr 1973; Cronquist; 1984) while others have suggested a closer relationship between *Hackelia* and *Eritrichium* (Johnston 1923; Ovczinnikova 2007, 2009; Popov 1953). Morphological distinctions between the two genera were made by (Johnston 1923) and summarized by Gentry and Carr (1976).

The phylogenetic data lend support to maintaining *Lappula* and *Hackelia* as separate genera; however they do not speak to higher level relationships among *Lappula*, *Hackelia*, and *Eritrichium*. For example, *Eritrichium thymifolium*, as treated in the Flora of China (Zhu et al 1995), has also been treated as *H. thymifolia* (Johnston 1935; Ovczinnikova 2007). It is not supported here as part of *Hackelia*. *Amblynotus rupestris* was recently inferred to be nested within a larger clade of *Eritrichium* (Nazaire and Hufford 2012), a finding consistent with morphological studies that showed similarities between it and certain *Eritrichium* species (Ovczinnikova personal communication).

Conclusions

Despite the presence of morphologically anomalous taxa, such as *L. sessiliflora* and *L. spinocarpos*, there is strong support for a monophyletic *Lappula* s.str. and for a close relationship between the North American *Lappula* and the Eurasian members of Section *Lappula*, to which they are most similar in terms of morphology. Sampling of the genus throughout Central Asia and the Middle Eastern regions will provide insight into the relationships between morphologically anomalous species such as *L. sessiliflora*, *L. spinocarpos*, and the more northerly distributed *Lappula* s.str. species.

This study supports the presence of a distinct lineage that includes the North American species and Asian *L. redowskii*. Phylogenetic study did not recover evidence of other introduced Asian species besides *L. squarrosa.*

Here we conclude that *Lappula*, is the strict sense, is monophyletic, but that taxonomic adjustments will be likely be necessary as sampling of sections *Sclerocaryum* (the section that includes *L. spinocarpos*), and *Sinaicae* M. Pop.(the section that includes *L. occultata*) may suggest closer relationships with other members of Cynoglosseae s.l. Our results reveal potential problems within the current circumscription of *Lappula*, however without broader sampling within *Lappula* and its hypothesized relatives, we do recommend any taxonomic changes at the generic level, rather we suggest an integrative approach to future classification in the genus that includes additional molecular data, and draws from the existing morphological (including micromorphology), developmental, and cytological work.

This phylogenetic study, the first to include sampling of both Eurasian and North American taxa, revealed a close relationship between species from North America, and *L. redowskii*, a Siberian species. This lineage, while not as speciose in North America as the genus is overall in Asia, is diverse in terms of morphology and habitat, occurring throughout western North America in grasslands, deserts, intermountain basins and Rocky Mountain meadows. Rather than a series of introductions from Asia, it appears that diversification has occurred in western North American, a phylogenetic hypothesis that opens door for further study into evolutionary relationships, biogeography, and ecology.

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Chapter 2 - A taxonomic revision of *Lappula* (Moench) in North America

Introduction

The genus *Lappula* includes approximately 70 species of annual, biennial rarely perennial herbs worldwide. Many species grow in semiarid grasslands, steppes and deserts. *Lappula* has much of its diversity in the Siberian and Irano-Turaniean provinces of the Holarctic kingdom (following Takhtajan 1986) where up to 62 species were recognized in the most recent treatment of the Eurasian species (Ovczinnikova 2009). The genus is less diverse in North America, where approximately ten species are estimated to occur north of Mexico. There are also few outlying species in temperate Africa, South America and Australia (Popov 1953; Edmondson 1978; Ovczinnikova 2009).

Two species in the genus are considered invasive weeds. *Lappula squarrosa* is introduced from the steppes of Asia and naturalized throughout North America and Europe with a widespread northern distribution. *Lappula patula* is presumed to have spread with human activity throughout Europe and into northern Africa (Popov 1953). There are also a number of narrow endemics in the genus, especially in parts of Kazakhstan and parts of China (Popov 1953; Ovczinnikova 2010).

Lappula is a member of the large, cosmopolitan family Boraginaceae. Historically, the genus has been considered part of Eritrichieae, a tribe characterized by corollas with a short tube, a distinct limb with rounded-obtuse floral lobes, and a pyramidal to subulate gynobase (Popov 1953). However, as early as 1884, Gray criticized Bentham and Hooker's separation of Eritrichieae from Cynoglossaeae [treated as sub-tribes of tribe Boraginoideae in (Bentham and Hooker 1876)], noting that there were too many overlapping characters between the genera of these two groups to separate them (Gray, 1884). Phylogenetic investigations into tribal classification in Boraginaceae using data from nuclear and chloroplast DNA support the

recognition of a broader Cynoglosseae including Eritrichieae (Långström and Chase 2002; Weigend 2010; Cohen and Davis 2012; Nazaire and Hufford 2012).

Relationships between *Lappula* and other genera have been proposed based on morphological similarities between the fruits. *Lepechiniella* Popov and *Hackelia* Opiz. have each been suggested as close relatives of *Lappula*. *Lepechiniella,* a narrowly distributed Central Asian genus, was suggested to be the sister genus to *Lappula* (Popov, 1953) and was included with it in the sub-tribe Echinosperminae (Ovczinnikova 2007). Several species from the western United States, later treated by Johnston (1923) as *Hackelia,* were classified informally as a non-ranked group of perennials and biennials in the genus *Lappula* (Nelson and Macbride 1916). In distinguishing *Hackelia*, Johnston reasoned the two genera were clearly morphologically distinct, basing this separation upon inferences from a number characters including gynobase morphology, shape of the fruit attachment scar, life history traits and vegetative characters (Johnston 1923). Furthermore, he asserted, *Hackelia* shared more characteristics with *Eritrichium*, in particular section Coloboma D.C. (Johnston 1923). Though *H. deflexa* is occasionally treated as part of *Lappula*, e.g. Flora Europea (Chater, 1972), *Lappula* as treated here excludes *Hackelia*.

The genus *Lappula* has been variously divided into sub-sections. Popov recognized a broad section *Lappula* DC. with a separate section Sclerocaryum D.C (Popov, 1953). More recently, Ovczinnikova recognized eight sections, primarily on the basis of gynobase, nutlet shape, and corolla height, elevating to section groups treated by Popov as series (2006). The three North American species Ovczinnikova surveyed in her monograph were placed into two sections. *Lappula occidentalis* (S. Watson) Greene was placed with *L. redowskii* (Hornem.) Greene in Section *Lappula*, Series Redowskianae Ovczinnkova. *L. texana* (Scheele) Britton and

L. cupulata (Gray) Rydberg (here as *L. occidentalis* var. *stricta*) were treated in Section *Omphalolappula* (Brand) Ovczinnikova, Series *Omphalolappula* (Brand) Ovczinnikova along with Central Asian and Australian species. The phylogenic hypotheses developed in Chapter 1 do not resolve interspecific relationships within the genus and do not support separating the North America species into series, though they are most closely related to species currently classified into Section *Lappula* (Ovczinnikova 2007, 2009).

Morphology

The morphological terms used in this treatment of the genus follow terminology used in Edmonston (1978), Popov (1953), and Ovczinnikova (2006), and terms used for fruit morphology were chosen to be in line with recent treatments of North American Boraginaceae genera (Ronald Kelly, personal communication). Edmonson (1978) discusses morphological terminology specific to Boraginaceae and gives examples from several genera to illustrate commonly used terms and continues to be useful resource.

Lappula includes annual, biennial, and occasionally perennial herbs (Asia) with or without a basal rosette of leaves and one to many stems. The basal leaves when present frequently wither once the plant produces fruits. Hairs are simple and stiff. Plant vestiture varies from sparse hairy to gray canescent. Flowering branches typically arise from a single main stem (or several stems from crown of basal leaves), branching in the upper half or third of the plant. Another common growth form, typically found in arid habitats, produces several stems highly branched from the near their bases, with long flowering branches. Sepals are free to the base and become accresscent in fruit, either widely spreading or clasping at maturity. Corollas are generally funnel shaped (infundibular) with limbs spreading 2—7 mm wide (Popov 1953; Ovczinnikova 2009). Most species have flowers in shades of blue, some have white or cream.

The fruit in *Lappula* is a schizocarp of four mericarps (also called nutlets). Fruits are important for identification of species (Edmonson 1978). The mericarps are ovate to pear-shaped and have clearly defined abaxial (outward facing) surface and an angled adaxial surface (inward facing). The abaxial surface of the mericarp is divided into a margin and a disk, ornamented with a row of spines [sometimes referred to in the literature as "glochids", e.g. "Edmonson", (1978), or "prickles", e.g. Popov (1953)] which can be free or variously connate into a dentate wing. The

spines often have anchorlike projections at their tips. In a few species marginal spines are absent or reduced to short turbercles, in others a second or third row of spines is present directly "behind" the primary row, on the sides of the nutlet. The abaxial disk is muricate, tuberculate or smooth, convex or flat, sometimes a line of short spines, ("tubercles" in Popov (1953)), or a raised crest ("keel" in Popov (1953) is present along the median line. The adaxial (inward facing) mericarp surface has a keel, formed by a narrowing of the nutlet in its upper half or third.

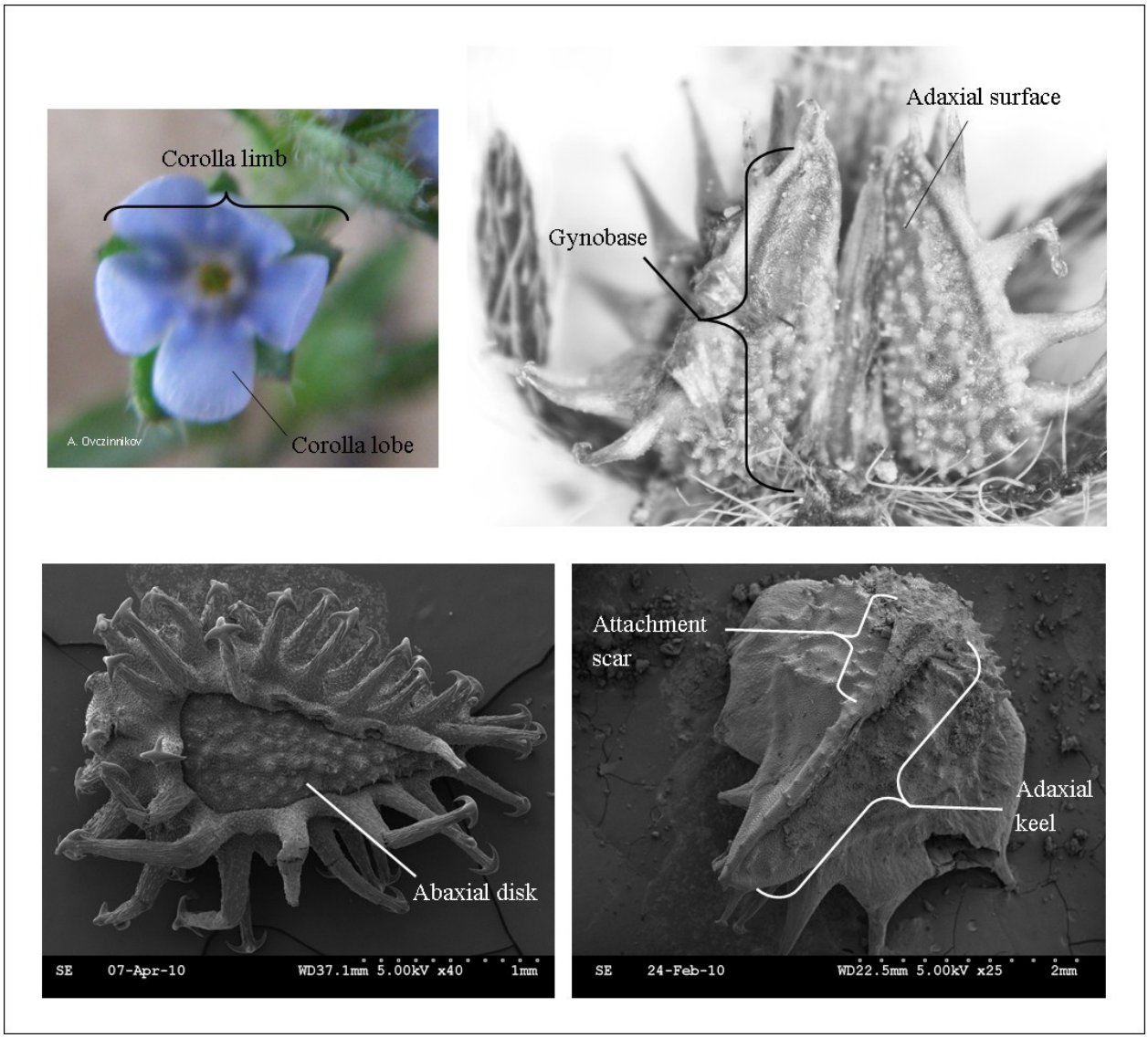


Figure 2.1. Image of flower and fruit morphology illustrating terms used throughout the taxonomonic treatment.

Following dehiscence, a linear or teardrop shaped scar (cicatrice) remains along the adaxial keel of the nutlet. The gynobase is formed from the receptacle (Edmonson 1978). In the North American species, the gynobase is triangular to subulate, gradually tapering to the style which is generally persistent in fruit. There is not a strong demarcation line between the style and gynobase in fruit, but in the literature the thin projection near the apex of the gynobase among the nutlets is referred to as the style for purposes of discussing its relative position. In some Asian species the style and part of the gynobase is visible above the fruit as what Popov (1953) describes as "a thick, more or less angular mucro", but this does not occur in the North American species. Mericarps can be identical, or variously heteromorphic, having differences in surface sculpturing or texture, degree of connation of spines, and in persistence of attachment to gynobase. The general fruit and flower morphology is illustrated in **Error! Not a valid bookmark self-reference.**.

Heteromorphic fruit morphology has been recognized for species in the Eurasian flora (Ovczinnikova 2006a; Popov 1953; Zhu et al 1994). For the North American species heteromericarpy was observed, but different fruit types in a single plant or populations was not reported, and this may have complicated species identification and classification. Based on observations of herbarium species and field collections of the author, a general classification of fruit types in the North American *Lappula* is presented in Table 2.1 (below) that summarizes which species (as treated below) produce heteromericarpic fruits, and which species are thought to be heterocarpic (rather than each fruit type representing a separate species)

.

Table 2.1 Variation in *Lappula* fruits. Species vary in whether they have highly variable fruits or not. They can be classified into four groups. Some species are so variable that they appear in more than one category. The asterisk (*) indicates that the species only occasionally produces plants with homomorphic nutlets in a population with either inflated or uninflated margins and free spines.

	One fruit type (Fruits homomorphic)	**More than one fruit type (Fruits heteromorphic)**
One nutlet type nutlets: homomorphic	fruits: homomorphic nutlets: homomorphic Examples: *L.coronata, L. fremontii*, *L. occidentalis* var. *occidentalis*, *L. longispina*, *L. squarrosa*	fruits: heteromorphic nutlets: homomorphic Examples: *L. cucullata, L. occidentalis* var. *stricta*
More than one nutlet type: heteromericarpic	fruits: homomorphic nutlets: heteromericarpic *L. cucullata, L. texana,* L. heterosperma*, L.desertorum* (weakly heteromorphic)	fruits: heteromorphic nutlets: heteromericarpic Examples: *L. cucullata, L. occidentalis* var. *stricta*

Cytology

Chromosomes in *Lappula* are extremely small, measurements of less than 2 micrometers was reported for a Spanish population (Luque 1992). Small chromosomes (<10 micrometers) are apparently typical for a number of genera in Eritrichieae (Britton 1951; Luque 1992). Numbers reported from North America to date are 2x=48 for *L. squarrosa* (as *L. echinata* (Mulligan 1984)] *L. occidentalis* (Löve and Löve 1975). Recent counts reported from Siberia for two specimens of *L. redowskii* were 2n=24 (Probatova et al. 2011, 2012). The same numbers were reported for *L. anisacantha* (morphologically similar to *L. fremontii*) and *L. consanguinea* (Probatova 2011, 2012). Mitotic counts for *Lappula fremontii* from root tips grown from seeds of Rolfsmeier collections 401I , and 401L, two plants from the same population, were 2n=48 (Figure 2.2).

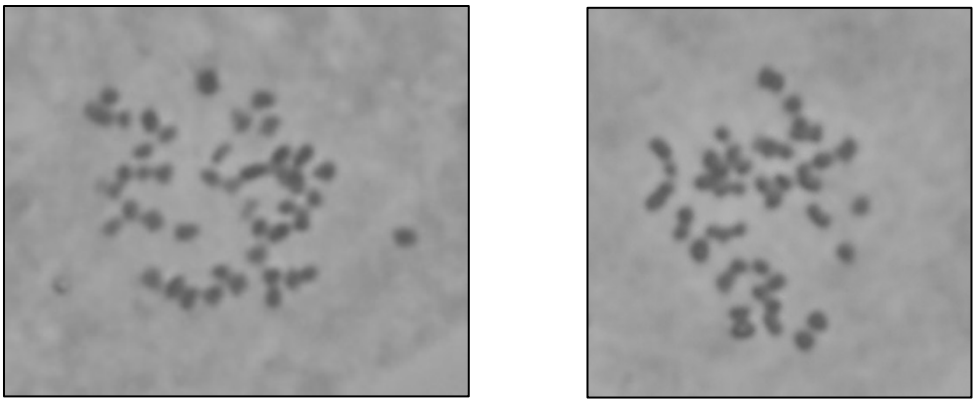


Figure 2.2. Mitotic chromosomes from root squashes of *Lappula fremontii* (Torr.) Greene 2n-48, seeds germinated from SJR 401I (left) and SJR401L (right)

Taxonomic background

The genus *Lappula* has a complicated taxonomic history in North America. Over 26 combinations were published based on western North American material of *Lappula* between the

mid-19th and early 20th centuries (IPNI, 2012). The oldest named North American species, originally described under the broadly circumscribed genus *Echinospermum*, were *E. texanum* Scheele (Scheele 1852 [=*L. texana* (Scheele) Britton]), *E. fremontii* Torr. (Torrey 1860), *E. redowskii* (Hornem.) Lehm. var. *occidentalis* S. Watson (Watson 1871) and *E. redowskii* (Hornem.) Lehm. var. *strictum* S. Watson (Watson 1871). Greene, addressing priorities in generic nomenclature determined the genus name *Lappula* had priority over *Echinospermum* (Greene 1899).

Botanists focused on studying western North American species including A. Nelson, E. L. Greene, and P. A. Rydberg, described the majority of *Lappula* species from the Rocky Mountains and the intermountain basins. Attempts were made early in the twentieth century to more clearly circumscribe the North American taxa and to clarify the nomenclature. Nelson and Macbride's revision recognized seven North American species (Nelson and Macbride 1916). Their concept included *L. cenchrusoides* A. Nelson as a species endemic to southeastern Wyoming, and included *L. erecta* A Nelson in synonymy under *L. fremontii* (Torr) Greene (Table 2.2). They recognized two groups of taxa with cupulate margins. The ones having a narrow wing they placed as varieties under *L. cupulata* (Gray) Rydb. (applied to Gray's *E. occidentalis* (S. Watson) var. *cupulatum* Gray (a superfluous replacement name for *Echinospermum redowskii* var. *strictum*, as the epithet "*strictum*" is an available name at the varietal level, see discussion under the section "Dubious names and Excluded Species"). The ones with inflated margins were considered varieties of *L. texana*. *Lappula occidentalis* and *L. patula* were considered varieties of *L. redowskii*.

Johnston's (1924) study on the North American species recognized ten native and two introduced taxa (*L. echinata* Gilib. = *L. squarrosa* (Retz). Dumort. and *L. redowskii* (Hornem.)

Greene var. *patula* (Lehm.) A. Nelson & J. F. Macbr.). Johnston's concept of *L. texana* included everything with connate spines, regardless of the degree of nutlet inflation. However, he later revised his taxonomy of the species with heteromorphic fruits (Johnston 1932). Johnston had observed that some taxa had fruits with an obese or inflated nutlet margin from which the spines arose and that others had a narrow wing that appeared to be derived from basal fusion of the spines. He determined that specimens with connate spines forming a thin wing should referred to *L. redowskii* (S. Watson) Greene var. *desertorum* (Greene) I.M. Johnst. (equivalent in part to Nelson and Macbride's (1916) concept of *L. cupulata*), and that those with an inflated nutlet margin with short spines perched on top should be referred *L. texana* (Johnston I. M., 1932). Johnston put the varieties of L. texana that he had recognized in his 1924 treatment into synonymy under these two names (Johnston 1932).

Brand's monograph placed the New World taxa in the context of Eurasian diversity (Brand 1931) though he considered much of the variation he observed to be "monstrosities" or varieties of Eurasian taxa. Ovczinnikova's monograph of *Lappula* considered only three North American species (Ovczinnikova 2007) and did not attempt to revise the North American taxonomy (Ovczinnikova, personal communication).

While the work of Nelson and Macrbride (1916) and Johnston (1924, 1932) did much to clarify the nomenclature and concepts in the genus, there were multiple problems. One was that Nelson and Macbride did not address some of Greene's name in synonomy. The other was they did not follow what is now accepted practice regarding nomenclatural priority (Nelson and Macbride 1916). Neither Johnston nor Nelson and Macbride had clear concepts for some of Greene's taxa, indicated in Johnston's work as question marks after names when he placed them in synonomy (Johnston, 1924). Greene's names that were based upon collections that were

widely distributed were not problematic, but those from his herbarium may not have been studied by Nelson and Macbride. What appears to be Johnston's handwriting was observed on the type specimen of *L. desertorum* from (E.L. Greene s.n. 16 July 1896, ND-G 42397), but there is no date or other notes to indicate when he studied this specimen.

A morphological species concept was used to delineate species for this treatment. When available, information from geography and ecology was included as a source of secondary data. The species concepts followed here are narrower than those of Johnston and in some cases a different suite of characters was used to distinguish among them. The primary reason for reexamining characters was that keys from both North American revisions often led to specimens of the same species keying to different species because of the nature of variation. Literature review of treatments from Asia suggested characters that had formerly not been addressed (at least in published treatments) for the North American species. The arrangement of species recognized here is alphabetical by species and then by variety. Throughout the text thee are references to specimens collected by the author. These are referenced by the initials "SJR" followed by the collector number. These specimens are deposited at the Kansas State University Herbarium (KSC) unless indicated otherwise.

Table 2. Summary of synonymy in taxonomic treatments of North American *Lappula* species. The taxon names highlighted in bold were accepted by the author.

Nelson and Macbride 1916	Johnston 1924	Brand 1931
***L. echinata* Gilib.** (=L. squarrosa (Retz.) **Dumort.)** ***L. cenchrusoides* A. Nelson** ***L. fremontii* (Torr.) Greene** *L. erecta* A. Nelson	***L. echinata* Gilib.** ***L. cenchrusoides* A. Nelson** ***L. fremontii* (Torr.) Greene** *L. erecta* A. Nelson	***L. echinata* Gilib.** *L. echinata* Gilib. var. *erecta* (A. Nelson) Brand ***L. cenchrusoides* A. Nelson**
***L. brachystyla* (A. Gray) J.F. Macbr.** ***L. redowskii* (Hornem.) Greene var. *occidentalis* (S. Watson) Rydb.** *L. occidentalis* (S. Watson) Greene ***L. redowskii* (Hornem.) Greene var. *patula* (Lehm.) A. Nelson & J.F. Macbr.** ***L. cupulata* (A. Gray) Rydb.** *L. columbiana* A. Nelson ***L. cupulata* (A. Gray) Rydb. var. *foliosa* (A. Nelson) A. Nelson & J.F. Macbr.** *L. foliosa* A. Nelson	***L. brachystyla* (A. Gray) J.F. Macbr.** ***L. redowskii* (Hornem.) Greene** ***var. occidentalis* (S.Watson) Rydb.** *L. montana* Greene *L. calycosa* Rydb. *L. leucotricha* Rydb. ***L. redowskii* (Hornem) Greene var. *patula* (Lehm.) A. Nelson & J.F. Macbr.**	***L. brachystyla (A. Gray) J.F. Macbr*** ***L. redowskii* (Hornem.) Greene.** *L. fremontii* (Torr.)Greene *L. occidentalis* (S. Watson) Greene ***L. redowskii* (Hornem.) Greene var. *texana* (Scheele) Brand** *L. heterosperma* Greene *L. desertorum* Greene var. *foliosa* A. Nelson *L. cupulata* (A. Gray) Rydb *L. cucullata* A. Nelson *L. foliosa* A. Nelson *L. texana* (Scheele) Britton. var. *heterosperma* (Greene) A. Nelson & J.F. Macbr. *L. texana* (Scheele) Britton var. *genuina* I.M. Johnst.

Nelson and Macbride 1916	Johnston 1924	Brand 1931
***L. texana* (Scheele) Britton** *L. collina* Greene ***L. texana* (Scheele) Britton. var. *heterosperma* (Greene) A. Nelson & J.F. Macbr.** *L. heterosperma* Greene *L. desertorum* Greene *L. cucullata* A. Nelson ***L. texana* (Scheele) Britton. var. *homosperma* (A. Nelson) A. Nelson & J.F. Macbr.** *L. heterosperma* Greene var. *homosperma* (A. Nelson) A. Nelson & J.F. Macbr. ***L. texana* (Scheele) Britton var. *coronata* (Greene) A. Nelson & J.F. Macbr.** *L. coronata* Greene	***L. texana* (Scheele) Britt. *var. genuina*** *L. texana (Scheele)Britt.* *L. cupulata (Gray) Rydb.* ***L. texana* (Scheele) Britt. var. *heterosperma*** *L. heterosperma Greene* *L. desertorum Greene* *L. cucullata A. Nelson* ***L. texana* (Scheele) Britt. var. *columbiana*** *L. infelix* Greene *L. anoplocarpa* Greene *L. cupulata (Gray) Rydb.* ***L. texana* (Scheele) Britt. var *foliosa (Nels.) Johnston*** *L. desertorum Greene var. foliosa Nels.* *L. foliosa Nels.* *L. cupulata (Gray) Rydbg. var. foliosa Nels. & J.F. Macbr.* ***L. texana* (Scheele) Britt. var. *homosperma (Nels.) Nels. & Macbride*** *L. heterosperma Greene var. homosperma (Nels.)* *L. montana Greene* ***L. texana* (Scheele) Britt. var *coronata*(Green) Nels. & Macbride** *L. coronata Greene*	**L. redowskii (Hornem) Green var *diploloma* Brand** *L. heterosperma Greene* *L. coronata Greene* *L. montana* Greene *L. columbiana* A. Nelson *L. infelix* Greene *L. collina* Greene *L. texana* (Scheele) Britt. var. *heterosperma* *L. texana* (Scheele) Britt. var. *columbiana* *L. texana* (Scheele) Britt. var. *homosperma (Nels.) Nels. & Macbride. texana* (Scheele) Britt. var *coronata*(Green) Nels. & Macbride

Taxonomic Treatment

Genus description (as applicable to the North American species)

***Lappula* Moench**, *Lappula* Moench, 1794, Method.: 414. Meth.:1794. *Lappula* Wolf, 1776. *Lappula* Gilib., 1782 Fl. Lithuan.: 25. nom. inval.

Type: *L. squarrosa* (Retz.) Dumort. (=*L. myosotis* Moench) (Following Ovczinnikova 2009; Al-Shebaz, 1991; Popov 1953) .

Etyology: from diminutive of *Lappa*, with small burs

Common name: Stickseed,

Native and Introduced

Echinospermum Swartz ex Lehm. Pl. Asperif. 2:113. 1818.

Growth form, annual (biennial), various but often upright or branching from the base; hairs single, frequently with pustulate bases. **Root** simple taproot. **Stem**: ascending to erect, green, height. **Leaf**: alternate; petiole present on basal leaves only, absent on cauline leaves, 4-9 mm; lanceolate to oblong, veins inconspicuous, margin entire, frequently with ciliate hairs. **Inflorescence**: arising at base or in upper half of plant, scorpiod cymes (typically raceme-like, panicle-like), tip coiled or not; bracts distributed throughout inflorescence, leaf-like reduced above; flowers one per axil. **Pedicel** reflexed, ascending or erect. **Flowers**: radial, brachymorphic; calyx lobes 5, free to base, accresscent in fruit, widely spreading or clasping in fruit; corolla blue white (cream or white), tube shorter than calyx, constricted at throat; appendages 5, narrow ovate, above anthers; throat tubular, glabrous, lobes spreading, more or less equal; stamens attached in tube, anthers not excerted from corolla; ovary deeply lobed, style

1, not exserted, gynobasic, 1 stigma per flower, capitate. **Fruit** gynobase subulate, slightly shorter than to slightly taller than nutlets fruiting style may be visible above fruits, apex usually obscured by apical spines; nutlet orientation, 4 nutlets per fruit, ripening tan to brown, attached along adaxial surface by narrow keel, adaxial attachment scar linear- lanceolate, narrow keel above scar, adaxial surface sculpturing various, marginal rim smooth to tuberculate, abaxial surface (disk) shiny or not, sculpturing various, prickle shape flat and subulate to terete and swollen.

Species number in the flora (9): Primarily Eurasia (65), a smaller number of species in North America with one or two species in temperate zones of Africa and South America.

Key to Species

1a. Nutlets with two or more rows of spines on the margin …….....……..…….. 2.

1b. Nutlets with a single row of spines on the margin, or spines absent ..... 3.

2a. Inner row of nutlet marginal spines 2 times longer than outer row, longest spines greater than 2 mm long, third row of marginal spines absent. Style obscured by in mature fruits, exceeded by nutlet apical spines. Corolla limb (3)—4 —7 mm wide ……. 4. *L. fremontii*.

2b. Inner and outer rows of marginal spines subequal, longest spines less than 1mm long, a third row of reduced marginal spines usually present. Style visible in mature fruits, not exceeded by nutlet apical spines. Corolla limb 2—3 mm wide ……..…. 9. *L. squarrosa.*

3a(1). Marginal spines of nutlets distinct to base. The annular margin at the base of the spines inconspicuous or as thin rib, spines may be reduced or absent (rarely) ……..… 4.

3b. Marginal spines of nutlets connate (one or more nutlets). The annular margin at the base of the spines conspicuous, forming a thin wing involving at least basal spines, or an inflated crown-like rim (resembling a horseshoe collar in shape) in one or more nutlets ……..……..…….. 7.

4a. Disk inside annular margin small, relative to rest of nutlet. Marginal spines of nutlets absent, or if present, reduced and lower spines inserted one-third from the base of the nutlet. Nutlets typically less than 2mm long ……..…..... 8. *L. montana.*

4b. Disk inside annular margin large, relative to rest of nutlet. Marginal spines present, and lower spines inserted near the base of the nutlet. Nutlets typically greater than 2mm long ……..…...……. 5.

5a. Disk of nutlets less than 0.5 mm wide at broadest part, narrow lanceolate, disk surface with three or more uneven rows of spiny tubercules, more prominent at midline. Adaxial (inward facing) surface spiny tuberculate, surface texture same as on disk. 4—5 spines per side ……..…… 6. *L. longispina.*

5b. Disk of nutlet typically greater than 0.5 at broadest part, broadly lanceolate to sub-ovate, surface various (verrucose, finely to broadly muricate), or if spiny tuberculate then tubercles not arranged in uneven rows, prominent midline of tubercles absent. Adaxial (inward facing) surface texture usually the same as disk, but may be smooth apically. 5—8 spines per side ……..……..... 6.

6a. Plants low and spreading, fruiting branches arising from base, plant olive-green sparsely short pubescent. Flowers pale blue with slight purple tint. Nutlet height 3—3.5mm. Disk

of nutlet smooth or wrinkled, some fruits coarse tuberculate along midline. Adaxial nutlet surface smooth toward the apex on one or both sides of nutlet

…….…… 2. *L. cucullata* (in part).

6b. Plants with 1 or more erect stems, branching throughout or in upper half, fruiting branches often arising in upper part of plant. Flowers pale to sky blue, white or cream. Nutlet height 2—2.5 mm Disk of nutlet otherwise (usually muricate or tuberculate). Adaxial nutlet surface muricate or tuberculate on both sides of nutlet

.....… 8. *L. occidentalis.*

7a(3). Margins of two or more of the nutlets completely inflated (looks similar to a horseshoe collar), with a row of short terete prickles arising from the top ……...

8.

7b. Margins of two or more of the nutlets forming a thin wing or cup-shaped margin, may be slightly inflated basally, but appearing as teeth or lobes) ……..……..……

13.

8a. Nutlet margins homomorphic with all nutlets with an inflated margin .....

9.

8b. Nutlets margins heteromorphic with at least two nutlets with an inflated margin

……...…….……..… 11.

9a. Many arcuate stems arising from base, fertile branches arising from near the base of each stem. Inflorescence not much branched, cymose. Nutlet margins generally only slightly inflated, abaxial surface wide, smooth with raised crest along midline

……..…… 2. *L. cucullata* (in part).

9b. One or more erect stems arising from a single crown, fertile branches arising primarily in upper half of each stem. Inflorescence raceme-like or paniculately branched cymes. Nutlet margins strongly inflated

……...…… 10.

10a. The nutlet disk completely smooth, shiny, frequently with a raised keel along the midline, nutlet adaxial (inward facing) surface smooth to scabrous …… 1. *L. coronata*.

10b. The nutlet disk finely muricate or smooth with fine line of murication along the midline, nutlet adaxial (inward facing) surface fine to rough tuberculate

……..……. 5. *L. heterosperma.*

11a(8). Style clearly visible among the nutlets. Apical spines reduced and shorter than style. Three nutlets with a completely inflated margin and one nutlet with a tear shaped disk smaller than the nutlet body with 3-6 spines per side. Disk surface of all nutlets papillate to muricate. Nutlet adaxial (inward facing) surface papillate to muricate throughout

…..…….……..……..…… 10. *L. texana.*

11b. Style hidden among the nutlets, shorter than or equal to the nutlet apex, apical spines, three nutlets with a completely inflated margin, and one with a narrow to lanceolate disk with 5 spines per side. Disk of nutlet with horseshoe shaped margin smooth or finely muricate along midline. Nutlet adaxial (inward facing) surface tuberculate to verrucose throughout or smooth apically …...…….……..…. 12.

12a. Plant sparsely short-cinereous pubescent throughout. Many arcuate stems arising from base, basal rosettes absent. Fertile branches arising from near the base of each stem, bracts more or less equal in length to leaves, plant appearing foliose throughout. Two or more nutlets with inflated margin that does not obscure the disk. Nutlets with inflated margin

have ovate disk > 2mm at broadest point, disk smooth often with raised crest along midline. Nutlet shape broadly ovate, apex acuminate (viewed from adaxial (inward facing) surface), adaxial (inward facing) surface various usually muricate or tuberculate below becoming smooth toward apex

…….…...… 2. *L. cucullata* (in part).

12b. Plant appearing green and short pubescent or appearing gray and long-cinereous, pubescence harsh. One to many erect stems, some plants with basal rosettes. Fertile branches arising throughout or in upper half of plant, bracts broadly leafy or reduced and linear, plant may appear foliose throughout or divided into clear stem and inflorescence. Two or more nutlets with inflated margins obscuring all or part of the disk. Nutlets with inflated margin with disk (if visible) appearing linear to narrow lanceolate < 2mm at broadest point, disk smooth and muricate along midline or thoughout. Nutlet shape narrow to broadly lanceolate, apex acute (viewed from adaxial (inward facing) surface), adaxial (inward facing) surface various usually muricate or tuberculate below becoming smooth toward apex ……..… 5. *L. heterosperma.*

13a (7). Stems erect, simple up to inflorescence, frequently arising from basal rosette of spatulate leaves. One to few stems per plant. Fruiting pedicels erect. More than on fruit type often present on a single plant(some fruits having a thin cuplike margin and some with marginal spines free to base), or fruits may be heteromericarpic having 2–3 nutlets with a thin shallow cuplike margin, and others with spines free or connate only at bases. Frequently the spines, with bristles along their margins, and on the undersides of the spines near the bases (may also be present on the underside of marginal wing). 6—7 conspicuous spines per side. Styles equal to or exceeding nutlets and visible among or

above them… ……..……..……... 8. *L. occidentalis* var. *stricta.*

13b. Stems arcuate to ascending, diffusely and branched and floriferous from base, basal rosette absent. Many stems arising from single root. Fruiting pedicels weakly to strongly reflexed. Only one fruit type present on a single plant, nutlets more or less the same in a single fruit though some margins may have more prominent wing. Bristles on spines absent. 3—4 conspicuous spines per side. Styles shorter than nutlets and hidden among them …….. 3. *L. desertorum*

1. Lappula coronata Greene

Lappula coronata **Greene**. Pittonia. 4:94. 1899 Type: U.S.A. Arizona, Mesas near Tucson. 18 Apr. 1884, C.G. Pringle *s.n*. (Lectotype designated here: US- 26390!, Duplicates of type: NY! image seen MO!) *Echinospermum coronatum* Schuman. Just's botanischer Jahresbericht. 27(1[3]): 522. 1901. *Lappula texana* (Scheele) Britt. var. *coronata* (Greene) A. Nelson & MacBride. The Botanical Gazette. 61(1):41. 1916.

The specimen at US was chosen as the lectotype for the species because there was no specimen at NDG. Greene was working in Washington D.C. at that time and in the same publication (Greene 1899) he referred to other specimens he had seen at the National Herbarium (US).

Description

Herbs annual. **Roots** single, long and narrow. **Stems** 1—3 stems main stem erect, branching in upper third, flowering stems ascending, 0.3—2 dm, mixed short appressed hairy and pilose, canescent. **Leaves** basal leaves withered at maturity (basal rosette not observed). **Stem leaves** narrow oblong to narrow lanceolate, 2—3 cm x 2—4 mm, abaxial surface long spreading hairy, may be glabrous near midvien and more densely hairy near margins, adaxial surface long spreading hairy, canescent; leaf bases attenuate to cuneate, apex subacute to obtuse, margins long spreading hairy. **Inflorescences** to 10 cm in fruit, raceme like cymes, erect to ascending, bracts oblong to linear, 5—10 mm becoming progressively smaller near branch tips. **Fruiting pedicels** erect, length in fruit 2—3 mm. **Calyx lobes** linear to narrow lanceolate, 1.5—2 mm to 3.5—4 in fruit, slightly accresscent (clasping or stellate spreading). **Corollas** (color not seen), 1.5—2.5 mm corolla lobes erect and spreading, oblong. **Fruits** homomorphic, subglobose (wider than tall), 4—6mm x 2.5—4 mm. **Nutlets** homomorphic, ovate to broad ovate, 2.5 mm, bases

rounded, apices sub-acute to acute.; four nutlets with 1 row of spines arising from a broadly inflated margin, 5 spines per side, terete, 0.5—1 mm long, 2 spines per side free from margin near apex. Abaxial disk lanceolate to broadly ovate (or partially obscured by margin), 1—2.5 x 1—1.5, disk surface smooth with raised crest at midline. Adaxial surface smooth throughout. (equally adhering equally to gynobase?). **Style** taller than nutlet body, obscured by apical spines. **Gynobase** 2.5 mm.

Discussion

This species is most similar to *L. heterosperma* and *L. texana*, but the smooth abaxial and adaxial surfaces of the fruits distinguish *L. coronata* from both species. *L. cucullata* has mericarps with smooth disks and a raised line or crest down the midline, and frequently will have four mericarps with an inflated marginal wing, but even then the two species can be distinguished by the ventral surface which is smooth in *L. coronata* and tuberculate in L. cucullata (at least below). The style is usually completely hidden in *L. cucullata* but visible among the apical spines in *L. coronata*. The two species have completely different ranges.

Observations were made from herbarium specimens only, because this species was not observed in the field. Measurements of the corolla limb width were made from dried specimens, and it is expected that measurements from fresh specimens will be wider. It was not possible to confirm the corolla color because the flowers change color as they dry, but observations of dried specimens suggest that it may be white.

Distribution and Ecology

Southern Arizona, Sonoran desert, 3000-4500 ft

The distribution map was made in ArcGIS online by entering the locality name into the search field and placing the marker dot by eye. If localities were specified to be a certain distance

from a town or landmark, the distance was estimated using the "measure tool." Each dot represents an herbarium specimen observed and cited below in the specimens cited section.

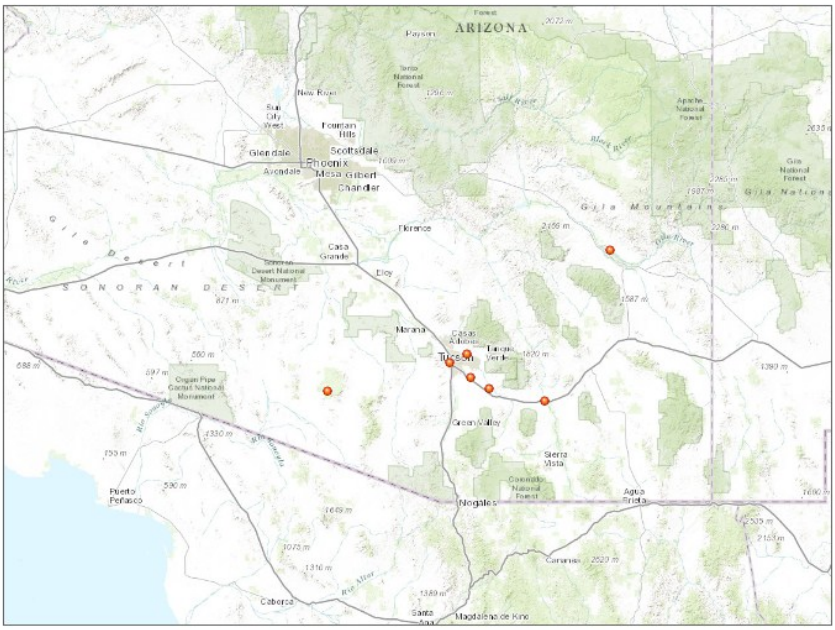


Figure 2.3 Map showing distribution of *L. coronata* Greene. Dots represent fruiting specimens identified as *L. coronata* Greene listed under specimens cited. The collections are mostly from historical localities now located in vicinty of Tucson.

Phenology

Flowering and fruiting: March-April—(June)

Specimens cited

The locality data from the specimens listed below were used to make the distribution map above. Each locality was searched by address in ArcGIS online and dots were placed by eye. Distances were estimated using the measuring tool. The specimens mapped were identified to species with confidence. Other specimens not cited were left unmapped because they were immature and it was not possible to confidently identify them to species.

UNITED STATES. ARIZONA. [GRAHAM CO.:]: On mesa 5 mi N. W. Safford, N of Gila River, Bassett Maguire, B. L. Richards, Jr., Theo. Moeller 10107, 16 March 1935 (RM, ARIZ) [co]: Mesas above [name is unreadable], Thornber s.n., 18 March 1906. (ARIZ); [co]: Small range reserve, Wilmot, J. J. Thornber 5325, 23 March 1905 (ARIZ); [PIMA CO.]: Dry plains near Camp Lowell [=Tucson], C.G. Pringle s. n. 16 April 1881 (GH); [CO.]: Santa Cruz. Dry hills. W. F. Parish 164, April-May 1884 (GH); [PIMA CO.]: Tucson, J. W. Toumey s.n., 10 June 1892; [PIMA CO]: Hills east of Vail, R. H. Peebles 11367, 28 April 1935 (ARIZ); [PIMA CO.]: Tucson, flats southwest of Tumaroc Hill near 22nd Street, 32.2ºN Latitude, 111.0ºW Longitude, 29 March 1983 (ARIZ); [COCHISE CO.]: Benson. Clay creek bottoms, Delzie Demaree 42055, 31 March 1960 (ARIZ)

2. Lappula cucullata A. Nelson

***Lappula cucullata* A. Nelson**. Botanical Gazette 34(1): 29. 1902. Type: U.S.A. Wyoming, Carbon Co.: Fort Steele, dry sandy slopes. 16 June1900, Nelson 7250. (Holotype: RM! Isotype: image seen US!)

Description

Herbs annual **Roots** single, narrow. **Stems** (1)—4—10+ ascending to erect, branching primarily from just above base of plant, heights (0.5)—1 —2 dm, strigose and hispid. **Basal leaves** absent. **Stem leaves** narrowly lanceolate or narrowly oblong, length 1—1.5 cm, width 2—3 (5) mm, strigose to short hispid, adaxially strigose to short hispid (typically more densely than above) bases sessile or cuneate, margin ciliate hairy, apex subacute to acute. **Inflorescences** to 10 cm fruit, cymose not much branched (fruits may appear secund along branches) bracts leaf like throughout, reduced distally, shape narrow lanceolate to lanceolate, 1.5—2 (2.5) cm, upper bracts shape narrow lanceolate, 0.5—1 cm length. **Fruiting pedicles** 1—2 mm, ascending to reflexed but often appearing sessile on branch. **Calyx lobes** linear to lanceolate 1—2 mm, to 4 in fruit, erect or clasping the fruit. **Corollas** pale blue or lavender (fading darker blue), limb 2—3 mm wide, lobes erect to spreading, lobes linear, oblong. **Fruits** heteromorphic, some plants with homomorphic nutlets (either nutlet type), some plants with heteromorphic nutlets, ovate (if fruits homomorphic and nutlet margins uninflated and spines free), globose (if fruits homomorphic with margins inflated and spines connate, or fruits heteromorphic with both nutlet types present) 3—5 mm high. **Nutlets** heteromorphic, broadly ovate to orbicular, 3—3.5 mm long, bases rounded, apices acute to acuminate; 1—4 nutlets with one row of spines arising from inflated deeply involute or revolute margin; 6—8 spines per side, arising from margin up to 1mm long, at least 2 of these apical spines free sub-terete to subulate, disk broadly lanceolate to broadly ovate,

completely visible or partially obscured by margin, 2.5—3 x 1—2 mm abaxial disk smooth to rugose with raised crest along midline smooth or striate with fine papillae, adaxial surface with a narrow keel above middle, muricate, smooth apically or one side smooth the other muricate, nutlets easily released from gynobase or not; 1—4 nutlets with 6—8 spines along each side arising from a smooth or muricate margin, longest spines bases free to confluent, disk shape lanceolate to broad lanceolate, 2—2.5 x 0.8—1.5mm, abaxial disk rugose, or finely muricate, adaxial disk sparsely to densely muricate. Nutlets frequently clinging to gynobase. **Gynobase** 2.8. **Style** shorter than or equal to nutlet body, not visible, obscured by nutlet apex and spines.

Discussion

One difficulty in delineating *L. cucullata* was the discovery that it can produce monomorphic, weakly heteromericarpic, or strongly heteromericarpic fruits in the same or separate populations. Plants collected from the eastern part of its range (NORTH DAKOTA. BOWMAN COUNTY: S. J. Rolfsmeier 1102; WYOMING. CARBON COUNTY S.J.R 670) were initially thought to be a new species. The fruits had homomorphic nutlets with spines that were free to the base and horizontally spreading. The nutlet disk was wide, smooth, and smooth somewhat wrinkled, and the flowers were pale blue to lavender (See image of fruit below, Figure 2.5) . However examination of the type specimen (cited above), and comparison with specimens with heterormorphic fruits (cited below under specimens examined), suggested that the plants with homomorphic fruits and nutlets with free spines are likely members of the same species as those with connate and hooded nutlet margins.

On the herbarium sheet, two collections from the same population may initially appear to be separate species. Fruits on a single plant can have three consimilar nutlets with connate bases and one nutlet with free spines. In the same population plants may be found with four consimilar nutlets with free spines (less common). Or there may be plants that have dissimilar nutlets that

vary in degree of dissimilarity. When the fruits are heteromorphic seems to be a correlation between nutlets having cupulate margin and a smooth disk surface (Figure 2.6). However plants that have fruits without connate margins can have muricate or smooth to rugose nutlets. In plants with two fruit types, the nutlets with free marginal spines may be smaller and have narrower abaxial disks than those with a cupulate margin, the midlines on these nutlets are demarcated by a line of muricate bumps (sometimes on a raised ridge) rather than a smooth raised keel with a sharp crest.

When this plant has strongly heteromericarpic fruits it may appear similar to *L. heterosperma*, but it can be separated by the larger nutlets which have wider abaxial disks, and styles shorter than the nutlets. It also typically has smaller flowers and a lower, more widely spreading growth form than *L. heterosperma*. This species frequently grows with *L. fremontii* (Torr.) Greene in sparsely vegetated areas with clay soils, but *L. fremontii* has larger blue flowers, fruits with multiple rows of spines and a different habit (see description of that species).

Observations of fresh plants in the field were based on individuals from a population in North Dakota (SJR 1102). Corolla lobes were narrow (less than 1 mm wide), and the angle between the lobes was 50º —90º. The corolla appendages (fornices) were light yellow to white, minute and bead-like, and sepals were narrow and linear. When unripe, the fruits were green and the spines were tinged blue.

In the western part of its range, *L. cucullata* is very similar to a form here treated as *L. desertorum* (described by Aven Nelson as *L. desertorum* var. *foliosa*, elevated to species by him and then treated as *L. cupulata* var. *foliosa*). Both of these species can have foliose bracts and are low growing and bushy branched from the base. One difference that seems to separate them is size of the fruits. The fruits in *L. cucullata* A. Nelson are larger than those of *L. desertorum* by

1—1.5 mm. The abaxial disk in the former is typically broader, though both have smooth wide surfaces when the bases are connate. The nutlet apex is acuminate, not acute. The adaxial surfaces of the nutlets are smooth, at least apically. Also, adaxially, the sides are often oblique, where one side is acuminate and the other acute; also the surfaces may differ with one half being smooth apically and the other muricate. However, specimens from the Snake River Plains of Idaho and Oregon, Lincoln and Sublette counties in Wyoming are difficult to place without carefully examination. Both of these species have a low spreading growth form and are foliose throughout. However, *L. desertorum* seems to have narrower leaves and smaller more widely spaced. It may also be possible that the number of marginal spines may be a good character, with *L. cucullata* consistently having 5 to 6 or more spines per side and *L. desertorum* having 3 or 4 spines per side. Another character that seems to distinguish the two species, when the spines are free, is that *L. cucullata* spines are usually ascending and get progressively smaller apically and *L. desertorum* seems to have spines that are horizontally spreading with relatively longer spines at the bottom "corners" of the nutlets and very reduced spines above. The lowermost spines in the nutlets of *L. desertorum* are sometimes connate and form a thin cup, or wing and this can be similar in appearance to the thin, hooded margin observed in *L. cucullata* (though the fruits in *L. cucullata* are often larger). Further evaluation is needed to determine if these two species are in fact the same, if they intergrade, or if they simply share some morphological characters that make it difficult to distinguish them; it is included here, but with low confidence in the delineation. The specimens cited below best represent the species as circumscribed here, but some confusing specimesn are cited with comments in brackets.

Distribution and Ecology

Sandy basins of South-central Wyoming, Salt desert scrub with *Atriplex*, clay shale barrens, sparsely vegetated sagebrush slopes, clay soils in badlands of the Missouri Plateau. The

map below was made in ArcGIS online and is based on localities from herbarium specimens listed below under specimens cited.

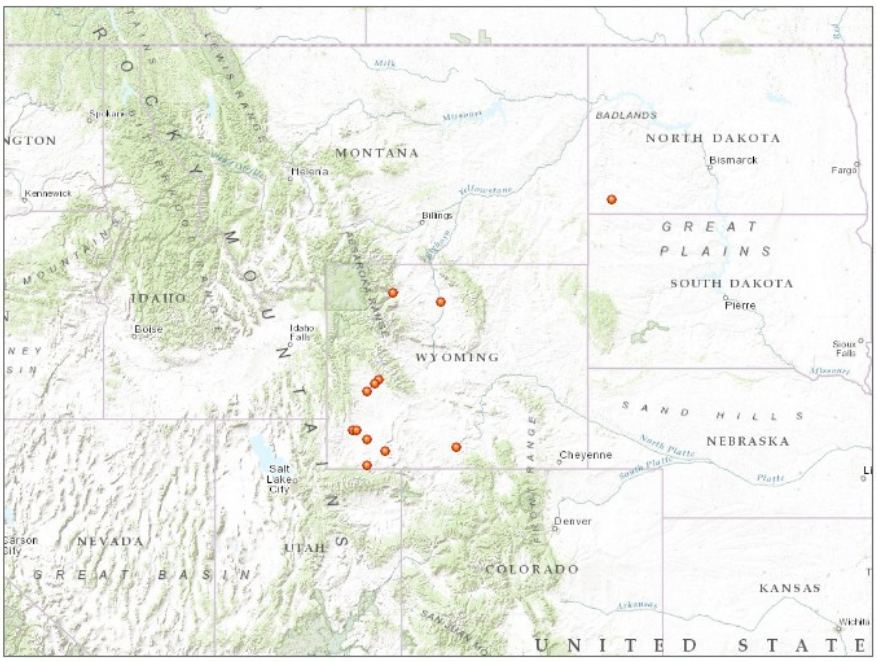


Figure 2.4 Map showing distribution of *L. cucullata* A. Nelson

Phenology

Flowering and Fruiting: June-July

Specimens cited

U. S. A. **COLORADO**.[MESA CO.]: DeBeque, 22 June 1912, G. E. Osterhout, RM)**WYOMING**. BIG HORN CO: Legal description [only] R92W T50N NE NW Sec 20, 6 June 1967, H. G. Fisser 16 (RM). CARBON CO.: 20 miles north of Baggs, sagebrush slopes. Common on disturbed soil of bottom land, 20 June 1957, C. L. Porter 7296 (ARIZ, TEX, RM). LINCOLN CO.: ca 4.5 air mi SW of Opal, 4.7 mi S on Wagon Wheel Road off of U.S. Hwy 30, 1 June 1995, C. H. Refsdal, Larry Refsdal 4750 (RM). Ca 10 air mi ENE of Opal, 30 June 1995, C. H. Refsdal 4701 (RM); Between Zieglers Wash and Dry Muddy Creek ca 9 air mi WNW of

Granger, 3 July 1995, B. E. Nelson, C. H. Refsdal 36074 (ARIZ, RM); .PARK CO.: Absaroka Mountains: along south side of inlet to Buffalo Bill reservoir, ca 13 mi W of Cody, 3 June 1988, Erwin F. Evert, 14142 (RM); SUBLETTE CO.: Ca 11. 5 air mi SW of Boulder, 7 Junl 1995, Tom Cramer 7423 [seems like it is approaching *L. foliosa* sensu Nelson-SR](RM);North rim of Dry Basin just off Calpet Road, ca 10 air mi SW of Big Piney, 28 June 1993, B. E. Nelson 26578 (RM); Green River Basin, ca 1.5 air mi E of Marbleton, 21 June 1995, Tom Cramer, Jane T. Kellett 6533 (RM) SWEETWATER CO.: along Henry's Fork near McKinnon, 28 June 1951, C. L. Porter, R. C. Rollins 5667 (GH); 22 miles South of Green River, 29 June 1951, C. L. Porter, R. C. Rollins 5714 (GH). WASHAKIE CO.: Big Horn Basin; on Lightning Ridge above Homestead Gulch on the Nowater Trail, ca 3 air mi NNW of Nowood, ca 20 air mil S of Tensleep, 8 July 1980, B. E. Nelson 5883 (RM); 19 miles NW of Worland at Hawk Exclosure, 31 May 1979, H. G. Fisser s.n. [mixed sheet w/ *L. fremontii*, 3rd specimen on sheet is cited here] (RM).

U. S. A. **WYOMING**. LINCOLN CO.: Ca 13 air mi N of Opal, 11 July 1995, Tom Cramer, Jane T. Kellett 7769 [Specimen seems between *L. desertorum* (recurved pedicles, branching from base),and *L. cucullata*](RM)

Figure 2.5 Image of *L. cucullata* fruit with free spines (SJR 1102).

Figure 2.6 Image of *L. cucullata* fruit with inflated margin (SJR 757).

3. Lappula desertorum Greene

***Lappula desertorum* Greene var. *desertorum*.** Pittonia. 4:95. 1899. Type: U.S.A.: Nevada [Elko Co.]: "deserts of central Nevada; described from specimens obtained by the writer near Holborn," E. L. Greene s.n. 16 July 1896 (Holotype: ND-G 042397!) Note: "Type" is written on Greene's specimen label, but the handwriting matches I.M. Johnston's (in particular the "y") and not Greene's.

Echinospermum desertorum K. Schum. Just's Bot. Jahresber. 27, Abt. 1: 522. 1899.

Lappula desertorum Greene var. *foliosa* A. Nelson Bull. Torr. Bot. Club. 27(5): 267-268. 1900. Type: U.S.A. Wyoming [Uinta]: Evanston. 4 June 1898, A. Nelson 4502, 13 June 1898 A. Nelson 4685. (Lectotype designated here: RM!). *L. foliosa* A. Nelson in A. Nelson and J.M. Coulter, Man. Rocky Mount. p 413. 1909. *L. cupulata* Rydb. var. *foliosa* A. Nelson & MacBride. Bot. Gaz. 61(1): 40. 1916. *L. redowskii* (Hornem.) Greene var. *desertorum* I. M. Johnston pro parte. J. Arnold Arb. 3: 92-94. 1932.

Description

Herbs annual. **Roots** single, narrow. **Stems** (1)—4—10+ ascending to erect, branching primarily from just above base of plant, heights (0.5)—1 —3 dm, strigose and hispid. **Basal leaves** absent. **Stem leaves** narrowly lanceolate or narrowly oblong, length 1—1.5 cm, width 1—3 mm, strigose to short hispid, adaxially strigose to short hispid (typically more densely than above) bases sessile or cuneate, margin ciliate hairy, apex subacute to acute. **Inflorescences** to 20 (30) cm fruit, cymose not much branched (fruits may appear secund along branches) bracts leaflike or narrow throughout, reduced distally, shape narrow linear lanceolate to narrow lanceolate, 1.5—2 (2.5) cm long, upper bracts shape narrow lanceolate, 0.5—1 cm long. **Fruiting pedicles** 2-4 mm, ascending to reflexed. **Calyx lobes** narrow lanceolate 1—2mm, to 5

mm in fruit, clasping or spreading. **Corollas** white, pale lavender-blue, limb 2—3 mm wide, lobes erect, lobes linear. **Fruit** homomorphic, **Nutlets** heteromorphic (not strongly pronounced), ovate, 2—2.5 mm long, bases rounded, apices acute; *1—4 nutlets* with 4—5 spines arising from a thin wing (may be inflexed at base of spines), longest spines 1—1.5 mm long, bases confluent or closely adjacent, disk ovate 1.5—2 x 0.3—0. 5 mm; disk surface finely muricate with a line of closely muricate bumps along midline, or smooth with striations of muricate or papillose bumps along midline. Adaxial surface muricate or smooth or muricate below and smooth above; *1—4 nutlets* with 4-5 spines arising from obscure margin, longest spines 1—1.5 mm long, bases free or closely adjacent, disk ovate 1.5—2 x 0.3—0.5 mm; disk surface finely muricate with a line of closely muricate bumps along midline, or smooth with striations of muricate or papillose bumps along midline. Adaxial surface muricate or smooth or muricate below and smooth above. **Gynobase** 2—2.5 **style** shorter than or equal to nutlet body, not visible, obscured by nutlet apex and spines.

Discussion

Johnston (1932) considered *L. desertorum* Greene a variety of *L. redowskii* (S.Watson) Greene, making the combination *L. redowskii* (S.Wats) Greene var. *desertorum* (Greene) I. M. Johnst. He submerged *L. cupulata* (Gray) Rydb., *L. desertorum* Greene*, L. foliosa* A. Nelson and *L. columbiana* A. Nelson into synonomy under *L. occidentalis* var. *desertorum*. His earlier work had largely followed that of Nelson and Macbride in recognizing six varieties with variously inflated margins, but Johnston placed all of these as varieties under *L. texana* (Scheele) Britt. and put Greene's name *L. desertorum* into synonomy under *L. texana* var. *heterosperma* (Greene) I. M. Johnst. with a question mark (Johnston 1923).

When Johnston published his new combination based on Greene's basionym, he determined that some nutlets had an inflated margin upon which the spines were perched, and

others formed a wing by becoming connate during development (Johnston 1932). Specimens with the later type of nutlets were all referred to *L. redowskii* var. *desertorum*. Here, *L. desertorum* is retained as a species distinct from *L. occidentalis* and from *L. redowskii*. There are differences in habit, vegetation, and fruits that support this delineation. In particular, *L. desertorum* is low growing, the fruits have fewer spines on the nutlets and overtop the styles, and the longer spines at the basal corners of the nutlet give the disk (and the fruit overall) a more triangular shape, compared with the ovate shape of the fruits in *L. occidentalis*.

Here, Nelson's variety *L. desertorum* var. *foliosa*, is treated within the species without varietal separation, but this merits further study. Nelson thought the variety was distinct enough to be considered a separate species, *L. foliosa* A. Nels. (Coulter and Nelson 1909), but later he placed it a variety of *L. cupulata* (Gray) Rydb. (a combination based on a superfluous name, here treated as *L. occidentalis* (S. Watson) Greene var. *stricta* (S.Wats.) *comb. nov*). The habit of the plants described as *L. desertorum* var. *foliosa* are very bushy branched and leafy and have widely spaced fruits, whereas the plants of the typical form are more closely fruited and the bracts less leaf-like. Some specimens labeled by Nelson as *L. foliosa,* have very large fruits and look very similar to *L. cucullata*. One possibility is that *L. cucullata* and *L. foliosa* are the same, and should take the older name *L. foliosa*. For now, the name is left as a synonym under *L. desertorum*.

Distribution and Ecology

Clay hillsides and badlands, Cold desert basins, Rolling plains, 2000-7000 ft

The distribution map shown below is based on specimens observed and determined to be L. desertorum. Each dot was placed manually in ArcGIS online. The locality listed on the label was entered into the search field, the dot was placed manually. Distances from towns or landmarks

were estimated using the measurement tool in the mapping application and dots were placed manually. Specimens mapped are listed below under the specimens cited section. General habitat data was compiled from herbarium specimens.

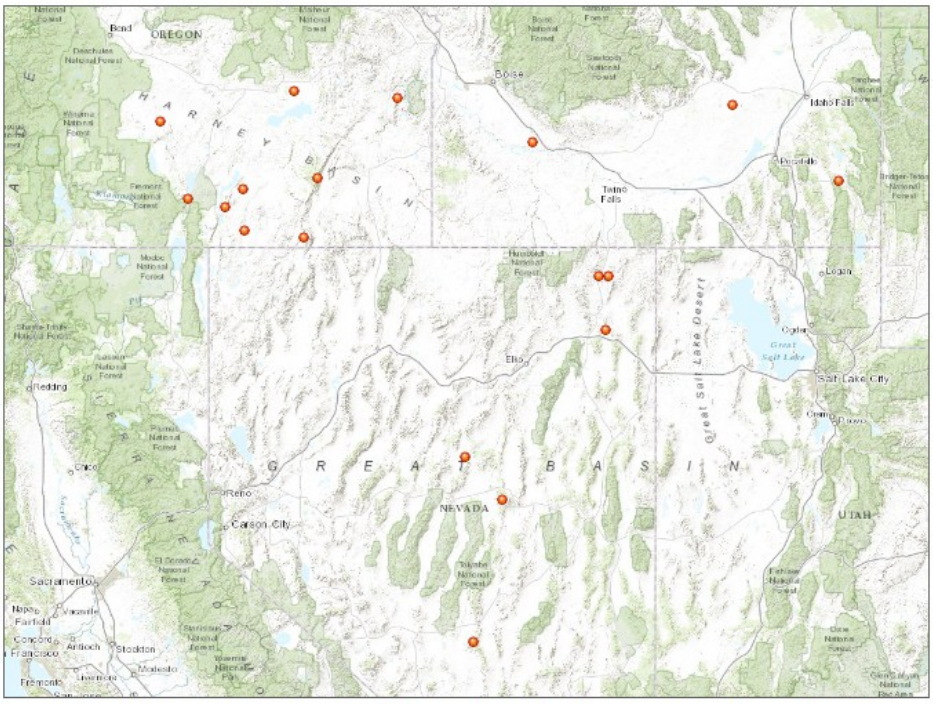


Figure 2.7 Distribution of *L. desertorum*. Dots represent examined specimens.

Phenology

Flowering and Fruiting: June-July

Specimens cited

U. S. A. **CALIFONIA.** MODOC CO.: Upper Alkali Lake, E side of Surprise Valley, 2 June 1989, B. Bartholomew, B. Anderson 4821 (NY); **IDAHO**. Snake Plains, 1893, Dr Edward Palmer 280, 115, 19 (NY); BANNOCK CO.: Soda Springs, 18 June 1920, Edwin B. Payson, Lois B. Payson 1714 (RM). BUTTE CO.: Big Butte, 27 May 1938, Ray J. Davis 140 (GH)20 miles northeast of Arno, 8 June 1941, J. H. Christ 12263 (NY). ELMORE CO.: 9 miles south of Mountain Home, 29 May 1953, William H. Baker 10193 (RM). **NEVADA.** ELKO CO.: South

of Contact, 29 June 1941, R. L. Riemeisel 261 (GH). ESMERALDA CO.: Trail Canyon, White Mountains, 15 June 1930, Victor Duran 2709 (ARIZ, NY, OSU, RM). EUREKA CO.: 5 mi S of Walti Hot Springs, ca 55 mi NE of Austin (Lander Co.), 13 June 1964, R. Spellenberg 366 (NY). NYE CO.: South end of the Monitor Range, 3.7 km (2.3 mi) North of U.S. Highway 6 from a turnoff 29 km (18mi) east of Tonopah, 9 June 1976, Noel H. Holmgren, Patricia K. Holmgren 8158 (NY). WASHOE CO.: Granite Range, upper meadows at the south fork of Rock Creek, ca 1.6 km (1 mi) east of Granite Peak, 16 km (10 mi) airline distance north-northwest of Gerlach, 29 June 1980, Noel H. Holmgren, Patricia K. Holmgren 9685 (NY). **OREGON**. Big Butte Station, 20 June 1893, Dr. Edward Palmer 200 (WTU); Harney Valley, 27 May 1885,Thomas Howell s.n. (NY). BAKER CO.: 1 mi E of Unity, 18 June 1928, M. E. Peck 16050 (WILLU). HARNEY CO.: Steins, June 1927, Lilla Leach 684 (OSU); Pueblo Mt. Mining Co., Pueblo Mts., 3 July 1927, L. F. Henderson (OSU); Silvies River, 23 June 1912, M. E. Peck 7838 (WILLU). LAKE CO.: Warner Valley, ¼ mile north of junction of road into Hart Mtn. refuge and road between Flagstaff and Wagner Lakes, just north of CCC Camp, 17 June 1977, Virginia Crosby 1300 (OSU); Near Guano Lake, 4 July 1936, Roy C. Andrews 633 (OSU); Along State Route 140, 44 miles S.E. of junction with State Route 395 mile post 44, 24 June 1986, Thomas W. Nelson, Jane P. Nelson 8212 (RM); Hart Mountain Headquarters, 25 June 1941, Lilla Leach s.n. (OSU); Road near Flook Lake, about 6 mi NE of Refuge Headquarters, Hart Mountain National Antelope Refuge, 9 June 1996, David Giblin 023 (WTU); Chewaucan River, 6 miles northwest of Valley View, 30 May 1940, C. L. Hitchcock 6752 (NY, WTU); West side of the Black Hills, 5 miles SSW of the town of Christmas Valley, 7 June 1983, Stephen Shelly 517; 5 mi S Valley Falls; 31 May 1948 M.E. Peck 25034 (WILLU). MALHEUR CO.: Owyhee Uplands, Dry Creek basin, hills northwest of Eddy Spring, 37 air miles south-southwest of Vale, 27 May 2004,

Danna Lytjen, R. E. Brainerd, N. Otting176 (OSU);. 21 km E of Whitehorse Ranch, 13 km W of hwy #95, crest of ridge above hairpin turn, 3 June 1983, Elaine Joyal 451 (OSU); Blue Mountain Pass, 19 June 1958, L. E. Detling (OSU). **WYOMING**. Yellowstone Park, Junction Butte, 15 July 1899, Aven Nelson, Alias Nelson, 5888 (RM); CARBON CO.: Sand Creek, 17 July 1973 M. H. Schroeder, G. L. Ranick, s.n.(RM). LINCOLN CO.: N of Opal, 8 June 1987, R. Dorn 4613 (RM); Holden Hill above Fontenelle Reservoir, ca 8.5 air mi NW of Fontenelle Dam, 5 June 1995, Tom Cramer 5586 (RM); Sugar Loaf, ca 26.5 air mi NW of Farson, 17 June 1995; Ca 13.5 air mi NE of Kemmerer, 4 July 1995, Tom Cramer 7096 (RM); Ca 15.5 air mi SSW of La Barge, 21 June 1995, Tom Cramer, Jane T. Kellett 6607 (RM); SUBLETTE CO.: Ca 9.5 air mi E of La Barge, 8 July 1995, Tom Cramer 7562 (RM); Ca 10. 5 air mi SSW of Big Piney, 24 July 1993, Ronald L. Hartman 41806 (RM);12 air mi N of Farson, 18 July 1995, Tom Cramer, Jane T. Kellett 8583 (RM); Southern end on the east side of the Prospect Mountains, ca 17 air mi W of South Pass City, 16 June 1994, Tom Cramer 752 (RM); ca 20 miles N of Farson, 17 June 1995, Tom Cramer, Jane T. Kellett 6163 (RM); Near Cora, 9 July 1925, Edwin B. Payson, Lois B. Payson 4317 (RM); ca 17.5 air mi NW of Farson, 2 August 1995, Tom Cramer, Jane T. Kellet 10184 (RM). SWEETWATER CO.: Delaney Rim, Ca. 4 air mi S of Tipton, 19 June 1980, Kieth H. Dueholm 10120 (RM); Ca 15 air mi s of Red Desert, 8 June 1980, Keith H. Dueholm 9916 (RM). Ca 11. 5 air mi NW of Farson ice cream store, 18 July 1995, Tom Cramer, Jane T. Kellett 8504 (RM). UINTA CO.:Kemmerer, 1 June 1907, Aven Nelson 9015 (RM);

4. Lappula fremontii (Torr.) Greene

Key to varieties:

Fruits 4 mm high (including apical spines), spines of secondary row half as long as those of main row, dorsal face of nutlet ca. 1 mm wide …… 4a. *Lappula fremontii* var. *fremontii.*

Fruits 3 mm high (including apical spines), spines of secondary row reduced to tubercles, dorsal face less than 1 mm wide ……..……. 4b. *Lappula fremontii* var. *nelsonii.*

4a. Lappula fremontii (Torr.) Greene *var. fremontii.*

Lappula fremontii* (Torr.) Greene var. *fremontii, Pittonia. 4:96. 1899. *Echinospermum fremontii* Torr. Pacif. R.R. Prep. 12(2): 46. Type: U.S.A. California: Creek of the [...]" in the Sierra Nevada. 1860, J. C. Frémont *s.n*. (Holotype: NY!). The label was not legible, but the publication lists the locality as "Pass Creek, near the Southern extremity of the Sierra Nevada" (Torrey, 1899).

Lappula cenchrusoides A. Nelson. Bull. Torr. Bot. Club. 1899. Type: U.S.A. Wyoming Laramie Hills, 14 Sept. 1898, Aven Nelson 5339. (Holotype: RM! Isotype: NY!).

Echinospemum cenchroides [sic] K. Schum. Just's Bot. Jahresber. 27, Abt. 1: 522. 1899.

Lappula erecta A. Nelson Bull. Torr. Bot. Club. 27(5): 268. 1900. Type: U.S.A. Wyoming [Platte County]: Uva, July 7 1894 , A. Nelson 424. (Lectotype designated here: RM!, Isolectotype: NY!) Nelson referred to two specimens in his publication, but wrote "type" on Nelson 424, which was selected for the lectotype. *Lappula echinata* var. *erecta* (A. Nelson) Brand. In Engler, H.G. Das Pflanzenreich IV. 252 (Heft 97): 140. 1931. *Lappula squarrosa* var. *erecta* (A. Nelson) Dorn. Vascular Plants of Wyoming 295. 1988.

Description

Herb Annual or biennial, **Roots** single, narrow or stout and conical. **Stems** 1—3 (occasionally more) arising from crown with basal rosette, or simple stem arising from root, ascending or, erect, branching throughout from near base, or primarily in upper third of plant, (0.5)—1—3—(4) dm high, strigose or appressed long hairy. **Basal leaves** absent or withering at maturity or present and lanceolate or spatulate (1—4 cm x 3—5 mm), strigose or densely appressed long hairy, bases attenuate, apices obtuse to subacute. **Stem leaves** narrow oblong to narrow lanceolate, or oblong elliptic; 1—4 cm long, 3—6—(10) mm wide; abaxial surface frequently sparsely pustulate hairy approaching glabrous at midline or appressed long hispid, adaxial surface more densely pubescent; bases cuneate to rounded, apices rounded or subacute, margins ciliate or long hairy. **Inflorescences** 5—30 cm, ascending raceme-like cymes or erect and paniculately branched in upper part of plant; bracts oblong to ovate, becoming progressively smaller near branch tips 0.5—1.5 cm. **Fruiting pedicels** 2—3 mm ascending **Calyx lobes** linear oblong or lanceolate, 0.5—3—(4) in fruit, stellate spreading. **Corollas** blue, limb (2)—4—5—(7) mm wide, lobes ovate to broadly ovate. **Fruits** homomorphic, 2.5—4—(5) mm, broadly lanceolate to triangular. **Nutlets** homomorphic 4 mm high, broadly lanceolate, nutlets with 2 rows of spines along disk margin; *spines of inner row* arising from inconspicuous margin, spines of primary row 6—7—(9) spines per side, free or closely adjacent sometimes fusing to form a thin wing, 1.5—3.5—(5)mm long; *spines of outer row* half as long, terete 0.5—1.5 mm long, bases free, abaxial disk triangular or lanceolate 3—3.5 mm long x 1—1.5 mm wide, disk surface scabrous tuberculate with prominent line of taller tubercles (frequently glochidiate) along midline. Adaxial surface scabrous tuberculate; one nutlet adhering more strongly to gynobase. **Style** exceeding nutlet body, style exceeded by apical spines. **Gynobase** 3.5—3.8 mm high.

Discussion

This species has two growth forms which may be recognized as varieties. One is found throughout the Missouri Plateau physiographic region and the Wyoming Basin (Chapman et al. 2004) and north to badlands in Saskatchewan and Alberta, consistently growing in gray smectite clays derived from volcanic ash. The other appears to be a biennial or winter annual (at least in some populations, but not confirmed empirically), and is found throughout Wyoming, the Rocky Mountains, and the Yukon and Alaska (see specimens cited below). The basin dwelling plants are typically bright green, short hispid, branching throughout from the base, with ascending fertile branches. The leaves are appressed hairy (sparsely so above) and usually leaf hairs have pustulate bases. The plants found in the hills and mountain zones tend to branch above and to be more robust, frequently with multiple stems arising from a leafy crown, and have a more gray hairy appearance. These two forms may constitute separate varieties, but in Wyoming and North to Alaska, they can be difficult to tell apart as the fruits are the similar and the combination of vegetative characters that distinguish them varies inconsistently.

The taxonomic identity of *L. fremontii* has been unclear. Greene considered Nelson's *L. cenchrusoides* synonymous with it (1899). Nelson and Macbride put *L. erecta* into synonymy under it and retained *L. cenchrusoides* as a distinct species (1916). Johnston determined the collection must have been *L. occidentalis* since he considered that species common to the region (1923). In part, the confusion arose because the type locality, recorded as Pass Creek in the Sierra Nevada Mountains of California, was considered doubtful.

The basionym, *Echinospermum fremontii* Torr., was published in a report on a survey of collections from the Missouri Plateau region, but Torrey typified it with Frèmont's specimen from California and not Suckley's. By the time Greene transferred the name from *Echinospermum* to *Lappula*, the species had not again been reported from California so he

inferred that the collection had been misattributed to that locality. Greene examined the type specimen, as well as that for *L cenchrusoides*, and determined the two were the same. Nelson continued to retain *L. cenchrusoides* as distinct on the basis of its vestiture, branching and flowering time and the minute flowers observed on the fall collected plants. On the other hand, he considered his *L. erecta* to be a synonym of *L. fremontii* on the basis of the vegetative characters. Specimens from California were not observed but one from Nevada (cited below) was, so it is possible that it is present in California.

An attempt was made to separate the two vegetative forms as varieties, but the morphology was extremely variable, even in the field. While plants in eastern part of its range were collected exclusively in badlands habitats, further west, they seem less restricted in their habitat preferences and were found in sandy and clay soils, in basins and montane woodlands. Furthermore, it was observed in the field (observations by SJR in 2003, 2005, and 2006 at Toadstool Park in that plants in the Missouri Plateau behave annuals and complete their life cycles by mid-July. Nelson collected the type of *L. cenchrusoides* in the fall in the Laramie Hills of Wyoming, finding them still in flower. He made additional collections in subsequent years at the same time, from the same general locality. The minute flowers he reported in his type description were also observed on later flowering plants of the strict annual form.

A third form was also observed and was separated out as a distinct variety on the basis of the fruits (see *L. fremontii* var. *nelsonii* described below). It was included under Nelson's concept of *L. erecta*, but the specimen on which he wrote "type" was of the form discussed above, with larger fruits, hence that name was put into synonymy under *L. fremontii* var. *fremontii*. The "co-type" of *L. erecta*, as labeled by Nelson (Wyoming. Park Co: Soda Butte, Yellowstone Park, July 15, 1899. Nelson 5872 RM!) was chosen as the type for a new variety

described below. Plants of this variety observed in the Uintah Mountains of Utah, and similar specimens were seen from Alaska. It branches in the upper third of the plant with erect branches and has fruits with shorter spines in the main row, and a second row of much shorter spines which may appear only as tubercles and may be visible only with a hand lens.

Plants with fruits like *L. fremontii* and vegetative morphology like that of *L. squarrosa* were observed. These specimens many aborted fruits and were found where their ranges overlap in the Rocky Mountains and Alaska. In North Dakota, where the two species also co-occur, living plants were observed growing in the same area but they were distinct in their morphology, and phenology with plants of *L. squarrosa* in early flower state, and those of *L. fremontii* were in late fruit. As both species produce large flowers, and *L. squarrosa* is reported to be both selfing and outcrossing (Frick, 1984) it is possible that there may have been past or ongoing introgression between the two species.

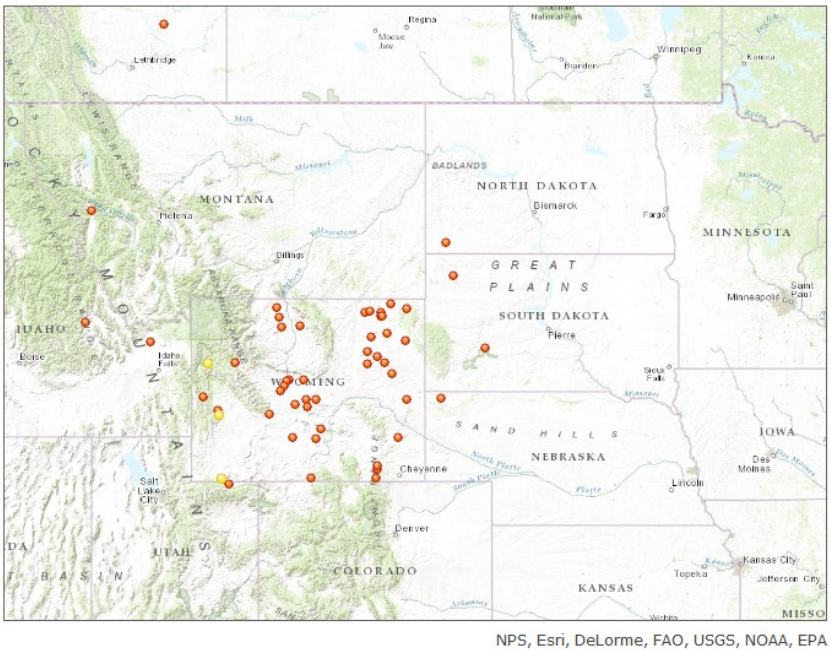


Figure 2.8. Distribution map of *L. fremontii* (both varieties). Map based on specimens observed and identified as *L. fremontii* var. *fremontii* (red dots), and *L. fremontii* var. *nelsonii* (yellow dots).

Distribution and Ecology

Habitat data for this variety is based on observations and herbarium label data. Sparsely vegetated areas in clay soils along eroding badlands slopes. Sparsely vegetated sagebrush slopes and sandy soils in foothills. The map shown in Figure 2.8 is based on specimens of both varieties. More specimens were observed of *L. fremontii* var. *fremontii*. Specimens chose represent morphological variation across a broad geographic range and these specimens were mapped. The maps were produced in ArcGIS online by using the search feature to find localities listed on the specimen labels. The dots were placed by eye and when the locality was a specified distance from a locality or landmark, the distance was estimated using the measure tool in ArcGIS and the dot was placed manually.

Phenology

Flowering and fruiting: May- July (September)

Specimens cited

The locality data was copied from the labels as written and historic locality names were not updated. As mentioned above, sometime two forms can be observed, but the pattern was not consistent enough to distinguish them at the varietal level. An attempt was made below to group the specimens by whether they had an erect stem and were branching above (usually the plants are also more canescent), or whether they were spreading (often these were robust bushy plants with very bright green color on the sheet). This was not exact however and some plants that were cited could just as easily be placed in one category or another. It is hoped however that citing the specimens this way might be useful for organizing the locality data for further study into variation in habit and growth form.

CANADA.**YUKON**: White Horse, Upper Yukon River 14 August 1932, L. F. Henderson 14646 (OSU); Haines Junction, 14 September 1999, P. Caswell 2000-408 (ALA). ALBERTA:

South of Brooks, 28 June 1932, J.W. Eastham 3867 (UBC); below Sunalta School, Calgary, 26 August 1948, W. C. McCalla 10272 (UBC). Along road on N. side of Slims River, from Alaska Hwy. ca. 5 mile up river from Kluane Lake, 15 July 1974, K.I. Beamish s.n. U.S.A.; Whitehorse, 18 July 1949, J. M. Gillett, D. A. Mitchell 3859 (RM); Contact Creek Esso Station Alaska Hwy. 953.5, 12 July 1983,W.J. Cody 32637 (UBC); U.S.A. **IDAHO.** CUSTER CO.: 10 miles west of Clayton, 5 August 1944, C. L. Hitchcock, C. V. Muhlick 10769 (WTU). CLARK CO.: 9 miles s.w. of Dubois, along Highway #22, 19 June 1963, C. L. Hitchcock, C. V. Muhlick 22777 (WTU). Challis, 15 July 1915, J. F. Macbride, Edwin B. Payson (RM); **MONTANA** [MISSOULA CO.] Fort Missoula, July 1914, Chas Lively (NEB). **SOUTH DAKOTA**. BUFFALO CO.: T107N, R71W, SEC 36, 11 June 1997, James R. Johnson 346 (OSU). PENNINGTON CO.: Buffalo Gap National Grasslands, 5 mi SE, 3.2 mi S Wall, 18 June 1971; Garrett Severson (USFS-RM). **UTAH.** [DAGGETT CO.]: Carter Dugway,Uintah Mts., 19 July 1899, Leslie Gooding (NEB). **WYOMING**. ALBANY CO.: North of Tie Siding, 24 June 1919, George E. Osterhout 5959 (RM); Chug Creek, 29 June 1900, Aven Nelson 7302 (OSU). CARBON CO.: Pryor Mountain desert: narrow canyon on E flank of Pryor Mountains ca 0.4 miles N of the Wyoming State line, 30 May 2001, Walter Fertig 19428 (RM). FREMONT CO.: E of Agate Flat or BLM Road 2404, ca 15.7 air mi NW of Three Forks Junction, ca 9 air mi NE of Jeffrey City, 3 July 1997, Amy J. Roderick, Pamela Foster 1528 (RM); Atlantic City, 22 June 1946, Helen L. Cannon, Maude C. Weigand s.n. (RM); White Pass and vicinity, ca 6 air mi S of Ramshorn Peak, ca 9 air mi NW of Dubois, 28 June 1984, B. E. Nelson 10927 (RM); Across US hwy 26 from Haines' Farm, ca 9 mi W of Riverton on Wyo Hwy 26, 2 June 1986, June Haines 6106B (RM); Laramie Hills, 10 August 1910, Aven Nelson 9569 (RM); August 1912, Aven Nelson 9665 (WTU); BIG HORN CO.: Six Mile Reservoir and vicinity, ca 9 air mi SW of

Manderson, 15 air mi S of Basin; 5 June 1981, B. E. Nelson 7585 (RM); Potato Ridge, ca 14 air mi ESE of Greybull, 7 June 1981, B. E. Nelson 7736 (RM); Sore Finger Reservoir and vicinity, ca 15 air mi S of Lovell, ca 7.5 air mi N of Emblem, 25 June 1987, B. E. Nelson 13931 (RM); Little Sheep Mountain, ca 7 air mi ESE of Lovell, 25 June 1987, B. E. Nelson 13888 (RM); Rainbow Canyon, ca 18.5 air mi ESE of Lovell, 23 June 1987, B. E. Nelson 13761 (RM). CAMPBELL CO.: Ca. 8 (air) miles SW of Spotted Horse, 12 July 1978, Keith H. Dueholm, Mary Alice Sanguinetti 4008 (RM); ca 4.5 (air) miles W of Pine Tree, 14 July 1978, Keith H. Dueholm, Mary Alice Sanguinetti 4210 (RM); Deadhorse Creek, ca 2.5 miles south of Interstate 90 and 19 miles SW of Gillette, 16 June 1992, Michele Barlow 350 (RM); Ca 14 (air) miles ESE of Reno Junction, 20 June 1978, Ronald R. Hartman, Keith H. Dueholm, Mary Alice Sanguinetti 6819 (RM); Ca. 12 (air) miles NNE of Recluse, 10 July 1978, Keith H. Dueholm, Mary Alice Sanguinetti 3902 (RM); Ca. 14 (air) miles NW of Savageton, 11 July 1978; Keith H. Dueholm, Mary Alice Sanguinettii 3960; 6 ½ miles S of Weston, 21 June 1978, Keith H. Dueholm, R. L. Hartman, Mary Alice Sanguinetti 2397 (RM). CARBON CO.: W of Seperation Rim, ca 14.5 air mi SE of Bairoil, 26 June 1995 B. E. Nelson 35527 (RM); Fort Steele, 16 June 1900, Aven Nelson (NEB); Near Table Mountain ca 6 air mi SE of Ferris, ca 3 air mi N of Windy Ridge, 21 July 1995, Laura Welp 6511 (RM). Along Buzzard Road, ca 2 air mi NE of Rendle Point above Separation Flats ca 16 air mi NNW of Rawlins, 3 June 1994, B. E. Nelson, Laura Welp 30950 (RM). Stinkhole Draw and ridges to NE, ca 16.5 air mi N of Sinclair; ca 17.5 air mi NE of Rawlins, 20 June 1997, B. E. Nelson, Amy J. Roderick 40467 (RM); Pathfinder Reservoir, Tye Draw leading into reservoir, ca 8 air mi N of Seminoe Dam, ca 38 air mi NE of Sinclair, 12 July 1997, Amy J. Roderick 2095 (RM); Ca. 5 air mi NW of Muddy Gap Junction (Three Forks), 30 June 1985, June Haines 4503 (RM). CONVERSE CO.: Ca 15 miles ENE of Bill, ca 43 air mi NE

of Douglas, 21 June 1994, B. E. Nelson 31858 (RM); Above the head of Shonsy Draw off Pine Ridge, ca 28 air mi NNW of Glenrock; ca 47.5 air mi NW of Douglas, 13 July 1994, B. E. Nelson 32808 (RM); Ca 4 air mi SSE of Douglas, 1 July 1993, Ronald L. Hartman 39399 (RM); Along Spring Canyon or County Road 11 and La Prele Main Canal at the base and NNE of Table Mountain, ca 7.8 air mi W of Douglas, ca 6.8 air mi S of Orpha, 26 August 1993, B. E. Nelson 29292 (RM); Flats N of Betty Reservoir, 5 July 1978, Keith H. Dueholm, Mary Alice Sanguinetti 3292 (RM); . FREMONT CO.: Sweetwater Rocks; ca 8 air mi ENE of Jeffrey City, 4 August 1985, June Haines, Georgia Haines 5357 (RM); 5 miles west of Shoshoni, 21 June 1947, A. A. Beetle 4548 (RM); East Fork of the Big Wind River, 7 air mi ESE of Dubois, 23 June 1983, Ronald L. Hartman 15606 (RM); Wyo Game and Fish Dept's Whiskey Basin Big Game winter range, ca 4-5 air mi S of Dubois, 31 August 1985, Scott Benson 40 (RM); Beaver Rim, ca 17 air mi NE of Jeffrey City, 3 July 1981, Ronald L. Hartman 13604 (RM); Badwater Road near East Fork of Dry Creek crossing, 4 July 1998, R. Scott 11250 (RM); Lysite Badlands, Pony Cr #1 gas line site just W of Moneta-Lysite Rd, 3.3 rd mi N of Moneta, 16 June 1986, Hollis Marriot 10062 (RM). HOT SPRINGS CO.: 22.5 mi SE of Hot Springs-Park Co. line on Wyo. 120, 16 June 1968, James and Helen Mears, 2297 (LL); S of Thermopolis, 13 June 1973, B. L. Turner 8085 (LL); On the road to Grass Creek, ca 3 air mi N of Grass Creek, ca 40 air mi NW of Thermopolis, 19 June 1983, B. E. Nelson 9513 (RM); Ca 3.5 air mi N of Hamilton Dome; ca 22 air mi NW of Thermopolis along Wagonhound Creek, 16 June 1983, B. E. Nelson 9398 (RM). JOHNSON CO.: Culp Draw, ca 22 (air) miles NNE of Sussex, 27 June 1978, Ronald L. Hartman, Mary Alice Sanguinetti 7750 (RM); Ca. 9 (air) miles S of Arvada, 22 June 1979, Kieth H. Dueholm 7720 (RM). LINCOLN CO.: Commissary Ridge, 0.5 air mi SE of Kemmerer Reservoir along power lines E of paved road; ca 12 air mi NW of Kemmerer, 27 June 1992,

Ronald L. Hartman 33477 (RM); Tunp Range, Rock Creek Ridge, ridge along upper reaches of Antelope Creek, 27 June 1992, Ronald L. Hartman 33630 (RM). NATRONA CO.: Laramie Range, County Road 403, ca 0.2 to 1.2 air mi W of Twin Buttes, 11 June 1997, Ronald L. Hartman, Amy J. Roderick, Cherie Winner 57528 (RM); Casper Mountain area, Just behind Casper College on "C" Hill, 19 June 1962, Francis X Joswik 117 (RM); Ca 6 air mi NW of Arminto, 6 July 1993, Ronald L. Hartman 40451 (RM); Ca. 24 (air) miles N Natrona, 3 July 1979, Keith H. Dueholm 7707 (RM); Ca 1.5 mi E of Arminto, 6 July 1993, Ronald L. Hartman, T. W. Nelson 40322 (RM); 11. 75 mi S of Alcova on Rd. to Alcova Dam, 17 June 1968, James and Helen Mears, 3021 (LL); Near the end of Ormsby or County Road 705 ca 2.3 air mi w of Converse County on the divide between Sand Spring Creek and McKenzie Draw, ca 21 air mi NNE of Casper, 27 June 1994, B. E. Nelson 32163 (RM); Ca 3.5 (air) miles SE Powder River, 5 July 1979, Keith H. Dueholm 7825 (RM); Along west side of County Road 410, ca. 4.4 air mi E of Independence Rock; ca 22.5 air mi NE of Three Forks Junction, 14 August 1997, Amy J. Roderick 3665 (RM). NIOBRARA CO.: Ca. 6 (air) miles southwest of Redbird, 23 June 1979, Kieth H. Dueholm 7366 (RM); Ca. 31 air miles NW of Lusk, ca. 8 air miles WSW of Lance Creek, 2 June 1978, B. E. Nelson 1607 (RM). PARK CO.: Near the head of Spring Creek, ca 6 air mi S of Cody, 26 June 1983, B. E. Nelson 9916 (RM); Shearing Pens Reservoir above West Branch Whistle Creek, ca 12 air mi SSE of Powell, 30 Jun 1987, B. E. Nelson 14097 (RM); Ca 2.3 air mi W of Fannie on the road from Elk Basin Oil Field to Fannie, ca 16 air mi NNE of Powell, 21 June 1987, B. E. Nelson 13752 (RM). SUBLETTE CO.: Southeast end of Deer Hill and lower slopes, ca 9 air mi W of Big Piney, 23 June 1992, Ronald L. Hartman 33177 (RM); SWEETWATER CO.: Ca 3 air mi e of Fontenelle, 22 May 1994, Ronald L. Hartman, Tom Cramer, Charmaine Refsdal 45152 (RM)Drainage to Gap Creek and along Gap Creek, ca 2.5 air

mi N of Red Creek badlands; ca 5 air mi S of Titsworth Gap; ca 31 air mi SSE of Rock Springs, 26 June 1997, Beth Ward 6324 (RM); North facing slope of Rifles Rim, ca 1 air mi W of Wyo Hwy 430; ca 35.5 air mi SSE of Rock Springs, 9 June 1997, Beth Ward 4853 (RM); ca 13.5 air mi SW of Green River, 3.9 mi W of Wyo Hwy 530 on 2 track, 10 June 1995, C. H. Refsdal 3839 (RM); Steamboat Mt., 9 June 1900, Aven Nelson 7049 (RM, NEB); Along Lost Soldier Creek on Bairoil or County Road 22, ca 4.5 air mi W of Bairoil, ca 42 air mi NNE of Wamsutter, ca 36.5 air mi NW of Rawlins, 5 June 1994, B. E. Nelson, Laura Welp 31084 (RM); NE of Cedar Mountain, ca 35 air mi SW of Green River and 10 ½ air mi N of Burntfork, 19 July 1979, Ann Aldrich 495 (RM); Flaming Gorge National Recreation Area, ca 8 air mi NW of Dutch John; 2.1 mi W of the Forest boundary, 7 June 1995, C. H. Refsdal, S. Goodrich 3771 (RM); Slopes of Simpson Gulch and Big Sandy River and river bottom area adjacent to Big Sandy River, ca 9 air mi SW of the confluence of Big Sandy River and Little Sandy Creek, ca 9.5 air mi SW of Farson, 24 July 1997, Beth Ward 6117 (RM); Ca 5 air mi E of the green River, ca 1 air mi W of Alkali Creek; ca 18 air mi WNW of Rock Springs, 24 June 1997, Beth Ward 6230 (RM); Great Divide Basin, ca 7.5 air mi N of Eagle's Nest; ca 14 air mi NE of Bastard Butte, 24 June 1994, Laura Welp 5752 (RM); Battle Spring Draw, ca 27 air mi SW of Bairoil, ca 26 air mi N of Wamsutter, 21 July 1995, Laura Welp 6636 (RM); Between Red Lake and Chalk Butte at the edge of Red Desert Basin along County Road 20, ca 30 air mi NW of Wamsutter, ca 49 air mi ENE of Rock Springs, 5 July 1995, B. E. Nelson 36336 (RM); Near Dugout Wash in Red Desert, ca 25.5 air mi WNW of Wamsutter; ca 46 air mi ENE of Rock Springs, 5 July 1995, B. E. Nelson 36264 (RM); UINTA CO.: Lower east flank of Hickey Mountain, ca 3 air mi NNW of Lonetree, 13 July 1995, C. H. Refsdal 5334 (RM); East end of Wildcat Butte, ca 14.8 air mi NE of Lyman, 5.4 mi E of on Church Butte Road, 18 June 1995, C. H. Refsdal, B. E. Nelson 4167

(RM).WASHAKIE CO.: Dry Cottonwood Creek just above Fifteenmile Creek, ca 20 air mi NW of Worland, 12 June 1988, B. E. Nelson, Erik Nelson 15710 (RM); Ca 14 air mi SSW of Tensleep on Blue Bank Road, 11 June 1981, B. E. Nelson 8009 (RM);Ca 15 air mi SSE of Worland on the Nowater Trail, 9 June 1981, B. E. Nelson 7884 (RM); WESTON CO.: Black Hills, W of WY Hwy 116 near Jct with Arch Cr Rd, ca 5 air mi NNE of Upton, 27 June 1984 (RM);

4b. Lappula fremontii (Torr.) Greene var. *nelsonii* var. novem

***Lappula fremontii* (Torr) Greene** (Type: U.S.A. Wyoming Park Co.: Soda Butte, on the disintegrated formation. Aven Nelson and Elias Nelson 5872, July 15, 1899. (Holotype designated here: RM-19715!).

The specimen chosen as the holotype of this new variety was labeled by Nelson as a "Co-type" of *L. erecta* A. Nelson, but represents a different form from the specimen on which he wrote "Type". This variety is named in Aven Nelson's honor for the work that he did on the North American species, particularly in Wyoming where he collected many *Lappula* specimens throughout his career.

Description

Herb Annual (biennial?), **Roots** single, narrow or stout and conical. **Stems** 1—4 (occasionally more) arising from crown with basal rosette, erect, branching primarily in upper third of plant, 1—3.5—(4) dm high, strigose or appressed long hairy. **Basal leaves** absent or withering at maturity or present and lanceolate or spatulate (1—4 cm x 3—5 mm), strigose or densely appressed long hairy, bases attenuate, apices obtuse to subacute. **Stem leaves** narrow oblong to narrow lanceolate; 1—4 cm long, 3—6—(10) mm wide; abaxial surface frequently sparsely pustulate hairy approaching glabrous at midline or appressed long hispid, adaxial surface more

densely pubescent; bases cuneate to rounded, apices rounded or subacute, margins ciliate or long hairy. **Inflorescences** 5—10 cm, erect and paniculately branched in upper part of plant, and some short single cymes arising from upper half of stem; bracts linear oblong to broad lanceolate, becoming progressively smaller near branch tips 0.5—1.5 cm. **Fruiting pedicels** 2—3 mm ascending **Calyx lobes** linear oblong or linear lanceolate, 0.5—3 in fruit, clasping or spreading. **Corollas** blue, (2)—4—(5)mm wide, lobes ovate to broadly ovate. **Fruits** homomorphic, 2.5—4—(5) mm, broadly lanceolate to triangular. **Nutlets** homomorphic 2—2.5 mm high, lanceolate, nutlets with 2 rows of spines along disk margin; *spines of inner row* arising from inconspicuous margin, spines of primary row 6—7 spines per side, bases free, 1.3—1.5 mm long; *spines of outer row* reduced to glochidate tubercles, primarily in lower half, terete 0.5—1mm long, bases free, abaxial disk narrow lanceolate 2—2.5—(3) mm long x 0.5—1 mm wide, disk surface scabrous tuberculate with prominent line of taller tubercles or triangular tooth-like spines along midline. Adaxial surface scabrous tuberculate; nutlets equally adhering to gynobase (otherwise?). **Style** exceeding nutlet body, style barely exceeded by apical spines. **Gynobase** 2.5 mm.

Discussion

Nelson's initial concept of *L. erecta* was based upon the erect stem and upright branching. His description of the species mentioned a single row of spines on the fruit, though he later noted that his earlier description was an "oversight" (Nelson and Macbride, 1916). He referred to two specimens in his description, but wrote "Type" on the one from Uva, which is cited above in synonymy under *L. fremontii* var. *fremontii* (see discussion above). The second specimen, on which he wrote "Co-type" is selected as the type for this variety. It has smaller fruits that the typical variety and highly reduced spines, a character that is invariant in this

variety, as is the consistently erect branching and long gray canescent vestiture. This variety was found only at higher elevations and in Alaska.

Distribution and Ecology

Montane zone Rocky Mountains, openings in Aspen and Pine and Spruce woodlands, found at higher elevations than the typical variety. Specimens were observed from Alaska, Yukon Territory, Utah, and Wyoming. The specimens cited below are mapped along with the typical variety (as yellow dots) in Figure 2.8

Phenology

Flowering and fruiting: June-July

Specimens cited

CANADA. YUKON. Roadside turnout at KM 1539 of the Alaska Hwy, ca. 2 miles N of Stoney Creek, 3 September 1985, LuDean Marvin 2215 (ALA), Vicinity of Pine Creek, near mi 1019, 28 June 1944, H. M. & L. G. Raup 12091 (ALA). Mile 1019 Alaska Highway, 4 July 1968, S. L. Welsh, G. Moore 7801 (ALA). U.S.A. ALASKA. 3 miles south of Chicken, 25-27 June 1954, Galen Smith, Leslie Viereck 2419 (ALA). Fairbanks Quad, College, University of Alaska campus, 17 June 1969, Pat Rutledge 59 (ALA). Tok, along Alaska Highway, 17 June 1986, R. Lee 86-48 (ALA). WYOMING. SUBLETTE CO.: Black Canyon Creek at base of grade, ca 18 air mi SW of Big Piney, 27 July 1993, Ronald L. Hartman 42384 (RM). TETON CO.: E of Alkali Creek ¾ -1 mi S of the Gros Ventre River, Bridger-Teton National Forest, 23 mi NE of Jackson, 8 July 1996, Erwin Evert 31858 (RM). SWEETWATER CO.: Cedar Moutain, ca 11 air mi NNE of Burntfork, 4 July 1980, Keith Duoholm 10274. UINTA CO.: North Slope Uinta Mountains, ca 7.5 road mi W from Wyo Hwy 414 on County Road 291; Ca 6 air mi SW of Lonetree, 3 July 1994, C. H. Refsdal 1422 (RM); Ca 2 air mi E of Lonetree; ca 8.0 road mi e of

the junction of County Road 1 with Wyo Hwy 414 on south side of Wyo Hwy 414, 7 June 1994, C. H. Refsdal 525 (RM).

5. Lappula heterosperma Greene

Lappula heterosperma* Greene var. *heterosperma. Pittonia. 4:94: 1899. Type: U.S.A. Colorado [Montezuma]: Mancos. Messrs. Baker, Earle, and Tracy 826. (Lectotype designated here: ND-G 042417 image seen! Duplicate of Lectotype: NY!)

Greene lists two collections, the earliest, by him (dried up) from Peach Springs in northern Arizona 2 July 1899 and the second, widely distributed collection, which he noted were in better condition. The latter has been selected as the lectotype. *L. texana* (Scheele) Britt. var. *heterosperma* Greene (A. Nelson & Macbride). Bot. Gaz. 61(1):41. 1916.

L. heterosperma Greene var. *homosperma* A. Nelson Bot. Gaz. 34:29. 1902. Type: U.S.A. Colorado [Weld Co.] New Windsor, June 23, 1899, Mr. G. E. Osterhout (Holotype:RM!)L. *texana* (Scheele) Britt. var. *homosperma* (A. Nelson & Macbride). Bot. Gaz. 61(1):41. 1916.

Description

Herbs annual. **Roots** single, narrow. **Stems** 1—4+, frequently ascending but sometimes erect, much branched from below, sometimes branching above from an erect stem. 0.5—3—(4) dm high, mixed strigose and spreading hairy. **Basal leaves** withering or absent at maturity, or if erect stem then forming a basal rosette, leaves spatulate, 1—4 cm x 0.3—10 mm, abaxial surface long spreading hairy, adaxial surface long spreading hairy, base attenuate, margin long hairy, apex obtuse. **Stem leaves** oblong to broad lanceolate, 0.3—4 cm x 3—5mm, abaxial surface strigose, adaxial surface strigose, bases cuneate, margins ciliate, apices obtuse to subacute. **Inflorescences** up to ca. 20 cm in fruit (variable, some plants low and 5—10 cm long cymes), cymes raceme like or paniculiform, fruiting branches frequently appearing secund. bracts leaflike throughout

becoming progressively smaller, oblanceolate to lanceolate, 1.5—2.5 cm long, upper bracts narrow lanceolate to lanceolate 0.5—1cm long. **Fruiting pedicles** 2—3 mm, erect to ascending. **Calyx lobes** narrow lanceolate 1—2mm, to 4mm in fruit (variable, sometimes enclosing fruit), stellate spreading or accresscent. **Corollas** blue or white limb (2)— 3—4mm wide, lobes divergent, oblong to subovate. **Fruit** homomorphic, subglobose (wider than long), 3—4 mm high **Nutlets** ovate to broadly ovate, 2—2.5 mm long, bases rounded, apices acute, heteromorphic, (*0)—3—4 nutlets* with 4--5 spines arising from highly inflated disk margin; 1.5—2mm and 1-2 spines per side free; disk narrow lanceolate to broadly lanceolate, 2 mm x 1mm disk surface frequently obscured by inflated margin, smooth and frequently with a slight muriculate crest along midline, ventral surface tuberculate throughout, nutlets not adhering to gynobase at maturity; *remaining nutlet/s wingless* with 5 spines along each side of margin (spines ascending), spines subulate and closely adjacent to connate at bases, disk lanceolate 2.5 x 1mm, disk surface muricate, ventral surface tuberculate throughout, nutlet adhering firmly to gynobase. **Style** surpassing nutlets, exceeded by spines. **Gynobase** 2.5—3 mm.

Discussion

This species was considered a variety of *L. texana* in revisionary work on the North America species (Nelson and Macbride 1916; Johnston 1923) and synonymous with *L. texana* Johnston when he put all species with inflated nutlet margins under that species. Here, L. heterosperma is treated as distinct on the basis of its nutlet characters, habit, ecological affinities and geographic distribution. Whereas *L. texana* has strongly dimorphic nutlets with either 4 spines per side (clearly visible on the nutlet with free spines), or nutlets with 6 or more spines per side (see photographs under the treatment for that species), *L. heterosperma* has variable nutlets where even the five free spines on the "odd" nutlet tend to be inflated and connate into a wing (Figure 2.10). The spines on *L. heterosperma* are ascending, rather than widely spreading as in

L. texana, and the style, while visible among the nutlets is exceeded by spines near their apices. This plant is common on the Mancos shale and occurs frequently in openings in sagebrush and pinyon-juniper woodlands throughout the Colorado Plateau region of southern Colorado and Utah. Collections from British Columbia and Montana have also been referred to this species, but not many specimens were seen, and they are not confidently placed here (see specimens cited below).

Distribution and Ecology

Open, sparsely vegetated areas in sagebrush and Mancos shale , pinyon pine-juniper association, Colorado Plateau, Chihuahua desert scrub. Specimens were mapped by manually placing dots on a basemap in ArcGIS online. The address search feature was used to find localities and the placement of the dot was done manually. The measure tool was used to estimate distances from towns and landmarks. All dots represented in the map are cited below. The Mexico localities were not found and so they were not mapped.

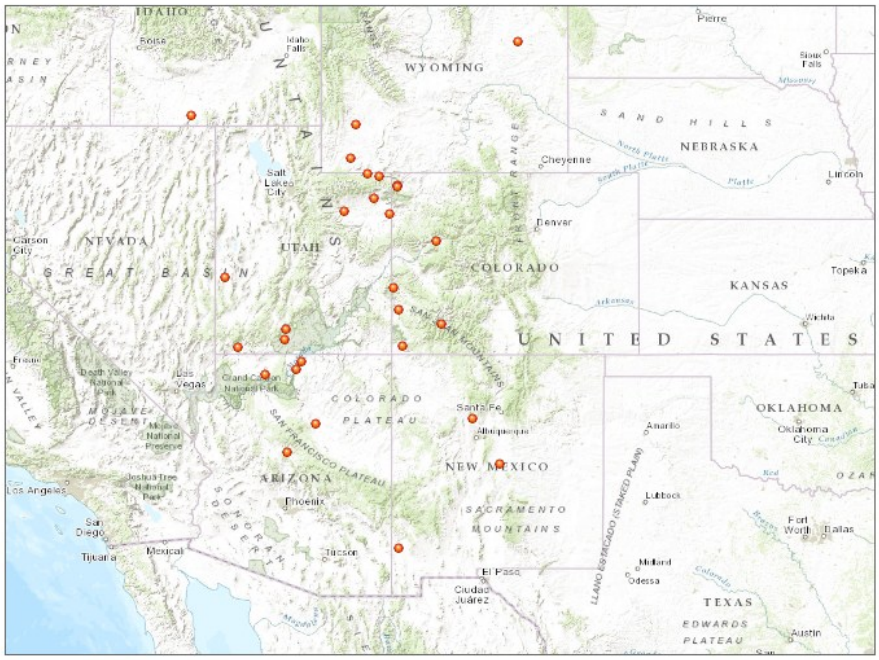


Figure 2.9. Map of *L. heterosperma* based on specimen data.

Phenology

Flowering and fruiting: May—June

Specimens cited

MEXICO. **SONORA.** Municipio de Aqua Prieta, Animas Valley, 58.7 km (by air) E of Agua Prieta, Cuenca Los Ojos Foundation property, 15 May 2010, T. R. Devender, A. L. Reina-G., C. Roll, 2010-407 (ARIZ).,; 33 km east of Aqua Prieta on MEX 2, Rancho Guadalupe, 1 May 2007, T. R. Van Devender, A. L. Reina 2007-503 (ARIZ). U. S. A**. ARIZONA.** COCONINO CO.: Road south of Hwy 89 in House Rock Valley; 26 May 1999, Steven McLaughlin 7909 (ARIZ). MOHAVE CO.: Hack Canyon about 1.0 mile below Hack tank and junction with highway to Grand Canyon National Monument, 2 June 1977, C. T. Mason, 3247, C. T. Mason, J. R. Reeder, 3247 (ARIZ). COCONINO CO.: In loose, sandy soil on east-facing slope at base of cliff opposite falls; Grand Falls of the Little Colorado River, 7 June 1966, C. T. Mason, Jr, 2547, W. E. Niles 775, W. S. Phillips, E. F. Haase (ARIZ), YAVAPAI CO: Tuzigoot National Monument.

East of Tavasci Marsh on path to ridgetop, 8 April 2003, Meg M. Quinn, James B. MacAdam 680 (ARIZ). **COLORADO**: GARFIELD CO.: Ca 5 air mi N of Rifle, 25 May 1991, James P. Vanderhorst 2163 (RM). MESA CO.: At base of Mount Garfield, 5 mi N of Clifton, 16 May 1978, W. A. Weber 15326 (RM). MONTEZUMA CO.:: Ca 12 air mi NW of Cortez at Burro Canyon, 1 June 1995, Lynn Marie Moore 4662 (RM) Ute Indian Reservation, near Towaoc, 23 May 1936, David F. Costello 2026 (USFS-RM). MOFFAT CO.: Ridge separation Conway from Vermillion drainage, between Greystone and Gates of Lodore, 26 June 1965, William A. Weber and Peter Salamun 12630 (WTU). MONTROSE CO: Sinbad Valley, south end, 30 May 1995, Ronald L. Hartman, Timothy K. Lowrey, Robert Sivinski 50941 (RM); 6 mi S of Silvey's Pocket, Little Gypson Valley, 30 May 1982, W. A. Weber, R. & J. Wittman 106048 (WTU). SAN MIGUEL CO.: Ca 15 air mi NE of Dove Creek, Disapointment Valley, 21 June 1995, Lynn Marie Moore 5843 (RM). **IDAHO**. CUSTER CO: Challis, 15 July 1916, J. F. Macbride, Edwin B. Payson 3227; 8 miles south of Challis, 7 June 1941, J. H. Christ 12216 (NY). LEMHI CO. 42 miles southwest of Salmon City, 7 June 1941, J. H. Christ 12222 (NY). **MONTANA.** Jack Creek Canyon, 19 July 1897, P. A. Rydberg, Ernst A. Bessey 4892 (NY). Yankee Jim Canyon, Gardiner, 4 July 1899 (WTU). GALLITIN CO.: Lombard, 1 June 1901, E. J. Moore (RM). **NEW MEXICO.** Chaco Canyon Nat'l. Monument, May 1937, Hastings, s.n. (ARIZ). Rio Puerco at crossing near village of Guadalupe 7 June 1974, Vorsila L. Bohrer 1863 (ARIZ). HILDAGO CO.: Lordsburg Mesa, along Redrock-Duncan shortcut, 4.6 miles west of New Mexico Highway 464, 17.5 airline miles north-northwest of downtown Lordsburg, 1 May 1973, Noel H. Holmgren, Patricia K. Homgren 7033 (WTU) SANDOVAL CO.: San Ysidro Pasture Allotment, 18 mi SW of San Ysidro, 21 July 1979, C. Pase (RM). **UTAH.** DAGGETT CO.: Ca 15.3 air mi E of Dutch John, 31 May 1995, C. H. Refsdal 3418 (RM), 1 mi S of Manila, 12 July

1935, Bassett Maguire 12373 (GH). DUCHESNE CO. About 18 miles west of Duchesne, 5 July 1947, Roxana S. Ferris 11294 (WTU). GARFIELD CO. 1.3 miles south of the junction of the Cottonwood Wash Road with Utah 54 at Cannonville in upper Cottonwood Wash, 3 June 1967, James L. Reveal, Johnnie L. Gentry, Jr. Gerrit Davidse (RM, TEX, WTU). KANE CO.: along the Paria "River", 8 road miles northwest of highway 89A,, 28 May 1965, Arthur Cronquist 10203 (WTU). MILLARD CO. South of Tunnel Spring Mountain, 4 June 1965, Sam F. Brewster, Jr., 4 June 1965, Sam F. Brewster, Jr. 18 (USFS-RM)**,** UINTAH CO.: 15 miles west of Vernal on US 40, 11 June 1965, Don G. Despain 42 (RM, WTU). Coyote Basin, 13.4 road mi S of Naples, thence E of dirt road0.3 mi, 19 May 2001, N. Snow 8420 (RM). 5 miles west of Vernal, on US 40, 20-21 June 1967, C. L. Porter & Marjorie W. Porter 10417 (RM, TEX, WTU); WASHINTON CO.: Ten miles east of St. George, 10 May 1938, Fred A. Barkley 3220 (WTU). WAYNE CO. near Capitol Reef National Monument, Pleasant Creek Ranch, ca 10 mi S of Fruita, 5 June 1953, Rogers McVaugh 14463 (TEX). WASHINGTON CO.: White Cliffs NW of Diamond Valley Ranch, 28 May 1986, R. B. Warrick 1614 (RM). **WYOMING.** BIG HORN CO.: Sykes Mt. 10 June 1983, Robert W. Lichvar 6030 (RM); CAMPBELL CO.: ca 15 (air) miles SSE of Reno Junction, 10 June 1978, Ronald L. Hartman, Kieth H. Dueholm, 6521a (RM). LINCOLN CO.:South end of Fontenelle Reservoir, ca 2 air mi NW of Fontenelle Dam, 5 July 1995, Tom Cramer 7305 (RM). PARK CO.: Along W side of YU Bench Rd. ca 8 mi S of Hwy 14, 16, 20 SE of Cody, 13 June 1990, E. Evert 18925 (RM). SWEETWATER CO.: ca 18 air mi SW of Green River, 4.7 air mi S of FMC access road off of Westvaco Road, 27 June 1995, C. F. Refsdal 4447 (RM). UINTA CO.: 6 mi east of Lyman, 19 June 1956, C. L. Porter 7009 (TEX), Wildcat Butte between Church Butte Road and I-80 at Sweetwater County, ca 14.8 air mi NE of Lyman, 18 June 1995, B. E. Nelson, C. H. Refsdal 35233 (RM).

Figure 2.10 Nutlet variation in *L. heterosperma.* Images showing some of the variation in the degree of inflation of the nutlet margin among individuals. Some specimens can have fruits where all the nutlets have inflated margins, in others the one or more nutlets have margins that are barely inflated. In all specimens, a line of muricate bumps was observed along the median line of the abaxial surface in the nutlets with inflated margins.

6. Lappula longispina

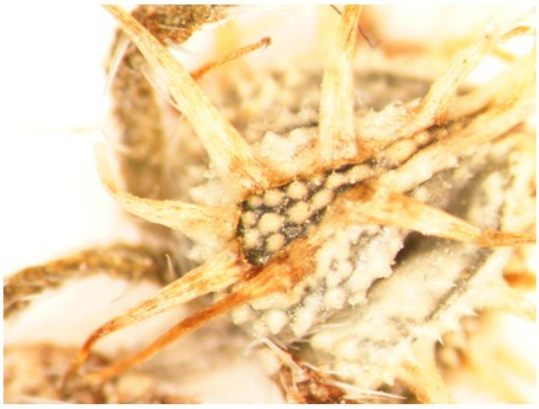
Lappula longispina sp. nov. TYPE: USA Washington Adams Co.: North of Othello, vicinity of Lyle Lake, 49.8955º N, -119.20310Wº, gentle to moderate slope above Lyle Lake. *Artemesia tridentata* and bunchgrass, moderately vegetated. Susan J. Rolfsmeier and Steven B. Rolfsmeier 1123, 20 June 2009 (Holotype designated here: deposited at KSC).

Description

Herbs Annual **Roots** single, narrow. **Stems** single (or up to 7 arising from single crown) erect, ca. 30 cm, branching from the middle or throughout, mixed short appressed and long pilose hairy. Basal leaves absent or withered at maturity, **Stem leaves** linear oblong to oblong-lanceolate, 1.5—4 cm x 2—5 mm wide, abaxial surface dense tuberculate hairy, adaxial surface long hairy less densely hairy, bases cuneate, margins ciliate, apices subacute to acute. **Inflorescences** raceme-like, ascending, 5—15 cm long; bracts lanceolate becoming smaller at branch tips 3 mm-1.5 cm. **Fruiting pedicels** 2-3 mm. erect, becoming arcuate in fruit, **Calyx lobes** linear, 0.5 to 4mm in fruit. Corollas white, 0.5—1mm (only late flowers observed), lobes narrow and erect, linear **Fruits** homomorphic, **Nutlet** margins with a single/other row of 8-10 spines total (4-5 per side) spines horizontally spreading, angled more or less 45º relative to disk surface, adjacent or connate at their bases, strap-like and frequently with hairlike spines near the base, lateral and basal spines > 2 times longer than apical spines, length of longest spines 1.5-2mm, shortest spines .7-.8 , abaxial disk (outer facing surface) 1.5-2 x .5-.8 mm wide, disk with irregular rows of tubercles, surface becoming smooth at disk margin, keel of taller tubercles at midline, ventral surface of nutlets evenly spiny tuberculate throughout; none of the nutlets adhering more firmly to the gynobase. **Style** more equal to nutlet apex, nutlet exceeded by apical spines. **Gynobase** 1.6—2 mm.

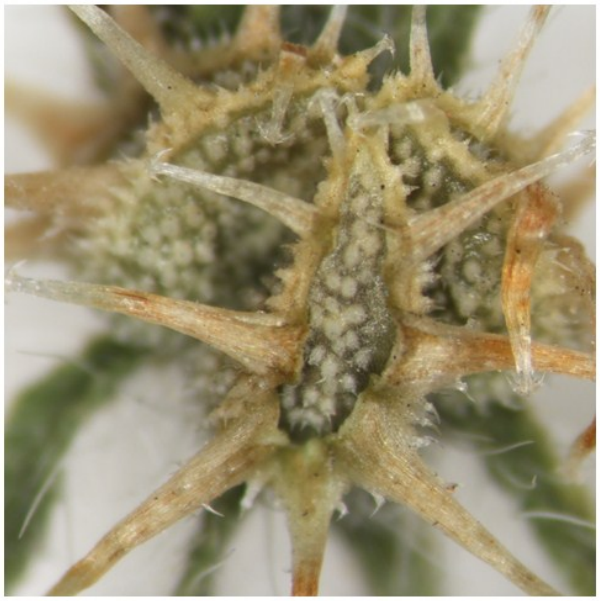
Discussion

Lappula longispina is distinct from other North American species and from *Lappula patula* Asch. ex Gürke to which it is superficially similar. What is here treated as *L. occidentalis* var. *stricta* also has secondary spines or fine bristles on the outer surface of the spines, although that variety has a wider dorsal face and spines that are frequently connate into a thin margin in most fruits. Other characters that distinguish this species are the uniformly spiny tuberculate surface of the fruits, the spines that extent from the disk surface at forty-five degree angle, and the narrow width of the disk. It is similar to the Eurasian species *L. patula*, however in that species the tubercles on the disk are arranged in orderly lines, and the sides are not uniformly spiny tuberculate. Below the fruits of both species are shown for comparison (**Error! Reference ource not found.**).



Lappula patula Asch. ex Gürke .

Left hand side, image showing abaxial surface of fruit. Right hand side, image showing adaxial surface.



L. longispina sp. nov.

Left hand side, image of fruit showing narrow adaxial disk and angle of spines relative to the surface. Right hand side, image of fruit showing tuberculate adaxial surface and uneven rows of tubercles on the abaxial disk.

Figure 2.11Figure 2.11 Fruit characters in *L. longispina*. Differences in fruit morphology between *L. patula* (above) and *L. longispina* (below) Adams Co. Washington, 16 Jun 2009, SJR 1122.

Distribution and Ecology

Canada: British Columbia; United States: Idaho, Oregon WashingtonSagebrush steppe, basalt scablands, rocky hillsides, sand dunes.

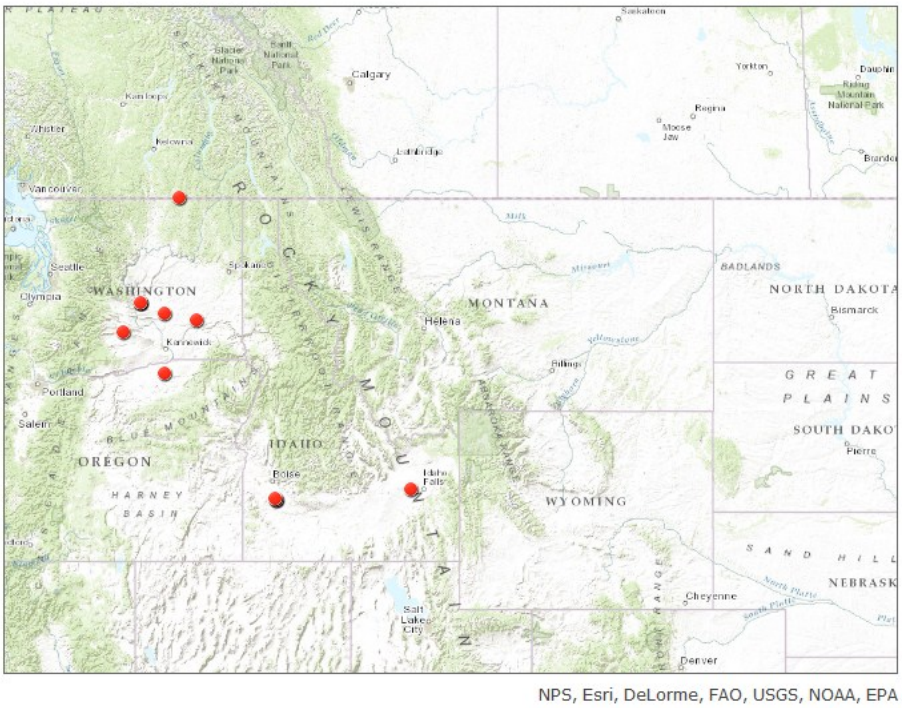


Figure 2.12. Distribution of *L. longispina*

Phenology

mid April -June- (July)

Specimens cited

CANADA. British Columbia: Midway, 25 June 1938, J. W. Eastham *s. n.* (UBC); UNITED STATES. Idaho. Bonneville Co.: 25 mi west of Idaho Falls, 19 June 1953, J. H. Christ 53-92 (WTU); Idaho. Ada Co.: 14 miles southeast of Boise, 15 June 1955, William H. Baker 12920 (WTU); Idaho. Boise Co.: ca. 10 miles southeast of Boise, 2 June 1944, C. L. Hitchcock and C. V. Muhlick 8638 (WTU); Oregon. Morrow Co.: near Lexington, 7 May 1894, J. B. Leiberg 35 (RM); Oregon. Morrow: about 13 air miles south southeast of Boardman, 4 June 1987, Richard R. Halse 3450 (OSU, ARIZ); Oregon. Umatilla Co.: near Echo, 16 May 1923, William

Sherwood 12974 (OSU); Washington. Adams Co.: 31 May 1950, about 10 miles west of Washtucna, Arthur Cronquist 6482 (WTU); Washington [Benton Co.]: Rattlesnake Mountains, 5 June 1901, J. S. Cotton 407 (ND, RM); Washington. Douglas: Badger Mountain, 1 June 1940, J. William Thompson 14641 (UBC, RM, WTU); Washington. Grant Co.: near Vantage, 18 May 1935, J. William Thompson 11489 ½ (ND,NY, WTU x2) Washington. Lincoln Co.: near Clark, 17 June 1935, J. William Thompson 11681 (WTU x2, NY); Washington. Yakima Co.: 5 mi. south of Toppenish Creek, 8 May 1938, C. L. Hitchcock and J. S. Martin 3405 (WTU, RM);

7. Lappula montana Greene

Lappula montana Greene. Pittonia. 4:96. 1899. Type: U.S.A. Montana [Lewis and Clark County]: Helena. 1887, Rev. F. D. Kelsey [192] (Holotype: NDG: 42423).

Echinospermum brachycentrum Ledeb. var. *brachystyla* A. Gray, Proc. Acad. Nat. Sci. Philadelphia. 21 (2): 413. 1886. CANADA. BRITISH COLUMBIA: [Kamloops Division Yale Land Distr.] Spence's Bridge, Thompson River. "J. Fletcher, fide Macoun" (Holotype:image seen DAO!). *Lappula brachystyla* (Gray) Macbride. Contr. Gray Herb. 48: 40.1916. Canada. British Columbia: [Kamloops Division Yale Land Distr] Spence's Bridge, Thompson River, James 29 May 1885, James Fletcher 1371 (Holotype: image seen DAO!)

Boivin annotated the specimen in 1970 and noted that the number 1553 published by Macbride, and 1371, listed on the specimen, were not collection numbers but reference numbers to two catalogs that were published, one detailed and one not. Note that Gray was not specific in his description about the collection details writing only "Fletcher fide Macoun", but Macbride, in elevated Gray's variety to the species level did specify a collection number.

Lappula echinata fo. brachystyla (A. Gray) B. Boivin. Le Naturaliste Canadien 93(6): 1060. 1966[1967]. *Lappula redowskii* fo. *brachystyla* (A. Gray) Scoggan. Scoggan, H. J.. Dicotyledoneae (Loasaceae to Compositae). Part 4.. In Fl. Canada. National Museums of Canada, Ottawa. 1979]

Lappula anoplocarpa Greene, Ottawa Nat. 16: 39. 1902

Canada: British Columbia, [Kamloops Division Yale Land Distr]Spence's Bridge, 25 May 1889, Mr. John Macoun, 17038 of Canadian Survey Herbarium (Holotype: CAN; fragment of Holotype: ND-G- 042391!).

Herbs Annual. **Roots** single, narrow and straight. **Stems** single, erect, branching in upper forth of plant,1.4—4 dm, appressed hairy. Basal leaves spatulate 1—2 cm x 5-10mm. **Stem leaves** narrow lanceolate to oblanceolate 2—4 cm x 2.5—4 mm, abaxial surface densely appressed hairy, adaxial surface densely appressed hairy, bases cuneate, margins long hairy, apices subacute to acute. **Inflorescences** to 3—5 cm (more?) in fruit. raceme like, erect. Bracts not leaflike, narrow oblong to linear becoming progressively smaller above 0.5—1 cm long. **Fruiting pedicles** 2—3 mm, erect. **Calyx lobes** linear 2—2.5 mm to ca. 4mm in fruit. **Corollas** not observed. **Fruits** homomorphic 2 mm, subovate. **Nutlet** homomorphic, broadly lanceolate, 1.5 mm long, bases rounded, apices acuminate, nutlets with a single row of thin spines 1—1.2 mm long or absent, arising from a thin smooth margin, bases free; disk lanceolate smaller than nutlet body, 1 x 0.5 mm, no obvious central keel, disk surface smooth to papillate or muriculate, adaxial surface muriculate or papillate becoming smooth toward nutlet apices, all nutlets releasing from gynobase. **Style** surpassing nutlets, about equal with or surpassing spines. **Gynobase** 2—2.3 mm long.

Discussion

The specimen from Helena by which Greene typified as *L. montana* seemed similar enough to those of *L. anoplocarpa* to consider them the same species (see Figure 2.13 which shows an image of fruits from the packets attached to the sheets). If however it is determined that the two are separate, then the oldest available name at the species level for the Canadian species is *L. anoplocarpa* Greene. The reduced size of the fruit, the disk smaller than the nutlet body and the narrow erect growth form with reduced leaves separate it from *L. occidentalis*. The species is maintained here, primarily because it is distinctive and it is not clear at present whether it is a variety of *L. occidentalis* or not and it should be studied in more detail before further nomenclatural changes are made. *L. occidentalis* is variable throughout its range, further study is needed to tease apart the geographic and morphological variation, as it is possible that fruits become smaller in the northern part of its range. However, if this is a species distinct from *L. occidentalis* with a narrow range within British Columbia and Montana, then submerging it within the widespread and common *L. occidentalis* would seem a mistake. *Lappula brachycentroides* M. Pop. a species remarkable similar to this one occurs in Siberia. I was able to observe this species in the herbarium and to sample DNA from a specimen of that species from Asia and it grouped with samples of *L.squarrosa*, *L. tuvinica,* and *L. consanguinea,* all species with multiple rows of spines (See phylogenetic study). What those species had in common was short, needle-like spines. Samples of *L. montana* were not included in the study, so its relationship to the other North American and Eurasian species is still unknown. Given its known narrow range in British Columbia, and that it was difficult to determine from the specimens on hand the extent of its variation relative to *L. occidentalis*, this is a species that could benefit from more intense field and herbarium study.

Figure 2.13 Close up of *L. montana* fruits. The image on the left is of fruits in the packet of ND-G 042391, considered by Greene to be *L. anoplocarpa*. The image on the right is of fruits in the packet on the type specimen of *L. montana* (ND-G 642423). Here they are treated as *L. montana* (see discussion in text).

Distribution and Ecology

British Columbia, Northern Rockies Mountains, western Montana.

Distribution is not well known. The distribution map is based on specimens observed and confidently identified as *L. montana*. The map was made in ArcGIS online by searching for the locality by name and mapping each dot by hand. Distances from localities and various landmark features was estimated using the measureing tool. The specimens included in the map are listed below under specimens cited.

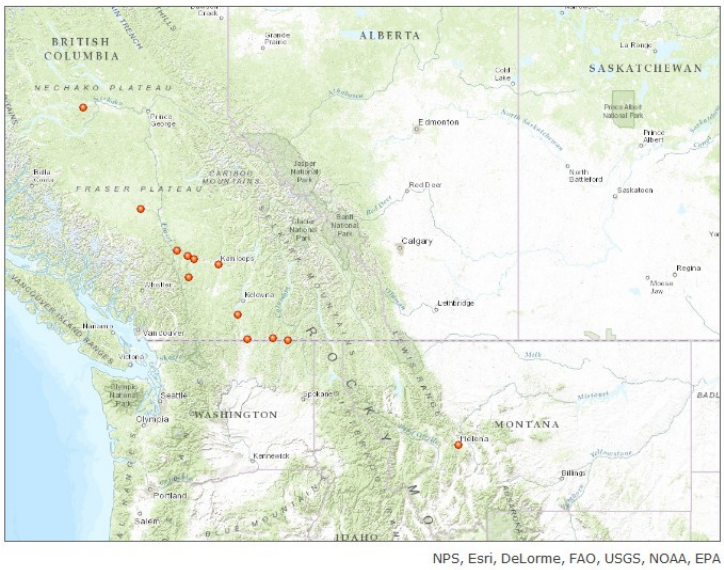


Figure 2.14. Distribution map of *L. montana*. Dots represent mature specimens confidently identified to species.

Phenology

Flowering and Fruiting: June—August

Specimens cited

Since immature fruits of *L. occidentalis* are also small, specimens with mature fruits were chosen as representative. These were mapped CANADA. **BRITISH COLUMBIA.** Trout Creek near Summerland, July 1974, Larmour, Ng s.n. (UBC); Junction of Hanceville River & Farwell Canyon Rd (Forestry Rd. 2000), ca 70 km SW of Williams Lake, 23 June 1995, O. Lee 342 (UBC); 14 miles west of Keremeos on road to Princeton, 17 June 1956, J. A. Calder, J. A. Parmalee, R. L. Taylor 17549 (ALA); 2 ½ miles north of Grand Forks on east side of Granby River, 21 June 1953, J. A. Calder, D. B. O. Savile, 9490 (RM); Along Fraser River, 3 km south of Sheep Creek Bridge (between Williams Lake & Riske Creek), August 1977, C. J. Marchant s.n.(UBC). Upper Hat Creek, Marble Mts., 14 July 1938, J. William Thompson, Emily M. Thompson 487 (WTU). Hat Creek Valley, 26 June 1938, J. William Thompson, Emily M. Thompson 204 (WTU); Anarchist Mt. just east of Lake Osooyoos, 18 July 1938, J. William Thompson 14385 (WTU); Arid Slopes in Thompson River Canyon near Spences Bridge,25 June 1938, J. William Thompson, Emily M. Thompson 199 (WTU), Near Haylmore 693, 28 July 1938, J. William Thompson, Emily M. Thompson 693 (WTU); 13 miles NNW of Savona along Deadman River, 31 May 1956, J. A. Calder, J. A. Parmelee, R. L. Taylor 16867 (WTU).

8. *Lappula occidentalis* (S. Watson) Greene

Key to varieties

Spines of nutlets widely spaced to closely adjacent but not connate into a wing. Secondary prickles not observed on adaxial surface of spines. Fruits typically homomorphic (single fruit type on plant, single nutlet type)…….*L. occidentalis* var. *occidentalis*.

Spines of nutlets typically connate into a thin wing (at least in some nutlets in a fruit or on some fruits on a single plant). Secondary prickles observed on adaxial surface of spines (sometimes only at base of spines). Fruits typically heteromorphic (more than one fruit type may be present on plant, or more than one nutlet type in a single fruit)…*L. occidentalis* var. *stricta*.

8a. Lappula occidentalis (S. Watson) Greene var. *occidentalis.*

Lappula occidentalis* (S. Watson) Greene var. *occidentalis. 1899. Pittonia. 4: 97.

Echinospermum redowskii Lehm. var. *occidentale* S. Watson, United States Geological Expolration [sic] of the Fortieth Parallel. Vol. 5, Botany: 246. 1871. TYPE: U.S.A. Nevada. [Washoe Co.]: Truckee Valley. July 1867, W.W. Bailey 861 (Lectotype designated here: GH 0092811!; Duplicate of Lectotype: US-26367!)

Watson wrote: “From Western Texas to Arizona and northward to the Saskatchewan, Bear Lake and Fort Youkon [sic]. Frequent in the valleys and on the mountains from the Sierras to the Wahsatch [sic] 4-8,000 feet altitude (861). Syntypes (GH, US, NY) were collected at various stations in Nevada all with the same number. Bailey’s collection at GH had more mature fruits compared to the other specimens and chosen for the lectotype. Watson’s collection from Pleasant Valley NV (GH: 0009813) also had mature fruits but this was a mixed sheet included a specimen of *L. desertorum* (Greene).

Lappula occidentalis (S. Watson) *Rydberg*, Mem. N. Y. Bot. Gard. 1: 329. 1900.

L. calycosa Rydb. Bull. Torrey Bot. Club 28(1): 30–31.1901. Type: U.S.A. Colorado: [Huerfano Co.]: Walsenburg 1900, Rydberg & Vreeland, 5715. (Holotype: NY!).

Description

Herbs annual. **Roots** single, narrow to conical. **Stems** 1—2 (3+) or one with flowering branches emerging from root crown, erect, branched from above (or throughout) cymes arising along stem in robust plants, erect or ascending, 2—6 dm high mixed strigose and spreading hairy. **Basal leaves** forming a forming rosette in more robust plants, typically withering in fruit, spatulate, 2—4 cm x 3—8mm (or more?) abaxial surface hirsute, adaxial surface more densely pubescent,attenuate, ciliate hairy, obtuse to subacute. **Stem leaves** narrow oblong to lanceolate or oblong, 2—4 cm x 4—6 mm,abaxial surface appressed hairy with fewer hairs toward midline, adaxial surface densely appressed hairy, more so along mid-vein, bases cuneate or leaves sessile, margins ciliate hairy, apices obtuse to subacute. **Inflorescences** 6—10 cm in fruit, paniculiform, branches ascending or virgate and spreading; bracts 5—10 mm becoming progressively smaller toward branch tips, narrow lanceolate. **Fruiting pedicles** 2—3mm erect. **Calyx lobes** linear to narrow lanceolate, 1.5—2 mm to 3.5— (4.5) mm in fruit, slightly spreading to stellate spreading and exceeding fruit. **Corolla** blue (white), limb 1.5—2—(3) mm wide, lobes divergent, oblong to subovate. **Fruit** homomorphic, ovate. 2—2.5 mm high. **Nutlets** homomorphic, lanceolate, 2—2.5 mm, nutlets with 1 row of spines along disk margin; 5—7—(8) spines arising from narrow smooth or muricate margin, longest spines 1.2—1.5 mm long, bases free to closely adjacent or connate that their bases, terete to flattened and grooved; disk lanceolate to broadly lanceolate, 1.8—2 mm x 0.5—1.2 mm, disk surface variable typically muricate, but also papillate, granulose, or verrucose and tuberculate, adaxial surface texture typically the same as abaxial disk, **Style** surpassing nutlets more or less equal to or surpassing spines. **Gynobase** 2—2.2 mm.

Discussion

Watson cites DeCandolle's Prodromus for his concept of *Echinospermum redowskii* (Hornem.) Lehm. and compared his collection from Nevada with Siberian material at the Gray herbarium (Watson, 1871). He and Bailey collected specimens from various stations in Nevada over a period of months. Watson separated the American and the Siberian material on the basis of nutlet characters, noting that while the tubercles on Asiatic *E. redowskii* were rounded and obtuse, those of var. *occidentalis* were acute and irregularly spaced and abundant on the dorsal (abaxial) surface. He distinguished both species from *E. patula* noting that the latter had longitudinal rows of tubercles on the sides, and along the dorsal (abaxial) face (Watson, 1871). The plates accompanying Watson's description illustrated the mericarp surface features and number of marginal spines, highlighting differences in nutlet characters among the three. Ovczinnikova refined the characterization of these three species identifying macro and micromorphological features that distinguish among these two species and others in Section *Lappula* (Ovczinnikova 2005).

It is clear from Watson's discussion that he based his interpretation of the species upon Lehmann's concept, and distinguished his North American variety based upon comparison with Siberian material. Field observations of *L. redowskii* (Hornem.) Greene sensu Ovczinnikova and comparison of herbarium material are consistent with Watson's and Ovczinnikova's observations that the two species can be separated by morphology. The dorsal face of the fruits fruits in *L. occidentalis* have rounded bases (Figure 2.16), and are more strongly tuberculate than those from Siberia (Figure 2.15). Molecular phylogenetic study based upon ITS and two chloroplast markers supports a close relationship between the Siberian material referred to *L. redowskii* and North American *L. occidentalis* (S. Watson Greene). While mitotic chromosome counts for the species

in North America have been reported as 2n=48 (Löve and Löve 1974) diploid counts for *L. redowskii* were reported as 2n=24 (Provatova et al. 2011, 2012)

Figure 2.15. Image of fruit of *L. redowskii*. Fruit from a specimen from Lake Baikal in Siberia. The fruit has a long style, a broadly triangular abaxial surface with angled corners.

Herbarium and field observations suggest that *L. occidentalis* (S. Watson) Greene is a species that varies considerably in size, branching, fruit characters, and habitat over its range. Johnston wrote in a letter to regarding *L. anoplocarpa* (treated here as *L. montana*)

> "During the past 20 years I have seen many specimens of *Lappula* from Asia, North America and South America and I must confess that I grow in the opinion that the Good Lord did not expect the species of that genus to be classified. The variations of the L. Redowskii-complex seem to be endless, as if the complex was a great heterozygous

population constantly throwing off forms representing every possible combination of characters, some sporadic and sometimes geographically correlated" (Johnston, 1956). Though there is much variability, some forms can be readily associated with particular regions. In the vicinity of the type locality in Nevada, plants grow erect, with flowering branching is the upper quarter of the plant and the leaves are short sparsely appressed hairy above having hairs tiny pustulate bases. However, in the same region, plants are found that are long canescent hairy like those in *L. occidentalis* var. *stricta* have fruits of the typical variety except for a few hairlike spines at the base of the nutlet marginal spines which are barely noticeable except with a hand lens. Additionally, Ron Kelly reported finding extremely large basal rosettes of L. occidentalis some with flowering/fruiting stems and others still in vegetative more while hiking in the mountains of Utah and Arizona (R. Kelly personal communication).

In the Great Plains, the species is characterized by an upright growth form, a single erect stem with an open short-paniculate inflorescence in the upper third of the plant, a blue corolla and asymmetrical tear drop shaped mericarps curved at their apices. Generally, the narrowly subulate or straplike marginal spines are often grooved (at least along their bases) which are closely adjacent but not connate. The dorsal (abaxial) surface of the mericarps are convex with a weak crest along its midline and the surface is muricate to spicate. The style is even with the mature nutlet and a pit is present between the apices of each nutlet pair. These forms may represent varieties worthy of taxonomic distinction, but more study of variation and habitat associations in this species is necessary before those determinations could be made.

In Montana, Manitoba, British Columbia, a common form is upright with a single erect stem, branching in the upper third, leaves narrow linear, the fruits are reduced in size (1.7 mm) with spines, narrow distinct and widely spaced along the margin, 5 spines per side. These seem

closest to *L. montana* collected in the vicinity of Spences Bridge, British Columbia discussed above, but based on the available collections which are frequently immature it is difficult to determine to which species they belong (see discussion of *L. montana* above).

In the Colorado Plateau, there are a few distinctive forms in additional to the typical form. One tends to have long spreading branches and long spreading sepals. These were separated out by Rydberg as *L. calycosa*, but specimens matching his description were found scattered throughout the range of the species and it was impossible to consistently assign species on the basis of these vegetative characters. Others are lower and have fruits with strongly connate bases.

Despite the variability of the North American material specimens from throughout the continent were determined to be distinct from *L. redowskii* and referred to *L. occidentalis*. Specimens of *L. redowskii* were not observed among the specimens examined, however, given its distribution in Siberia and China, it may yet be found in Alaska.

Lappula occidentalis (S.Wats.) Greene was first described as *Echinospermum redowskii* Lehm. var. *occidentale* S. Watson. If *L. occidentalis* is considered equivalent to or related to *L. redowskii*, what then is *L. redowskii*? The identity of *Lappula redowskii* is not as straightforward as it would seem. The oldest species now considered part of *Lappula* (and included in *Echinospermum* at the time of Watson and Lehman) were originally described as species of *Myosotis*. This includes *Myosotis redowskii* Hornem., the basionym of *E. redowskii* var. o*ccidentale*. Hornemann's (1813) description served only to distinguish the species from others in the garden where he worked. It was not detailed enough to distinguish the species from other species of *Lappula*, referring only to vegetative and floral characters (shared by many species in the genus), and noting that the collection in the garden was from Imperial Russia. Watson based

his description upon comparisons of North American material collected from various localities in Nevada with representative Asian species from the Gray Herbarium (Watson 1871). He concluded that the North American material was distinct, and included in the description of his new variety illustrations of the Asian species *E. redowskii* and *E. patula* Lehm. for comparison (Watson 1871). Watson cited DeCondolle (1846) who followed Lehmann's (1818) characterization of *E. redowskii* which was based upon material from the vicinity of Lake Baikal in eastern Russia. Thus Watson based his concept of *Echinospermum redowskii* var. *occidentalis* upon Lehman's. Ovczinnikova (2005) chose a lectotype for the species from the Lake Baikal region, following Lehman's concept of *E. redowskii*. She was unaware of a specimen in Hornemann's herbarium at Copenhagen (S.V. Ovczinnikova, pers. comm.). However another author, Riedl came to a different conclusion regarding the nature of *M. redowskii*. He reported that the specimen at Copenhagen (C) was the holotype (2000), though Hornemann (1813) did not specify a type in his description. The specimen cited by Riedl as Hornemann's type was in early flower and largely vegetative. His conclusion was that it is an immature specimen of *L. squarrosa*. Riedl based his conclusion upon the inference that Lehman and Hornemen would have had access only to plants from the region around Ukraine. Riedl determined that *L. patula*, *L. squarrosa*, L. *anisacantha*, or *L. stricta* would have been the only species these authors would have had access to that time and did not include Siberia in his delineation of imperial Russia. He inferred based on morphological comparisons among the species cited above, that Hornemann's *M. redowskii* was actually *L. squarrosa* (Retz.) Dumort., and he picked a specimen of *L. squarrosa* as an epitype (Riedl 2000). Ovczinnikova later listed the specimen recognized by Riedl as the Hornemann's type as the holotype, but she retained *M. redowskii* as the basionym of *L. redowskii*. While the identity of Hornemann's type is unclear, the species as characterized by

Lehmann was recognized by Watson. In our study, we follow Ovczinnikova's concept of *L. redowskii* as an eastern Asian species, also in line with Lehman's and Watson's concept of the species.

Figure 2.16 Fruit images of *L. occidentalis*.

Distribution and Ecology

Grasslands, pinyon juniper woodlands, ponderosa pine forests, sagebrush steppes, meadows, and roadsides throughout western North America collected occasionally from eastern North America. The distribution map below (Figure 2.15) is based on specimens determined to be *L. occidentalis* var. *occidentalis* and was made in ArcGIS Online. Label locality data was entered into the search address window, and checked by eye. If the label data indicated a mileage distance from a town, the dot was placed by eye using the measurement tool to get an estimate. Dots represent specimens observed for this study, therefore the density of occurrences is not necessarily indicative of abundance; rather it reflects collecting patterns of the herbaria from which specimens were loaned.

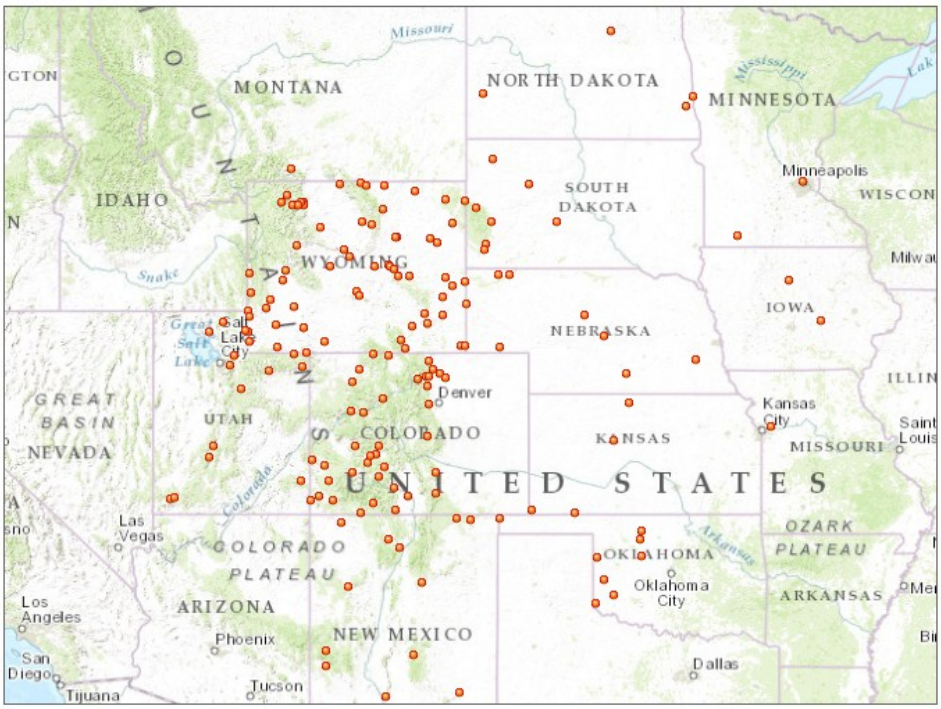


Figure 2.17 Distribution of *L. occidentalis* var. *occidentalis* based on specimens observed. Each dot represents a specimen studied and determined to be *L. occidentalis* var. *occidentalis.*

Phenology

May-July

Specimens cited

The specimens cited below were determined to be *L. occidentalis* var. *occidentalis* and are representative of geographic and developmental variation. The majority of specimens cited below are also represented in the map above (Figure 2.15), excluding specimens with ambiguous locality data. General locality data were included in the citation, but township and range data were not unless a locality was not listed on the label. Information in square brackets was not included on the label. All names on the label were listed, followed by the collector number. CANADA. **BRITISH COLUMBIA.** Spotted Lake, 23 May 1978, A. A. Rose 7942 UBC).

UNITED STATES. **COLORADO.** Colorado Territory, Clear Creek Cañon, 14 June 1873, J.M. Coulter s.n. (WTU). ALAMOSA CO.: Dry flat west of Alamosa, 11 June 1924, Hazel M. Schmoll 1005 (RM). ARCHULETA CO.: Arboles, June 1899, C.F. Baker 544 (RM), Pagosa Springs, 15 June 1924, Hazel M. Schmoll 1070 (RM). BOULDER CO.: Near Eldora, 22 July 1953, George Neville Jones 20125 (WTU); 4 miles north of Boulder, on foothill road to Lyons, 8 June 1941, Joseph A.Ewan 12936 (TEX). Nederland, Roosevelt National Forest, 6 August 1973. Andrew Moldenke, Harold N. Moldenke 27524 (LL). CHAFFEE CO.: Middle Cottonwood Creek, Cocheotopa [National] Forest, 4 September 1940, Ralph K. Gierisch 1326 (RM-USFS). CONEJOS CO.: Conejos River Canyon, 12 mi w. of Antonito, 19 July 1952, W. A. Weber 7819 (WTU). DELORES CO.: Upper east end of Disapointment Valley, County Road D.00, Warden Draw, ca 26 air mi N of Dolores, 16 June 1995, Lynn Marie Moore 5438 (RM). DELTA CO. Needle Rock, south and east slopes to north side, rock face, ca 3.5 mi NE of Crawford. 19 May 1997, Ronald L. Hartman, Kevin Taylor 56503 (RM); Youngs Peak and lower instrusive mountain immediately SE; adjacent to Crawford, 20 May 1997, Ronald L. Hartman, Kevin J. Taylor 56644 (RM). EAGLE CO.: Red Dirt Creek, ca 14 air mi NW of Eagle, 11 June 1990, James P. Vanderhorst 380 (RM). EL PASO CO.: Mountain View, 7 August 1901, F.E Clements, E. S. Clements 143 (RM). Along R.R. near Half-way house Pikes Peak, 2 August 1919, Edwin B. Payson 1567 (RM). GARFIELD CO.: Glenwood Springs, 6 June 1902, G.E. Osterhout 2578 (RM). South side of Grand Hogback, ca 6 air mi NNE of Rifle, 28 May 1990, James P. Vanderhorst, Walter Fertig 89 (RM). GUNNISON CO.: Between Stubbs Gulch and Gold Basin Creek just N of Saguache County, ca 8.3 air mi SSE of Gunnison, 1 September 1999, Melanie Arnett 7993 (RM);Curecanti National Recreation Area: between U.S. Hwy 50 and blue Mesa reservoir, W of Willow Creek, ca .32-3.7 air mi W of intersection of U.S. Hwy 50 and Colo Hwy

149, 20 May 1999, Melanie Arnett 3805 (RM); Ca 4 air mi NNE of Almont, 10 June 1997, Kevin J. Taylor 1164 (RM). Ca 2 air mi SW of Almont, 19 June 1988, Keven J. Taylor, 6909 (RM). HINSDALE CO.: La Garita Wilderness: heading S of west side of Mineral Creek from northern boundary of Wilderness for ca 1.5 mi…ca 14 air mi E of Lake City, 10 August 1999, Melanie Arnett 6605 (RM). JACKSON CO.: Along County Road 6 in the vicinity of Trappers Gulch at the south end of Battle Ridge, ca 11 air mi WNW of Cowdrey, 29 August 2001, B.E. Nelson 56414 (RM). HEURFANO CO.: Cuchara River, below La Veta, 28 May 1900, P.A. Rydberg, F.K. Freeland 5708 (RM). LARIMER CO.: Howes Gulch, 13 June 1889, W.F. Marshall 1663 (RM). Big Thompson Canyon, 19 miles west of Loveland, 14 June 1937, A.A. Beetle 1459 (TEX); North Park, 5 September 1900, G.E. Osterhout 4208 (RM), Livermore, 25 July 1904, G.E. Osterhout 2874 (RM); Estes Park, 11 August 1904, W.S. Cooper 1904; Moraine Park, 21 July 1903, G.E. Osterhout 2812 (RM). Big Thompson Canyon, 19 miles west of Loveland, 14 June 1947, A.A. Beetle (OSU). LAS ANIMAS CO.:South slopes of Jesus Mesa, 19 May 1993, Tim Hogan 2044 (RM). MOFFAT CO.: Monument Butte, ca 6 air mi SW of Hamilton, 22 June 1990, Ronald L. Hartman 25702 (RM). Cedar Mountain, ca 6 air mi NW of Craig, 23 May 2001, Ronald L. Hartman 70455 (RM). MONTEZUMA CO.: Mancos, 22 June 1898, C.F. Baker, F.S. Earle, and S.M. Tracy 29 (RM). Ca 3 air mi W of Cortez, northwest side of ridge overlooking Alkali Canyon, Indian Camp Ranch, jeep trail W of County Road 23, 26 May 1995, Lynn Marie Moore 4524 (RM); Circa 17.5 air mi S of Dove Creek, side road ca ¼ road mi W of County Road Y, on Ridge between Hovenweep Canyon and Negro Canyon, 23 May 1994, Lynn Marie Moore 1746 (RM). Entrance to McPhee Recreation Area on County Road 25, 25 May 1995, Ronald L. Hartman 50552 (RM). MONTROSE CO.: Paradox, 13 June 1912, Ernest P. Walker 80a (RM); Hwy. 347 ca. 1 mile S of entrance to Black Canyon National

Monument, 29 June 1984, Bruce Stein, D. Neill 1821 (RM); Cimarron 5 July 1901, C.F. Baker 327 (RM). Naturita, 27 May 1917, Edwin B. Payson (RM) OURAY CO.: Ouray, 27 June 1927, G.E. Osterhout 6783 (RM), E of County Road 4B, ca 0.5 air mi S of Chaffee Gulch; ca 8 air mi NNE of Ridgeway, 20 May 1999, Melanie Arnett 3755 (RM). PUEBLO CO.: 8 miles west of Buelah, 23 June 1936, Reed C. Rollins 1215 (ND). RIO GRANDE CO.: Del Norte, 15 June 1935, Francis Ramaley, K. Richard Johnson 14569 (TEX). ROUTT CO.: At the junction of Bedrock and Tennessee creeks, along Beeler Gulch and vicinity, ca 35.5 air mi NNW of Steamboat Springs, 27 June 2001, B.E. Nelson 53285 (RM). SAGUACHE CO.: Cochetopa Park: Gunnison National Forest: north side of Forest Road 804, ca 1.5 road mi from intersection with County Road NN-14; ca 2.2 air mi ESE of Cochetope Dome. 5 August 1999, Melanie Arnett 6442 (RM). SAN MIGUEL CO.: 27 mi NE of Egnar at Gypsum Valley, 11 June 1973, B.L. Turner 8061 (LL) Norwood Hill, 12 August 1912, Ernest P. Walker 459 (RM). WELD CO.: Windsor, 20 June 1917, G.E. Osterhout 5614 (RM); Pawnee Butte, 13 July 1920, G.E. Osterhout 6076 (RM), Banks of Cache la Poudre River near Fort Collins, 9 June 1896, C. S. Crandell (RM). TELLER CO.: Near Florissant, 1-8 August 1905, Francis Ramaley 1384 (RM). **ILLINOIS** [CHAMPAIGN CO.]: along railroad near Urbana, June 1928, W.G. Solheim 14 (RM). IOWA. [POWESHIEK CO.]: Grinnell, 22 Sept 1921, G. L. Wittrock s.n. (WTU). **KANSAS**. BARTON CO.: Pawnee Rock, Pawnee Rock Monument, 19 May 1982, Ralph E. Brooks, R.L. McGregor 15922 (RM). ELLIS CO.: Waste land on college campus, Hays, 12 May 1936, Earle Bondy 854 (ARIZ, WTU); MEADE CO.: 17 mi s Plains, sandy flats along Cimarron River 15 May 1981, R.L. McGregor 322247 (RM); MORTON CO.: 6 mi N, 4 mi W Elkhart, 10 June 1982, R.L. McGregor 33051 (RM); OSBORNE CO.: Collected within a radius of five miles of Osborne City, 24 May 1894, C.L. Shear s.n. (RM) RILEY CO.: North side of Sand lake near

Manhattan. 14 May 1927, Frank C. Gates 14732 (ND). SMITH CO. 3 mi. W. Smith Center, 3 June 1937, W.H. Horr E132 (OSU)**MINNESOTA.** [HENNIPEN CO.]: Minneapolis, 5 June 1890, T. H. B. 7486 (WTU); [Jackson CO.]: Prairie Junction [historical locality], 7 July 1898, Edward L. Greene s.n. (ND-G). **MISSOURI.** Atherson, 7 June 1858, B.F. Bush 34 (ND-G). **MONTANA**. STILLWATER CO.: Pine Grove Campground, Custer Natl. Forest, ca 20 nw of Red Lodge, 28 June 1991, Erwin Evert 21262 (RM). **NEBRASKA**. [CHEYENNE CO.]: N of Sidney, 18 June 1930, G. E. Osterhout 7195A (RM). [DAWES CO.]: Chadron, 8 June 1896, J. M. Bates s.n. (RM). [KEARNEY CO.]: Minden, 3 June 1940, H. Hapeman s.n. (WTU); 3 June 1929, H. Hapeman s.n. (TEX); 25 May 1938, H. Hapeman s.n. (ARIZ). [LANCASTER CO.]: On State Fair Grounds, 26 June 1893, C.A. Turrell s.n. (ARIZ). SHERIDEN CO.: Metcalf Public Hunting Grounds, 13 miles north of Hay Springs. 1 July 1964, Elray S. Nixon 140 (RM). THOMAS CO.: On Middle Loup River, near Thedford, 14 June 1893, P.A. Rydberg 1259 (ND-G). **NEW MEXICO.** CATRON CO.: Mogollon Range, Gila National Forest, 60 miles northwest of Silver City, 18 miles east of Mogollon, 18 July 1964, Michael Baad 736 (WTU). CIBOLA CO.: Along I-40 near Grants, 30 May 1992, Larry E. Brown 16340 (TEX). COLFAX CO.: Mesa between Sugarite Creek and Raton about 4 miles east of Raton on highway to Capulin, 17 June 1941, G.T. Robbins 575 (ARIZ). DONA ANA CO.: 2 air km NNW of Bishop's Cap on N limestone slope, 17 April 1988 R.D. Worthington 13601 (RM). EDDY CO.: 7.5 miles south of Carlsbad on U.S. 62, 6 April 1975, T.R. Van Devender s.n. (ARIZ). GRANT CO.: Howell's Ridge, Little Hatchet Mts. 31 May 1973, T. R. Van Devender, W.G. Spaulding (ARIZ). HIDALGO CO.: Peloncillo Mts., Post Office Canyon, 19 April 1973, William H. Moir (ARIZ). RIO ARRIBA CO.: Arroyo de Agua, 21 June 1934, Joseph T. Gregory 592 (WTU). Roadside, rt 84 in vicinity of Echo Ampitheater, approx.. 15 mi nw of Abiquiu, 10 May 2011,

Carolyn Ferguson, Mark Mayfield, Clara Mayfield, Helen Mayfield 835 (KSC). SANDOVAL CO.: Gonzales Ranch, Cerro Tinaja Quadrangle, 9 June 1973, Vorsila L. Bohrer 1677b (ARIZ); In Guadalupe Canyon near Guadalupe Spring, 3 June 1975, Mary B. Losure 115. (ARIZ), SAN JUAN CO.: Valley floor, floodplain of master stream, Horn Canyon Quadrangle, T29N, R11W, section 30; Zone 12, 5 June 1976, Geoff Levin SJVAP 410 (ARIZ); Rito de los Frijoles, August 1910, W.W. Robbins (RM). SOCORRO CO.: Mogollon Mountains, on Mogollon Greek, 20 July 1903, O.B. Metcalfe 275(RM). UNION CO.: On Johnson mesa, Folsom, 17 June 1941, Aven Nelson, Ruth Nelson 4630 (RM).VALENICA CO.: In the vicinity of Ice Caves, 30 miles south of Grants on State Highway 53, 31 July 1964, Michael Baad 1107 (WTU). **NEVADA.** Snow Creek, Summit Lake Indian Reservation, 12 June 1939, Percy Train 3081 (GH). **NORTH DAKOTA**. BENSON CO.: Leeds, 29 July 1909, J. Lunell s.n. (RM). BILLINGS CO.: Near Medora and Theodore Roosevelt National Memorial Park, in the badlands, 7-10 June 1967, C.L. Porter, Marjorie W. Porter 10364 (TEX). [CASS CO.]: Kindred, 4 July 1929, W.G. Solheim, A.O. Stevens 171 (RM); Fargo, along railroad, 20 June 1934, O.A. Stevens s.n. (RM). **OKLAHOMA**. ALFALFA CO.: Carmen, 1 May 1936, Delzie Demaree 12363 (TEX). BLAINE CO.: Roman Nose State Park, 14 May 1966, George J. Goodman 7676 (TEX). CIMARRON CO.: Black Mesa country of the Cimarron River, 2 mi N of Kenton, 17 May 1941, M. Hopkins, M. Van Valkenburgh 5766 (ARIZ, RM). North Slope of Black Mesa, 1 June 1947, George J. Goodman 4373 (TEX). GREER CO.: Lake Altus, 4 mi N., Granite 11 June 1966, Rudy Koch 1260 (OSU). KIOWA CO.: Quartz Mountain State Park, 30 April 1944, Milton Hopkins, Aven Nelson, Ruth Nelson, 243 (WTU, RM). MAJOR CO.: 3 miles west of Orienta, 21 May 1951, U.T. Waterfall, Patsy L. Coryell 9924 (ARIZ) ROGER MILLS CO. Slopes and tops of Antelope Hills, 31 May 1947, George J. Goodman 4312 (TEX). **SOUTH DAKOTA**. CUSTER CO.:

Jessie Elliot Ranger Station, Slim Buttes Div. C. M Hubbard 61 (RM-USFS); Wind Cave, 29 June 1927, Herman E. Hayward 1663 (RM). [FALL RIVER CO.]: Hot Springs, 28 June 1927, Herman E. Hayward 1635 (RM). LAWRENCE CO.: Deadwood, 10 July 1913, W.P. Carr 32 (RM); LAAKON CO.: Along U.S. highway 14, 2 miles north of Midland, 25 June 1953, C.G. Gilly, G.W. Parmelee, Stella M. Wilson and P.G. Coleman 827 (RM); MEADE CO.: Boke Ranch House yard, 5 mi south of Faith, 8 June 1972, Norman H. Boke 496 (TEX). [PENNINGTON CO.]: Rapid City. 22 July 1912. S.S. Visher 1525 (WTU) **UTAH.** BOX ELDER CO.: Bear River Canyon, 20 June 1909, Charles Piper Smith 1678a (RM). CACHE CO.: Bench S. of College, Logan, 26 May 1932, Bassett Maguire, Ruth Maguire 3710 (RM). DAGGETT CO.: Teepee Mountains, ca 11.5 air mi ENE of Dutch John, 5 July 1995, C.H. Redsdal (RM). 4822. DUCHESE CO.: Ashley [National] Forest, Yellowstone, 26 June 1928, K.E. Weight W-24 (RM-USFS). GARFIELD CO.: T33S, R7E, S9. South of Lamb Stand, 30 May 1992, Larry Higgins 18839. [PIUTE CO.]: Along Sevier River, below Marysvale, 20 July 1905, P.A. Rydberg, E.C. Carlton, 6978 (RM); RICH CO. ca 3 air mi NE of Woodruff; 1 mi N of Little Crawford Road, 8 July 1995, C. H. Refsdal, B. E. Nelson 5058 (RM). SALT LAKE CO. Summit of Murdock Peak, Lambs Canyon, 16 July 1959, R.K. Vickery, Jr. 2360 (WTU). SAN JUAN CO.: Meadow south of Monticello, 24 July 1911, P.A. Rydberg, A. O. Garrett 9148 (RM). SEVIER CO.: 2 miles north of Elsinore…at the mouth of a canyon, 2 June 1967, James L. Reveal, Johnnie L. Gentry, Jr., Gerrit Davidse 734 (WTU). [SUMMIT] Red Rock Canyon, 11 June 1905, P.A. Rydberg 6086 (RM). [UINTAH CO.:] Diamond Valley, 16 May 1902. Leslie N. Goodding 825 (RM) WASATCH CO.: Uinta [National] Forest, Mud Spring, 11 August 1927, Lynn Alleman A-7 (RM-USFS). WASHINGTON CO.: Pine Valley, 14 July 2000, L. Higgins 21601 (RM); Pine Valley Mountains, Santa Clara River, 30 July 1968, Johnnie L. Gentry, Jr.,

Earl Jensen, Jr. 2206 (WTU). **WYOMING**. ALBANY CO.: Blue Grass, 8 July 1894, Aven Nelson 305 (ND-G, RM); Near Centennial,15 July 1946. E.C. Yunker, T.G. Yunker (TEX); North Fork, Centennial, 26 July 1900, Aven Nelson 7705 (RM); Wood's Creek, 9 Aug 1900, Aven Nelson s.n. (RM); Cooper Lake, 17 June 1901, Leslie N. Goodding 23 (TEX); Ca 25 mi SW of Wheatland on Nueces Ranch (old Adam Boyd Ranch) along Bluegrass Creek on Tunnel Road, 7 June 1985, Ruth O'Brien 1329 (RM); South Sybille, 3 July 1900, Aven Nelson 7372 (RM); Laramie Exp. Farm, 28 June 1894, Aven Nelson 294 (ND-G, RM). CAMPBELL CO.: Ca. 31 miles NNW of Gillette on US Hwy. 14- 16, then 11.4 miles NNE on the Recluse-Olmstead Creek Road, 2.5 miles E of the road. Ca. 8 ¼ miles NE of Recluse. 19 June, 1975, B. E. Nelson, Linda Nelson 1251 (RM). CONVERSE CO.: 2.5 air mi S of Glenrock, 27 Jun 1993, Ronald L. Hartman 38701 (RM). ca 40 air miles NW of Douglas, Hardy Project Uranium Mine, 14 June 1978, Steve Skelton s.n.; Ca 2.5 air mi SSW of Douglas, 29 June 1993, Ronald L. Hartman 39117; CROOK CO.: Devils Tower National Monument, prairie dog town near amphitheater, 27 July 1982, Hollis Marriot 1690 (RM); Sand Creek Canyon, near Beulah, 20 June 1950, C.L. Porter 5347 (RM) FREMONT CO.: Riverton, late May 1920, Aven Nelson s.n. (RM). Haines' Farm, ca 9 mi W of Riverton on the US Hwy 25. 19 July 1985, June Haines 4960 (RM) Sweetwater Rocks, Cranner Rock, ca 14.75 air mi ESE of Jeffrey City, 13 June 1986, June Haines 6350 (RM), Big Camp Creek Area, ca 6 air mi WSW of Muddy Gap Junction (Three Forks), 4 July 1985, June Haines, Georgia Hains, Nora Little 4741 (RM); Wiggins/East forks confluence: ca 8 air mi E of Dubois, 29 May 1995, C. Lynn Kinter 1031 (RM); Southwest flank of Copper Mountain, ca 14 air mi NNE of Shoshoni, 29 June 1981, Ronald L. Hartman, Keith H. Dueholm 13247; Lysite badlands, drainage between Day and Fuller Gulches, ca 6 air mi NNW of Moneta, 30 July 1986, Hollis Marriot 10532; GOSHEN CO.: Ca 7.5 air miles SE of

Torrington, ca 1.25 air miles NW of Henry, Nebraska, 4 June 1978, B.E. Nelson 1633 (RM) on the Goshen-Niobrara County Line. Near the east side of Rawhide Buttes and west of US 85, 6 July 1955, C.L. Porter 6712 (TEX, WTU). HOT SPRINGS CO.: along north side of Grass Creek road, ca 6 mi W of Wyo Hwy 120, 27 June 1993, Erwin F. Evert 253424 (RM); JOHNSON CO.: Buffalo, September 1900, Frank Tweedy 5066 (RM); ca 22 (air) miles NNE of Sussex, 27 June 1978, Ronald L. Hartman, Mary Alice Sanguinetti 7487 (RM); Ca 1 air mi W of Dullknife Reservoir spillway, 27 June 1979, Ronald L. Hartman 6549 (RM). LARAMIE CO. Ca. 0.5 miles S of I-80 in Pine Bluffs, S of Pine Bluffs Rest Area, 20 June 1978, B. E. Nelson, Paul Ehrmann 1744 (RM). 3-5 miles west of Granite Canyon on the Harriman Road, 3 July 1968, C.L. Porter, Marjorie W. Porter, 10539 (RM) Ca 22.5 air mi W of Cheyenne, ca 3.5 air mi NE of Buford, 26 June 1979, William C. Edwards 94. LINCOLN CO.: Star Valley, Strawberry Creek 0.3 mile E of US 89. 4 June 1977, Orval C. Harrison 179 (RM); Ca 2.5 air mi SE of Thayne, 10 June 1989, Orval C. Harrison 539 (RM); ca ¾ air mi E of Utah off Wyo Hwy 89 ca 4 air mi SW of the intersection of U.S. Hwy 30 and Wyo Hwy 89, 24 May 1995, B.E. Nelson, Tom Cramer 34759 (RM); Ca 3 air mi N of Sage at Boulder Ridge. 3 June 1995, Tom Craver 5412 (RM); ca 13.5 air mi N of Cokeville, Sublette Range at Raymond Creek, 11 July 1995, Tom Cramer, Jane T. Kellett 7696 (RM); Benchland between Zieglers Wash and Dry Muddy Creek ca 13 air mi WNW of Granger, 3 July 1995, B.E. Nelson, C.H. Refsdal 36162; Hogsback Ridge: lower slopes on southeast end of Hogsback Ridge, circa 5.7 air mi W of La Barge, 23 June 1993, B.E. Nelson, Russ Nelson 26315; NATRONA CO.:ca 12.5 (air) miles North of Casper, 26 June, 1979, Kieth Dueholm 7434 (RM). Rattlesnake Mountains; Burnt Wagon Draw and surrounding N slope of range. 26 June, 1981, Ronald L. Hartman, Gael Fonken 12900 (RM); Ca. 22 (air) miles S of Kaycee in Sectoins 32 and 33, 10 June 1979, Keith H. Dueholm 6932, (RM); Emigrant Gap

Ridge, ca 12 air mi W of Casper. 23 June 1993, Ronald L. Hartman 38061 (RM); ca 10 mi SW of Casper. 2 June 1988, Ronald L. Hartman 23598 (RM); ca 18.5 air mi NW of Casper. 16 June 1993, B.E. Nelson 25781 (RM); U.S. Hwy 20, 26, less than 1 air mi E of Fremont County. 6 July 1993, Ronald L. Hartman with T.W. Nelson 40177 (RM); Hwy 253, ca 9 air mi SE of Casper. 26 June 1993, Ronald L. Hartman 38462 (RM), 3.5 (air m) SE Powder River…along Middle Casper Creek. 5 July 1979, Keith H. Dueholm 7825A (RM); Ca 3 air miles SSE of Powder River and 1 air mi NW of Middle Fork Casper Creek crossing. Ronald L. Hartman 38356 (RM). North Fork Casper Creek, east of County Rd 110, 9.5 miles N of WY Highway 20, 21 June 1991, George P. Jones 220 (RM); Sentinel Rocks 2.5 air mi SE of Independence Rock, 2 June 1985, Ronald L. Hartman, June Haines 20290 (RM); Ridge w of Hemingway draw along Thirtythree Mile or County Road 110, ca 24.5 mi NW of Casper. 15 June 1993, B.E. Nelson 25840 (RM); Bates Creek, 5 July 1901, Leslie N. Goodding 198 (RM, TEX). NIOBRARA CO.: Jireh, 25 June 1915, Wright L. Hess 123 (RM); Sand hills near Van Tassel, 11 June 1957, C.L. Porter 7259 (ARIZ,GH, RM, TEX,) PARK CO.: ca ⅛ mi W of Horse Creek and ca 1-2 mi N of W.S. Hwy 14, 16, and 20. 16 June 1987, Erwin F. Evert 12261 (RM); Ridge between big Creek and Wall Creek, ca 203 mi N of W.S. Hwy 14, 16, & 20, 14 June 1987, Erwin F. Evert 12175 (RM). N Fork Shoshone River drainage, W of Wapati Ranger Station, 21 July 1980, E. F. Evert 2153 (RM), Ridge ca. 3 mi. E of Hwy. 120 ca 9 mi N of Meeteese, 21 June 1990, E. Evert 19214 (RM); West ridge leading to summit of Heart Mountain. 1 July 1981, Ronald L. Hartman 13451 (RM); Along S side of Buffalo Bill Reservoir ca. 10 mi SW of Cody, 9 June 1989, E. Evert 16559 (RM); On hill just S of Wapiti, 17 June 1981, E. F. Evert 2730 (RM); Bull Creek, Ca. 2 air mi SE of the South Fork Shoshone River, 19 June 1983, Ronald L. Hartman, Robert S. Kirkpatrick 15429 (RM); SW flank of Rattlesnake Mtn. ca 6 miles W of Cody and ca ½ mile N

of Hwy 14, 16, & 20, 15 June 1989, E. Evert 16751 (RM); Absaroka Mountains: along north side of North Fork Shoshone River, ca 0.5 mi W of the mouth of Canyon Creek, 13 June 1986, Ervin F. Evert 9956 (RM).North Fork Shoshone River drainage, Logan Mountain Springs, 18 June 1981, E.F. Evert 2766 (RM). PLATTE CO.: E side of Guernsey Lake reservoir, 14 June 1967, James Mears, Helen Mears 2250 (TEX); Ca 2 mi E of Slater on breaks, 11 July 1993, Ronald L. Hartman 40691(RM). TETON CO.: Jackson Hole Wildlife Park, 19 August 1947, John F. Reed, Mildred S. Reed 1640 (RM); Goosewing Creek, 27 June 1977, Robert Lichvar 526 (RM); Vicinity of Hoback Canyon, 24 June 1932, Louis Williams, Rua Pierson 703 (RM); SUBLETTE CO.: Between east shore of Fremont Lake and Skyline Drive, ca 4 air mi NE of Pindale, 11 July 1990, Walter Fertig 3462 (RM); Western slope of the Wind River Range, east of Pinedale near Fremont Lake, 11 July 1967, C.L. Porter, Marjorie W. Porter 10423 (TEX, WTU); The Mesa, ca 9.5 air mi WSW of Boulder, 27 July 1995, Tom Cramer, Jane T. Kellet 9634; SHERIDAN CO.: Ca. 6.5 air mi WNW of Parkman, ca. 12 air mi NW of Dayton. 16 July 1979, B. E. Nelson 3826 (RM); Ca. 14.5 (air) miles northeast of Sheridan, 2 Jun 1979, Keith H. Dueholm 6336; Ca. 8 (air) mi E of Wyarno. Hills above SR Creek, 7 June 1979, Keith H. Dueholm 6716 (RM). SWEETWATER CO.: ca 8 air mi W of Farson, 18 July 1995, Tom Cramer, Jane T. Kellett 8562 (RM). UINTA CO.: North end of Woodruff Narrows Reservoir, ca 16 air mi N of Evanston; 8.5 mi E on County Road 101, 22 June 1995, C. H. Refsdal 4231 (RM); Ca 9 air mi N of Lonetree; 2.5 mi s of Cedar Mountain Road on jeep trail, 14 June 1995, C. H. Refsdal 4066 (RM). WASHAKIE CO.: Near the mouth of Tensleep Canyon, ca 5 air mi NE of Tensleep, 6 June 1980, B.E. Nelson 5170 (RM) WESTON CO.: Ca 4 (air) miles SSE of Rochelle, 20 June 1978, Ronald L. Hartman, Keith H. Dueholm, Mary Alice Sanguinetti 6739 (RM).

***8b. Lappula occidentalis* var. *stricta* (S. Watson) comb. nov.**

***Lappula occidentalis* var. *stricta (S. Watson)* comb. nov**. *Echinospermum redowskii* Lehm. var. *strictum* S. Watson. United States Geological Expolration [sic] of the Fortieth Parallel. Vol. 5, Botany: 246. 1871. Type: USA. Nevada [Pershing County]: Trinity Mts. 5000 ft. May 1868. S. Watson 862. (Holotype: GH! Isotype: YH).

Tiehm (1984) lists the specimen at Harvard (GH) as the holotype and that at YH

Watson cites in synomy Nees' name *Echinospermum strictum*, a later homonym of *Echinospermum strictum* Ledeb. However, Watson provides a diagnosis for his variety and cites a collection (Watson 862). His combination was a combination novem and a nomen novem and as "*stricta*" is available at the varietal level, *E. redowskii* var. *strictum* S. Watson was a valid combination. A new combination is made in *Lappula* based upon Watson's name. See discussion of *Echinospermum strictum* Nees under dubious and excluded names.

Echinospermum redowskii Lehm. var. *cupulatum* Gray. Superfluous name. Replacement name for var. *strictum*; Geological Survey of California, Botany 1: 530. 1876. *Lappula cupulata* (Gray) Rydberg. Bulletin of the Torrey Botanical Club 28(1): 31. 1901. Invalid name, based on Gray's illegitimate name. *Lappula occidentalis* (S. Watson) Rydb. var. *cupulata* (Gray) Higgins. 1972. Brigham Young Univ. Sci. Bull., Biol. Ser. 16(3): 62.

L. collina Greene. Pittonia. 4:96 1899. Type: U.S.A. Utah [Piute Co.]: Kingston, alt. 5,300 ft. (Lectotype designated here: NY 01156455!). Greene wrote, "I know the plant only as in the U.S. Herbarium from Marcus Jones, who obtained it at various stations in Utah in 1894; one being Kingston, at 5,300 feet; another Pahria Cañon, same altitude." Neither specimen was found at US, but the Kingston specimen (M. Jones 5317, 20 May 1894) was located at NY and is selected as the lectotype here. This name is reluctantly placed into synonomy here, and needs more study to determine if it should be considered distinct. Early observations suggested that it

was a specimen of *L. heterosperma*. The fruits are finely muricate on all surfaces, not tuberculate, and the nutlet margin is very delicate and thin and thus may be more appropriately identified as *L. occidentalis* var. *stricta*. The type specimen was found late in the study and specimens with a similar morphology were not observed. More work is needed to determine if this specimen represents an anomalous individual or not, and to determine if the name should be put into synonomy or not. The fruits were extremely small (less than 2mm), and the stems were thin and delicate.

L. columbiana A. Nelson 1902. The Botanical Gazette.34:28. Type: U.S.A. Idaho, Nez Perces Co.: Snake River. A.A. & Gertrude Heller *s.n*. April 1896 (Lectotype: RM!). Nelson's publication referred to multiple collections, but he wrote "type" on the one selected above as the the lectotype.

L. infelix Green. 1901. Pittonia. 4:235. Type: U.S.A. : Oregon, Malheur River. Wm. C Cusick, 1945. 20 June 1898. (Holotype: NDG-042421!) "…distributed for *L. occidentalis*, some specimens of which are mixed with the new one in the distribution; on which account the label number (1,945) is useless, and not be cited as certainly representing *L. infelix*."

L. leucotricha Rydberg, 1909. Bulletin of the Torrey Botanical Club 36(12): 676–677. USA: Arizona [Pima]: Tucson 20, Toumey 1909. April 1894. (Holotype: NY!).

L. echinata fo. *cupulata* (A. Gray) B. Boivin . Le Naturaliste Canadien 93(6): 1060. 1966[1967]

L. redowskii (Hornem.) Greene fo. c*upulata* (A. Gray) Scoggan. 1979. Dicotyledoneae (Loasaceae to Compositae). Part 4. 1117–1711 pp. In Fl. Canada. National Museums of Canada, Ottawa.

Lappula redowskii (Hornem.) Greene var. *cupulata* M. E. Jones. 1910. Biological series of the bulletin of the state university of Montana 15: 44. 1910

Description

Herb, Annual. **Roots** single, thick from a stout crown, thin. **Stem** one or 2—(4+) from basal rosette 20-50 cm, erect, densely pilose to densely appressed and spreading hairy, little to much branched in upper half or upper third. **Basal leaves** if present, spatulate, 2—4 cm long, densely spreading hairy on both surfaces, bases attenuate, margins hairy, apices obtuse. **Stem leaves** linear or broadly oblong, (2—4 cm x 3—5 mm), abaxial surface with fine stiff hairs more densely arranged along margin and apex, adaxial surface with fine stiff hairs densely and evenly distributed on leaf, midvein densely hairy additionally with longer pustulate hairs, bases clasping or cuneate, apex acute to obtuse,. **Inflorescences** strongly paniculate branching from the middle to upper third of main stem, with numerous long branches or simple branched above to 4—10+ cm long; bracts oblong to sub-ovate, frequently leaf-like but variable, becoming progressively smaller at branch tips, 0.5—3cm. **Fruting pedicels** 3—4 mm, ascending. **Calyx lobes** lanceolate, 1—2 mm to 3—4 mm in fruit, spreading. **Corollas** white (blue? not seen), limb 2—3mm, lobes spreading, oblong. **Fruits** Variously heteromorphic with one or more types of fruit on a single plant, or heteromorphic within a single fruit, when spines connate appearing broader than tall due to thin wing, 3—4 mm. **Nutlets** homomorphic or heteromorphic. 2.5—3 mm, bases ovate, apices acute to acuminate; *0—4 nutlets* with obscure margin. 4—6 spines on each side confluent and forming a thin spreading dentate wing and 0—2 spines per side free, 1—2mm long, often with bristles or finely aculeate near the base of the wing, spines subulate to broadly triangular and tooth like, disk lanceolate to broadly lanceolate, 2 mm x 0.8—ca. 1mm wide, abaxial surface densely fine muricate, or smooth with a slight crest visible at midline, frequently with 3 muriculate lines, adaxial surface aculate often more densely so in lower third; *0—4 nutlets* with obscure margin, 5—7 (8) spines per side, 0.8—2 mm long, spines terete or subulate, often with hairs or fine aculae along the sides or restricted to the base of the spine, disk

lanceolate to broadly lanceolate, 2 mm x 0.8—ca. 1mm wide, nutlet surface muriculate to muricate, abaxial surface muricate to tuberculate. Did not observe either nutlet type tending to cling more strongly to the gynobase. **Style** more or less equal to or taller than fruits., frequently exceeded by spines. **Gynobase** [missing measurement].

Discussion.

Of the taxa treated here, what is here treated as *L. occidentalis* was the most problematic to circumscribe. In Southern Arizona specimens were easily referable to Rydberg's *L. leucotricha*. In the Snake River Plains and Columbia River Basin regions, there were distinctive specimens that could be assigned to *L. columbiana*. However, Watson's type specimen of *E. redowskii* var. *stricta* has characteristics of both, even while extremes of northern and southern forms when placed side by side look like separate species. In both regions, specimens can produce highly variable fruits with some plants having a majority of fruits that look like *L. occidentalis*, but with hairy leaves and stems, or plants that have the vestiture of *L. occidentalis* but fruits with broadly spreading wings. Additionally plants were found that had both fruit types on a single branch. There are species names available for each form discussed here, for ease of communication the species name is used to refer to each form despite their being treated as a single species here.

The southern form of this variety is equivalent to Rydberg's *L. leuchotricha*. This form seems to be most similar to *L. occidentalis*. The presence of *L. occidentalis* type fruits on some specimens and the difficulty distinguishing the two varieties from some specimens lends support to treating it variety of that species. However, there are compelling reasons to maintain it as distinct. In southern Arizona it is morphologically and ecologically distinct. The majority of collections referable to *L. leucotricha* were made in riparian zones and along ephemeral washes,

whereas *L. occidentalis* tends to occur at higher elevations. Observed at 10x magnification, the fruits were frequently observed to have secondary bristles near their bases. Rydberg observed the fruits ripened a light tan. This characteristic has been observed on several specimens, but field observations were not made and the coloring may be artifactual. Typical *L. occidentalis* ripens from green to brown, light tan forms were not observed, nor were heteromorphic fruits. Specimens referable to *L. leuchotricha* frequently were observed to have robust basal rosettes. The vegetative parts were observed to be very long hairy and the plants appear gray. This is especially noticeable on the leaves, which have long hairs except for the midvien on the upper surface, which was frequently observed to be free of pubescence. The typical variety of *L. occidentalis* usually has shorter hairs on the stems and leaves. Another observations made in the southwestern plants was that the stems were long, the branches often equallying or exceeding the stem length, robustly branching above.

In the northern part of the range of this variety, plants circumscribed as *L. infelix* Greene and *L. columbiana* A Nels. (different types but similar morphology) from eastern Oregon, Washington and parts of Idaho have gray pilose stems, white flowers (reported, not observed) and variable fruits similar to those from Arizona. Typically specimens from this region are are shorter and less branched.

Both forms were observed from herbarium specimens and photographs only. It was not possible to determine flower color from herbarium specimens white flowers often faded blue. However, label data from multiple specimens of both the northern and southern indicated white flowers. In the course of preparing this treatment, the two forms were treated variously as separate species, as separate varieties and finally as a single variety under *L. occidentalis*. This

seemed the most conservative route as a varietal name was already available and only a new combination was needed to transfer it to *Lappula*.

In Figure 2.18, six hypotheses are presented diagrammatically in an attempt to address the variation observed. The boxes with gradient shading represent the hypothesis that L. occidentalis var. stricta varies along a North-South gradient whereas the solid boxes represent the taxonomic hypothesis that the two are separate taxa. When boxes intersect, the implication either that may have or are actively hybridizing. The relationship of the gray boxes to the white ones (representing *L. occidentalis*) reflect the following hypotheses: 1. The observed variation is within the taxonomic entity *L. occidentalis* in the western part of its range. 2. The variation observed is with one for more taxonomic entities separate from *L. occidentalis*. 3. The variation represents introgression among one or more separate entities and *L. occidentalis*. Treating the specimens with cupulate fruits as a single variety over simplifies the problem, as it is clear that at least at the extreme northern and southern parts of its range, *L. occidentalis* var. *stricta* seems to be distinctive in its habitat associations, but it was not resolvable in this revision.

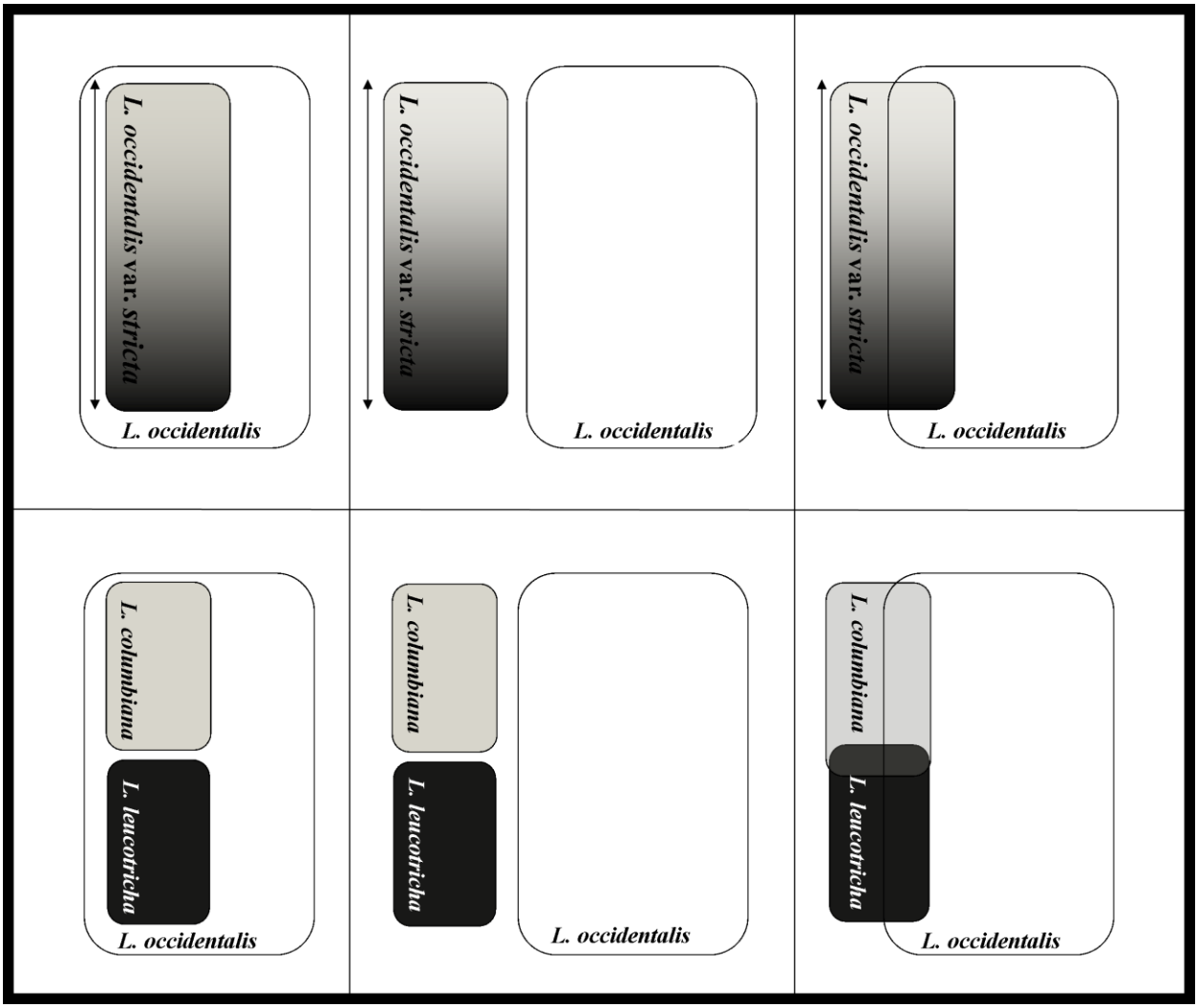


Figure 2.18. Diagram of hypotheses regarding variation in *L. occidentalis* var. *stricta.* See text for explanation.

Figure 2.19 Three forms of *L. occidentalis* var. *stricta*. Left nutlet from an Arizona specimen showing completely connate, bristly nutlet margin. (Center) Form with free spines but bristles at

the bases of the spines. Shannon Fehlberg 50208-3 (Right) Northern form typically found in Snake River Plains, Cusick 1945 ND-G 42421

Distribution and Ecology

Southern form: Riparian washes in Sonoran desert, Mexico, Northern form: yellow-pine belt foothills of Nevada, Great basin, along tributaries of the Snake River and Columbia River, grassland and sagebrush steppe, basaltic rocky soils.

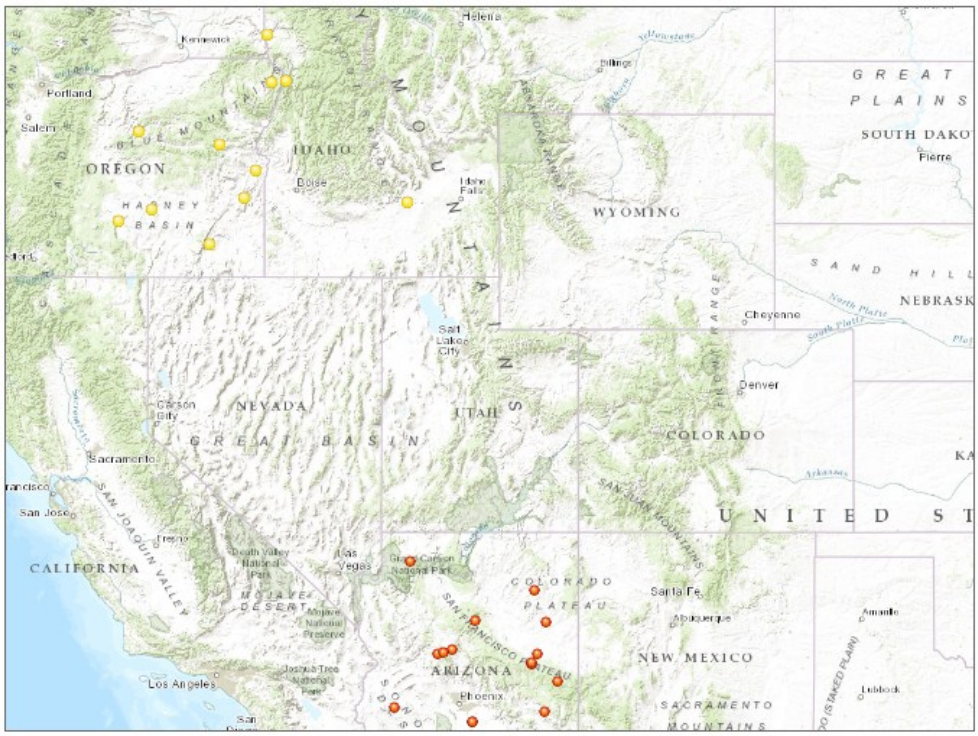


Figure 2.20. *L. occidentalis* var. *stricta*. Distribution of the two forms observed. Only cited specimens are mapped. The distribution is broader than shown and includes Nevada,.Utah and southwestern Idaho.

Phenology

Flowering and Fruiting: March--August. There are early and late season collections throughout the range of this variety.

Specimens cited

NORTHERN FORMS:U. S. A. **IDAHO.** IDAHO CO.: 2 mi N of Sheep Creek, 16 May 1936, L. Contance, R. C. Rollins, L. A. Dillon 1593 (WTU). Snake River adjacent to Sheep Creek, Snake River Canyon, C. W. Sharsmith 4020, 13 May 1939 (WTU). NEZ PERCES CO.: Valley of Clearwater River, 24 April 1892, J. H. Sandberg, D. T. MacDougal, A. A. Heller 17 (RM). **NEVADA.** LINCOLN CO.: Near Silver King Mine Rd, 14 May 1982, Margaret J. Williams 82-16-2 (GH). **OREGON**. CROOK CO.: Near camp on Hay Creek 12 June 1894, John Leiberg 213(OSU); Near camp on Pine Creek, 12 June 1894; J. B. Leiberg 213 (NY). HARNEY CO.: Alvord Desert, June 1937, Lilla Leach 5100 (OSU); Near Wagontire, 20 June 1927, Mr. and Mrs J.R. Leach s.n. (OSU); Approx. 5 mi SE of Squaw Butte, 2 mi NW of Hwy 395, 23 July 1956, R. E. Eckert s.n.; Long Draw RNA, 18 June 1986, Zika, Kemp 9682 (OSU); 8 mi W of Riley, 22 June 1925, M.E. Peck 13853 (WILLU). KLAMATH CO.: 2 mi SE of Reno, 8 July 1920, Morton E. Peck 9391 (OSU). MALHEUR CO.:Owyhee Uplands, Dry Creek Basin, 2/3 miles southwest of Wall Rock Spring and 32 air miles southeast of Juntura, 23 May 2003, Danna Lytjen 36 (OSU); Near Vale, 16 May 1896. John B. Leiberg 2057 (OSU). WALLOWA CO.: Battle Creek, 12 April 1923, Hazel Barton 19511 (WILLU); Cactus Mountain, southeast of the confluence of the Snake and Imnaha Rivers, 4.7 road miles north of Cow Creek Bridge, 19 May 1990, T. N. Kaye 1191 (OSU); Imnaha, 24 June 1923, Wm. Sherwood 22 (WILLU). WHEELER CO.: Near the summit of Sutton Mt., 10 miles north of Mitchell, 22 June 1953, Arthur Cronquist 7252 (NY, WTU).

9. Lappula squarrosa (Retz.) Dumort.

***Lappula squarrosa* (Retz.) Dumort.** Fl. Belg.:40. 1827. *Myosotis lappula* L. Species Plantarum 1: 131 (1753) TYPE: "Hab. in Europae argillosis nudis, ruderatis" (Lectotype, designated by Selvi in Cafferty and Jarvis (ed.). Taxon 53: 803. 2004.: LINN-180.9)

Description

Herbs annual, biennial, **Roots** single, narrow and slender to thick and conical. **Stems** single, or 2—(4) fascicled and caespitose, erect, divaricately branched in upper part of plant (rarely branching throughout), 2—6+ dm, hairs short appressed and long spreading becoming more appressed hairy above. **Basal leaves** withering at flowering or absent, spatulate, 2—3 cm x 3—6 mm wide, abaxially long spreading hairy to sericeous, adaxially long spreading hairy to sericeous, occasionally pustulate hairy, bases attenuate, margin pubescent and similar to surface hairs, apex rounded to acute. **Stem leaves** variable, narrow oblong to lanceolate, length (1)—2—5—(8) cm x 2—5— (15) mm, abaxially spreading hairy, adaxially hairy to pustulate hairy, bases attenuate to cuneate, margins ciliate hairy, apex acute to rounded. **Inflorescences** to 12+ cm in fruit, paniculiform frequently divaricate; bracts narrowly ovate or lanceolate, 1—3 cm long becoming progressively smaller distally and sepal like, 5—10 mm long, narrow lanceolate to linear. **Fruiting pedicles** 1-3 mm, erect to ascending. **Calyx lobes** linear, 1—2 mm, to 3—4 mm in fruit, spreading. **Corollas** pale to azure, 3—(5) limb mm wide, lobes horizontally spreading, narrow ovate to orbicular. **Fruit** homomorphic, globose, 2—3 mm high. **Nutlets** homomorphic, narrow ovate, 2 mm long, bases ovate, apices attenuate to acute; nutlets with 3 rows of spines along disk margin, subequal, spines smooth, needle-like to subterete; longest inner spines 2mm, arising from smooth marginal rim, bases free; longest spines of middle row 1mm bases free; spines of outer row 0.5 mm or reduced to tubercles, adaxial in lower part; disk

narrow lanceolate to lanceolate, 1.5 mm x 0.5mm, disk finely muricate throughout, central line occasionally marked by fine line of murication, but not raised; nutlets easily released from gynobase at maturity. Fruiting gynobase 2.5 mm. Style surpassing nutlets and apical spines.

Discussion

This species is presumed introduced into North America. Cronquist (1984) suggested that there may be a native form in the mountainous areas of North America, but as he considered *L. fremontii* as part of *L. squarrosa*, that may be the species to which he referred. In 2004, a population was observed that seemed intermediate between *L. fremontii* var. *nelsonii* and *L. squarrosa* in the Ashley National Forest. Several plants had produced flowers but had many aborted fruits. Potential introgression of the mountain populations with *L. fremontii* should be explored, as should relationships between the populations of *L. squarrosa* that occur in the mountains versus those in the mixed grass prairies and eastward. Plants from Alaska and the mountains have corolla widths at least 4mm wide and with dark blue flowers, like those observed in Siberia. Whereas the ones observed in the Great Plains and eastward typically had pale blue flowers and corollas that were 2—3 mm wide. The fruits seemed superficially similar with three rows of marginal spine.

Distribution and Ecology

Throughout the northern tier of states and all the Canadian Provinces, present as a waif in the southern United States.

Figure 2.21 Map of *L. squarrosa* specimens observed. Each dot represents a specimen studied and determined to be *L. squarrosa* (Retz.) Dumort.

Disturbed roadsides, crop fields, openings in grasslands, woodlands (aspen-spruce-Douglas fir).

Phenology

Flowering and Fruiting: June-August-(September)

Specimens cited

CANADA. ALBERTA. 65 mi. W of Calgary between Gap Lake and Hwy 1, 25 July, 1949. Frank Raymond F38 (OSU); Banff National Park, near 2nd and 3rd Vermilion Lakes, 23 June 1949, W.W. Mair 40a (UBC); Calgary, North Hill, 16 July 1941, W.C. McCalla 6752 (UBC); Craigmyle District, 10 July 1942, A.H. Brinkman 5227 (UBC); Jasper, 26 July 1957, F. Comte 1606 [specimen on right side of sheet] (WTU); 8 mi N of Red Deer; 28 July 1949, Frank Raymond F68 (OSU). **BRITISH COLUMBIA**. Fort Nelson near mile 300 of the Alaska Highway, 3 July 1970, R.M. Annas (UBC); West of Goose Lake, 7 June 1977, Robert K. Scagel 77-0-38 (UBC); Road to Glimpse Lake which is at the head of Lauder Creek, N. of Douglas Lake, 14 September 1975, Gerda Krause 64 (UBC); Near Hedley, Stemwinder Camp, 4 June 1957, K.I. Beamish, A. J. Gilmartin 7127 (UBC); Along Ashnola River Rd. 16 km west of jct. with Rt. 3 west of Keremeos, 11 June 1983, Gerald B. Straley 2649 (UBC); Prince George, 22 July 1946, J. W. Eastham s.n. (UBC);12 miles east southeast of New Hazelton. 15 July 1954, J.A. Calder, D.B.O. Savile, J.M. Ferguson 13032 (RM); 3 mi W of Princeton, 22 May 1964, V.J. Krajin, B. Fraser 645-08 (UBC) 7.0 km. from Post Office, Fort St. James, along Stone's Bay Road, 26 June 1981, Arle Kruckeberg 63 (UBC); Fairmont Hot Springs, 11 July 1947, J. W. Eastham s.n. (UBC); Spotted Lake near Osoyoos, 23 May 1978, A. A. Rose AAR78289 (UBC); About 4 miles west of Taylor Flats north of railway bridge; Ft. St. John area, 10 July 1960, J. a. Calder, I. Kokkonen 26787 (UBC); Longbeach , Nelson, 28 July 1937, J.W. Eastham s.n. (UBC); KC-2 Alex Fraser Research Forest, approximately 5 kilometers south of 150 Mile House, Knife Creek, 21 July 1997, Claudia Hanel 173 (UBC); Cranbrook, 23 July 1938, J.W. Eastham (UBC); 12 km N of Clearwater Village, 8 September 1980, Trevor Goward 81-817 (UBC); Near Colony Farm Road, Coquitlam, 11 August 1988, Frank Lomer 88-116 (UBC);

Redbush Meadow Road, Chilcotin, 10 August 1975, D. Jenkins 10137 (BC); Columbia Valley High ground north of Kimberly, 23 July 1939, J.W. Eastham s.n. (UBC); Cache Creek, 12 July 1955, G. Mulligan, W. Woodbury 1619 (UBC); Creston, 18 September 1927, G.N. Jones 913 (WTU); Clinton, 9 July 1963, J.W. Eastham 747 (UBC); Cecil Lake, 8 July 1958, F. Mertens 13 (UBC); 110 Cariboo Road, 27 July 1945, J.W. Eastham (UBC) ; South of Quesnel, 21 August 1947, Hanson and Merkle 373 (OSU); Highway 26, ¼ mile east of junction of Highway 97, Quesnel, 14 July 1993, A.R. McCutcheon s.n. (UBC); Smithers, 2 September 1943, V.C. Brink (UBC); Kootenay National Park, Radium Hot Springs, 10 July 1937, Lewis S. Rose 37472; Along road below Sabine Mt. (north side of mt.), 25 August 1970, J. Maze 666 (UBC); South Peace River, 20 June 1958, R. Shearer (UBC); Picnic grounds along Hwy. 16, just N.W. of Topley, 7 July 1974, V.J. Krajina, J. Pojar, C. Parsons s.n. (UBC); Errington, V.I. [Vancouver Island], 1952, Geo. H. Larnder, s.n. (UBC); Vanderhoof, farm of E. Smedley, 10 August 1943, C. Tice s.n. (UBC); Vernon, 23 August 1949, T. C. Brayshaw 49418 (UBC); Along the banks of the Bull River 6 m. northeast of Wardner, 21 July 1941, W.A. Weber 2258 (UBC, WTU); Wasa, Premier Lake, 14 July 1946, F. Fodor 208, (UBC);Yale District, between Tulameen and Aspen Grove, 9 September 1963, A. R. Krukeberg 5730 (RM, WTU); Sandspit area, Moresby Island, in town and along roadside just south of town on road to Copper Bay, 17 July 1964, J.A. Calder, R.L. Taylor 36025 (OSU); Macalister, 18 June 1952, T.M.C. Taylor, W.H. Lewis 287 (UBC). Crown Lake, Marble Canyon, Pavilion area, 26 June 1963, K. Beamish 630011 (UBC); Kamloops on the road toward Merritt, 23 June 1965, V.J. Krajina 65062335 (UBC); Shuswap Falls, Lumby area, June 1957, K.I. Beamish, A.J. Gilmartin 7418 (UBC). MANITOBA. 0.1 m west of Ski lodge at Mt. Aggassiz along Mt. Aggassiz Rd. 16 July 1979, W.A. Wojtas 514 (UBC). Ft. Churchhill, August 1950, W.H. Lewis (UBC); Ethelbert: sandy roadside north of

village, 1 July 1950, H.J. Scoggan, W.K. W. Baldwin 7622 (UBC). **NORTHWEST TERRITORIES CO.** Mackenzie District, Experimental Farm, Fort Simpson, 7 July 1961, W.J. Cody, K.W. Spicer 11488 (ALA). **ONTARIO**. HURON CO.: Morris Tp, 8 July 1895, C. McLean Fraser s.n. (UBC). ["Michigan, U.S.A." was written in ink on the sheet above the label, but a search for Morris Twp. lists it Morris Twp as a former township (now the municipality of Morris-Turnberry) in Huron Co. Ontario:http://www.huroncounty.ca/cc/ mungov.php]; Capreol, 15 July 1949, V. Krajina 5 (UBC); Montreal Road near Ottawa, 13 July 1935, Mary E. Forward s.n. (UBC); ALGOMA DISTRICT: Mamainse Pt. 13 July 1935, T.M.C. Taylor et al. 1220 (UBC); THUNDER BAY DISTRICT: Heron Bay, vicinity of Peninsula, 22 July 1939, T.M.C. Taylor, M.W. Bannan, H.M. Harrison 185. (UBC); Railway tracks, Port Coldwell, vicinity of Peninsula, 7 July 1939, T.M.C. Taylor, M.W. Bannon, H.M. Harrison 185 (UBC). Old railway bank SW of Swing Bridge, Neebing Twp., 18 July 1965, W. Hartley 140 (ARIZ); Mortimer Island, North Schore of Lake Superior, 27 July 1937, R.C. Hosie, S.T. Losee, M.W. Bannan 555 (ALA). QUEBEC: Buckingham, cté Papineau, rang 4, 3 October 1944, Gaston Lamarre 44-202 (UBC); Cité Universitaire, 10 July 1964, C. Rousseau 64-1022 (OSU); Deschênes, 1 July 1919, Marie Victorin 10051 (ND); Ile du Calumet (Pontiac): ferme G. Kelly, 10 July 1056, G. Lamarre, G. Beaulieu s.n. (OSU); Lascelles, overlooking Johnston, 9 July 1942, H. Groh 1754 (RM); GASPE CO.: St. Pierre, 21 July 1934, H.K. Svenson 6257 (ND). SASKATCHEWAN: Regina, south side Wascan Lake between New Broad St. & Winnipeg St. 5 August 1963, J.F. Alex 1149 (ALA, OSU, UBC, WTU); South of Swift Current, 13 August 1959, R. Buchanan s.n. (UBC), McKague, 9 July 1941, A. J. Breitung 1259 (WTU).

U.S.A. **ALASKA.** Fairbank Quad., University of Alaska campus, 1 September 1970, Jinkinson 57 (ALA); Tanana Lowlands, Nenana, 15 August 1955, H. Schmuck 75 (ALA);

Gakona, 18 June 1944, J. P. Anderson 8519 (ALA); Unilaska Quad., Aleutian Island, Unilaska I., Unalaska village, 23 August 1996, C.L. Parker 6930 [this specimen with corollas >4mm wide –SJR] (ALA); Matanuska, 7 August 1931, J.P. Anderson 1334 (ALA). **ARIZONA**. GRAHAM CO.: Pinaleno Mountains: West Peak, 12 September 1989, Steven P. McLaughlin 5805 (ARIZ). PIMA CO.; Mt. Lemmon, Santa Catalina Mountains, about 0.5 mi E of the Santa Catalina Highway, August 1997, Stephanie Quick s.n. (ARIZ). **COLORADO**. DOLORES CO.: County Road 31.00, ca 22 air mi NNE of Dolores in the Belmear Lake drainage area. 13 July 1995, Lynn Marie Moore, Sierra Smith 7010 (RM); San Juan National Forest: beaver pond along Colo Hwy 145, ca 3 air mi N of Rico, 16 August 1994, Lynn Marie Moore 3955 (RM). EAGLE CO.: Park Range, ca 1.5 air mi ESE of McCoy, ca 18.7 air mi NNE of Eagle, ca 0.4 air mi below Copper Spur, along Yarmony Creek, 8 August 1989, B.E. Nelson, Michelle Nelson 17976 (RM); Slopes of Colorado River Canyon, ca 15 mi NNW of Eagle, 1.5 mi road mi SW of Burns, 3 June 1990, James P. Vanderhorst 132 (RM). GARFIELD CO.: East Elk Creek drainage, ca 12 air mi NW of Glenwood Springs, 25 August 1990, James P. Vanderhorst 1920 (RM); Rifle Gap Reservoir, east end along East Rifle Creek, ca 7.5 air mi NNE of Rifle, 23 June 1990, Ronald L. Hartman 25782 (RM). GRAND CO.: Gore Range: upper Gore Canyon, Inspiration Point and slopes below, 5 June 1990, Ronald R. Hartman 67147 (RM); Park Range; ca 9.5 air miles WSW of Kremmling, 11 August 1989, Nancy Kastning, with Sunny and Joel Kastning 2601 (RM). GUNNISON CO.: roadside along Cochetopa Pass Hwy, 4 mi S of junction with Parlin-Gunnison Road, 10 August 1955, W.A. Weber 9452 (RM, TEX,WTU). JACKSON CO.: Rabbit Ears Range: ca 1 ¼ air mi S of Slack-Weiss Reservoir and ca 2 air mi WNW of the north end of Arapaho Ridge, ca 21.5 air mi S of Walden, 17 July 2001, B.E. Nelson 54347 (RM); North Park, along County Road 6 in the vicinity of Trappers Gulch at the south end of Battle Ridge, ca 11 air mi WNW of Cowdrey,

ca 17 air mi NW of Walden, 29 August 2001, B.E. Nelson 56410 (RM), North Park, along Colo Hwy 125 just N of the Canadian River, ca 1/3 mi N of Cowdrey; ca 9.5 air mi N of Walden, 6 September 2000, B.E. Nelson 52176 (RM). MOFFAT CO.: Craig-Meeker road, 1.2 mi. N. Gossard Jnct, 16 July 1936, L-3 (USFS-RM); Williams Fork Mountains: KNEZ divide between Jeffway and Deacon gulches, ca 7 air mi SSE of Craig, 19 June 1990, B.E. Nelson 18722 (RM). RIO BLANCO CO.: Between junction Meeker-Rio Blanco and Strawberry Canyon roads, 14 June 1978, W.A. Weber, J. Wingate 15369 (RM); Oak Ridge, ca 13 air mi ESE of Meeker. 16 July 1990, James P. Vanderhorst 1182 (RM); ROUTT CO.: Steamboat Springs, bank of Yampa River, 3 September 1963, Robert Irving s.n. (TEX); Ca 16.5 air mi SE of Yampa, ca 4 air miles NNE of McCoy, 8 August 1989, B.E. Nelson, Michelle Nelson 17898 (RM); Elkhead Mountains: along Wolf creek and County Road 52, ca 5 air mi SW of Slippery Sides Mountain, ca 6.5 air mi ENE of Hayden, 28 June 2001, B.E. Nelson 53412 (RM). WELD CO.: Bluffs N.W. of Grover, 24 May 1926, E.L. Johnston 180 (RM). **IDAHO**. BANNOCK CO.: Sandy flat, Cache Valley, five miles south of Downey, 12 July 1952, William H. Baker 9228 (WTU). BONNEVILLE CO.: Big Elk Creek campground, 13 August 2003, J. F. Smith 4909; Targhee National Forest: Mike Spencer Canyon, SE of Ida Hwy 31, ca 6 air mi N of Swan Valley, 16 July 1991, Stuart Markow 3114 (RM); Targhee National Forest: West Slope Snake River Range: Rainey Creek from entrance to National Forest to Corral Canyon, ca 3 air mi E of Swan Valley, 28 June 1991, Stuart Markow 1539. CASSIA CO.: Formation Canyon, Black Pine Range, May 1978, Bob Thompson 323 (ARIZ). CLARK CO.: Warm Springs to mouth of Grouse Canyon, ca 22 air mi NW of Dubois, 21 June 1992, Stuart Markow 7870 (RM); Targhee National Forest: east Slope Big Hole Mountains, trail along South Fork of Horseshoe Creek, ca 10 air mi W of Driggs, 4 July 1991, Stuart Markow 2002 (RM); Western Centennial Mountains: 0.5 mi N of

entrance to Huntley Canyon, ca 1 air mi NW of Spencer, 24 July 1992 Stuart Markow 9782 (RM). CUSTER CO.: Near Double Springs Summit, 8 miles N.E. of Dickey, 16 July 1941, Arthur Cronquist 3163 (GH); Just S of Wildhorse Guard Station, on road to Wildhorse Creek Forest Camp, 27 July 1957, A.R. Krukeberg; FREMONT CO.: Vacant lot in Ashton, 8 July 1939, Arthur Cronquist 1514; FREMONT CO.: Henry's Lake Mountains, Targhee Creek Trail from trail head to Dry Fork Cutoff, ca 9 air mi W of West Yellowstone, Montana, 15 July 1992, Stuart Markow 9387 (RM). LEMHI CO.: Below Bannock Pass, Salmon National Forest, 11 miles northeast of Leadore, 18 August 1956, William H. Baker 14665 (WTU); Beaverhead Range: lower reaches of Scott Canyon, ca 6 air mi SE of Nicholia, 22 August 1992, Stuart Markow 10990 (RM); . MADISON CO.: Targhee National Forest: West Slope Big Hole Mountains: West Pine Creek Trail, just N of Ida Hwy 31, 28 July 1991, Stuart Markow 4227 (RM). ONEIDA CO.: Blue Spring Hills, Ida 37, 9 miles west of Malad City, 7 June 1969, Noel H. Holmgren, Earl Jensen 3452 (UBC); Along Weston Creek below the Weston Reservoir, 14 July 1952, William H. Baker 9274 (WTU). OWYNEE CO.: Triangle, 12 August 1951, William H. Baker 8567 (WTU). TETON CO.: Targhee National Forest: East slope Big Hole Mountains: south end of trail leading from Ida Hwy 31 to Corral Creek, ca 7 air mi SE of Victor, 10 July 1991, Stuart Markow 2552 (RM).VALLEY CO.: West slope of high ridge west of Cascade, Payette Nat. For. (WTU). **ILLINOIS**.[COOK CO].: Edgewater Chicago, 28 June 1896, Agnes Chase (RM); [DUPAGE CO.:] Naperville, 16 July 1897, L.M. Umbach; [JACKSON CO.]: Cedar Lake, July 1940, Ogden Glasow 72 (OSU). PEORIA CO.: Horse Shoe Bottom, 7 July 1919, Virginius H. Chase 3171 (ARIZ, WTU); Peoria, July 1900, F.E. McDonald s.n. (RM). STEPHENSON CO.: Freeport 19 July 1898, Charles F. Johnson (OSU). STARK CO.: East of Wady Petra, 14 July 1895, Virginius H. Chase (RM); **INDIANA.** NEWTON CO.: 1.5 mi W of

Goodland, 23 July 1949, Ray C. Friesner 22892 (TEX). **IOWA.** DICKINSON CO. Silver Lake Fen, 29 July 1950, Winona H. Welch 9860 (TEX). [JOHNSON CO.:] Iowa City, 26 June 1894, B. Shimek (TEX). PLYMOUTH CO.:1878, John Leiberg s.n. (OSU). SIOUX CO.: West Branch creek, Junct. Hwys. 10 and 75, 8 July 1956, Jack L. Carter 1386 (ARIZ).**MASSACHUSETTS.** NORFOLK CO.: Avon (near Stoughton line), 5 June 1958, S.F. Blake 12620 (LL); Canton, barnyard of Amos Holmes; 29 July 1923, S.F. Blake 8525 (LL). **MICHIGAN.** HURON CO.: Caseville, 11 July 1956, P.E. Hebert, 4447 (ND); Grindstone City, 15 July 1951, P.E. Herbert 3491 (ND); [INGHAM CO.]: Michigan Agricultural College. East Lansing. 24 July 1888, E.R. Lake s.n. (OSU); South of Harrison's, East Lansing, 27 June 1895, P.B. Cordley s.n. (OSU). LIVINGSTON CO.: Greenoak Twp. Island Lake State Rec. Area, 2 July 1947. Daniel Lynch s.n. (TEX). WASHTENAW CO.: Ann Arbor, 1 August 1903, Kirk Whited 2064 (OSU). **MINNESOTA.** CLAY CO.: 2 miles east of Glyndon, 11 June 1956, John W. Moore 22811 (TEX). HENNEPIN CO.: 15 June 1890, T.H.B. 7484 (WTU). Minneapolis, June 1895, E.P. Sheldon s.n. (RM). HUBBORD CO.: Sandy beach, 29 June 1939, Robert Bebb 4505 (ARIZ). PIPESTONE CO.: Pipestone, June 1895, Max Menzel s.n. (RM). ROCK CO.: River bank east of Luverne, 14 June 1941, Philip Johnson 307 (WTU). **MISSOURI.** CRAWFORD CO.: Courtois Creek, west of Berryman, 14 June 1941, Julian Steyermark 41284 (TEX). **MONTANA**. BEAVERHEAD CO.: Along the Johnson Gulch Road ca 10 mi southeast of Grant, 6 July 1984, Peter Lesica 3109 (RM); Horse Prairie (west end), along Lemhi Pass rd. 7 mi. E of Lemhi Pass; 20.2 mi N of Leadore, Idaho, 6 July 1970, Peter F. Stickney 2109 (USFS-RM); [FLATHEAD CO.]: Bet. Belton and Kalispell, 18 July 1934, George E. Osterhout 8027 (RM); 2 miles S of Columbia Falls, 16 July 1942; H.T. Rogers and J.M. Rogers 1082 (WTU). GRANITE CO.: Near the Lolo National Forest vic. North Fork Lower Willow Creek, 23 July 1958, Peter F. Stickney PFS-196 (USFS-RM); MADISON CO.: Madison Range: Beaverhead National Forest: ca ½ mi W of Hammond Creek Ranger

Station; 12 mi E of Ennis. 2 August 1993, Erwin F. Evert 26583 (RM); Bear Trap Canyon ca 1 mi N of dam, ca. 5 mi. ne. of McAllister, 18 June 1994, Erwin Evert 27247 (RM); Sandy plain 6 miles South of Ennis, 25 July 1947, C.L. Hitchcock 16815 (WTU). MEAGHER CO.: Helena National Forest, 24 April 1939, Wilfred W. White 300 (USFS-RM). MISSOULA CO.: Jocko Mts., La Valle Cr. Watershed 1.5 mi SW of TV Mtn.; 8 mi N of Missoula, 25 September 1968; Peter F. Stickney (USFS-RM). **NEBRASKA**.[OTOE CO.]: Nebraska City, 27 June 1901, Thornber s.n. (ARIZ). LANCASTER CO.: Near Steven's Creek. S.E. of Lincoln, 20 August 1893, C.A. Turrell s.n. (ARIZ). **NEW JERSEY**.: [CAMDEN CO.]: Cooper's Point R.R. freight yard, Camden, 20 June 1932, W.H. Witte (RM). [MIDDLESEX CO.]: New Brunswick, June 1891, Halsted 54 (ARIZ, RM) [SOMERSET CO.]: Rocky Hill, 1 August 1916, L.H. Lighthipe s.n. (TEX). **NEW YORK**. ALBANY CO.: Albany, 20 June 1945, H.D. House 29831 (TEX); 24 June 1891, C.L. Shear s.n. (RM). [TOMPKINS CO.]: Ithaca, 12 July 1889, W.W. Rowlee (RM); 30 July 1890, W.W. Rowlee (WTU). **NEW MEXICO**. OTERO CO.: Lincoln Nat. Forest, Aqua Chiquita Creek and Upper Pendleton Canyon, 12 August 1970, D.S. Correll, Helen B. Corell 39212 (LL, WTU). **NORTH DAKOTA**. BENSON CO.: Fort Totten, 12 July 1952, Vera Facey 278 (TEX). RAMSEY CO.: Edge of alkali flat 1 mile south of Devils Lake (town) and near former northeast arm of Devils Lake, 29 June 1952, H.H. Bartlett, John F. Grayson 345 (WTU). OHIO. [LORAIN CO.]: Brownhelm, 29 June 1892, Henry C. Cowles (WTU). **OREGON** GRANT CO.: 5 miles south of Seneca, 30 July 1954, Orlin L. Ireland 3393 (OSU); South of John Day, 24 July 1941, Reeder and Merkle 330 (OSU); HARNEY CO.: 3 miles south of Silvies, 30 July 1953, Arthur Cronquist 7671 (WTU). UNION CO.: alfalfa field, 4 August 2000, Darrin Walenta s.n. (OSU). WALLOWA CO.: By trail above Wallowa Falls, 15 June 1928, J. William Thompson 4823 (WTU); Near Enterprise, 25 July 1933, M.E. Peck 17890 (WILLU), Hurrican Canyon, Wallowa Mts., 3 August 1931, Lilla Leach 4010 (OSU). **SOUTH DAKOTA.** CLAY CO.: Vermillion, 3

July 1913, W.H. Over 5090 (OSU). [CODINGTON CO.]: Watertown, 27 July 1895, T.A. Williams s.n. (RM). CUSTER CO. Jewel Cave National Monument, Lithograph Canyon below Porthole, 24 June 1985, Hollis Marriot 9682 (RM); US Hwy 16 just E of Hell Canyon, 7 July 1985, Hollis Marriot 9788 (RM). FALL RIVER CO.: Hot Springs, 1 August 1924, W.H. Owen 16163 (RM). [LAWRENCE CO.]: East of Deadwood, 22 August 1931, George E. Osterhout 7530 (RM). MEADE CO. Black Hills 11 July 1932, George Osterhout 7812 (RM). [MINNEHAHA CO.]: Sioux Falls, August 1892, J.J. Thornber 268 (ARIZ). **UTAH.** Grand CO.: E. Tavaputs, Bookcliff Divide near Seep Ridge Rd., 7 September 1983, E. Neese 15292 (RM). SALT LAKE CO.: Red Butte Canyon, Wasatch Range, 0.5 miles northeast of intersection of Elk Ford Road, 19 July 1969, L. Arnow 2896 (ARIZ). SUMMIT CO.: North Slope Uinta Mountains: west flank of Bald Range, ca 4 air mi S of Lonetree; 4.5 mi S on Uinta County Road 295 on east side of the road, 3 August 1995, C. H. Refsdal 6514 (RM). Just south of I-80 at exit 193, 26 June 1986, Thomas W. Nelson, Jane P. Nelson 8248 (RM). UINTAH CO.: Ca 10 mi NW of Vernal, 31 June 1983. E Neese 14105 (RM). **VERMONT.** [ORLEANS CO.] Newport, 26 July 1904, A. A. Eaton M-223 (LL). **WASHINGTON**. CHELEN CO.: Camas Land, Wenatchee Mts., 26 June 1934, J. William Thompson 10788 (ND,WTU). FERRY CO.: Nancy Creek, 2 mi north of Kettle Falls, 20 June 1939, L. Boner, V. Weldert 165 (RM). OKANOGAN CO. Upper Tonk Creek Valley. 24 August 1931, Charles B. Fiker 426 (WTU); Near Wauconda Summit, 2 July 1932, J. William Thompson 8699 (WTU); Twisp, 17 July 1921, Harold St. John, W.D. Courtney, Charles S. Parker 5523 (WTU); By ditch between Conconully and Loomis, 28 June 1931, J. William Thompson 7095 (WTU). SPOKANE CO.: Spangle, 30 June, 17 July 1916, Wilhelm N. Suksdorf 8727 (WTU); Spokane, 3 October 1912, G.W. Turesson s.n. (RM). STEVENS CO.: near Cedonia, 10 July 1946, Mae E. Dennis 39 (WTU). **WISCONSIN**. FLORENCE CO.:

Nicolet National Forest, 13 July 1938, Clarence Anderson (Clarence V. Lovin), 346 (USFS-RM). MANITOWOC CO.: Along highway U.S. 141, 5.8 miles northwest of Francis Creek, 20 June 1952, H.H. Bartlett, John F. Grayson 17 (WTU). MILWAUKEE. Waumatosa, n.e. of Jacobus Park near Milwaukee road tracks, 23 July 1941, E. P. Kruschke K-41-79 (ND). **WYOMING**. [ALBANY CO.]: Summit rest area on US 80, between Laramie and Cheyenne, 36.5 mi W of Cheyenne, 11 August 1984, James S. Miller, Porter P. Lowry II 1971 (RM). CARBON CO.: Along Cottonwood Creek and McCarty Canyon or County Road 503, ca 5 air mi NNE of Dixon, ca 50.5 air mi SSW of Rawlins, 20 August 1996, B.E. Nelson 40106 (RM). CROOK CO.:Black Hills, Sand Creek, 11-12 air mi ESE of Sundance, 9 July 1984, Ronald R. Hartman 17706 (RM); Houston Cr where it turns S (near Harvey Divide), ca 10 air mi W of Sundance, 24 August 1983, Hollis Marriott 5720 (RM). FREMONT CO.: Junction of Little Atlantic Gulch and BLM Road 2324, ca 4 air mi S of Roundtop Mountain; ca 1 air mi E of Atlantic City, 11 August 1994, Laura Welp 3483 (RM). LARAMIE CO.: 0.5-1 air mi ESE of Federal, 13 July 1993, Ronald L. Hartman 41177 (RM). LINCOLN CO.: Vicinity of Coal Creek, ca 14 air mi N of Border Junction, 20 July 1994, Tom Cramer 2107 (RM); Diamondville, 27 August 1900, Aven Nelson s.n. (RM); Hills east of Afton, 30 June 1923, Edwin B. Payson, George M. Armstrong 3325 (RM) ; Star Valley, Wyoming Game and Fish fishing access area on Salt River; on Wyo Hwy 237 ca 2 road mi W of Grover, 17 August 1992, Ronald L. Hartman 36010 (RM); Star Valley, southwest end of Palisades Reservoir; 2.5 air mi SSW of Alpine Junction, 22 June 1992, Ronald L. Hartman, Bruce Embury 32928 (RM); Spring Lake Creek trail from divide to western end of Lake Alice, 22 August 1993, Ronald L. Hartman 44819 (RM); Tunp Range, Pine Creek, ca 2 road mi NNE of Pine Creek Ski Area, ca 8 air mi NE of Cokeville, 2 August 1993, Ronald L. Hartman 43205 (RM); Hams Fork, ca 1 air mi N of Frontier, 14

August 1994, Tom Cramer 3760; Green River Basin, near Elkol, 6 airmiles SW of Kemmerer, 28 July 1982, Alan T. Carpenter 105 (RM); Prater Canyon, ca 19 mi N of Afton, 19 June 1992, Ronald L. Hartman, Bruce Embury, 32606 (RM), Sublette Range ca 18 air mi N of Cokeville, 15 August 1994, Tom Cramer 3872 (RM); PARK CO.; Absaroka Mountains: just N of U.S. Hwy 14, 16 and 20, ca 40 mi W of Cody in Highway Department gravel storage and dump area. 23 July 1984, Erwin F. Evert 7098 (RM); Shoshone National Forest: Sunlight Basin, ca 30 air mi ENE of Cody, 29 July 1996, David Rosenthal 221 (RM); Northern Absaroka Wilderness: ca 2 mi up Crandall Trail ca 36 air mi WNW of Cody, 22 July 1997, David Rosenthal 2866 (RM). SUBLETTE CO.: Between Chall and the South Fork Middle Beaver Creek, S of South Rim; ca 19 air mi NW of Daniel Junction, 28 July 1992, Ronald L. Hartman 35181 (RM).; Soda Lake; 2 air mi S of Lander Peak; 26 air mi SW of Daniel Junction, 13 August 1992, Ronald L. Hartman 35558 (RM); Between Willow Lake and Fremont Lake near Trapper Lake Trailhead, 9 July 1990, Ronald L. Hartman 26774 (RM); South end of Fremont Lake adjacent to Skyline Drive, ca 2.5 air mi NE of Pinedale, 9 July 1990, B.E. Nelson, Walter Fertig 19345 (RM); West bank of Willow Lake, ca 9 air mi NNW of Pinedale, 10 August 1990, Walter Fertig 5837 (RM); Ca 1 mi N of Scab Creek Campground, 16 air mi E of Pinedale, 24 July 1991, Walter Fertig 10010 (RM); Green River Basin: South Rim, ca 8 air mi NW of Warren Bridge, 10 August 1994, Tom Cramer 3518 (RM); Bank of Green River just S of Bridger-Teton Forest Boundary, ca 19 air mi N of Cora, 30 June 1994, Tom Cramer 1345 (RM); Little Prospect Mountain, ca 11.5 air mi ESE of Big Sandy, 13 July 1995, Tom Cramer 7914 (Tom Cramer, Jane T. Kellett 7914 (RM), Hill just SW of Onion Springs, ca 7 air mi SW of Daniel Junction, 22 June 1994, Tom Cramer 1034 (RM); New Fork River, ca 10 air mi SW of Boulder, from old wooden bridge NE to section line, 30 July 1994, Ronald Hartman, Tom Cramer 48845 (RM); Horse Creek, ca 4.5 air mi SE of

Merna, 12 August 1994 (RM); South Cottonwood Creek, ca 11 air mi WSW of Daniel, 25 August 1994, Tom Cramer 4803 (RM); Pinedale Glacial Fields, E of Fremont Lake, 10 July 1973, R.J. Hill (RM); Apperson Creek to 1.5 mi upstream from road; ca 8 air mi E of Corral Creek Guard Station, 18 August 1992, Ronald L. Hartman 36188 (RM); Big Fall Creek, ca 24 air mi SW of Big Piney, 25 July 1993, Ronald L. Hartman 42155 (RM); Wyoming Range, at the confluence of North Horse and South Fork North Horse creeks, ca 34 air mi W of Pinedale, 7 August 1992, B.E. Nelson, Russ Nelson 23806 (RM); Wyoming Range: along Kilgore Creek ca 4 air mi E of Hoback Peak, ca 8.5 air mi SSW of Bondurant, ca 36 air mi NW of Pinedale, 15 July 1992, B.E. Nelson, Russ Nelson 23281 (RM). SWEETWATER CO.: Earnest Butte, ca 5 air mi SW of Quaking Asp Mountain, ca 14.5 air mi S of Rock Springs, 31 May 1997, Beth Ward 4427 (RM). Green River Basin: draws and slopes draining S to Sugarloaf Marsh Creek from Currant Creek Ridge, ca 0.5 air mi N of Spitzi Creek; ca 1.5 air mi W of Big Ridge; ca 29 air mi SSW of Rock Spings, 14 July 1997, Beth Ward 6441 (RM); West flank of Cedar Mountain, ca 5 air mi NE of Lonetree,; 2.6 mi E of junction of Sage Creek Mountain Road/ County Road 4-1, 23 July 1995, C.H. Refsdal 5833 (RM); E side of Pine Mountain, at head of Coyote Creek, 17 July 1980, Keith H. Dueholm 10734 (RM); Big Sandy River, ca 1 air mi SW of Farson, 21 August 1994, Tom Cramer, Ben and Becky Cramer, 4396 (RM). TETON CO.: Bridger-teton National Forest; East Slope Snake River Range: Coburn Creek trail, from Prichard Pass, 20 July 1991, Stuart Markow 3446 (RM); Targhee National Forest: West Slope Teton Range: trail from Grand Targhee Ski Area to Miles Creek Trail, ca 10 air mi NE of Driggs, Idaho, 19 August 1991, Stuart Markow 6222 (RM); Gros Ventre, along Camp Creek N of the Hoback River, ca 13.5 air mi SSE of Jackson, 21 August 1990, B.E. Nelson 19965 (RM); N of Dubois Highway, 15 August 1947, John F. Mildred S. reed 1365 (RM); West Slope Teton Range: Game Creek Trail,

ca 4 air mi SE of Victor, Idaho, 19 August 1991, Stuart Markow 6428 (RM); Flats along Blackrock Creek near Blackrock Ranger Station, ca 8 air mi E of Moran, ca 31.3 air mi NE of Jackson, 3 August 1987, B. E. Nelson, Neil Snow 14345 (RM). UINTA CO.: North Slope Uinta Mountains: Blacks Fork, ca 9.2 air mi SW of Robertson; 9.9 mi S of County Road 271, 29 July 1995, C.H. Refsdal 6115 (RM). Ca 10 air mi SW of Mountain View; 4.4 mi S on County Road 279, 13 July 1995, C.H. Refsdal 5380 (RM). WASHAKIE CO.: Big Horn Mountains, at the head of Tensleep Canyon on an old section of US hwy 16, ca 12.5 air mi NE of Ten Sleep, 14 August 1980, B.E. Nelson, Gael Fonken 7089 (RM). WESTON CO.: Black Hills, Cold Springs Cr near State line, ca 7 air mi NE of Four Corners, 3 July 1984, Hollis Marriott 7544 (RM).

10. Lappula texana (Scheele) Britton

Key to varieties

1. Nutlets with 5-6 spines per side, flowers white barely exserted from calyx…*L. texana* var. *texana*

2. Nutlets with 3-4 spines per side, flowers white barely exserted from calyx….*L. texana* var. *septemtrionalis*

10a. Lappula texana (Scheele) Britton *var. texana.*

Lappula texana (Scheele) Britt. **var.** ***texana.*** Mem. Torrey Bot. Club 5: 273. 1894.

Echinospermum texanum Scheele. Linnaea 25: 260.1853. Type: U.S.A. Texas. 1846. F. Lindheimer, 477. (Neotype designated here: PH-10004!).

Lappula redowskii var. *texana* (Scheele) Brand. 1931. Pflanzenr. IV. 252(Heft 97): 150

Echinospermum scabrosum Buckley. Proc. Acad. Nat. Sci. Philadelphia. 462. 1861 (1862). Type: U.S.A. Texas: "Upper Colorado" June S.B.Buckley (Holotype: PH-10001!).

Echinospermum pilosum Buckley. Proc. Acad. Nat. Sci. Philadelphia. 462. 1861 (1862). Type: U.S.A.: Texas Hills Northern Texas. June 1861. Buckley, S.B. s.n. (Holotype: PH-10000, first specimen at left on sheet (mixed sheet!)).

Description

Herbs annual. **Roots** single, narrow, straight. **Stems** 1—3 (up to 7) several stemmed, ascending to erect, branching in upper half, (0.5dm)—1—3 dm, mixed appressed hairy and pilose, canescent. **Basal leaves** forming loose rosette, withering in fruit, basal leaves spatulate, 2—4 cm x 3—6 mm, abaxially spreading hairy,adaxially spreading hairy, frequently minute pustulate, long hairy at midrib, bases attenuate, margins long hairy, apices obtuse. **Stem leaves** oblong-obovate, less than 2 cm x (1) 3—5—(9) mm wide, abaxially tomentose with a glabrous line along midrib, adaxially tomentose, bases cuneate to attenuate, margins densely ciliate hairy, apex rounded to acute, occasionally notched. **Inflorescences** to over 10 cm long in fruit, paniculiform, bracts linear to rhombic, 3 mm—1.5 (2)cm length, more or less similar somewhat reduced distally. **Fruiting pedicles** 0.5—2 mm ascending to shallowly recurved, appearing sessile. **Calyx lobes** narrow linear, 1mm—3mm long, to 4mm length in fruit, clasping often exceeding fruit. **Corollas** blue (white not seen), limb 1.5—2 mm wide, lobes divergent, oblong to subovate. **Fruits** homomorphic, sub-globose (wider than tall), 2—3 mm high. **Nutlets** heteromorphic, ovate, 2 mm long, bases rounded, apices acute; *3 nutlets* with 1 row of spines along highly inflated disk margin; 10—12 spines arising from margin, 1mm long, at least 1 spine per side free near apices, terete; disk ovate partially obscured by margin, 1.5 mm x 0.5 mm, abaxial disk evenly muricate-papillate; adaxial surface evenly muricate-papillate or becoming smooth apically; *remaining nutlet wingless*, with 5-6 spines along each side arising from raised margin, 1—2 mm long, bases free to adjacent, disk shape lanceolate to ovate, smaller than nutlet body,

1.5 mm x 0.5—1 mm, abaxial disk evenly muricate-papillate, adaxial surface muricate-papillate; nutlet clinging to gynobase at maturity. **Gynobase** 2—2.2 mm tall. Style surpassing nutlets, readily visible, even with or exceeding spines.

Discussion.

Scheele in naming *E. texanum,* referred to Roemer's collection from San Antonio (1853). Scheele wrote that the collection was made: "Im Gebüsch der *Algarobia glandulosa* (Musket-tree) bei San Antonio" (Scheele, 1853). Blankenship notes that a collection made by Lindheimer in April from San Antonio may be the type, but notes Scheele's attribution of the type to Roemer (Blankinship, 1907). Lindheimer collected with Roemer and traveled with him to San Antonio when this collection was made (Goyne, 1991), The location of Scheele's herbarium and type specimens is unknown and attempts to locate material associated with Roemer were unsuccessful. The collection of Lindheimer at the Philadelphia Herbarium (PH) from the type locality is designated the neotype. It was distributed by him as Fascicle 3 of "Flora Texana exsicatta."

The typical variety is typical larger and with longer branches than the northern one. Herbarium specimens appear gray canescent (living specimens not seen.) Specimens have blue flowers with petals extending beyond the calyx. The fruits are also different having more spines, and the free spines on the odd nutlet are long horizontally spreading, often pectinate and upcurved and fruiting characters reliably separate the two varieties. Species with heteromericarpic fruits occasionally produce homomorphic fruits. Though not observed in the specimens studied, it can be expected that occasionally plants may be found that have four nutlets with inflated margins or with none inflated.

The fruiting characters are pronounced and the two varieties do not seem to intergrade where they co-occur. Plants of the Texas variety have an earlier flowering and fruiting time. Further study may reveal evidence that the two represent separate species, but the two are maintained as a single species here. The majority of collections observed were from Texas, primarily from the Edwards Plateau, Trans-Pecos, and Rolling Plains vegetational areas of Texas (as defined in (Diggs et al. 1999)) and Oklahoma. Only a few specimens were observed from Mexico, but it is expected in similar habitats southward. Specimens of this species were not observed from Colorado, New Mexico where *L. heterosperma* becomes dominant, so it is not possible at this time to say whether the species occurs there.

Britton's concept of *L. texana* included *L. occidentalis* including the variety with connate spines. Nelson and Macbride (1916) and Johnston (1923) applied *L. texana* to all species with a broadly inflated margin separating out varieties which are here treated under *L. heterosperma* and *L. occidentalis* var. *stricta*.

Distribution and Ecology

Sands and gypsum soils, rocky and grassland slopes, along Nueces River and tributaries.

The distribution map for both varieties is shown in Figure 2.23 under the information for *L. texana* var. *septemtrianales*. The dots in the map represent specimens that were examined and confidently determined. The map was made in ArcGIS online. The search window in ArcGIS online was used to find the localities on the specimen labels and dots were placed manually.

Phenology

Flowering and fruiting: March-May

Specimens cited

TEXAS. CONCHO CO.: 25 April 1943, B. C. Tharp s.n. (TEX)COTTLE CO.: 14 mi W of Paducah, Rre. 70, 8 May 1968, D. S. Correll 35708 (LL). CROCKETT CO.: thirty miles north of Juno, 5 June 1957, Barton H. Warnock, W. D. McBryde 15303 (LL). **[**DIMMIT CO].: Dimmit and Maverick county line on road from Carrizo Springs to Eagle Pass, 31 March 1959, M. C. Johnston (TEX); Carrizo Springs-Eagle Pass, 6 April 1930, Eula Whithouse s.n. (TEX); CHILDRESS CO.: On hills on east edge of Childress, 1 June 1957, D. S. Correll 16550 (RM); EDWARDS CO.: Along West Fork of the Nueces River, southern part of county, route #674, 29 April 1959, D. S. Correll, I. M. Johnston 21211 (LL). Southernmost part of county ca. 5 miles south of intersection US377 and state hwy 2523, along the latter, 26 April 2001, B. L. Turner 21-369 (TEX); FISHER CO.: On east edge of Longworth, 14 May 1957, D. S. Correll 16376 (LL). FRIO CO.: 6 miles northeast of Pearsall, off U. S. 81, along railroad, C. L. Lundell 13627 (LL). GILLESPIE CO.: About 9 miles North of Willow City near Serpentine Quarry, 23 April 1966, Elray Nixon G45 (TEX); Along Delaware Creek, fork of the Pedernales, 29 April 1959, D. S. Correll, I.M. Johnston 21173 (LL). HARDEMAN CO. 2 miles west of Acme on Hy. 287, 1 June 1957, D. S. Correll 16524 (LL). HUTCHINSON CO.: Canadian River breaks, 24 May 1965, Mrs. Cliff Drake 86 (TEX). KIMBLE CO.: Buck Wildlife Management Area, 17 May 1989, W. R. Carr 9698 (TEX). SUTTON CO.: Southwestern most part of county where highway 189 enters Val Verde Co., 25 March 2001, B. L. Turner 21-144 (TEX). TAYLOR CO. east of Merkel, 29 April 1942, C. L. Lundell, Amelia A. Lundell 11362 (LL). UVALDE CO.: 19 miles NW of Uvalde, just past crossing of Nueces River going N of #55, 20 April 1974, Mary Butterwick, Jackie Smith, Arnold Cuba, B. L. Turner (TEX). North of Uvalde, 17 April 1949, B. C. Tharp, Charles Havard 49347 (ND), On hills and flats one miles north of Uvalde, 18 April 1949, D. S. Correll, R C. Rollins 20911 (LL).

10b. Lappula texana (Scheele) Britton var. *septemtrionalis* var. novem

Description

Herbs annual. **Roots** single, narrow, straight. **Stems** 1—3 (up to 7) several stemmed, ascending to erect, branching in upper half (throughout), 0.5dm—1—2 dm, long appressed hairy and pilose. **Basal leaves** forming loose rosette, withering in fruit, basal leaves spatulate, 2—3 cm x 3—4—(6) mm, abaxially spreading hairy, adaxially spreading hairy, frequently minute pustulate, long hairy at midrib, bases attenuate, margins long hairy, apices. **Stem leaves** oblong-obovate, less than 2 cm x (1) 3—5—(9) mm wide, abaxially tomentose with a glabrous line along midrib, adaxially tomentose, bases cuneate to attenuate, margins densely ciliate hairy, apex rounded to acute, occasionally notched. **Inflorescences** 3—10 cm long in fruit, raceme-like, bracts linear to lanceolate, 3 mm—1.5 –1—(2) cm length, more or less similar somewhat reduced distally. **Fruiting pedicles** 0.5—2 mm ascending to shallowly recurved, appearing sessile. **Calyx lobes** narrow linear, 1mm—3mm long, to 4mm length in fruit, clasping often exceeding fruit. **Corollas** white fading blue, blue, limb 1.5—2 mm wide, lobes erect spreading, narrow oblong. **Fruits** homomorphic, sub-globose (wider than tall), 2—3 mm high. **Nutlets** heteromorphic, ovate, 2 mm long, bases rounded, apices acute; *3 nutlets* with 1 row of spines along highly inflated margin; 6—8 spines arising from margin 0.5 mm long, at least 1 spine per side free near apices, terete; disk ovate partially obscured by margin, 1.5 mm x 0.5—0.7 mm, abaxial disk evenly muricate-papillate; adaxial surface evenly muricate-papillate or becoming smooth apically, nutlets easily released from gynobase at maturity; *remaining nutlet wingless*, with 3—4 spines along each side arising from raised margin, bases free to adjacent, longest spines 1mm, disk shape narrow lanceolate to narrowly ovate, smaller than nutlet body, 1 mm x 0.2—0.5 mm, abaxial disk evenly muricate-papillate, adaxial surface muricate-papillate, nutlet clinging

strongly to gynobase at maturity. **Gynobase** 2mm tall. Style surpassing nutlets, readily visible, even with or taller than spines.

Discussion

In the Northern part of its range this variety can be confused with *L. heterosperma* from which it can be distinguished by its fruits. This variety has four spines per side on the nutlets. The style is clearly and not surpassed by the apical spines, whereas in *L. heterosperma* the apical spines exceed the nutlet body and obscuring the style. The flowers are white or palest blue and 1-2 mm wide, barely exceeding the corolla. In *L. heterosperma* and *L. texana* var. *texana* the flowers are blue. *Lappula texana* var. *texana* is a larger more robust plant than the northern variety and the odd nutlet has more marginal spines that are horizontally spreading and upcurved at the tips. The northern variety has been collected from grasslands in western Kansas and western Nebraska, eastern Colorado, and parts of Okalahoma. Where the ranges of the northern and southern varieties meet, they remain distinct.

Figure 2.22. *L. texana* var. *septemtrianalis*. Closeup of fruit showing style clearly visible among nutlets, and "odd" nutlet with four free spines per side. SJR 1100.

Distribution and Ecology

Sandy grasslands and sparsely vegetated openings. The specimens listed below were included in the map in Figure 2.23. The variety also occurs in South Dakota, western Nebraska, and North Dakota, but only cited specimens were included in the map.

Figure 2.23. Distribution of *L. texana* (Scheele) Britt. *Lappula texana* var. *texana* (red dots), *L. texana* var. *septemtrianalis* (yellow dots)

Phenology

Flowering and fruiting: May—July

Specimens cited

U. S. A. **COLORADO.** BACA CO. Springfield, 21 May 1914, G. E. Osterhout 5066 (RM). **KANSAS.** CLARK CO.: North rim of Little Basin and St. Jacob's Well, 17 June 1957, Lloyd C. Hulbert.2760 (KSC). ELLIS CO.: July 1895, C. A. Hitchcock s.n. (KSC). ROOKS CO.: Rockport, 27 May 1889, E. Bartholomew s.n. (KSC). RAWLINS CO.: Atwood, S. S. Fry (KSC). SHERIDEN CO.: 1931, Clement Weber 164 (KSC). **WYOMING**. GOSHEN CO.: Along Horse Creek and adjacent plains W of County Road 191, ca 4 air mi S of La Grange; ca 34 air mi S of Torrington, 13 June 1993, 25679 (RM). LARAMIE CO. Ca. 0.5 miles S of I-80 in Pine Bluffs, S of Pine Bluffs Rest Area, 20 June 1978, B. E. Nelson, Paul Ehrmann 1745 (RM). NIOBRARA CO.: On the Goshen-Niobrara County Line, near the east side of Rawhide Buttes and west of US 85, 6 July 1955, C. L. Porter 6714 (RM, TEX). PLATTE CO.: Hartville, 30 June 1901, Aven Nelson 8324 (RM); Guernsey, 3 June 1940, M. Greenwald s.n. (RM); Camp

Guernsey, 0.5 km W of North Platte River, ca 0.2 km N of Cottonwook Creek, 12 June 1995, Douglas, Nelson, Popolizio, Smith 57; 7.5 air miles W of Wheatland, 1 July 1993, Ronald L. Hartman 39661 (RM).

Future Directions

There are a number of areas that would be interesting to explore in the North American *Lappula.* While hybridization has been invoked to explain puzzling variation in some of the Turkish *Lappula* species (Edmonson 1978), virtually nothing is know if hybridization is responsible for the complex patterns of variation, or what other processes are at work. The recent finding reported above of a diploid count of 2n=24 for *Lappula redowskii* is of interest, the few counts of American *Lappula* species were reported as 2n=48.It would be valuable to get chromosome counts for more North American species and to observe the behavior of meiotic chromosomes. More work is needed to understand variation and species boundaries, especially in *L. desertorum*, *L. occidentalis* var. *stricta* relative to *L. cucullata.* Are there mountain populations of *L. squarrosa* that may have a different introduction than those that stretch across the Northern plains and eastern North America? Perhaps further exploration may suggest that some populations of *L. squarrosa* do not represent recent introductions. In addition to possibilities of further taxonomic work, also of interest are questions of fruit ecology and reproductive biology. It is hoped that this work will result in more in depth study of the genus in North America.

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