

REVISION OF *SPHAEROCARDAMUM* (BRASSICACEAE)

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ABSTRACT

Sphaerocardamum (Brassicaceae) is a little known and rarely collected genus that includes eight species that are endemic to limestone soils of Mexico's Chihuahuan Desert and adjacent mountain regions. In the present study species boundaries were evaluated using data from morphology, crossing experiments, cytology, genome size, and AFLP-based molecular variation. Considering variation observed from herbarium accessions and individuals cultivated in a common environment, fixed morphological character state differences support the current circumscription of *S. compressum* and *S. nesliiforme*. However, no fixed morphological states were consistent with the segregation of *Sphaerocardamum macropetalum* from *S. divaricatum* or *S. fruticosum*, *S. macrum*, and *S. ramosum* from *S. stellatum*. Genome size variation partitioned the genome into two groups of taxa that are consistent with morphological variation and results from AFLP data are also consistent with the morphologically based groupings. In light of the available data, a taxonomic revision is presented recognizing four species: *S. compressum*, *S. divaricatum*, *S. nesliiforme*, and *S. stellatum*.

The genus *Sphaerocardamum* S. Schauer comprises eight species of Brassicaceae (Rollins 1984) native to north-central Mexico. It includes perennial or biennial herbs that typically flower from May through October following seasonal precipitation. The genus can be identified based on a combination of morphological characteristics including a caulescent diminutive habit, woody caudex, simple oblong leaves, indument of single-celled dendritically branched trichomes, white linear to spatulate petals, pale to purplish anthers, and small silicular fruits with two to eight ovules per locule (Rollins 1984; Bailey et al. 2002) (Fig. 1).

Members of the genus were primarily known from the Chihuahuan Desert and surrounding mountains in Aguascalientes, Coahuila, Hidalgo, Nuevo León, San Luis Potosí, Tamaulipas, and Zacatecas. More recent collections expand that distribution to as far to the south as Puebla and as far west as Guerrero. Populations typically occur in seasonally dry habitats on limestone soils at elevations ranging from 1560–2850 m.

In Rollins's (1941, 1984) treatments of *Sphaerocardamum*, he discussed the tentative nature of his circumscriptions because of the paucity of available material. From just 42 known sheets of *Sphaerocardamum*, he concluded that the variation could be segregated into eight putative species. The majority of the collections were designated as two widespread taxa, *S. macropetalum* Rollins and *S. stellatum* (S. Wats.) Rollins, whereas *S. compressum* (Rollins) Rollins and *S. ramosum* Rollins were known only from the type collections and the remaining species from fewer than five collections each.

The present study focuses on advancing our understanding of the taxonomy of *Sphaerocardamum* through an investigation of morphology, chromosome number, genome size, crossing studies, and amplified fragment length polymorphism data (AFLP).

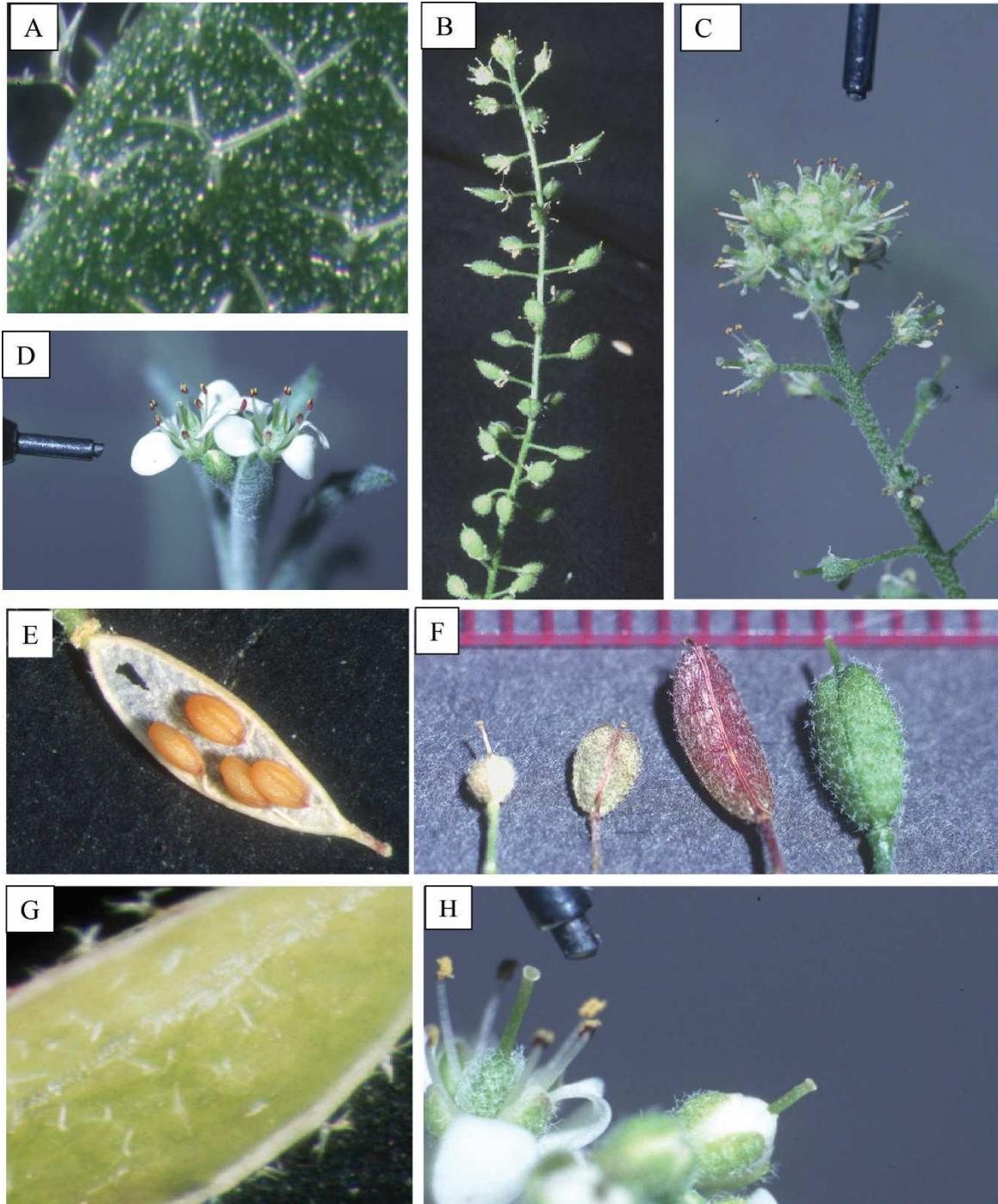


Figure 1. General morphology of *Sphaerocardamum*. A) Dendritically branched trichomes. B) Infructescence. C) *Sphaerocardamum neseliiforme* inflorescence (Bailey 157 [BH & MEXU]). D) *Sphaerocardamum macropetalum* inflorescence (Bailey 45). E) Replum funiculi and seeds (Bailey 57), seeds are 1 mm long. F) Siliques shape variation, left to right: *S. neseliiforme*, *S. stellatum*, *S. compressum*, and *S. macropetalum*. G) Interior fruit valve indument (Bailey 57). H) Protogyny and style morphology (Bailey 45). Scales are either a 1mm rule or the tip of a 0.5 mm diameter mechanical pencil tip. Vouchers noted are with BH and MEXU.

MATERIALS AND METHODS

Sampling. Specimens of *Sphaerocardamum* from AA, ANSM, BH, BM, ENCB, GH, JEPS, K, LL, MEXU, MO, TEX, and US herbaria were examined. New field collections were made in 1996 and 1997 (deposited in BH and MEXU). Fieldwork provided new herbarium samples as well as materials for DNA isolation, morphological studies, and seed for greenhouse-studies. Because of the limited available material, new collections from previously identified sites in addition to areas linking known localities were sought to evaluate the potential for clinal variation between the currently recognized species and/or new combinations of character states consistent with previously uncharacterized taxa. Initial comparisons of morphological variation indicated that the range of morphologies described by Rollins (1984) represented the maximum array of variation for the group (i.e., clinal variation was observed between populations but no new combination of variation were discovered). Therefore, Rollins's species limits were tested to determine whether the variation from the new collections supported the previous circumscription or if the observed intergradations blurred species boundaries, supporting more inclusive species. In cases where a collection showed intergradations between two of the species recognized by Rollins (1984), the collection was initially assigned to the species that it shared greatest geographic and morphological similarity.

Variation from all individual herbarium sheets and greenhouse grown individuals was accounted for in the morphological studies. The other sources of data (crossing studies, cytology, genome size, and AFLPs) incorporated a limited selection of the individuals (listed in subsequent sections). Because of the discrepancy of sampling and the desire to generate useful classifications, the morphologically defined species are referred to throughout and the support for those species provided by other data sources discussed within that context.

Morphology. Morphological features were compared within and between species to evaluate fixed differences between populations and to identify the range of variation within the genus. Observations were taken from herbarium sheets, 70% ethanol-pickled field collections, and live greenhouse-grown material.

Species Delimitation. The phylogenetic species concept (PSC; sensu Nixon & Wheeler 1990) was selected as the criterion for delimitation. Application of the PSC followed the general guidelines of population aggregation analysis (PAA) (Davis & Manos 1991; Davis & Nixon 1992). Those individuals sampled from a population were considered to represent the diversity of that population. Populations were compared and the minimally inclusive units maintained as distinct species if fixed characters or combinations of characters (sensu Nixon & Wheeler 1990) differed between them.

Reproductive Biology. The majority of the newly collected samples were not observed to be in flower at the time of collection. Therefore, observations and experiments regarding reproductive biology and crossing were made on plants grown from seed in the greenhouse. Artificial pollination experiments were carried out by taking anthers from the pollen donor and applying them to the stigmas of emasculated and bagged (to exclude pollinators) maternal flowers.

Cytology and Genome Size. Meiotic counts were taken from pollens mother cells (PMC) squashed from intact anther sacs of fresh greenhouse-grown material using the formic, lactic, propionic acid-orcein stain of Jackson (1973). Flow cytometry was used to corroborate ploidy estimates for additional accessions and to estimate genome sizes. Leaf tissue of greenhouse-grown samples was analyzed on a FACS Caliber flow cytometer (Becton Dickinson, San Jose, CA) using the citric acid buffer protocol of Otto (1990) modified by Dolezel and Göhde (1995). Following the recommendation of Dolezel (pers. comm.), the centrifugation and resuspension steps were skipped and nuclei were stained using a propidium iodide plus RNase solution. Internal size standards involved the combined use of *Brassica oleracea* subsp. *acephala* (kale) and *A. thaliana*. Kale was

selected as the primary standard and run with each *Sphaerocardamum* sample because it was easy to obtain large numbers of nuclei from a single plant and its genome size did not overlap and obscure resolution of size estimates in *Sphaerocardamum*. However, that genome is slightly more than double those of *Arabidopsis* and the similar sized *Sphaerocardamum*. Therefore, the kale genome size for our sample was established via an *A. thaliana* (0.30 pg/2C for *A. thaliana* (Arumuganathan & Earle 1991)) internal standard. The single kale plant used as a standard was calculated at 1.097 pg/2C (relative to *Arabidopsis*) and used in all subsequent analysis of *Sphaerocardamum* samples.

AFLP Data. DNA extraction and purification followed Bailey et al. (2002). AFLP Small Genome Kits were purchased from ABI (Applied Biosystems, Foster City, CA) and the amplification procedure adopted followed the manufactures protocol. Primer pairs EcoRI-AC/MseI-CTA, EcoRI-AG/MseI-CTA/, EcoRI-AT/MseI-CTA, and EcoRI-AA/MseI-CTA were initially screened prior to final primer selection. Primer combinations EcoRI-AC/MseI-CTA and EcoRI-AT/MseI-CTA were selected for the final amplification because of the reproducibly amplified polymorphic markers generated across accessions. Selective amplification reactions were run on an ABI 3100 (Genetics Testing Laboratory, NMSU, Las Cruces, NM) with the GeneScan Rox 500 internal standard. GeneScan (Applied Biosystems Inc.) was used to extract peaks between 75-500 bp for each sample. GeneScan project files were imported into GenoTyper (Applied Biosystems Inc.) to establish loci and score each individual in the final matrix. A locus bin was established for any peak at least 250 units in height. Overlapping loci (bins) were excluded from the final analysis. Tables were exported to Excel for editing and peak verification using GeneScan. Polymorphic loci were imported into MVSP (Kovach Computing Systems) and UPGMA cluster analyses were obtained using the Jaccard's Coefficient. In addition, Parsimony heuristics (1000 replicates holding 10,000 trees total and 10 trees per replicate) and bootstrap analyses (1000 replicates with up to 10 trees held per replicate) were run via WinClada (Nixon 2002) in Nona (Goloboff 2000).

RESULTS

Growth Habit. Field-collected *Sphaerocardamum* are mostly upright and 4-45 cm tall (Fig. 2A). Plants often topple over toward the end of the growing season and sometimes die back to the woody portion of the stem, which remains horizontal. Such stems can end up forming a 1-10 cm long rhizome-like structure from which upright shoots for subsequent season's growth originate. Although field-collected plants were typically upright, greenhouse-grown representatives of *S. divaricatum* and *S. macropetalum* sometimes showed a loosely decumbent habit.

The majority of greenhouse accessions began flowering within two to four months of germination. Following heavy fruitset, lateral branches from axillary buds basal to the inflorescence often form. These generally form small rosette-like structures that can apparently remain dormant for prolonged periods. During a secondary growth phase, these lateral branches become elongate stems.

Trichomes. All individuals have a moderate to dense indument of translucent dendritically branched single-celled eglandular trichomes (Fig. 1A) distributed over nearly all above-ground portions of the plant. Trichomes were never found on adaxial surface of the sepals or anywhere on petals, stamens, styles, or stigmas. Trichomes on the stem ranged from 0.05-0.8 mm tall. Occasionally (*Rollins 83347* [ENCB, GH]; *Moore 4253a* [GH]) larger trichomes (particularly on the exterior of fruit valves) appeared to have greenish spots, presumably due to the presence of chloroplasts. The relative number of ramifications of trichomes on the adaxial surface of upper cauline leaves were compared to determine whether species-specific distinctions might exist. Results from these measurements did not reveal differentiation into non-overlapping ranges (Fig. 2B). *Sphaerocardamum compressum*, *S. divaricatum*, and *S. macropetalum* showed greater average degrees of trichome branching than the other species, but each shared moderate overlap with some or all of the other taxa.

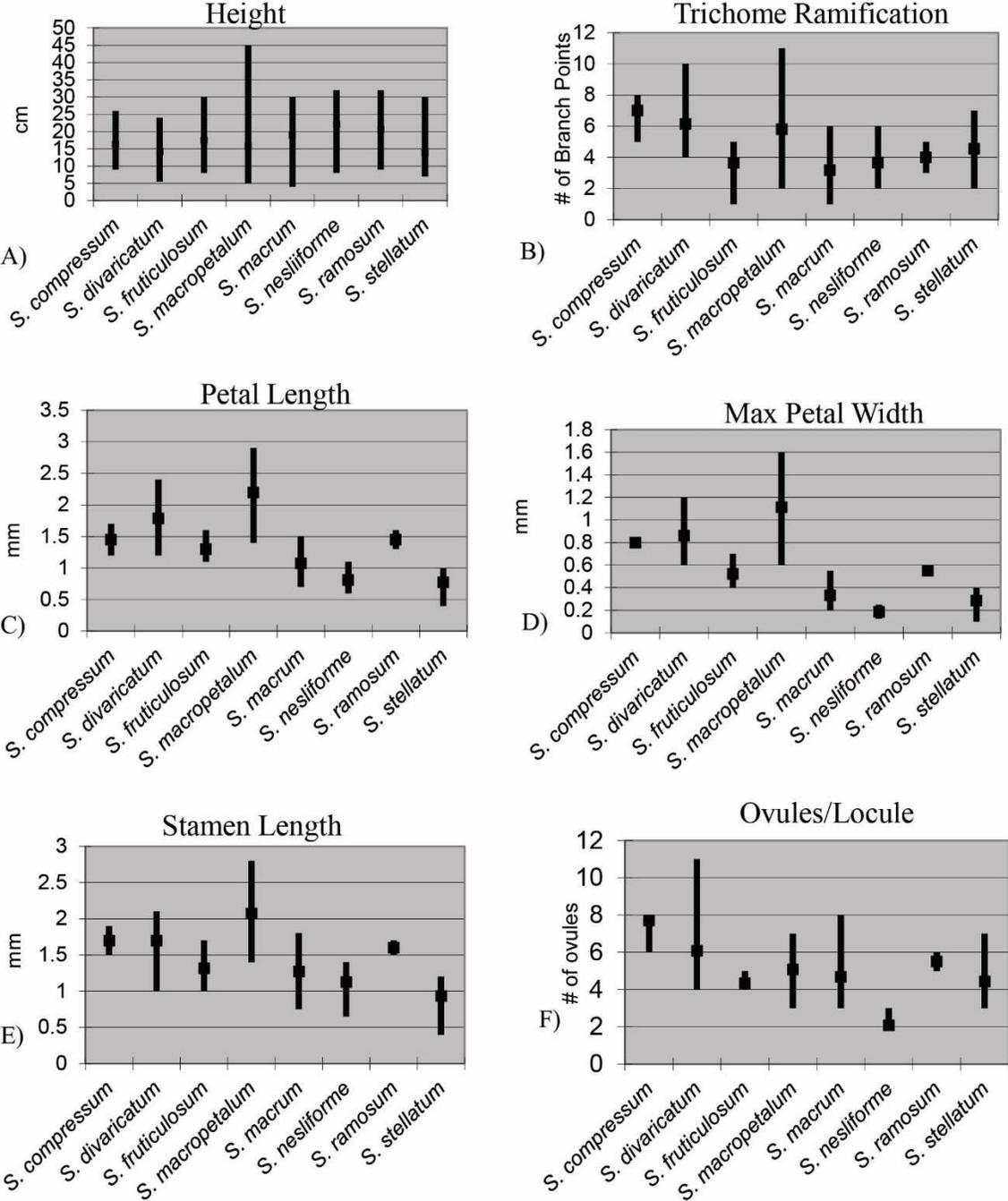


Figure 2. Morphological comparisons.

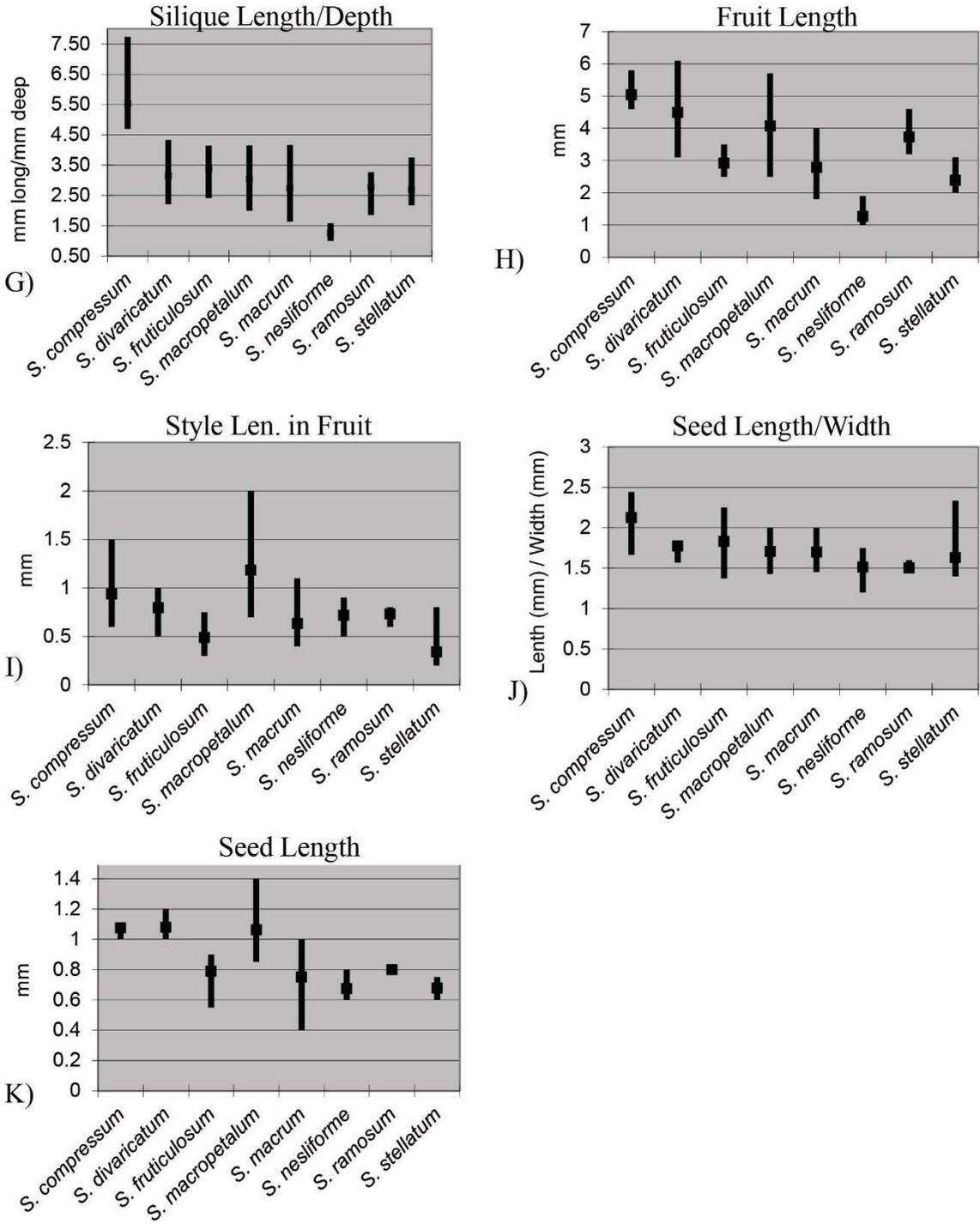


Figure 2 continued. Morphological comparisons.

Leaves. Field-collected plants were compared to identify the range of variation from natural populations. Leaf sizes ranged from 0.2-6 cm long by 0.1-1.2 cm wide, with leaves becoming progressively smaller distally. Considerable overlap in sizes and shapes were not consistent with differences between previously recognized species.

Inflorescences. The inflorescences are upright ebracteate corymbose racemes (Fig. 1B & C), which vary from simple, in some *Sphaerocardamum compressum* accessions, to paniculate in other *S. compressum* and individuals of all other *Sphaerocardamum* collections. Fruiting pedicels are straight, divaricately ascending to slightly descending, and pubescent.

Corolla. Contrary to Rollins's (1984) observations of herbarium material and a few cultivated accessions, my field and greenhouse observations did not uncover any apetalous individuals. Greenhouse observations suggest that plants pass through stages of rapid growth followed by quiescence. Quiescence follows an extended period of flowering and fruiting, and as plants become dormant they produce partially developed buds. This suggests that collections without petals may represent plants passing into a dormant phase rather than potentially apetalous species. Observations from new collections failed to identify unique differences in petal shapes and sizes between Rollins's (1984) species. These features vary both within and between species. In general, *Sphaerocardamum compressum*, *S. divaricatum*, and *S. macropetalum* have the largest petals and greatest degree of expansion from claw into a pronounced blade (Fig. 2C & D). *Sphaerocardamum macrum*, *S. nesliiforme*, and *S. stellatum* have the smallest and narrowest petals with little or no expansion.

Androecium. The subequal nature of stamens (Rollins 1984) was maintained (Fig. 1D) in greenhouse-grown accessions. Measurements from the long stamen sets ranged from ca. 0.4-2.8 mm and were exerted beyond the perianth in all collections. *Sphaerocardamum compressum*, *S. divaricatum*, *S. macropetalum*, and *S. ramosum* have the greatest average stamen lengths, but there is considerable overlap between previously recognized species (Fig. 2E).

Pollen. Pollen grains were mounted in glycerin and observed using light microscopy at 400X. All observed pollen grains conformed to the typical tricolpate Brassicaceae type, and they ranged from 27-30 μm long by 13-16 μm wide. No taxonomically informative characters were observed with respect to gross pollen morphology or size.

Gynoecium. The vast majority of collections displayed 2-8 ovules per locule (Fig. 2F), with a single collection of *Sphaerocardamum divaricatum* containing 10-11 ovules per locule (Rzedowski 6551[TEX]). *Sphaerocardamum nesliiforme* accessions contained two ovules per locule, with an occasional individual fruit having a third ovule (e.g., Moore 5443 [GH]; Bailey & Ochoterena 157 [BH, MEXU]). The other species range from four to eight ovules (occasional individual fruits with 3-9 ovules).

Fruit shape varies from spherical in *Sphaerocardamum nesliiforme*, to oblong in *S. compressum*, *S. divaricatum*, and *S. macropetalum*, to obovate in *S. fruticosum*, *S. macrum*, *S. ramosum*, and *S. stellatum* (Fig. 1F). Fruits can be uncompressed or compressed perpendicular to the septum. An estimation of compression relative to length was made to quantify the degree of compression (fruit length/depth ratio; Fig. 2G). Values greater than one identify angustiseptate-compressed fruits, whereas values closer to one identify relatively uncompressed spherical fruits. Estimates for *S. compressum* and *S. nesliiforme* revealed differentiable variation in silicle shape with greatest and least compression respectively. The remaining species share similar averages and ranges with respect to

Overall fruit size was estimated by length (Fig. 2H). *Sphaerocardamum nesliiforme* has the smallest fruits while *S. compressum*, *S. divaricatum*, and *S. macropetalum* have the largest fruits.

Considerable overlap exists between species with respect to fruit length except for *S. nesliiforme*, which rarely produces fruits that are long enough to overlap with variation from *S. macrum*.

Table 1. Interspecific crosses. The first four columns identify the species and accession of the maternal parent and paternal parent, respectively. The number of presumably viable (normal shape and size) seeds recovered from each fruit are provided in the fifth column. Note: not all crosses were attempted and crosses not included should not be considered unsuccessful. “*” – with the paternal donor cross indicates that F1 seed were grown to maturity. “1” - self-pollinated accessions producing seed.

Maternal Parent		Paternal Parent		Seeds
Species	Accession	Species	Accession	
<i>S. divaricatum</i> ¹	158	<i>S. fruticosum</i>	142	0
	158	<i>S. macropetalum</i>	137	0
	158	<i>S. macrum</i> *	57	4
	158	<i>S. macrum</i>	126	0
	158	<i>S. ramosum</i> *	125	3
	158	<i>S. ramosum</i>	125	2
	158	<i>S. nesliiforme</i>	157	3
<i>S. fruticosum</i> ¹	144	<i>S. fruticosum</i>	141	6
	144	<i>S. divaricatum</i> *	93	7
	144	<i>S. nesliiforme</i>	157	0
<i>S. macropetalum</i> ¹	137	<i>S. fruticosum</i>	144	1
	137	<i>S. macrum</i>	122	3
	137	<i>S. macrum</i> *	128	3
	137	<i>S. ramosum</i> *	125	4
<i>S. macrum</i> ¹	128	<i>S. divaricatum</i>	158	4
	128	<i>S. fruticosum</i>	141	2
	128	<i>S. fruticosum</i> *	142	5
	57	<i>S. fruticosum</i> *	141	10
	57	<i>S. macropetalum</i> *	93	2
	128	<i>S. divaricatum</i> *	93	5
	128	<i>S. macrum</i>	57	1
	128	<i>S. macrum</i>	57	8
	128	<i>S. nesliiforme</i> *	152	8
	57	<i>S. nesliiforme</i> *	157	2
	128	<i>S. nesliiforme</i> *	157	8
	128	<i>S. ramosum</i> *	125	6
<i>S. nesliiforme</i> ¹	157	<i>S. fruticosum</i>	141	3
	152	<i>S. fruticosum</i> *	142	4
	152	<i>S. macropetalum</i> *	137	2
	157	<i>S. macrum</i>	57	4
	152	<i>S. ramosum</i>	125	2

Interior Valve Indument. Trichomes on the interior of fruit valves are relatively uncommon within Brassicaceae. Aside from *Sphaerocardamum compressum*, *Sphaerocardamum* species all display a sparse to dense indument on the interior surface of the fruit valves (Fig. 1G). These trichomes are mostly dendritic, but often less ramified than the exterior valve trichomes on the same fruit. In a few cases (e.g., *Purpus* 5235 [UC], 5374 [US]; *Wells & Nesom* 99 [GH]), they show reduction to malpighiaceous or minute, apparently simple, forms. All observed valves of *S. divaricatum*, *S. macropetalum*, *S. macrum*, *S. nesliiforme*, and *S. ramosum* accessions showed some level of interior pubescence. Individual valves on two plants of some *S. stellatum* (*Pringle* 2844 [GH]; *Palmer* 752 [GH, NY]) ranged from glabrous to pubescent.

Style. Previous knowledge of style lengths suggested that mature styles ranged from ca. 0.5 mm in *Sphaerocardamum stellatum* to more than 2 mm in *S. macropetalum*. Observations for the present study identified style lengths from 0.2-2 mm (Fig. 2I). They are greatest in *S. compressum*, *S. divaricatum*, and *S. macropetalum* with the remaining species overlapping with the lower range for these two long-styled species.

Seed. All observed individuals had incumbent cotyledons. Seed shape was estimated by length to width ratio (Fig. 2J). This estimate supports strong similarity in overall seed shape within and between species. Relative seed size was subsequently estimated by length (Fig. 2K), which identified more variation than shape. *Sphaerocardamum compressum*, *S. divaricatum*, and *S. macropetalum* have the largest seeds, whereas the five other species have smaller seeds. Although there is variation in seed length, there is also considerable overlap in ranges. Seeds were viable for extended periods, with field-collected seed successfully germinated up to three years after collection following storage in paper envelopes at room temperature and humidity. However, a recheck of seeds stored under these conditions after five years recovered very low seed viability, highlighting the need to store these seeds under more optimal conditions.

Reproductive Biology. Protogyny was illustrated by stigmas protruding from the closed buds in greenhouse grown *Sphaerocardamum divaricatum*, *S. fruticosum*, *S. macropetalum*, *S. macrum*, and *S. nesliiforme* (Fig. 1H). Protogyny appeared was common in the early stages of flowering, with flowers/buds initiated later in the cycle rarely displaying the trait. *Sphaerocardamum stellatum* and *S. ramosum* often appeared to have fully developed stigmas well before the anther sacs matured and dehisced, suggesting additional cases of functional protogyny. No observations were made for *S. compressum*, because accessions rarely flowered in the greenhouse, and those that did finished flowering before protogyny in the genus was noted. Stamens were generally spreading at anthesis, but commonly flex inward, coming into contact with the style or stigma late in flower development. This was most frequently observed in the shorter-styled accessions. However, the timing of style elongation appeared to be variable in the longer-styled accessions and some long-styled accessions were observed with anthers touching the stigma prior to full elongation.

The shorter-styled species generally produced seed when bagged to exclude pollinators, suggesting that they are self-compatible and selfing under some conditions. The longer-styled species, *Sphaerocardamum divaricatum*, *S. macropetalum*, and *S. nesliiforme*, had to be intentionally self-pollinated to produce self seed. Seed set among field-collected individuals was noticeably higher than in cultivated accessions.

Artificial crosses were made as a measure of potential reproductive isolation. Individuals grown from accessions collected from populations used in Rollin's (1984) treatment were used in the crossing studies. Table 1 lists each cross and the resulting seed per fruit (abnormal seed morphologies were not observed). Because these experiments were dependent on accessions flowering simultaneously in the greenhouse, not all crosses were possible. However, given the results available, it appears that all of these populations, representing seven of eight of Rollin's species, can be

crossed. Although a few crosses failed to produce seed, these single attempts do not particularly support a conclusion of reproductive isolation. For all failed cases, alternative crosses involving the same species pairs were successful. Therefore, the unsuccessful crosses may have been due to poor timing or growth conditions during pollination and fruit development. Germination of F1 seed for a subset of crosses were all successful, but F1 fertility was not measured. Furthermore, a cross involving *Sphaerocardamum ramosum* (125) pollen and a *Halimolobos minutiflora* (145B; a diploid *Halimolobos* accession; Bailey unpubl.) stigma produced plump viable-looking seeds, suggesting that intergeneric crosses are also possible.

Chromosome number. Previous cytological studies of *Sphaerocardamum* were limited to three observations of $n = 8$ (a single accession of *S. macropetalum* and two accessions of *S. stellatum* (Rollins and Rüdberg 1971, 1977)). Table 2 lists haploid chromosome numbers observed in this study. Counts for *Sphaerocardamum* ranged from $n = 7-9$, with the majority considered $n = 8$. Photographs of representative meiotic squashes are provided in Fig. 3.

Table 2. Haploid chromosome counts.

Taxon	Voucher	squash date	$n =$
<i>S. compressum</i>	115	6 Dec '99	8
<i>S. divaricatum</i>	158	19 Nov '98	8
<i>S. fruticosum</i>	142	19 Aug '99	8
<i>S. fruticosum</i>	144	4 July '98	8
<i>S. macropetalum</i>	45	15 Oct '98	7 & 8
<i>S. macropetalum</i>	45	19 Aug '99	8
<i>S. macropetalum</i>	137	19 Nov '98	8
<i>S. macropetalum</i> *	—	—	8
<i>S. macrum</i>	128	15 Oct '98	8
<i>S. nesliiforme</i>	157	15 Oct '98	8
<i>S. ramosum</i>	125	19 Nov '98	8 & 9
<i>S. ramosum</i>	125	19 Nov '98	8
<i>S. stellatum</i>	122	5 Nov '98	7-8
<i>S. stellatum</i> *	—	—	8

Note: counts followed by a "*" are from Rollins and Rüdberg (1977, 1979). A "-" indicates that a clear distinction could not be made, whereas an "&" notes that two distinct numbers were clearly identified.

Flow cytometry. Genome sizes from greenhouse grown samples ranged from 0.29-0.36 pg/2C (Table 3). The genomes of these species can be divided into two size classes (two tailed unpaired t-test, p-value 0.00005): 1) 0.340-0.360 pg/2C for *Sphaerocardamum compressum*, *S. divaricatum*, and *S. macropetalum* genomes; and 2) 0.294-0.325 pg/2C for *S. fruticosum*, *S. macrum*, *S. nesliiforme*, *S. ramosum*, and *S. stellatum* (Fig. 4). Plants grown from F1 seed of greenhouse crosses between taxa with different genome sizes almost all displayed genome sizes intermediate between their parental types (Table 3). The one exception was the 128 x 152 cross, which displayed a larger genome size than either parent.

AFLP. AFLP runs resulted in the identification of 89 variable non-overlapping loci from 21 accessions (Table 4). Both UPGMA clustering (Fig. 5A) and parsimony analysis (Fig. 5B) clearly resolved representatives of *Sphaerocardamum compressum* and *S. nesliiforme* as distinct lineages within the genus. *Sphaerocardamum divaricatum* and *S. macropetalum* accessions resolved within a single mixed group/clade. In the parsimony analysis *S. fruticosum*, *S. macrum*, *S. ramosum*, and *S. stellatum* accessions resolved within a single mixed clade with low support and in the UPGMA dendrogram these taxa form a grade leading to *S. nesliiforme*.

Table 3. DNA Content. Vouchers replicated in two or more rows signify individuals measured on different days or, if they are followed by a superscript, different individuals from the same population.

Taxon	Voucher	pg/2C
<i>S. compressum</i>	104	0.347
	104	0.348
	115	0.354
<i>S. divaricatum</i>	158	0.340
	93	0.344
	99	0.348
<i>S. fruticosum</i>	142	0.319
<i>S. macropetalum</i>	45	0.359
	137	0.341
<i>S. macrum</i>	57	0.316
	122	0.326
	126	0.305
	128	0.309
	132	0.315
<i>S. nesliiforme</i>	152	0.306
	156	0.321
	157	0.319
<i>S. ramosum</i>	125 ¹	0.304
	125 ¹	0.294
	125 ²	0.311
<i>S. stellatum</i>	120	0.306
hybrid	137x125	0.315
hybrid	158x125	0.317
hybrid	57x93	0.327
hybrid	157x141	0.318
hybrid	128x152	0.316

Table 4. Molecular sampling and voucher Information.

Taxon	Collection/Herbarium
<i>Sphaerocardamum compressum</i> (Rollins) Rollins	Bailey & Ochoterena 104 / BH & MEXU
<i>Sphaerocardamum compressum</i> (Rollins) Rollins	Bailey & Ochoterena 115 / BH & MEXU
<i>Sphaerocardamum divaricatum</i> (Rollins) Rollins	Bailey & Ochoterena 99 / BH & MEXU
<i>Sphaerocardamum divaricatum</i> (Rollins) Rollins	Bailey & Ochoterena 158 / BH & MEXU
<i>Sphaerocardamum fruticosum</i> (Rollins) Rollins	Bailey & Ochoterena 142 / BH & MEXU
<i>Sphaerocardamum fruticosum</i> (Rollins) Rollins	Bailey & Ochoterena 144 / BH & MEXU
<i>Sphaerocardamum macropetalum</i> (Rollins) Rollins	Bailey 15 / BH & MEXU
<i>Sphaerocardamum macropetalum</i> (Rollins) Rollins	Bailey 45 / BH & MEXU
<i>Sphaerocardamum macropetalum</i> (Rollins) Rollins	Bailey 47 / BH & MEXU
<i>Sphaerocardamum macropetalum</i> (Rollins) Rollins	Bailey & Ochoterena 133 / BH & MEXU
<i>Sphaerocardamum macropetalum</i> (Rollins) Rollins	Bailey & Ochoterena 137 / BH & MEXU
<i>Sphaerocardamum macrum</i> (Standley) Rollins	Bailey 57 / BH & MEXU
<i>Sphaerocardamum macrum</i> (Standley) Rollins	Bailey & Ochoterena 126 / BH & MEXU
<i>Sphaerocardamum macrum</i> (Standley) Rollins	Bailey & Ochoterena 128 / BH & MEXU
<i>Sphaerocardamum macrum</i> (Standley) Rollins	Bailey & Ochoterena 132 / BH & MEXU
<i>Sphaerocardamum macrum</i> (Standley) Rollins	Bailey & Ochoterena 131 / BH & MEXU
<i>Sphaerocardamum nesliiforme</i> Schauer	Bailey & Ochoterena 152 / BH & MEXU
<i>Sphaerocardamum nesliiforme</i> Schauer	Bailey & Ochoterena 156 / BH & MEXU
<i>Sphaerocardamum nesliiforme</i> Schauer	Bailey & Ochoterena 157 / BH & MEXU
<i>Sphaerocardamum ramosum</i> Rollins	Bailey & Ochoterena 125 / BH & MEXU
<i>Sphaerocardamum stellatum</i> (S. Wats.) Rollins	Bailey & Ochoterena 120 / BH & MEXU

Note: Accessions in bold face type were used in Bailey and Doyle (1999).

DISCUSSION

The culmination of data from all available collections, including the 42 available to Rollins (1984) and 75 new samples, eliminated previously discrete boundaries between morphological features used to distinguish several species of *Sphaerocardamum*. Furthermore, the study of morphology did not identify any new characters or character combinations that would suggest the existence of previously uncharacterized species. Since the morphological data were recorded from all available collections, while all other studies involved subsampling accessions, I focus the initial evaluation of species boundaries on the morphological findings and then discuss whether the other relevant data sources support, refute, or provide no useful information in comparison to conclusions based on morphology.

The distinctiveness of accessions representing *Sphaerocardamum compressum*, relative to other species, was supported by the complete absence of trichomes on the interior of fruit valves and

by the fruit length to width ratio (Fig. 2G). Fruits of *S. compressum* are among the longest and are the widest, resulting in a highly compressed angustiseptate form with a greater than average number of ovules per ovary (Fig. 2F). These features were maintained in greenhouse-grown accessions and these individuals differed from accessions of other species by remaining largely unbranched and rarely flowering in cultivation. This group of accessions is clearly most similar to those representing *S. divaricatum* and *S. macropetalum*, which are also robust plants with relatively large petals and fruits, shared nuclear DNA content (Fig. 4), and greater ramification of leaf trichome branching (Fig. 2B). However, in addition to differing in the key traits noted above, *S. compressum* was supported as a distinct cluster and clade the UPGMA and parsimony trees (Fig. 5), respectively.

An assessment of morphology, geography, genome size, crossing data and AFLP data all failed to clearly differentiate accessions of *Sphaerocardamum divaricatum* and *S. macropetalum*. These accessions are distinct from *S. compressum* (noted above), but share overlap in essentially all other features. In general, it seems those individuals previously assigned to *S. divaricatum* display somewhat smaller flowers overall (petals, stamens, and style length), larger fruits, and shorter styles, but none of these are strikingly different. Furthermore, accession representing the geography of these two species were intermixed in the AFLP analysis (Fig. 5).

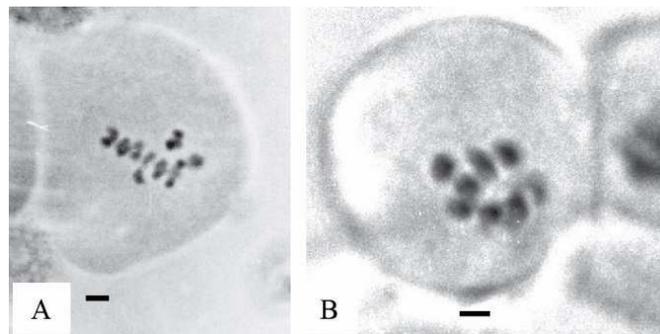


Figure 3. Representative meiotic chromosome counts. Oil immersion at 1000x (scales = 5 µm). A) *S. macropetalum*, $n = 8$ (Bailey & Ochoterena 45 [BH & MEXU]). B) *S. fruticosum*, $n = 8$ (Bailey & Ochoterena 142 [BH & MEXU]).

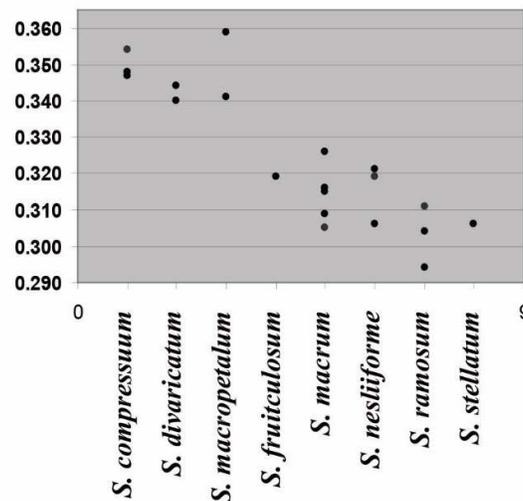


Figure 4. Genomic DNA content in picograms per diploid genome (pg/2C).

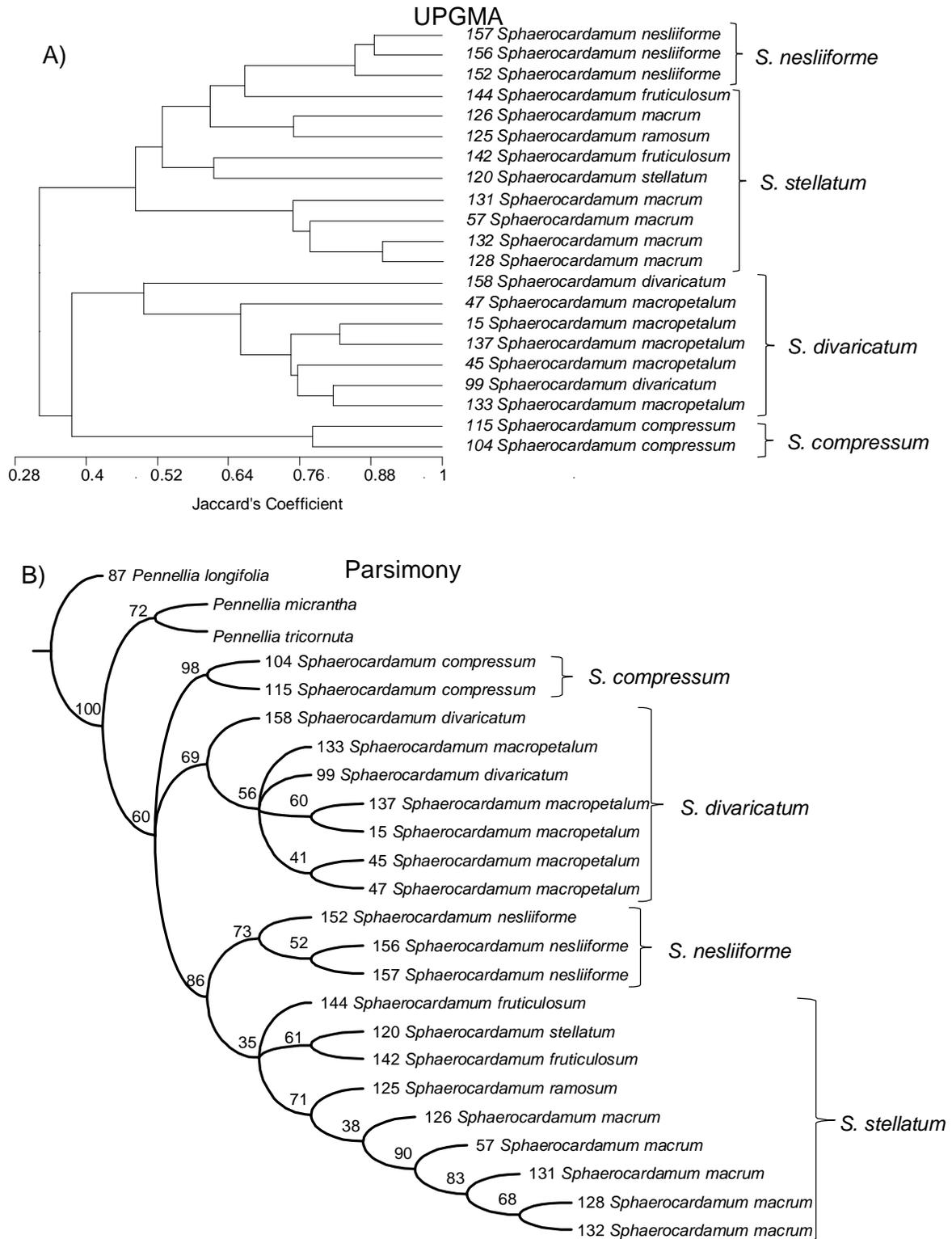


Figure 5. Analysis of AFLP data. A) UPGMA dendrogram derived from clustering using Jaccard's coefficient. B) Parsimony derived strict consensus tree with bootstrap percentages from 1000 replicates. Species names at the tips of branches represent *a priori* assignments and species names summarizing groups represent the species recognized herein.

Like *Sphaerocardamum compressum*, populations of *S. nesliiforme* were distinctive relative to all other species. They all displayed two ovules per locule with a very few individual plants displaying a third ovule in a couple of locules observed (Fig. 2F). This is in contrast to all other species, none of which were observed to ever have two ovules per locule. In addition, the small spherical fruits differ from all other species of *Sphaerocardamum* and these features were maintained in the common garden grown accessions. Though highly distinctive, the species is most closely aligned with *S. fruticosum*, *S. macrum*, *S. ramosum*, and *S. stellatum*. Results from the analysis of AFLP data group accessions of *S. nesliiforme* into an exclusive cluster (UPGMA, Fig 5A) and clade (parsimony, Fig. 5B)

The remaining four taxa (*Sphaerocardamum fruticosum*, *S. macrum*, *S. ramosum*, and *S. stellatum*) also shared considerable overlap in their morphology, genome sizes, and they resolved together in the UPGMA and parsimony analyses (Fig. 5). The key features used to previously distinguish these taxa were derived from observations of few accessions and it was often impossible to apply any trait other than geography when attempting to classify newly available accessions aligned with these taxa. Ultimately this group, like *S. divaricatum* plus *S. macropetalum*, appears to represent a fairly widespread and common lineage. They are clearly distinguished from the aforementioned groups by relatively short oblong (not spherical) fruits (Fig. 1F), short linear petals (Fig. 2D), and relatively short seeds (Fig. 2K). They also resolved as a weakly supported clade in the parsimony analysis (Fig. 5B) and as a grade of individuals in the UPGMA clustering (Fig 5A).

While it was hoped that chromosome and crossing data would identify additional features to differentiate these individuals and populations into putative species-level lineages, neither provided much in the way of variable characters. Lack of variability can be consistent with accessions that all represent single taxa, but when compared to other features that are fixed between populations these are interpreted as ancestral features that have simply not diverged in these cases (e.g., Rosen 1979), providing essentially no information to refute species limits relative to other characters that do show variability among populations.

TAXONOMIC HISTORY AND TREATMENT

The relatively short (1847-present) and convoluted taxonomic history of *Sphaerocardamum* is exemplified by the historical assignment of its species to four different genera (*Capsella* Medik., *Cibotarium* O.E. Schulz, *Lepidium* L., and *Sphaerocardamum*) and multiple Brassicaceae tribes. The type for the genus, *Sphaerocardamum nesliaeforme*, was described in 1847 by Sebastian Schauer to accommodate a specimen collected by Alwin Aschenborn from central Mexico. Sereno Watson described *Capsella stellata* in 1890 from Carneros Pass (Coahuila) collections of C. G. Pringle. The preeminent German cruciferologist O.E. Schulz, who wrote the Cruciferae treatment for Engler and Prantl's *Die Natürlichen Pflanzenfamilien*, erected *Cibotarium* in 1933 to accommodate *C. stellata*. A few years later, Standley (1937) described *Lepidium macrum* from Nuevo León collections of C.H. Mueller. About the same time, R.C. Rollins, who became the premier North American Cruciferae systematist of his time (see Al-Shehbaz 1999), began addressing the group as a side project to his dissertation research on *Arabis*. Rollins had collections for all the aforementioned species except the type of the monotypic *Sphaerocardamum*, which was housed in the Berlin herbarium and unavailable to Rollins during World War II. Rollins recognized the affinities between *Cibotarium stellatum*, *Lepidium macrum* and several newer collections available at the Gray Herbarium and concluded that these all belonged to *Cibotarium*. He subsequently transferred *L. macrum* and described *C. divaricatum*, *C. divaricatum* var. *compressum*, *C. fruticosum*, and *C. macropetalum* (Rollins 1941). In that treatment, members of *Cibotarium* were united and considered distinct from *Capsella* and *Lepidium* based on their exerted purplish anthers, three to eight ovules per locule, and nearly equal stamen lengths. Aside from Rollins's (1957) description of *C. microcarpum*, from a Hidalgo collection of H.E. Moore, no additions or changes were made to the genus until the early 1980's.

Forty years after Rollins revised *Cibotarium*, he had the opportunity to view the type material of *Sphaerocardamum nesliaeforme* for the first time. Comparison of this collection to members of *Cibotarium* were sufficient to recognize *C. microcarpum* was synonymous with *S. nesliaeforme*. Rollins concluded that Schulz had incorrectly erected *Cibotarium* for *Capsella stellata*, which Rollins decided best fit under *Sphaerocardamum*. Subsequently, Rollins abandoned *Cibotarium* in favor of *Sphaerocardamum*, which had priority. In addition, he elevated *C. divaricatum* var. *compressum* to *S. compressum*, described *S. ramosum* from a single new collection (Rollins 1984), and corrected an orthographic error in the type so that *S. nesliaeforme* has subsequently been known as *S. nesliiforme*.

In Schulz's 1936 classification, *S. nesliiforme* and species of *Arabidopsis* Heynhold, *Christolea* Camb., *Cymatocarpus* O.E. Schulz, *Drabastrum* (F.v. Mueller) O.E. Schulz, *Geococcus* J. Drummond, *Halimolobos* Tausch, *Harmsiodoxa* O.E. Schulz, *Lamphophragma* O.E. Schulz, *Lemphoria* O.E. Schulz, *Micromystrina* O.E. Schulz, *Nasturtiopsis* Boiss., *Pachymitus* O.E. Schulz, *Pennellia* Nieuwl., *Pseudarbidella* O.E. Schulz, and *Scambopus* O.E. Schulz were all placed in the subtribe Arabidopsidinae of the Sisymbriaceae. In contrast, the other species of *Sphaerocardamum* (known then as *Cibotarium stellata* O.E. Schulz) was assigned to subtribe Capsellinae of the Lepidieae along with *Capsella*, *Greggia* A. Gray, *Hartwegiella* O.E. Schulz, *Hedinia* Ostenfeld, *Hornungia* Reichenb., *Hutchinsia* R. Brown, *Hymenolobos* Nutt., *Mancoa* Weddell, *Phlegmatospermum* O.E. Schulz, and *Synthlipsis* A. Gray.

Recent phylogenetic studies based on DNA sequences and morphology have consistently resolved a well-supported *Sphaerocardamum* within a strictly New World group of Brassicaceae, the tribe Halimolobeae (Bailey & Doyle 1999; Bailey et al. 2002; Bailey et al. 2007). The latter is also well-supported within a larger "Arabidopsoid lineage" (Bailey et al. 2002) that has become known as Brassicaceae Lineage 1 (Beilstein et al. 2006; Beilstein et al. 2008). As currently recognized Halimolobeae comprise five genera (*Exhalimolobos* [9 spp.], *Halimolobos* [8 spp.], *Mancoa* [9 spp.], *Pennellia* [10 spp.], and *Sphaerocardamum* [4 spp. recognized here]) that are distributed from the southwestern USA to the Andes (Price et al. 2001; Bailey et al. 2007; Hernández-Sandoval & Martínez 2013). A combination of geography and morphological features can be used to help diagnose Halimolobeae. The morphological features include branched unicellular trichomes, ebracteate racemes, white petals, mucilaginous seeds, and $x = 8$ base chromosome numbers (Bailey et al. 2007). Nearly all these taxa occur in remote under collected areas and therefore little is known about their overall distribution, variation, or biology.

SPHAEROCARDAMUM S. Schauer, *Linnaea* 20: 720. 1847. **TYPE:** *Sphaerocardamum nesliiforme* S. Schauer

Cibotarium O. E. Schulz, *Engl. Jahrb.* 66: 91. 1933. **TYPE:** *Cibotarium stellatum* S. Wats.

Biennial or perennial **herbs**, sometimes subshrubs, with a woody caudex, 5-40 cm tall, plants often dying back to the caudex, which can form a short (≤ 10 cm) rhizome-like structure in subsequent seasons. **Roots** forming a taproot system without obvious adventitious roots. **Trichomes** translucent (rarely greenish), unicellular, eglandular, and dichotomous dendritically branched; covering most aerial portions of the plant. **Stems** erect to ascending or decumbent, terete, simple or branched apically and/or basally, sometimes developing from adventitious buds on roots, moderately to densely pubescent. **Leaves** cauline (not rosulate), petiolate to sessile, simple oblanceolate to elliptic, moderately to densely pubescent; blade margins entire to sparingly and irregularly dentate, apex and teeth terminating in a single trichome. **Peduncle** erect. **Inflorescence** a dense terminal corymbose ebracteate raceme, simple to compound. **Pedicels** divaricately ascending to slightly descending, 3-5 mm apart, straight terete, 2-6 mm long, pubescent. **Perianth** actinomorphic, 1-3 mm across. **Sepals** erect to spreading, oblong, non-saccate, hyaline-margined, 0.5-2.0 mm long, 0.3-1.0 mm wide, caducous; abaxial surface pale to purplish, sparsely to densely pubescent; adaxial surface smooth,

glabrous. **Petals** 4 (0), narrowly oblanceolate to spatulate with a claw, 0.4-2.9 mm long, 0.1-0.2 mm wide at the proximal end, 0.1-1.6 mm wide at the distal end, white; apex obtuse, glabrous; margin entire; petals occasionally absent. **Stamens** 6 (4+2), exerted, subtetradynamous; **filaments** white to translucent (sometimes with a purplish base), glabrous; **anthers** purple to pale yellow, dithecal, oblong, rounded at base, obtuse at apex, glabrous, dehiscence introrse; pollen yellow. **Gynoecium** spherical to oblong, moderately to densely pubescent; often protogynous; **styles**, 0.5-2 mm long, glabrous; **stigmas** capitate to obscurely bilobed with lobes over the septum margins, papillate; **ovules** biserially attached 2-8 (rarely 10-11) per locule, plump. **Fruit**, spherical to oblong, uncompressed to strongly angustiseptate, 1-6 mm long, minute apical notch present or absent, pubescent, dehiscent, some fruits remaining attached for extended periods; **valves** keeled or rounded on the dorsal side, densely pubescent on the exterior, glabrous to moderately pubescent on the interior; **septum** membranaceous to scarious, complete to perforate, glabrous; **funiculi** free from the septum, glabrous. **Seeds** uniserially to biserially arranged, 2-8 (rarely 10-11) per locule, oblong and plump; seed coat golden to brown, reticulate, mucilaginous when wetted, glabrous; cotyledons incumbent. **Seedlings** with epigeal germination; cotyledons entire, fleshy, glabrous to sparsely pubescent.

Species of *Sphaerocardamum* are restricted to Mexico on limestone soils in arid habitats of the central and southern Chihuahuan Desert. More specifically, populations are known from a fairly contiguous swath of the region from Sierra de Parras in southern Coahuila to Hidalgo with single disjunct populations found in Puebla and Guerrero. Each locality tends to have individuals broadly spaced across the landscape, making it difficult to find more than a few of these cryptic plants. However, the rarity of species within the genus is questionable. Just a few weeks of fieldwork following a good rainy season recovered many populations, suggesting more *Sphaerocardamum* populations exist that have not been discovered because of seasonality, the remoteness of localities, and difficulty involved in spotting individuals. Furthermore, the habitat for *Sphaerocardamum* species does not appear to be under threat from significant human related disturbance. Aside from grazing, little disturbance was noted within most *Sphaerocardamum* habitats and we rarely observed evidence of grazing on *Sphaerocardamum*.

Key to *Sphaerocardamum* species

1. Silique uncompressed-globose, 1–1.5 mm in diameter, septum nearly circular; seeds two per locule (rarely a third in a few fruits); styles ca. 0.5–0.7 mm long **Sphaerocardamum nesliiforme**
1. Silique moderately to highly compressed perpendicular to the septum (angustiseptate – fruits wider than deep), septum elliptic to narrowly oblong; seeds 3–11 per locule; styles 0.2–2.0 mm long.
 2. Petals mostly as long as sepals, 0.1–0.7 mm wide at the distal end; siliques obovate, ca. as long as wide, 2–4.5 mm long, moderately angustiseptate; valves keeled on the back, pubescent on the interior (rarely a mixture of pubescent and glabrous valves on the same individual); apical notch at the base of the style present or absent; styles in fruit 0.2–1.1 mm long; seeds 0.4–1 mm long
..... **Sphaerocardamum stellatum**
 2. Petals longer than sepals, 0.6–1.6 mm wide at the distal end; silique oblong, mostly twice as long as wide (or longer), 2.5–6 mm long, moderately to strongly angustiseptate; valves keeled or rounded on the back, pubescent or glabrous on the interior; apical notch mostly wanting; styles in fruit 0.5–2.0 mm; seeds 0.8–1.4 mm long.
 3. Silique weakly angustiseptate (septum length to depth ratio 1.75–4.4), septum elliptic; valves mostly rounded on back and pubescent on the interior **Sphaerocardamum divaricatum**
 3. Silique strongly angustiseptate (septum length to depth ratio 4.7–7.25); septum narrowly oblong; valves always keeled on back and glabrous on the interior **Sphaerocardamum compressum**

1. **SPHAEROCARDAMUM COMPRESSUM** (Rollins) Rollins, Contrib. Gray Herb. 213: 13. 1984.
Cibotarium divaricatum var. *compressum* Rollins, Contrib. Dudley Herb. 3: 180. 1941.
TYPE: MEXICO. Coahuila. Sierra De Parras, July 1910, C.A. Purpus 4603 (holotype: GH!; isotypes: UC!, US!). Figures. 6 & 7.

Biennial or perennial 9-26 cm tall. **Stems** erect, often unbranched, moderately to densely pubescent. **Leaf** margins entire to denticulate, trichomes with 5-8 ramifications. **Inflorescence** simple to compound. **Pedicels** 4-7 mm long, divaricately ascending. **Perianth** spreading. **Sepals** 1.2-1.4 mm long and 0.5-0.6 mm wide. **Petals** spatulate with distinct claw and blade, 1.2-1.7 mm long and ca. 0.8 mm wide at the distal end. **Filaments** 1.5-1.9 mm long; **anthers** purple. **Gynoecium** oblong; **ovules** 6-8 per locule. **Fruit** oblong, strongly angustiseptate, 4.6-5.8 mm long, 1.9-2.4 mm wide, 0.75-1.0 mm deep, minute apical notch mostly absent; **styles** 0.6-1.5 mm long; stigmas capitate entire to obscurely bilobed; **valves** keeled, densely pubescent on the exterior, glabrous on the interior. **Seeds** uniseriate to biseriate arrangement, 6-8 per locule, oblong and plump 1.0-1.1 mm long and 0.45-0.6 mm wide. $n = 8$.

Phenology. Only known to flower in July (information from the type specimen only, all other collections lack flowers).

Sphaerocardamum compressum is easily distinguished from other *Sphaerocardamum* species by its 6-8 seeds per locule, glabrous fruit valve interiors, and strongly angustiseptate-compressed siliques. The majority of specimens for *S. compressum* suggest that plants are among the shortest and least branched of *Sphaerocardamum* species. Geographically *S. compressum* is restricted to the mountains of southern Coahuila (Fig. 7), which limits the species to the northernmost range for the genus. Populations are only known from southern Coahuila on limestone soils of Sierra de Parras as well as the smaller ranges to the east of Saltillo. The distribution of *S. compressum* only overlaps slightly with the range of *S. divaricatum*, and these two species have only been collected growing in reasonably close proximity from one locality. *Sphaerocardamum compressum* have been found at the highest known elevations for *Sphaerocardamum*, from 2000-2900 m, with *Abies*, *Agave*, *Arctostaphylos*, *Dasyliirion*, *Pinus cembroides*, *Pseudotsuga*, *Quercus*, and *Spirea*.

The labels for the holotype and isotypes of *Sphaerocardamum compressum* (Purpus 4603) each have a hand written "4603=1027." Purpus 1027 sheets correspond to the type of *S. divaricatum*. The different dates and accession numbers on these presumably mean that Purpus believed that these represented collections of the same species from different localities. The idea that these two distinct morphological forms were not collected sympatrically is further supported by the morphology of the specimens in each of the two sets of collections. All specimens on the 1027 sheets are morphologically defined as *S. divaricatum*, whereas all specimens on the 4603 sheets correspond morphologically to *S. compressum*. If Purpus had collected these from the very same locality, on different dates, and considered them the same species, one would expect that a mixture of morphological forms would be found in the two sets

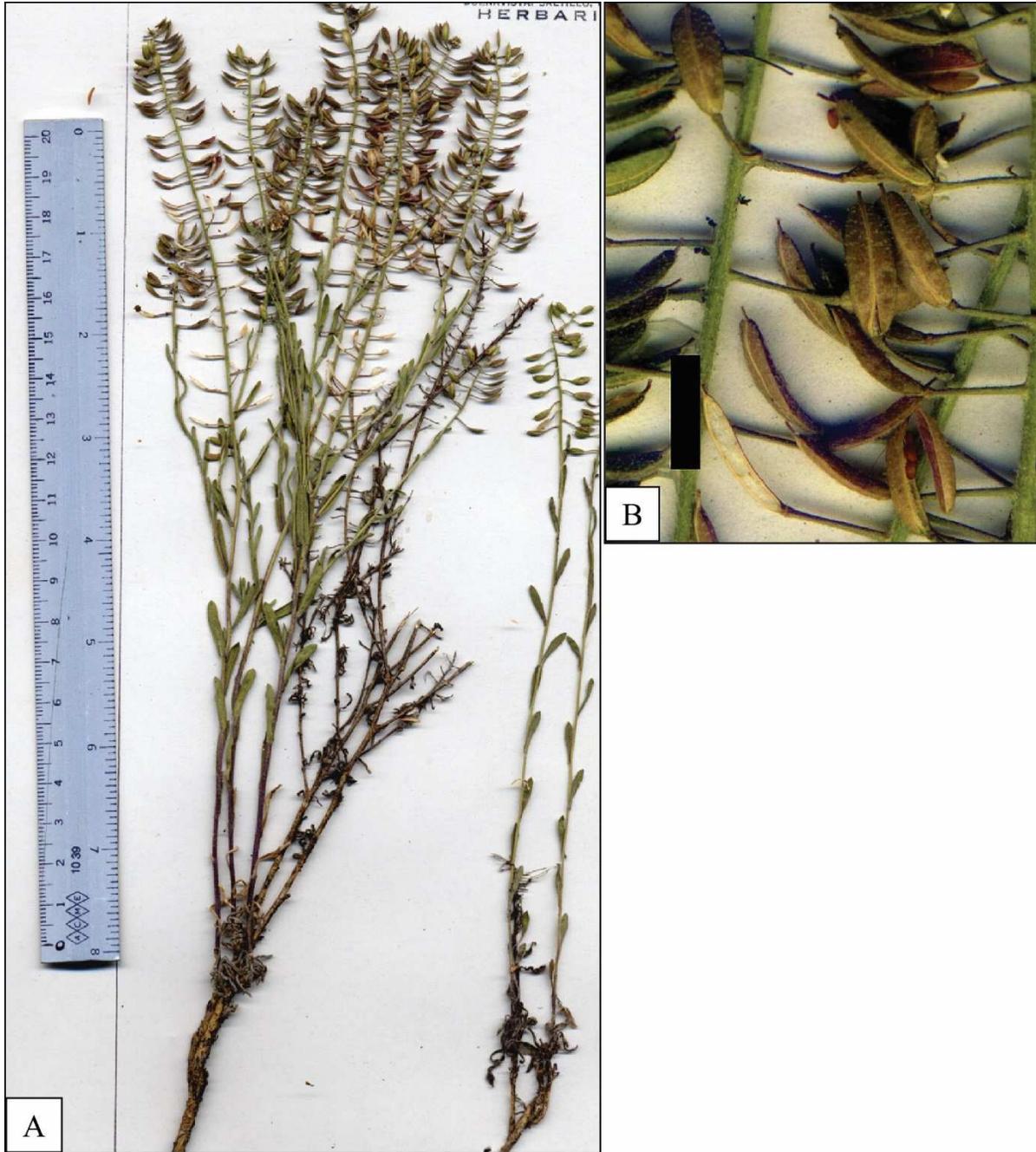


Figure 6. *Sphaerocardamum compressum* (Villarreal & Carranza 3773 [ANSM]). A) General habit. B) Close-up of fruit and infructescence (scale = 5 mm).

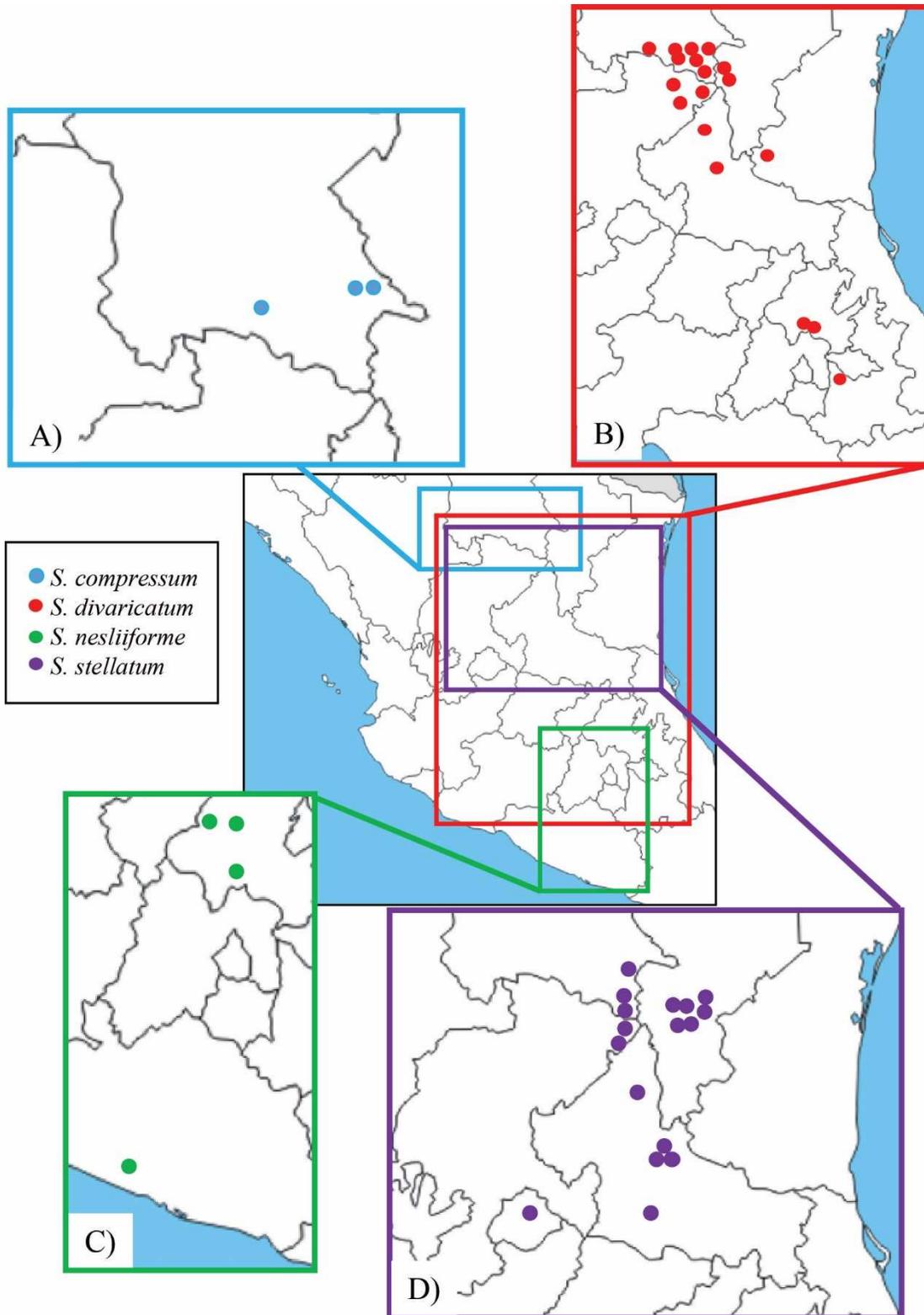


Figure 7. Distribution Maps. A) *S. compressum* (blue inset). B) *S. divaricatum* (red inset). C) *S. nesliiforme* (green inset). D) *S. stellatum* (purple inset). All base maps from <http://d-maps.com/m/america/mexico/mexique/mexique15.gif>

Additional collections examined. MEXICO. Coahuila. Las Vigas, Cañon de la Carbonera, Sierra de Arteaga 25° 20' N, 100° 39' W, 2100-2600 m, no date, *Villarreal & Carranza 3773* (ANSM); along the road that parallels the railroad tracks from Parras to Saltillo, 49 km E of Parras, 14 km W of the deviation to El Cinco (on some maps "Cinco de Mayo"), uphill side of the road (S), 2085 m, 30 Aug 1997, *Bailey & Ochoterena 97* (MEXU); Mpio. Arteaga, Sierra de Arteaga, Cañon de Jamé, 8 km past (E) of Jamé turn left on a small road to the residence Las Vigas, 2 km up the road, 25° 21' 312" N 100° 33' 741" W, 2850 m, 2 Sept 1997, *Bailey & Ochoterena 104* (BH, MEXU); Mpio. Arteaga, Sierra de Arteaga, small stone road leading from El Tunal to Arteaga, N25° 26' 599" 100° 37' 593" W, 2380 m, 2 Sep 1997, *Bailey & Ochoterena 115* (BH, MEXU).

2. SPHAEROCARDAMUM DIVARICATUM (Rollins) Rollins, *Contrib. Gray Herb.* 213: 16. 1984. *Cibotarium divaricatum* Rollins, *Contrib. Dudley Herb.* 3: 189-190, 1941. **TYPE: MEXICO. Coahuila.** Sierra de Parras, *Purpus 1027* (holotype: GH!; isotype NY! UC!). Figs. 7 & 8.

Sphaerocardamum macropetalum (Rollins) Rollins, *Contrib. Gray Herb.* 213: 16. 1984. *Cibotarium macropetalum* Rollins, *Contrib. Dudley Herb.* 3: 190-191. 1941. **TYPE: MEXICO. Zacatecas.** Near Concepción del Oro, 11-14 Aug 1904, *Palmer 297* (holotype: GH!; isotypes: MO!, NY!, UC!, US!).

Biennial or perennial, 3-45 cm tall. **Stems** erect, branched below and within the inflorescence, moderately to densely pubescent. **Leaf** margins entire to denticulate, trichomes with 4-11 ramifications. **Inflorescence** compound. **Pedicels** divaricately ascending, 2.0-10 mm long. **Perianth** widely spreading. **Sepals** 1.0-1.8 mm long and 0.45-1.0 mm wide. **Petals** spatulate with distinct claw and blade, 1.2-2.9 mm long and ca. 0.6-1.6 mm wide at the distal end. **Filaments** 1.0-2.8 mm long; **anthers** pale to purple. **Gynoeceum** oblong, often protogynous with styles protruding beyond the apex of the closed buds; **ovules** 4 (rarely 3)-8 (rarely as many as 11) per locule. **Fruit** oblong, weakly angustiseptate, 2.5-6.1 mm long, 1.0-2.5 mm wide, 0.8-2 mm deep; minute apical notch absent; **styles** 0.5-2.0 mm long; **stigmas** obscurely bilobed; **valves** unkeeled to slightly keeled, densely pubescent on the exterior, moderately to densely pubescent on the interior. **Seeds** biserially arranged, 4 (rarely 3)-8 (rarely as many as 11) per locule, 0.85-1.4 mm long and 0.5-0.8 mm wide. $n = 8$.

Phenology. Flowering March to November.

Sphaerocardamum divaricatum is distinguished from the other *Sphaerocardamum* by its oblong largely unkeeled fruits, large petals with expanded blades, internally pubescent fruit valves, and fruits lacking an apical notch below the style. The morphological distinctions between Rollins's (1984) *S. divaricatum* and *S. macropetalum* were not supported when considering information from newer collections.

Sphaerocardamum divaricatum is a widespread taxon, with populations in Coahuila, Nuevo León, Puebla, San Luis Potosí, Tamaulipas, and Zacatecas (Fig. 7) at elevations ranging from 1800-2900 m. This distribution overlaps slightly with *S. compressum* and *S. nesliiforme* and more extensively with *S. stellatum*. Populations of *S. divaricatum* have been noted growing on limestone soils with *Acacia*, *Agave*, *Dasyllirion*, *Larrea*, *Pinus cembroides*, *Opuntia*, and *Salvia*.

Additional collections examined. MEXICO. Coahuila. Limestone ledges on Carneros Pass, 9 Sep 1889, *Pringle 2848* (GH); Municipio de Saltillo, Estacion Carneros Camino, torre de

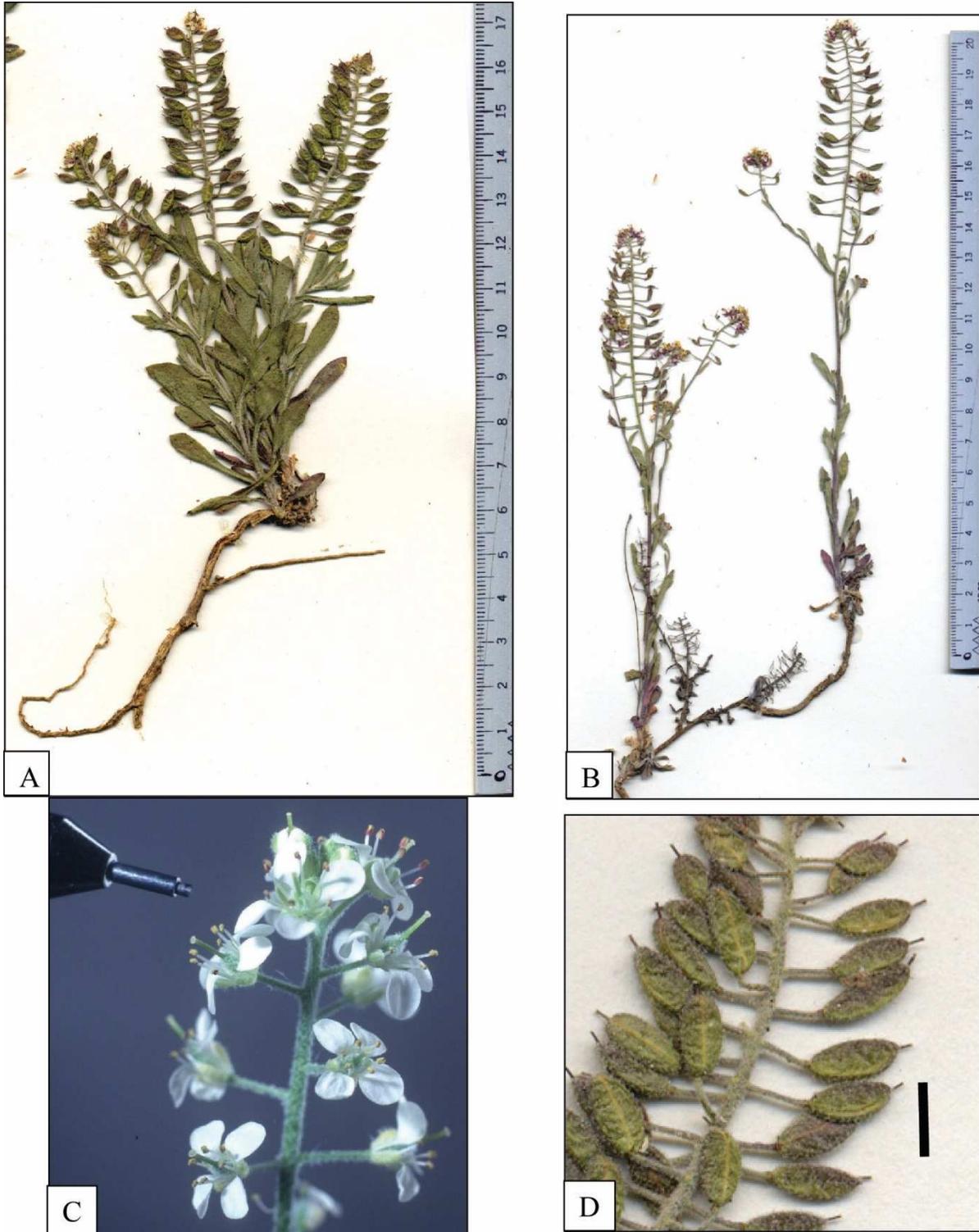


Figure 8. *Sphaerocardamum divaricatum*. A) Habit (Rollins & Ruby 74137 [GH]). B) Habit (Hinton 21852 [TEX]). C) Inflorescence (Bailey & Ochoterena 99 [BH & MEXU]). D) Infructescence (Rollins & Ruby 74137 [GH]) – scale = 5 mm.

microndas, 3 km al Poniente de la Estacion, 30 km Al Sur de Saltillo, 25° 07' 30" N 101° 07' W, 2100 m, 24 May 1982, *Villarreal s.n.* (ANSM); ca. 2 km N of Estación Carneros, E flank of Sierra El Chorreadero, 2150 m, 29 Mar 1973, *Johnston, Wendt, & Chiang 10497A* (TEX); Carneros Pass, 26 mi S of Saltillo, 7200 ft, 18 Nov 1958, *Rollins & Tryon 58134* (GH, MO NY, TEX, UC, US); belt in a mountain valley, about 4 mi E of Carneros Pass, on road to Hedionda Grande, 2 May 1959, *Correll & Johnston 21325* (GH, NY, TEX); rock crevices on steep hillside, first pass S of Carneros Pass, 29 mi S of Saltillo near Mex. Hwy. 54, 29 Sep 1974, *Rollins & Roby 7489* (ENCB, GH, MO, NY, US); Carneros Pass, limestone ledges, 12 Aug 1890, *Pringle 3195* (BM, GH, KEW, NY, TEX, UC, US); Sierra de Parras en el Capulín, 2050 m, 9 Jun 1981, *Rodríguez & Carranza 861* (ANSM); Saltillo and vicinity, Jun & Sep 1898, *Palmer 347* (BM, GH, MO, NY, UC, US); Fraile, 59 km S of Saltillo, in playa valleys with some considerable drainage from surrounding hills, 1967 m, 10 Jul 1941, *Stanford, Retherford, & Northcraft 290* (GH, MO); ca. 2-3 km up the road to the radio tower from Estación Carneros (Carneros Pass), 2200 m, 6 Sep 1997, *Bailey & Ochoterena 133* (BH, MEXU); 16 mi S of Arteaga, 18 Aug 1948, *Kenoyer & Crum 2807* (GH); Mpio G. Cepeta, 63 km E of Parras, take the deviation south toward El Cinco (on some maps "Cinco de Mayo") 18 km (as you pass through El Tejocote keep to the left, plants in canyon "Boca de Domingo"), 2050 m, 30 Aug 1997, *Bailey & Ochoterena 102* (MEXU); Mpio G. Cepeta, 63 km E of Parras take the deviation S toward El Cinco (on some maps "Cinco de Mayo") 14 km (as you pass through El Tejocote keep to the left, plants in canyon "Boca de Domingo, 2000 m, 30 Aug 1997, *Bailey & Ochoterena 99* (BH, MEXU); along the road that parallels the railroad tracks from Parras to Saltillo, 49 km E of Parras, 14 km W of the deviation to El Cinco (on some maps "Cinco de Mayo"), 2085 m, 30 Aug 1997, *Bailey & Ochoterena 93* (BH, MEXU); Carneros Pass, 26 mi S of Saltillo, 1885 m, *Bailey 45* (MEXU); valley 15 km W of Concepción del Oro just within Coahuila border, 2300 m, 19 Jul 1941, *Stanford, Retherford, & Northcraft 484* (GH, MEXU, MO, NY, UC); Coahuila/Zacatecas boarder, 9 km S of Parras on Sierras Negras, 3 Jul 1941, *Stanford, Retherford, & Northcraft s.n.* (NY). **Hidalgo.** El Capulin, near km 134 on highway between Actopan and Ixmiquilpan, 1800 m, 4 Aug 1948, *Moore & Wood 4253a* (GH); just S of Patria Nueva, 16 km N of Actopan near Mex. Hwy 85, 17 Oct 1983, *R. & K. Rollins with Sousa-Pena 83347* (ENCB, GH). **Nuevo León.** San Urbert, 1900 m, 20 Mar 1992, *Hinton 21852* (TEX); S.J. Las Joyas, 2420 m, 29 Jun 1983, *Hinton 18499* (TEX); low hill near Hwy. 57, 34 mi S of Saltillo, 5 Sep 1976, *Rollins & Roby 76065* (GH); 4 mi S of the turn-off to Hacienda de San Jose Raices, between Saltillo and Matehuala, 20 Nov 1958, *Rollins & Tryon 58181* (GH); 1.5 km E of El Barrosito, 1.5 km W of Puero Prieta in southern part of Sierra la Tomita, 2100 m, 19 Jun 1972, *Wendt, Chiang, & Johnston 8008* (GH). **Puebla.** Traveling from Puebla to Tehuacan turn off main Hwy 150 to Hwy 150 for Orizaba, plants found on N-facing slope ca. 200 m down the road from the interchange, 2120 m, 13 Jul 1996, *Bailey 15* (BH, MEXU). **San Luis Potosí.** Ca. 6 km al E de laguna seca Mpio. de Charcas, 2150 m, 10 Sept 1955, *Rzedowski 6551=628* (ENCB, MO, TEX); 2 km S on the road to Real de Catorce from the road between Matehuala and San Francisco de los Quijano, 2280 m, 8 Sep 1997, *Bailey & Ochoterena 138* (MEXU). **Tamaulipas.** 6 km al S de Bustamante, 1950 m, 15 Aug 1972, *Lopez y Dirzo 4651* (MEXU); Patria Nueva, 1 km S of town along interstate 85, N of Pachuca, 1980 m, 12 Sep 1997, *Bailey & Ochoterena 158* (BH, MEXU). **Zacatecas.** Sierra del Astillero (approached from the SE, from Tanque El Alto), 2500-3195m, 2 Jul 1973, *Johnston, Wendt, & Chiang 11551C* (TEX); 5.5 km by road E of Salaverna toward Concepción del Oro, 3 km W of Aranzazu, N side of pass in mountains, 2900 m, 29 Mar 1973, *Johnston, Wendt, & Chiang 10475A* (TEX); 4 km E of Salaverna, S side of a mountain pass, 2900 m, 29 Mar 1973, *Johnston, Wendt, & Chiang 10473A* (GH, TEX); hillside, 9.6 mi W of Concepción del Oro, 8 Oct 1974, *Rollins & Roby 74137* (ENCB, GH, MO, NY, US); Concepción del Oro, Sierra Madre Oriental, 2300-2700 m, 18-19 Jul 1934, *Pennell 17399* (GH, NY, US); ca. 16 air mi E of Concepción del Oro, 3 mi NE of Guadalupe Garceron in small igneous canyon of main canyon of Sierra del Astillero, 6350 ft, 22 Sep 1973, *Henrickson 13289* (GH); Sierra del Astillero (approached from SE, from Tanque El Alto), 2100-3195 m, 2 Jul 1973, *Johnston, Wendt & Chiang 11564* (GH, MEXU, TEX); Puerto de Rocamontes at the Zacatecas-Coahuila state line, 1990 m, 29 Mar 1973, *Johnston, Wendt, & Chiang*

10487 (GH, TEX); 1.5 km ESE of Salaverna, on road to Concepción del Oro, 2800 m, 17 Jun 1972, Chiang, Wendt & Johnston 7936 (GH, TEX); ca. 2 km E of Salaverna, 14 km W of Concepción del Oro, 2600 m, 7 Sep 1997, Bailey & Ochoterena 137 (BH, MEXU); K884-S of Saltillo, 29 July 1929, Runyon 1333 (TEX, US).

3. SPHAEROCARDAMUM NESLIIFORME S. Schauer, *Linnaea* 20: 720 1847. **TYPE: MEXICO.** Locality unknown, *Aschenborn* 209 (holotype: B!). Figs. 7 & 9.

Cibotarium microcarpum Rollins, *Rhodora* 59: 70. 1957. **TYPE: MEXICO.** District of Zimapán, dry rocky slopes of Barranca de Tolimán somewhat above the mines, 7.6 mi from Zimapán on road to Mina Loma del Toro and Balcones, 5000 ft, 30 Oct 1949, H.E. Moore Jr. 5443 (holotype GH!; isotype BH!).

Biennial, 8-35 cm tall. **Stems** erect, mostly distally branched. **Leaf** margins denticulate to dentate, trichomes with 2-6 ramifications. **Inflorescence** compound. **Pedicels** divaricately ascending, 2-6 mm long. **Perianth** spreading. **Sepals** 0.5-1 mm long and 0.3-0.6 mm wide. **Petals** narrowly oblanceolate, little distinction between claw, blade 0.6-1.1 mm long and 0.125 -0.25 mm wide. **Filaments** 0.65-1.4 mm long; **anthers** purple or pale. **Gynoeceum** spherical; often protogynous with styles protruding beyond the apex of the closed buds; **ovules** 2 (rarely 3) per locule, one attached on each side of the replum near the apex. **Fruit** spherical, uncompressed 0.9-1.9 mm in diameter; minute apical notch absent; **styles** 0.5-0.9 mm long; stigmas obscurely bilobed; **valves** rounded on the back, densely pubescent on the exterior, sparsely to moderately pubescent on the interior. **Seeds** 2 (rarely 3) per locule, 0.6-0.8 mm long and 0.4-0.5 mm wide. $n = 8$.

Phenology: Flowering in October (based on limited information).

Sphaerocardamum nesliiforme is easily distinguished by the 2 (rarely 3) seeds per locule and spherical fruits. The current study supports Rollins's (1984) decision to synonymize *Cibotarium microcarpum* and *S. nesliiforme*. Geographically *S. nesliiforme* is restricted (Fig. 7) to the southernmost range for *Sphaerocardamum*, with collections only known from limestone soils in mountainous areas of Hidalgo and a single disjunct locality in Guerrero. The distribution for *Sphaerocardamum nesliiforme* only overlaps slightly with that for *S. divaricatum*, and these two have only been collected growing sympatrically from a single locality. Populations grow at elevations from 1100-2000 m in association with *Acacia*, *Croton*, *Juniperus*, *Karwinskia*, *Pinus*, and *Yucca*.

Additional collections examined. MEXICO. Guerrero. Mpio. Atoyac de Alvarez, El Ranchito, 1100 m, 19 Aug 1985, Soto Nunez & Roman 10087 (MEXU). **Hidalgo.** Mpio. Zimapán, along a little used mining road, steep SE slope of Barranca de Toliman, 7.6 mi N of Zimapán, 18 Oct 1983, Rollins & Sousa-Pena 83349 (ENCB, GH); road from Ixmiquilpan to Tolontongo above the first 180° corner as you descend into Barranca de Tolantongo, 22 km NE of Ixmiquilpan, 12 km NE of Cardonal, 6 km NE of San Cristobal, 1850 m, 10 Sep 1997, Bailey & Ochoterena 152 (BH, MEXU); from Zimapán follow the mining road toward the mines in Barranca de Tolimán, ca. 8 km N of Zimapán turn right onto a (currently) less well used road, 2 km up this road you cross over a small pass and immediately after turn left down an abandon road ca. 1 km on uphill side of the road, 1760 m, 11 Sep 1997, Bailey & Ochoterena 156 (BH, MEXU); Patria Nueva, 1 km S of town along Interstate 85, N of Pachuca, 1980 m, 12 Sep 1997, Bailey & Ochoterena 157 (BH, MEXU).

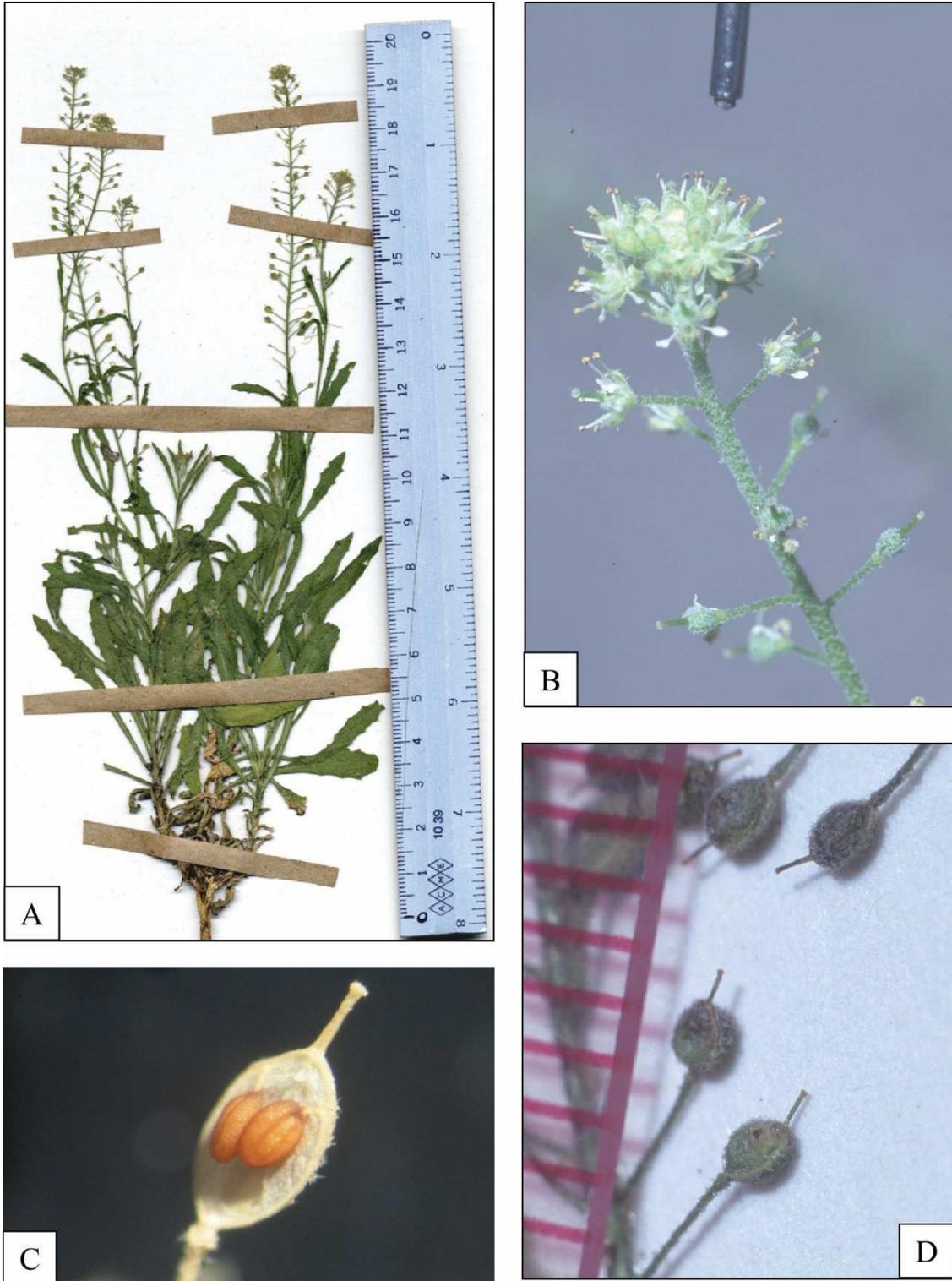


Figure 9. *Sphaerocardamum nesliiforme*. A) Habit (Rollins 83349 [GH]). B) Inflorescence (Bailey & Ochoterena 157 [BH & MEXU]). C) Open fruit with intact seeds (Bailey & Ochoterena 157 [BH & MEXU]). D) Infructescence (Rollins 83349 [ENCB]).

4. **SPHAEROCARDAMUM STELLATUM** (S. Wats.) Rollins, Contrib. Gray Herb. 213: 14. 1984. *Cibotarium stellatum* (S. Wats.) O.E. Schulz, Engl. Jahrb. 66: 91. 1933. *Capsella stellatum* S. Wats., Proc. Amer. Acad. 25: 142. 1890. **TYPE: MEXICO. Coahuila.** Limestone ledges on Carneros Pass, 9 Sep 1889, *Pringle 2844* (holotype: GH!). Figures. 7 & 10.

Sphaerocardamum fruticulosum (Rollins) Rollins, Contrib. Gray Herb. 213: 14-15. 1984. *Cibotarium fruticulosum* Rollins, Contrib. Dudley Herb. 3: 187. 1941. **TYPE: MEXICO. San Luis Potosí.** Minas de San Rafael, Jun 1911, *Purpus 5374* (holotype: GH!; isotype NY!, US!).

Sphaerocardamum macrum (Standl.) Rollins, Contrib. Gray Herb. 213: 15. 1984. *Cibotarium macrum* Rollins, Contrib. Dudley Herb. 3: 189. 1941. *Lepidium macrum* Standl., Publ. Field Mus. Nat. Hist., Chicago, Bot. Ser. 17: 248. **TYPE: MEXICO. Nuevo León.** Municipio de Derrumbadero, Cañon de los Capulines, above San Enrique, Hacienda San Jose de Raices, 6 Aug 1935, *Mueller 2411* (holotype: F; isotypes GH!, MO!).

Sphaerocardamum ramosum Rollins, Contrib. Gray Herb. 213: 15. 1984. **TYPE: MEXICO. Nuevo León.** Cerro Potosí, E slope, dry rocky open places between corn fields, 6050 ft, 9 Jul 1963, *MacGregor, Harms, Robinson, Rosaria & Segal 413* (holotype: GH!).

Biennial or perennial, 4-40 cm tall. **Stems** erect, branched below and within the inflorescence. **Leaf** margins entire to dentate; trichomes with 1-7 ramifications. **Inflorescence** compound. **Pedicels** divaricately ascending to slightly descending, 1-7 mm long. **Perianth** widely spreading to somewhat closed. **Sepals** 0.6-1.4 mm long and 0.3-0.9 mm wide. **Petals** strap shaped to spatulate (limited distinction between claw and blade), 0.4-1.6 mm long and ca. 0.1-0.65 mm wide at the distal end. **Filaments** 0.4-1.8 mm long; **anthers** pale to purple. **Gynoecium** obovate, sometimes protogynous; **ovules** 4 (rarely 3) -8 per locule. **Fruit** obovate, strongly angustiseptate, 1.8-4.6 mm long, 1.0-2.9 mm wide, 0.6-2.2 mm deep; minute apical notch often present; **styles** 0.2-1.1 mm long; stigmas capitate to obscurely bilobed; **valves** keeled, densely pubescent on the exterior, pubescent on the interior (sometimes individual fruits with glabrous valves); septum complete or slightly perforate. **Seeds** biserially (occasionally nearly uniserially) arranged, 3-8 per locule, 0.4-1 mm long and 0.3-0.75 mm wide. $n = 8$.

Phenology. Flowering March to November.

Sphaerocardamum stellatum is recognized by its obovate keeled fruits, short styles and petals. Populations are known from Aguascalientes, Coahuila, Nuevo León, San Luis Potosí, and Zacatecas (Fig. 7), making it another widespread species. Its range only overlaps with *S. divaricatum*, but it has been collected growing sympatrically with this species at three different localities. Habitats for *S. stellatum* typically include limestone soils from 1555-2470 m in association with *Acacia*, *Agave*, *Dasyllirion*, *Larrea*, *Pinus cembroides*, *Opuntia*, and *Toxicodendron*.

Additional collections examined. MEXICO. Aguascalientes. Ladera S del Cerro Palmira, 4 km al W de Asientos, 2300 m, 1 Nov 1967, *Rzedowski 25059* (ENCB). **Coahuila.** MEX 57 ca. 9 km SE of the deviation to Huachichil and 2 km NW of the border with Nuevo León, NW-facing slope on W side of road, 2080 m, 3 Sep 1997, *Bailey & Ochoterena 120* (BH, MEXU); Saltillo and vicinity, June 1898, *Palmer 347* (BM, US); Saltillo and vicinity, 1898, *Palmer 347.5* (UC); Saltillo, 10 Aug 1905, *Palmer 752* (GH, NY); limestone ledges on Carneros Pass, 9 Sep 1889, *Pringle 2844* (GH); limestone ledges, Carneros Pass, 12 Aug 1890, *Pringle 3195* (K); rock crevices first pass S of Carneros Pass, 29 mi S of Saltillo near Mex. Hwy 54, 29 Sep 1974, *Rollins & Roby 7490* (GH, NY); ravine, Carneros Pass, 26 mi S of Saltillo, 7200 ft, 18 Nov 1958, *Rollins & Tryon 58133* (MO, NY, TEX, UC, US); ca. 2 km N of Estacion Carneros, E flank of Sierra El Chorreadero, 2150m, 29 Mar

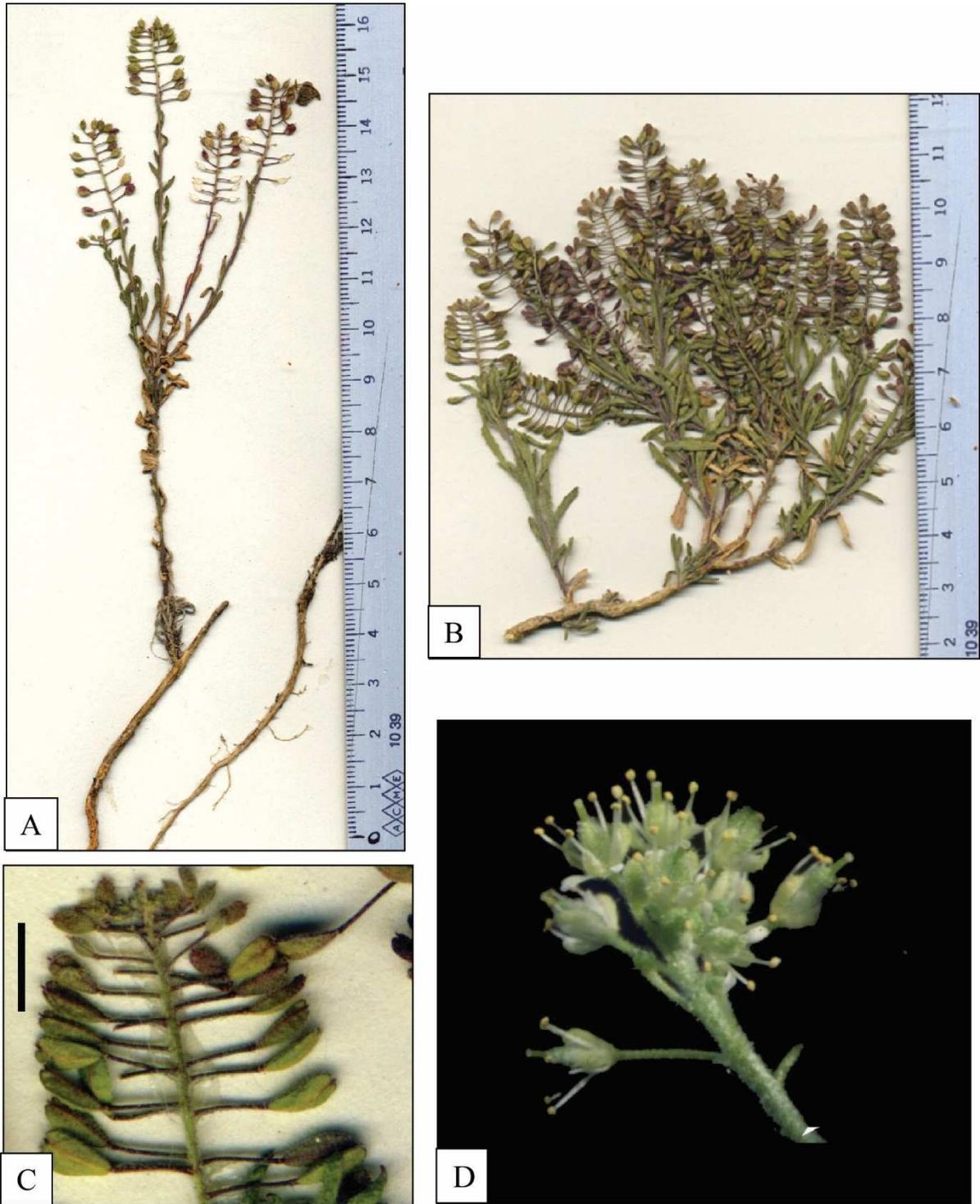


Figure 10. *Sphaerocardamum stellatum*. A) Habit (Wells & Nesom 99 [LL]). B & C) Habit and infructescence (Chiang et al. 8143 [LL]), scale = 5 mm. D) Inflorescence.

1973, *Johnston, Wendt, & Chiang 10497A* (GH, TEX); Cuesta de Palmas Altas, 2250 m, 21 Aug 1975, *Robert & Passini s.n.* (ANSM); Rancho Demonstrative "Los Angeles" 34 km al S de Saltillo, Aug 1972, *collector unknown s.n.* (ANSM); 16 mi S of Arteaga, 18 Aug 1948, *Kenoyer & Crum 2807* (GH). **Nuevo León.** Dirt road ca. 2 km WSW of San Pablo, 16 km E of San Rafael on the road between San Pablo and San Rafael, 2400 m, 3 Sep 1997, *Bailey & Ochoterena 122* (BH, MEXU); Hwy 58 between San Roberto and Linares, km marker 54, 10 km W of Iturbide, 1 km E of the deviation to Las Delicias, 1780 m, 5 Sept 1997, *Bailey & Ochoterena 131* (MEXU); Cerro Potosí, 19 km NE of Galeana, 3 km up the road to radio tower on the mountain, gradual E-facing slope, 2130 m, 4 Sep 1997, *Bailey & Ochoterena 125* (BH, MEXU); 20 km NW of Galeana, 4 km NW of Marzo on the road from Marzo to La Lagunita, above the very steep roadcut, 2170 m, 4 Sep 1997, *Bailey & Ochoterena 126* (BH, MEXU); 37 km NW of Galeana, 3 km NE of the deviation to San Jose de la Joya on the road between Galeana and Los Mimbres (km marker 13.5), 2470 m, 4 Sep 1997, *Bailey & Ochoterena 128* (BH, MEXU); 7 km E of Cienaga del Toro on the road to Santa Rosa and Rayones, 1980 m, 4 Sep 1997, *Bailey & Ochoterena 130* (BH, MEXU); 3 km SE of Santa Clara de Gonzáles on a dirt road to San José de Raices, S.C. de Gonzáles is ca. 20 km S of Galeana, 2130 m, 5 Sep 1997, *Bailey & Ochoterena 132* (BH, MEXU); Iturbide to Camarones, 1570 m, 13 Sep 1991, *Hinton 21455* (TEX); low hills E of Hwy 57, turn-off to La Boca, 177 km N of Matahuala, 5 Sep 1976, *Rollins & Roby 76067* (ENCB, GH2, US); 8 km S of Galeana at fork in the road to Dr. Arroyo and San Roberto, small limestone hill 300 m W of junction, 1630 m, 29 Jul 1996, *Bailey 57* (BH, MEXU); 15 mi E of San Rafael off Hwy 57, 100° 26' W 25° 03' N, ca. 1 mi WSW of San Pablo in narrow valley, 8000 ft, 22-23 July 1977, *Wells & Nesom 99* (GH, LL); Sierra Madre Oriental, San Francisco Canyon, about 15 SW of Pueblo Galeana, 7500-8000 ft, 12 May 1934, *C.H. & M.T. Mueller 317* (AA); on Route 60 at the village of Iturbide, 8 Oct 1962, *Turner & Powell 1070* (TEX); 1-2 mi SW of Pablillo, 21 Jul 1958, *Correll & Johnston 1929* (TEX); arid calcareous-gypseous hillside in thin pine-pinyon woodland, 9 mi W of Galeana, 13 Nov 1964, *Ripley & Barneby 13800* (NY); Galeana to Rayones + 19 km, Rayones, 1560 m, 20 Oct 1990, *Hinton et al. 20831* (GH, TEX). **San Luis Potosí.** Hwy 57, 1 km N of Charco Blanco, then 200 m up the small road to the statue of Benito Juárez, plants on the steep N-facing slope adjacent to the parking lot, 1650 m, 8 Sep 1997, *Bailey & Ochoterena 141* (BH, MEXU); road between Moctezuma and San Lorenzo, 2 km W of Salitrillos (21 km E of Arista), S side of the road at the base of a hill, 8 Sep 1997, *Bailey & Ochoterena 140* (MEXU); Hwy 57, 1 km N of Charco Blanco, then take the road going E toward Guadalcázar for 2 km, 1645 m, 8 Sep 1997, *Bailey & Ochoterena 142* (BH, MEXU); 9 km N of San Jose and ca. 10 km S of Armadillo (Armadillo de los Niños), 2045 m, 9 Sep 1997, *Bailey & Ochoterena 144* (BH, MEXU); Minas de San Rafael, Jun 1911, *Purpus 5235* (BM, UC); Minas de San Rafael, Jul 1911, *Purpus 5235'* (UC); ca. 12 km al SE de Armadillo, ca. 2000 m, 10 Aug 1956, *Rzedowski 7964* (ENCB); steep hillside, 50 mi NE of San Luis Potosí on the road to Matehuala, 5100 ft, 21 Nov 1958, *Rollins & Tryon 58191* (GH, MO, NY, TEX, UC, US); 6 km E of Estación Catorce on the winding road to Real de Catorce, NW portion of the Sierra de Catorce, 2160 m, 17 May 1973, *Johnston, Wendt, & Chiang 11078D* (TEX); 7.4 km E of the San Luis Potosí-Matehuala highway on the road to Cerritos, 1800 m, 29 Jun 1972, *Chiang, Wendt & Johnston 8143* (TEX). **Zacatecas.** Ca 15 (air) mi E of Concepción del Oro, 2.5 mi NE of Guadalupe Garceron in small ravine NW of summit of igneous Sierra del Astillo, 6500 ft., 22 Sep 1973, *Henrickson 13302 B* (GH); Municipio de Saltillo a 60 km, carretera a Concepción del Oro, Rancho "Dos Arbolitos," 15 Aug 1981, *Vásquez, Tera, & de León s.n.* (ANSM).

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