

Generic Limits in Tribe Halimolobeae and Description of the New Genus *Exhalimolobos* (Brassicaceae)

C. DONOVAN BAILEY,^{1,3,4} IHSAN A. AL-SHEHBAZ,^{2,4} and GOVINDARAJULU RAJANIKANTH¹

¹Biology Department, Foster Hall, New Mexico State University, P.O. Box 30001, Las Cruces, New Mexico 88003 U.S.A.;

²Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299 U.S.A.;

³Author for correspondence (dbailey@nmsu.edu)

⁴Authors contributing equally to this research

Communicating Editor: Gregory M. Plunkett

ABSTRACT. In 2002, a monophyletic group previously unrecognized within Brassicaceae was identified through phylogenetic analysis of morphological characters in combination with data from three DNA sequences (Bailey et al.: Syst. Bot. 27: 318–332). As understood at that time, the halimolobine alliance (herein tribe Halimolobeae) comprised ca. 44 species from *Halimolobos*, *Mancoa*, *Pennellia*, and *Sphaerocardamum*. Within this group, a number of nomenclatural problems have remained unaddressed, including the polyphyly of both *Halimolobos* and *Mancoa*. With a developing understanding of Brassicaceae phylogeny, the Halimolobeae is robust in the context of higher level analyses and therefore in need of formal nomenclatural revision. The present study uses new and existing data in phylogenetic analyses based on *trnL-F*, ITS, and *pistillata* intron 1 data along with SEM studies of *Synthlipsis elata* and *S. greggii* to provide the bases for recircumscription of taxa assigned to the Halimolobeae. As recognized herein, the tribe includes five genera [*Exhalimolobos*, *Halimolobos* (including *Synthlipsis elata*), *Mancoa*, *Pennellia*, and *Sphaerocardamum*] and 39 species with two centers of distribution, one in north-central Mexico and the other in the Andes. A synopsis and keys to all taxa of the tribe are presented. Fifteen new combinations are proposed (*E. arabioides*, *E. berlandieri*, *E. burkartii*, *E. hispidulus*, *E. palmeri*, *E. parryi*, *E. pazense*, *E. polyspermus*, *E. weddellii*, *H. elatus*, *H. henricksonii*, *H. pubens*, *H. stylosus*, *P. lechleri*, and *P. parvifolia*).

KEYWORDS: *Halimolobos*, *Mancoa*, *Pennellia*, Phylogeny, *Sphaerocardamum*, *Synthlipsis*.

Generic delimitation and tribal classifications are among the most controversial problems in the systematics of the Brassicaceae (e.g., Al-Shehbaz 1973, 1984; Appel and Al-Shehbaz 2003). The use of molecular data in assessing phylogenetic relationships within the family (Koch 2003; Koch et al. 2003; Mitchell-Olds et al. 2005; Beilstein et al. 2006) has demonstrated that morphological data alone can be insufficient or even misleading with respect to phylogeny, and that fruit characters, the most frequently used characters in the taxonomy of Brassicaceae, are subject to high levels of homoplasy.

Recognition of the informal “halimolobine Brassicaceae” was first suggested by Bailey et al. (2002). This previously unrecognized but well-supported group included taxa with a cohesive general morphology as well as genera with similar geographic distributions. Members of the tribe have branched trichomes, ebracteate racemes (except in two species of *Mancoa*), often spreading sepals, white (rarely purplish) petals, seeds that produce mucilage when wetted, and a chromosome base number of $x = 8$. They are distributed from the southwestern United States to Argentina, with two centers of diversity, one in north-central Mexico and the other in the Andes.

The wide variety of fruit morphologies represented among taxa of the Halimolobeae provided

striking examples of homoplasy in fruit form among closely related Brassicaceae. In fact, the taxa included in the halimolobine clade contradicted Brassicaceae classification to the tribal level. While there are several historical tribal treatments for the Brassicaceae, only that of Schulz (1936) is comprehensive enough to be of use here. Of the five clades resolved in the halimolobine alliance, Schulz (1936) placed *Sphaerocardamum* (1 sp.), *Halimolobos* (11 spp.), *Pennellia* (5 spp.), and *Lamprophragma* (1 sp.) in the Sisymbrieae subtribe Arabidopsinae, assigned *Cibotarium* (1 sp.) and *Mancoa* (4 spp.) to the Lepidieae subtribe Capsellinae, and *Poliophyton* (1 sp.) to the Lepidieae subtribe Cochealiinae. *Lamprophragma* is now united with *Pennellia*, *Cibotarium* with *Sphaerocardamum*, and *Poliophyton* with *Halimolobos*. The main feature used by Schulz (1936) to distinguish the tribe Sisymbrieae from the Lepidieae is terete rather than angustiseptate fruits (flattened at a right angle to the septum). He distinguished the subtribe Capsellinae from the Cochleariinae by strongly compressed fruits with a linear replum and slightly compressed fruits with elliptic replums, respectively.

The results put forward by Bailey et al. (2002) provided strong support for recognition of the halimolobine alliance as tribe Halimolobeae (sensu Al-Shehbaz et al. 2006). With the obvious discon-

nect between previous classification and observed results (Bailey et al. 2002), a number of taxonomic changes are warranted, including a realignment of generic limits within Halimolobeae. Of the 12 species of *Halimolobos* sampled by Bailey et al. (2002), only five were resolved in the clade with the type of *Halimolobos*, *H. lasioloba*. *Halimolobos virgata* was clearly not a member of the Halimolobeae and was transferred to *Transberingia* of the tribe Camelinae (Al-Shehbaz and O'Kane 2003; Al-Shehbaz et al. 2006). Other problems have remained unaddressed. For example, all other sampled members of *Halimolobos* formed a divergent monophyletic group within the halimolobine clade and were informally referred to as "xhalimolobos" (Bailey et al. 2002). *Mancoa* was also polyphyletic within the halimolobine clade. Nevertheless, without higher-level Brassicaceae phylogenetic analyses, it was unclear whether Bailey et al.'s (2002) analyses were sufficiently sampled to warrant formal taxonomic revision of *Mancoa* and *Halimolobos* or the recognition of "xhalimolobos".

With the presentation of family-wide Brassicaceae analyses (e.g., Bailey et al. 2006; Koch et al. 2000; Koch et al. 2001a; Koch et al. 2001b; Koch 2003; Beilstein et al. 2006) it is clear that recognition and formal revision of taxa within the alliance are necessary. In this paper, we provide new data relevant to the Halimolobeae, erect a new genus (*Exhalimolobos* for the informal "xhalimolobos"), and provide a synopsis and keys that reflect our current understanding of the group's five genera.

MATERIALS AND METHODS

Most of the data underlying the phylogenetic background for this revision were put forward by Bailey et al. (2002). Using a combination of DNA sequence data (nrDNA ITS, cpDNA *trnL-F*, and nuclear *pistillata* intron 1) and morphology, Bailey et al. (2002) identified high support for the halimolobine alliance, suggesting that the alliance includes all those taxa discussed above. As an up-date to those analyses, we have included additional sequence data in the matrices presented by Bailey et al. (2002). The newly added material includes ITS (GenBank DQ336388) and *trnL-F* (GenBank DQ336387) sequences from the holotype of *Synthlipsis elata* (Correll and Johnston 20149, GH) and previously published ITS data for *S. greggii* (AF137590). These data were generated because we suspected that *S. elata* is a member of the Halimolobeae rather than *Synthlipsis* s.s. (Physarieae). Attempts to amplify *pistillata* intron 1 from the degraded DNA of *S. elata* failed. The phylogenetic analysis presented here includes all three gene sequences with both species of *Synthlipsis* having missing data for genes that were not available. Molecular and phylogenetic protocols followed Bailey et al. (2002) and the data matrix (15% missing values) is available from TreeBase (study number S1596). In addition to the molecular phylogenetic work, scanning electron micrographs of pollen grains and fruit valve trichomes were studied from the type material of *S. elata* and non-type representative material of *S. greggii* (McVaugh 7832, GH). Other voucher information is provided in Appendix 1.

RESULTS

Figure 1 depicts the strict consensus of 32 equally most parsimonious trees ($L = 1191$; $CI = 0.62$; $RI = 0.66$) along with strict consensus bootstrap support (sensu Davis et al. 1998). Contrary to its assignment to *Synthlipsis* by Rollins (1959; 1993), *S. elata* was not supported as a member of that genus, but rather as a member of *Halimolobos*. The halimolobine alliance (Bailey et al. 2002) was recovered with 96% support. Within this group, five monophyletic clades were recovered with a minimum of 77% support. These include *Mancoa* s.s. (100%), the group previously referred to as "xhalimolobos" and herein as *Exhalimolobos* (99%), *Halimolobos* (77%), *Pennellia* (86%), and *Sphaerocardamum* (100%).

Figure 2 presents the results of SEM studies carried out on two of the three species of *Synthlipsis*. *Synthlipsis elata* (Figs. 2A and 2B) has typical Brassicaceae tricolpate pollen grains (Rollins and Banerjee 1979) while *S. greggii* (Fig. 2C) has polycolpate pollen (also supported by the results of Rollins and Banerjee 1979). *Synthlipsis elata* also displays a trichome size dimorphism (Fig. 2D) on the exterior surface of the fruit valves unknown in other members of *Synthlipsis*.

DISCUSSION

Phylogenetic analysis of ITS, *trnL-F*, and *pistillata* intron data, including the newly obtained sequences, gave results that are entirely congruent with those found by Bailey et al. (2002). However, *Synthlipsis elata* was strongly supported within *Halimolobos* s.s. while *S. greggii*, the type species for *Synthlipsis*, was supported in a divergent monophyletic group containing *Nerisyrenia* and *Physaria* (formerly *Lesquerella*). The position of *S. elata* outside of *Synthlipsis* s.s. is also supported by the SEM work, which revealed that the type material for *S. elata* has tricolpate pollen grains rather than the polycolpate pollen of *S. greggii* [Fig. 2C (see also Plate 13 in Rollins and Banerjee, 1979)]. Brassicaceae with polycolpate pollen are only known from members of *Dimorphocarpa*, *Dithyrea*, *Lyrocarpa*, *Paysonia*, *Physaria* (including *Lesquerella*), and *Synthlipsis* (e.g., Rollins and Banerjee 1979), and current family-level analyses based on a variety of data suggest these taxa represent a well-supported monophyletic group (e.g., Bailey et al., 2006; Beilstein et al. 2006) recently placed in the tribe Physarieae (Al-Shehbaz et al. 2006). Tricolpate pollen represents a plesiomorphic feature in Brassicaceae and therefore does not support a position of *S. elata* within the Halimolobeae. However, the position of *S. elata* within *Halimolobos* s.s. (Halimolobeae) is supported by the molecular

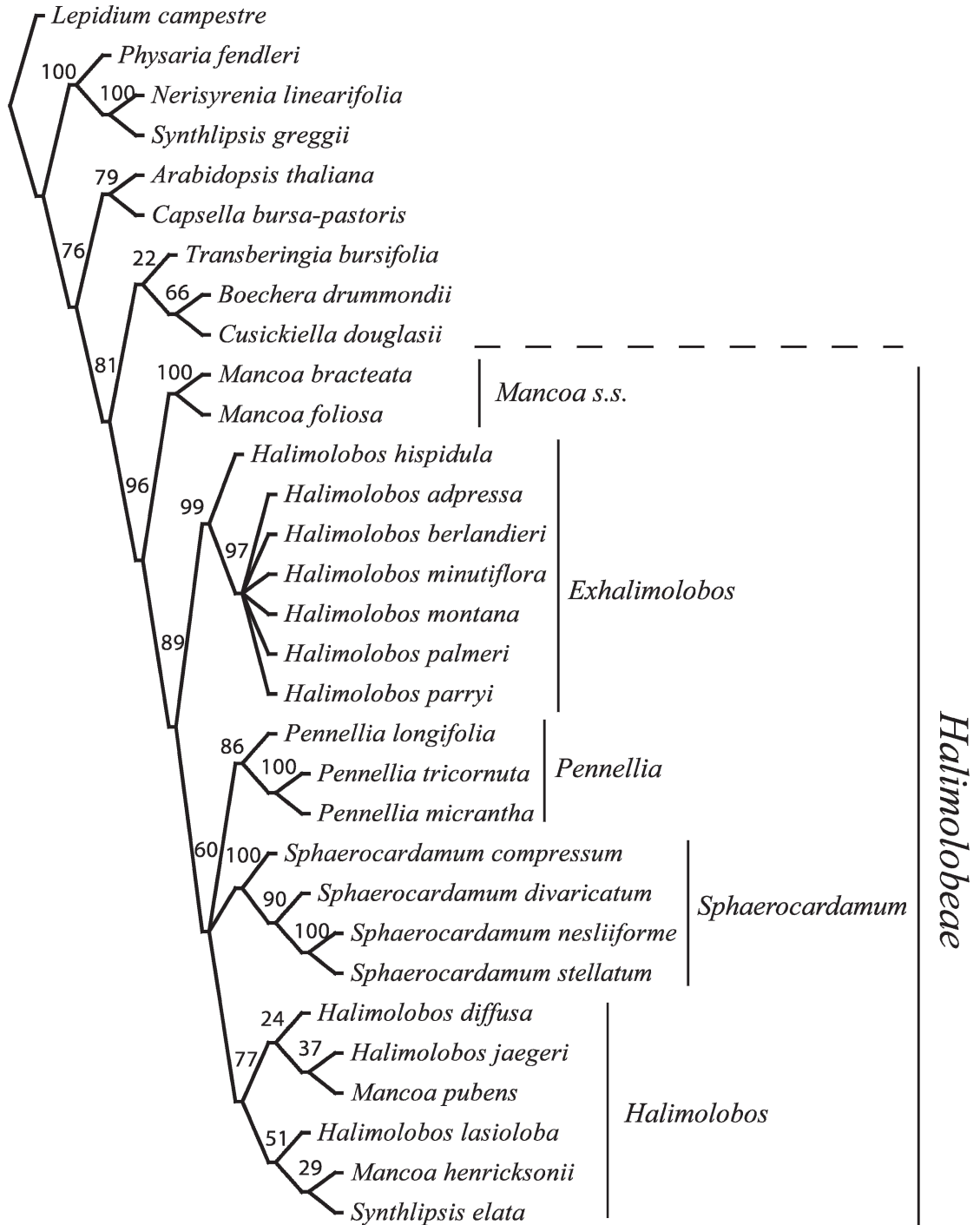


FIG. 1. Strict consensus of 32 equally most parsimonious trees ($L=1191$; $CI=0.62$; $RI=0.66$) resulting from the simultaneous analysis of ITS, pistillata intron 1, and trnL-F DNA sequence data. The Halimolobeae is outlined by the most inclusive bracket and the other genera presented in the revision are noted within this group. Note that *Synthlipsis elata* and *Synthlipsis greggii* (in bold font) do not form a monophyletic lineage. *Synthlipsis elata* is strongly supported as a member of *Halimolobos* within the alliance. Strict consensus bootstrap support values are provided above each node.

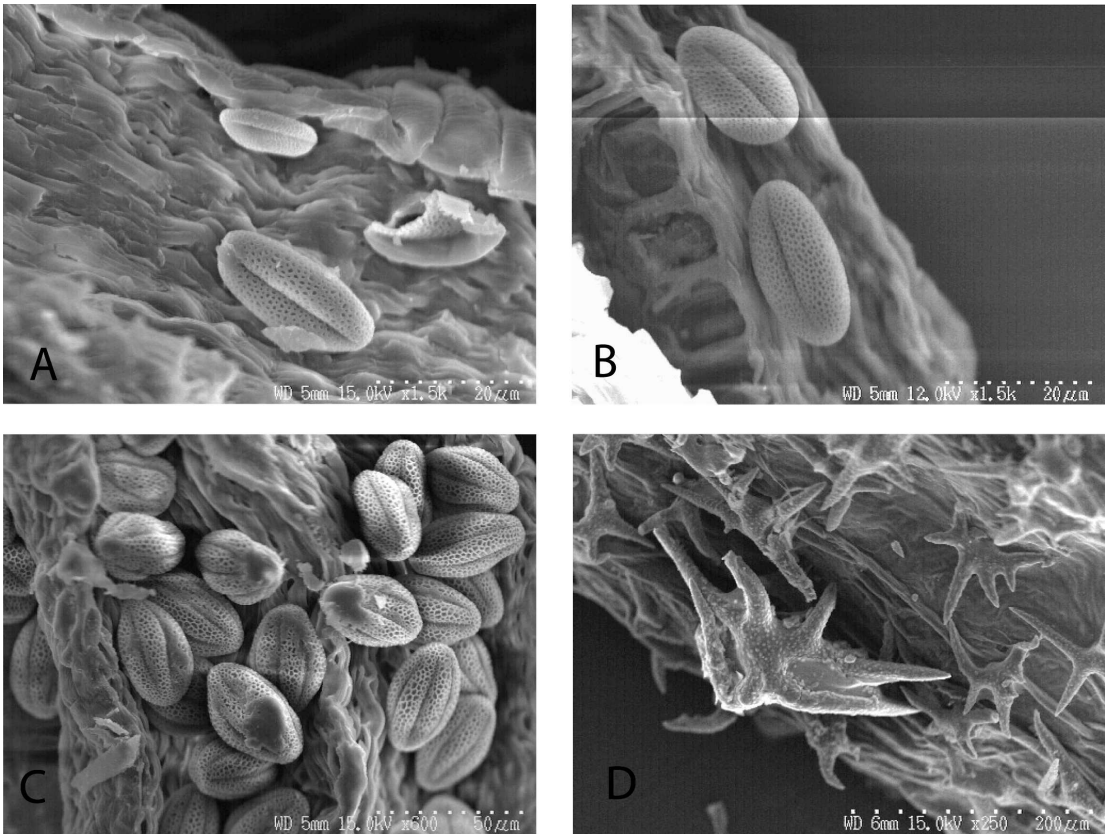


FIG. 2. Representative SEMs of *Synthlipsis*. A, B. Pollen grains from the type material of *S. elata* (Correll and Johnston 20149, GH). C. Representative material of pollen from *S. greggii* (McVaugh 7832, GH). Note that these non-type images of *S. greggii* corroborate previously published data on pollen of *S. greggii* (Rollins and Banerjee 1979). D. Image of the exterior surface of fruit valves in the type material of *S. elata*. Striking dimorphism in trichome size has been noted in members of *Halimolobos* (Bailey et al. 2002), but not *Synthlipsis*.

analysis and by the presence of trichome dimorphism on the fruit valves (Fig. 2D). Within the Halimolobae, these types of trichomes are known only from *Halimolobos s.s.*

Within tribe Halimolobae, both *Mancoa* and *Halimolobos* were polyphyletic with species resolved in two or more divergent lineages. These results continue to support the need for revision of these taxa (as noted by Bailey et al. 2002). Herein, we recognize five genera within the alliance: *Exhalimolobos*, *Halimolobos*, *Mancoa*, *Pennellia*, and *Sphaerocardamum* (Fig. 1). These taxa are all restricted to the New World, with two major centers of distribution. The majority of the species are centered in northern and central Mexico and some extend their ranges northward into the southern United States and southward to Costa Rica. The other center is Bolivia and northern and central Argentina, with fewer species distributed in northern Chile and Peru northward into Ecuador and Colombia. The affinities of species from these genera that were not available for the molecular

analysis were discussed by Bailey et al. (2002). With few exceptions, we follow these authors in assigning taxa to genera in the treatment that follows.

All species in the alliance have dendritic trichomes (sometimes mixed with simple and forked trichomes), incumbent cotyledons (accumbent in *Pennellia tricornuta* and *P. microsperma*), simple, subsessile or sessile, dentate leaves (pinnately lobed and petiolate in some *Mancoa*), mucilaginous seeds, ebracteate racemes (bracteate in some *Mancoa*), nonsaccate sepals, white flowers (lavender or purple in some *Pennellia*), subequal stamens, distinct styles, often slightly ascending floral parts, and dehiscent, several- to numerous-seeded fruits. Latiseptate fruits (flattened parallel to the septum) are known only in the above two species of *Pennellia*, whereas angustiseptate fruits typically characterize all species of *Mancoa*, three of four species of *Sphaerocardamum*, and four species of *Halimolobos*, though the fruits can be slightly angustiseptate in some *Exhalimolobos*. Three species

of *Halimolobos* with angustiseptate fruits were previously assigned to *Mancoa* (Rollins 1941, 1976) and one to *Synthlipsis* (Rollins 1959). *Halimolobos* is unique in the tribe by having fruit valves with large dendritic trichomes mixed with more numerous and much smaller ones (Fig. 2D). In the remaining species of the tribe, the fruit valves are either glabrous or pubescent with trichomes uniform in size. The number of ovules/seeds per ovary/fruit ranges from as few as four (*Sphaerocardamum nesliiforme*) to as many as 120–270 (*E. polyspermus*) or 140–230 (*E. weddellii*).

TAXONOMIC ACCOUNT AND GENERIC SYNOPSES

As delimited herein, the tribe Halimolobeae includes 39 species distributed in *Exhalimolobos* (9 spp.), *Halimolobos* (8 spp.), *Mancoa* (8 spp.), *Pennellia* (10 spp.), and *Sphaerocardamum* (4 spp.). Members of the tribe have branched trichomes, ebracteate racemes (except in two *Mancoa*), often spreading sepals, white (rarely purplish) petals, seeds that produce mucilage when wetted, and a chromosome base number of $x = 8$. A key to the last four genera was provided by Fuentes-Soriano (2004). However, due to the expansion of the limits of *Halimolobos*, a new generic key is required.

KEY TO THE GENERA OF THE HALIMOLOBEAE

1. Fruit a silicle (length $< 3 \times$ width), narrowly oblong, ovate, or globose, distinctly angustiseptate or rarely terete . . . 2
 2. Fruit valves with large trichomes mixed with much smaller ones *Halimolobos*
 2. Fruit valves glabrous or pubescent with trichomes uniform 3
 3. Fruits/ovaries with 4–16(–22) seeds/ovules; funicles straight, shorter than seeds; leaves all cauline, dentate to entire *Sphaerocardamum*
 3. Fruits/ovaries with (30–)40–100 seeds/ovules; funicles often tortuous, longer than or as long as seeds; leaves often basal and cauline, pinnatisect or dentate *Mancoa*
1. Fruit a silique (length $> 3 \times$ width), terete or latiseptate, rarely slightly angustiseptate 4
 4. Petals purple tipped; flowers cupulate, petals and stamens subequalling or only slightly longer than sepals *Pennellia*
 4. Petals white; flowers not cupulate, petals and stamens longer than sepals 5
 5. Fruit valves with large trichomes mixed with smaller ones, midvein and marginal veins obscure; seeds uniseriate, 16–46 per fruit; cauline leaves not auriculate *Halimolobos*
 5. Fruit valves glabrous or pubescent with trichomes uniform in size, midvein and marginal veins distinct; seeds biseriate or multiseriate, (40–)60–270 per fruit; cauline leaves auriculate or not *Exhalimolobos*

HALIMOLOBOS Tausch, Flora 19: 410. 1836.—TYPE: Lectotype (here designated): *H. patulus* Tausch (= *H. lasiolobus* (Link) O. E. Schulz). Tausch (1836) did not designate a type for *Halimolobos*, but he described two species, *H. patulus* and *H. strictus*, under which he listed the earlier published *Sisymbrium polystachyum* Link and *Arabis lasioloba* Link as synonyms, respectively. All four names were considered by Schulz (1924) and Rollins (1943) as conspecific, a position with which we agree. *Poliophyton* O.E. Schulz, Bot. Jahrb. Syst. 66: 93. 1933.—TYPE: *P. pubens* (A. Gray) O.E. Schulz.

Biennial or perennial herbs with woody base; trichomes dendritic, short stalked or subsessile. Stems erect, simple or branched above. Basal leaves petiolate, not rosulate, dentate or sinuate; uppermost leaves sessile, base cuneate to truncate, rarely auriculate. Sepals oblong, slightly spreading, caducous, pubescent, base of lateral pair not saccate; petals white, oblanceolate or spatulate, apex obtuse; stamens slightly tetradynamous, somewhat spreading; anthers ovate or oblong; nectar glands confluent, subtending bases of all stamens; ovules 16–110 per ovary. Fruits linear siliques or ovoid to oblong silicles, terete or slightly

angustiseptate; valves obscurely veined, pubescent with small, appressed, subdendritic trichomes mixed with coarser, short-stalked dendritic ones; style distinct, to 1.5 mm; stigma entire. Seeds uniseriate in silique fruits and biseriate in silicles, wingless; cotyledons incumbent. Basic chromosome number, $x = 8$.

Eight species: southwestern United States and northern and central Mexico.

Six species of *Halimolobos* were initially placed by Fournier (1865) in *Sisymbrium* L., but as pointed out by Warwick et al. (2002), his concept of that genus involved dozens of other genera. Schulz (1924) transferred these six species along with five species from other genera to *Halimolobos*. *Halimolobos* then consisted of 11 species distributed exclusively in North and South America. Rollins (Rollins 1943, 1976, 1993) further expanded the genus to include 18 species, and Martinez-Laborde (1992) recently added another. Of these 19 species, two are now treated as *Sandbergia* Greene, two as *Transberingia* Al-Shehbaz and O’Kane (Price et al. 2001b; Al-Shehbaz and O’Kane 2003), and eight as *Exhalimolobos* (see below). With the transfer of three species of *Mancoa* and one of *Synthlipsis* to what remains of *Halimolobos*, the genus includes eight species.

KEY TO THE SPECIES OF *HALIMOLOBOS*

1. Fruits oblong-linear, oblong, to ovoid, 1.5–5 mm wide, angustiseptate; seeds biseriate, 30–110 per fruit 2
2. Fruits obtuse at apex; fruiting pedicels (6–)8–15(–18) mm long 3
 3. Style 0.2–0.8 mm long; seeds to 0.5 mm long, (60–)70–110 per fruit 7. *H. pubens*
 3. Style 2.5–3.5 mm long; seeds ca. 1 mm long; 40–60 per fruit 8. *H. stylosus*
2. Fruits emarginate at apex; fruiting pedicels 4–8 mm long 4
 4. Middle and upper cauline leaves not auriculate; fruits 8–12 mm long; styles ca. 2 mm long 5. *H. elatus*
 4. Middle and upper cauline leaves auriculate; fruits 5–6 mm long; styles ca. 1 mm long 6. *H. henricksonii*
1. Fruits linear, 0.5–1.5 mm wide, terete; seeds uniseriate, 16–46 per fruit 5
 5. Fruits 1–1.5 mm wide, not or obscurely torulose; plants annual or biennial, not woody at base 6
 6. Lower fruiting pedicels 5–12 mm long; petals 2.5–3.5 × 1–1.5 mm; infructescence lax, racemose 1. *H. lasiolobus*
 6. Lower fruiting pedicels 1.5–4 mm long; petals 0.7–1.2 × 0.2–0.4 mm; infructescence congested, paniculate 2. *H. multiracemosus*
5. Fruits 0.5–0.8 mm wide, torulose; plants perennial, with woody base 7
 7. Fruits 0.6–1.4(–1.7) cm long, 16–24-seeded; sepals 1.2–2 mm long; petals 1.8–2.5 mm long; southeastern Arizona, New Mexico, southwestern Texas and northern Mexico 3. *H. diffusus*
 7. Fruits 1.5–2.6 cm long, 28–38-seeded; sepals 2–4 mm long; petals (3.5–)4.5–6 mm long; eastern California and adjacent Nevada 4. *H. jaegeri*

1. *HALIMOLOBOS LASIOLOBUS* (Link) O.E. Schulz, Pflanzenreich IV. 105(Heft 86): 287. 1924. *Arabis lasioloba* Link, Enum. Pl. Hort. Berol. 2: 163. 1822.—TYPE: MEXICO. Grown at B from seeds by anonymous collector (holotype: B, not seen; isotype: LE!).

Halimolobos lasiolobus var. *pedicellatus* Rollins, Contr. Dudley Herb. 3: 360. 1943; *H. pedicellatus* (Rollins) Rollins, Contr. Gray Herb. 206: 5. 1976.—TYPE: MEXICO. Durango: Tejamén, 21–27 Aug 1906, E. Palmer 491 (holotype: GH!; isotypes: F!, NY, UC!, US!).

Halimolobos rigidus Rollins, Contr. Gray Herb. 206: 4. 1976.—TYPE: MEXICO. San Luis Potosí: 12 km north of El Cubo, 43 km north of Charcas on road to Catorce, 23°26'N, 101°00'W, 1700 m, 3 July 1972, F. Chiang, T. Wendt and M. C. Johnston 8321 (holotype: GH!).

Distribution. Mexico (Chihuahua, Durango, Jalisco, Querétaro, San Luis Potosí, Zacatecas).

Notes. Rollins (1976, 1993) overemphasized the orientation of the fruiting pedicels to distinguish taxa in this complex. There can hardly be much of a difference between fruiting pedicels that are horizontal vs. divaricate, or divaricate vs. divaricately ascending, and one often finds considerable variation on the same plant. A case in point is the holotype of *Halimolobos pedicellatus*, which has pedicels ranging from horizontal to ascending. Furthermore, the presence of about ten smaller lateral branches on the lowermost 15 cm of the stem of *H. rigidus* does not justify its recognition as independent species because this branching aspect occurs sporadically in other species of *Halimolobos*, such as *H. jaegeri* and *H. diffusus*. In fact, a critical comparison of the holotypes of *H. rigidus* and *H. pedicellatus*, along with a good number of collections of *H. lasiolobus*, leaves little doubt that these

represent the same taxon. These “taxa” are indistinguishable in every aspect of leaf and fruit morphology, flower size, and indumentum. They are considered herein as conspecific.

2. *HALIMOLOBOS MULTIRACEMOSUS* (S. Wats.) Rollins, Contr. Dudley Herb. 3: 260. 1943. *Sisymbrium multiracemosum* S. Wats., Proc. Amer. Acad. Arts 26: 132. 1891.—TYPE: MEXICO. San Luis Potosí: Las Canoas, 8 Oct 1890, C. G. Pringle 3522 (holotype: GH!).

Distribution. Mexico (Hidalgo, Michoacán, San Luis Potosí).

3. *HALIMOLOBOS DIFFUSUS* (A. Gray) O.E. Schulz, Pflanzenreich IV. 105(Heft 86): 288. 1924. *Sisymbrium diffusum* A. Gray, Smithsonian Contr. Knowl. (Pl. Wright.) 3: 8. 1852.—TYPE: U.S.A. Texas: Pass of the Limpia, Aug 1849, C. Wright 10 (holotype: GH!; isotypes: UC!, US!).

Distribution. United States (southern Arizona, New Mexico, southwestern Texas) and Mexico (Chihuahua, Coahuila).

4. *HALIMOLOBOS JAEGERI* (Munz) Rollins, Harvard Pap. Bot. 4: 46. 1993. *Sisymbrium diffusum* A. Gray var. *jaegeri* Munz, Bull. S. Calif. Acad. Sci. 31: 61. 1932; *Halimolobos diffusus* (A. Gray) O.E. Schulz var. *jaegeri* (Munz) Rollins, Contr. Dudley Herb. 3: 258. 1943.—TYPE: U.S.A. California: Inyo Co., Westard Pass, July 1928, M. E. Jones s.n. (holotype: POM; isotype: GH!).

Distribution. United States (southeastern California and adjacent Nevada).

5. *Halimolobos elatus* (Rollins) Al-Shehbaz and C.D. Bailey, comb. nov. *Synthlipsis elata* Rollins, *Rhodora* 61: 255. 1959.—TYPE: MEXICO. Durango: 9 miles northeast of Durango on route 31, 25 July 1958, D. S. Correll and I. M. Johnston 20149 (holotype: GH!).

Distribution. Mexico (Durango). Known only from the type collection.

6. *Halimolobos henricksonii* (Rollins) Al-Shehbaz and C.D. Bailey, comb. nov. *Mancoa henricksonii* Rollins, *Contr. Gray Herb.* 206: 8. 1976.—TYPE: MEXICO. Zacatecas: Pico de Teyra, 15 miles northeast of Estacion Cmacho, near 23°33'N, 102°10'W, 8,200 ft., 23 Sep 1973, J. Henrickson 13471 (holotype: GH!; isotypes: GH!, MO!).

Distribution. Mexico (Zacatecas). Known only from the type collection.

7. *Halimolobos pubens* (A. Gray) Al-Shehbaz and C.D. Bailey, comb. nov. *Hymenolobus pubens* A. Gray, *Smithsonian Contr. Knowl. (Pl. Wright.)* 3: 9. 1852; *Mancoa pubens* (A. Gray) Rollins, *Contr. Dudley Herb.* 3: 192. 1941; *Poliophyton pubens* (A. Gray) O.E. Schulz, *Bot. Jahrb. Syst.* 66: 93. 1933.—TYPE: U.S.A. Texas: valley about 80 miles beyond the Pecos, Aug 1849, C. Wright 12 (holotype: GH!; isotype: US!).

Distribution. United States (southwestern Texas), northern Mexico (Coahuila).

8. *Halimolobos stylosus* (Rollins) Al-Shehbaz and C.D. Bailey, comb. nov. *Mancoa stylosa* Rollins, *Contr. Gray Herb.* 206: 7. 1976.—TYPE: MEXICO. Durango: Carcaria, 5 Aug 1898, E. W. Nelson 4657 (holotype: US!).

Distribution. Mexico (Durango). Known only from the type collection.

The last three species were placed by Rollins (1993) in *Mancoa*, a genus that he and Appel and Al-Shehbaz (2003) distinguished from *Halimolobos* using somewhat angustiseptate silicles instead of

terete siliques. However, as discussed by Al-Shehbaz et al. (2006) the relative length to width of fruit, on which the distinction of siliques vs. silicles is based, is quite artificial and can be found within numerous genera of the family, as can the fruit compression (terete vs. slightly angustiseptate). In our opinion, these fruit characters can be unreliable and should be evaluated with extreme care in the delimitation of genera. All eight species of *Halimolobos* are readily distinguished from the other members of the Halimolobeae by fruit valve of the trichome types (discussed above).

Exhalimolobos Al-Shehbaz and C.D. Bailey, gen. nov.—TYPE: *Exhalimolobos palmeri* (Hemsl.) Al-Shehbaz and C.D. Bailey.

Herba biennis, pilis simplicibus et dendritis; folia basalia nonrosulata, dentata vel sinuata; folia caulina sessilia, aruiculata vel amplexicaulis; sepala nonsaccata; petala alba; ovula 40–270; fructus lineares, teretes vel angustiseptates, glabres vel pubescentes; semina biseriata, oblonga; cotyledones incumbentes.

Biennial herbs; trichomes dendritic, stalked or subsessile, sometimes mixed with simple ones. Stems erect, simple or branched above. Basal leaves petiolate, not rosulate, coarsely dentate or sinuate; cauline leaves sessile, base auriculate to amplexicaul, dentate or sinuate-dentate. Sepals oblong, erect or rarely ascending, caducous, pubescent, base of lateral pair not saccate; petals white, oblanceolate or spatulate, apex obtuse; stamens slightly tetradynamous, anthers ovate or oblong, obtuse at apex; nectar glands confluent, subtending bases of all stamens; ovules 40–270 per ovary. Fruits dehiscent, linear or rarely oblong siliques, terete or slightly angustiseptate; valves with a prominent midvein extending at least to middle and distinct marginal veins, glabrous or uniformly pubescent with subsessile or short-stalked dendritic trichomes, not torulose; style distinct, to 3.5 mm; stigma entire. Seeds usually biseriate or multiseriate, wingless, oblong; cotyledons incumbent. Basic chromosome number, $x = 8$.

Nine species: Argentina, Bolivia, Colombia, Ecuador, Mexico, Peru, Venezuela.

KEY TO THE SPECIES OF EXHALIMOLOBOS

1. Plants densely pubescent throughout with predominately simple trichomes, branched trichomes restricted to leaf margins 1. *E. polyspermus*
1. Plants pubescent with appressed or short-stalked 2–8-rayed trichomes, simple trichomes (if present) restricted to lower portions of stems and leaf veins, always fewer than branched trichomes 2
2. Fruits and fruiting pedicels appressed to rachis 6. *E. pazense*
2. Fruits and fruiting pedicels descending, horizontal, divaricate, or ascending, never appressed to rachis 3

3. Cauline leaves cuneate, neither auriculate nor amplexicaul 4
 4. Fruit glabrescent; style ca. 0.1 mm long; seeds 0.4–0.5 mm long; Argentina 9. *E. burkartii*
 4. Fruits pubescent; style 0.5–1 mm long; seeds 0.7–1 mm long; Mexico 4. *E. berlandieri*
 3. Cauline leaves amplexicaul or auriculate 5
 5. Petals 5–6.5 × 1.5–2 mm; fruits horizontal to somewhat reflexed, 2.5–3 mm wide; style (1–)1.5–2.5 mm long 8. *E. arabioides*
 5. Petals 1.5–4(–4.5) × 0.3–1.2 mm; fruits divaricate to ascending or erect, 1–1.7(–2) mm wide; style 0.2–1(–1.5) mm long 6
 6. Fruit valves sparsely pubescent on the inside; seeds/ovules 40–60(–84) per fruit; fruits 0.4–1.2(–1.5) cm long 3. *E. parryi*
 6. Fruit valves glabrous on the inside; seeds/ovules (80–)100–250 per fruit; fruits (0.8–)1–3.8 cm long 7
 7. Fruits moderately to densely pubescent; stems without setose trichomes 7. *E. weddellii*
 7. Fruits glabrous or sparsely pubescent; stems with setose trichomes to 1.5 mm long 8
 8. Fruits glabrous; style obsolete or to 0.2 mm long; seeds 0.5–0.6 mm long; north-central Mexico 2. *E. palmeri*
 8. Fruits sparsely pubescent; style 0.5–1.5 mm long; seeds (0.6–)0.7–0.9(–1) mm long; south-central Mexico, South America 5. *E. hispidulus*
1. *Exhalimolobos polyspermus* (E. Fourn.) Al-Shehbaz and C.D. Bailey, comb. nov. *Sisymbrium polyspermum* E. Fourn., Recherch. Crucif. 103. 1865; *Hesperis polysperma* (E. Fourn.) Kuntze, Revis. Gen. Pl. 2: 935. 1891; *Halimolobos polyspermus* (E. Fourn.) O.E. Schulz, Pflanzenreich IV. 105(Heft 86): 294. 1924.—TYPE: MEXICO. San Luis Potosí, 1851, V. d' Aoust 570 (holotype: P!; photo, F). Hemsl., Dign. Pl. Nov. Mexic. 2: 19. 1879; *Hesperis parryi* (Hemsl.) Kuntze, Revis. Gen. Pl. 2: 935. 1891; *Halimolobos palmeri* (Hemsl.) O. E. Schulz var. *parryi* (Hemsl.) O.E. Schulz, Pflanzenreich IV. 105(Heft 86): 291. 1924; *Halimolobos parryi* (Hemsl.) Rollins, Contr. Dudley Herb. 3: 249. 1943.—TYPE: MEXICO. San Luis Potosí, 22°N, 6,000–8,000 ft., 1878, C. C. Parry and E. Palmer 15 (holotype: K!; isotype: GH!).
- Distribution.* Mexico (Hidalgo, Puebla, Querétaro, San Luis Potosí).
2. *Exhalimolobos palmeri* (Hemsl.) Al-Shehbaz and C.D. Bailey, comb. nov. *Sisymbrium palmeri* Hemsl., Dign. Pl. Nov. Mexic. 2: 19. 1879; *Hesperis palmeri* (Hemsl.) Kuntze, Revis. Gen. Pl. 2: 935. 1891; *Halimolobos palmeri* (Hemsl.) O.E. Schulz, Pflanzenreich IV. 105(Heft 86): 290. 1924.—TYPE: MEXICO. San Luis Potosí: 22°N, 6,000–8,000 ft., 1878, C. C. Parry and E. Palmer 13 (holotype: K!; isotypes: F!, GH!). *Halimolobos palmeri* var. *acutilobus* Rollins, Contr. Dudley Herb. 3: 249. 1943.—TYPE: MEXICO. Hidalgo: Sierra de Pachua, 17 August 1898, C. G. Pringle 7651 (holotype: GH!).
- Distribution.* Mexico (Hidalgo, Querétaro, San Luis Potosí, Zacatecas).
- Notes.* Rollins (1943) recognized two varieties (*palmeri* and *acutiloba*) in this species and in some cases (e.g., Parry and Palmer 13; K) on the same herbarium sheet. He distinguished them primarily by the density of the trichomes on the leaves and the frequency of occurrence of simple trichomes on the leaf veins. Such distinction is tenuous at best, and we believe that the recognition of such infraspecific taxa in this group has little if any value.
3. *Exhalimolobos parryi* (Hemsl.) Al-Shehbaz and C.D. Bailey, comb. nov. *Sisymbrium parryi* Hemsl., Dign. Pl. Nov. Mexic. 2: 19. 1879; *Hesperis parryi* (Hemsl.) Kuntze, Revis. Gen. Pl. 2: 935. 1891; *Halimolobos palmeri* (Hemsl.) O. E. Schulz var. *parryi* (Hemsl.) O.E. Schulz, Pflanzenreich IV. 105(Heft 86): 291. 1924; *Halimolobos parryi* (Hemsl.) Rollins, Contr. Dudley Herb. 3: 249. 1943.—TYPE: MEXICO. San Luis Potosí, 22°N, 6,000–8,000 ft., 1878, C. C. Parry and E. Palmer 15 (holotype: K!; isotype: GH!).
- Distribution.* Mexico (San Luis Potosí).
- Notes.* The holotype and isotype of *Halimolobos minutiflorus* each has a plant with glabrous fruits, a feature not reported by Rollins (1976, 1993). The remaining six plants on the holotype and four on the isotype sheet have pubescent fruits. However, all plants of this species have fruit valves sparsely pubescent on the inside. In this aspect, the species is exactly the same as *E. parryi*, but Rollins (1943, 1976, 1993) did not observe this similarity between the two taxa. The fact these two taxa have the smallest fruits [0.5–1.2(–1.5) mm long vs. longer] and fewest number of seeds per fruit [40–60(–84) vs. (80–)90–270 in the other species], as well as being both restricted to San Luis Potosí, clearly support the placement of *H. minutiflorus* in synonymy of *E. parryi*. Bailey et al. (2002) stated that *H. palmeri* var. *acutilobus* has valves pubescent on the inside, but an examination of the holotype and all collection of this taxon at GH and MO show that the valves are always glabrous inside. It is likely that the taxon meant by these authors was *H. parryi*, not *H. palmeri*.

4. *Exhalimolobos berlandieri* (E. Fourn.) Al-Shehbaz and C.D. Bailey, comb. nov. *Sisymbrium berlandieri* E. Fourn., Recherch. Crucif. 105: 1865; *Hesperis berlandieri* (E. Fourn.) Kuntze, Revis. Gen. Pl. 2: 934. 1891; *Halimolobos berlandieri* (E. Fourn.) O.E. Schulz, Pflanzenreich IV. 105(Heft 86): 289. 1924.—TYPE: MEXICO. Near Mexico City, 31 July 1827, *M. Berlandier* 579 (holotype: P!; isotype: F!).

Distribution. Mexico (Aguascalientes, Distrito Federal, Guanajuato, Hidalgo, Michoacán, Nuevo León, Oaxaca, Puebla, San Luis Potosí).

5. *Exhalimolobos hispidulus* (DC.) Al-Shehbaz and C.D. Bailey, comb. nov. *Turritis hispidula* DC., Syst. Nat. 2: 213. 1821; *Sisymbrium hispidulum* (DC.) Triana and Planch., Ann. Sci. Nat. Bot. IV. 17: 63. 1862; *Hesperis hispidula* (DC.) Kuntze, Revis. Gen. Pl. 2: 934. 1891; *Halimolobos hispidulus* (DC.) O.E. Schulz, Pflanzenreich IV. 105(Heft 86): 291. 1924.—TYPE: ECUADOR. Cotopaxi, *Humboldt and Bonpland s.n.* (P-Bonpl.).

Halimolobos acutifolius O. E. Schulz, Pflanzenreich IV. 105(Heft 86): 291. 1924. *H. hispidulus* var. *acutifolius* (O. E. Schulz) Rollins, Contr. Dudley Herb. 3: 252. 1943.—TYPE: MEXICO. Federal District: Eslaba, 23 Sep 1903, C. G. Pringle 11370 (holotype: B!; isotypes: BH!, F!, GH!, US!).

Distribution. Mexico (Distrito Federal, Guanajuato, Puebla), Bolivia (Cochabamba, La Paz), Colombia (Cauca, Cundinamarca, Magdalena, Norte de Santander), Ecuador (Azuay, Chimborazo, Cotopaxi, Imbabura, Loja, Pichincha, Tungurahua), Peru (Ayacucho, Cajamarca, Cusco, Junin, La Libertad), Venezuela (Merida).

6. *Exhalimolobos pazense* (Rusby) Al-Shehbaz and C.D. Bailey, comb. nov. *Sisymbrium pazense* Rusby, Mem. Torrey Bot. Club 3(3): 5. 1893.—TYPE: Bolivia. Vicinity of La Paz, 10,000 ft, 1890, A. M. Bang 172 (holotype: NY!; isotypes: E!, GH!, MO!, NY!, US!, W!).

Halimolobos adpressus O.E. Schulz, Pflanzenreich IV. 105(Heft 86): 293. 1924.—TYPE: ARGENTINA. Catamarca, lomas arriba de Yacutula, cerca Belen, Dec 1879, F. Schickendantz 69 (lectotype: here designated, B!).

Distribution. Argentina (Catamarca, La Rioja, Mendoza, San Luis, Tucuman), Bolivia (La Paz).

Notes. It is a puzzle why Rollins (1943) did not take the earliest name (*Sisymbrium pazense*) for the species but listed its type collection

under the later published *Halimolobos adpressus* (as *adpressa*). By contrast, Schulz (1924) listed the type collection of *S. pazense* as a probable synonym of *H. weddellii* and as a syntype of *H. adpressus*.

Schulz (1924) cited eight syntypes under *Halimolobos adpressus*, and Rollins (1943) did not designate a lectotype for the species. The most complete specimen at B, which carries Schulz's annotation, is designated herein as the lectotype.

7. *Exhalimolobos weddellii* (E. Fourn.) Al-Shehbaz and C.D. Bailey, comb. nov. *Sisymbrium weddellii* E. Fourn., Recherch. Crucif. 104. 1865; *Hesperis weddellii* (E. Fourn.) Kuntze, Revis. Gen. Pl. 2: 935. 1891; *Halimolobos weddellii* (E. Fourn.) O.E. Schulz in Engler, Pflanzenreich IV. 105(Heft 86): 292. 1924; *Sisymbrium hispidulum* (DC.) Triana and Planch. var. *weddellii* (E. Fourn.) Baehni and J.F. Macbr., Candollea 7: 296. 1937; *H. hispidula* (DC.) O.E. Schulz var. *weddellii* (E. Fourn.) Rollins, Contr. Dudley Herb. 3: 252. 1943.—TYPE: BOLIVIA. Taperazi, *H. I. Weddell* 3596 (lectotype: here designated, P!; isolectotypes: 2P!).

Greggia montana Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 72. 1874; *Halimolobos montanus* (Grieseb.) O.E. Schulz, Pflanzenreich IV. 105(Heft 86): 292. 1924.—TYPE: ARGENTINA. Catamarca, Feb. 1872, P. A. Lorentz 573 (holotype: GOET!).

Halimolobos boelckeii Martinez-Laborde, Hickenia 11: 63. 1992.—TYPE: ARGENTINA. San Juan: Depto Valle Fértil, Sa. de Elizondo, ceros y alrededores, 1700 m, 17 Dec 1987, *M. Múlgura*, C. Antuña and E. Ulibarri 880 (holotype: SI!).

Distribution. Argentina (Buenos Aires, Catamarca, Chaco, Córdoba, Corrientes, Entre Rios, Formosa, Jujuy, La Pampa, La Rioja, Mendoza, Salta, San Juan, San Luis, Santiago de Estero, Tucuman), Bolivia (La Paz, Santa Cruz, Tarija), Peru (Apurimac, Cuzco, Moquegua), Uruguay.

Notes. Fournier (1865) cited four syntypes under *Sisymbrium weddellii*, of which two were from Bolivia (*Weddell* 3596 and *Mandon* 907) and one each from Argentina (*Bonpland s.n.*) and Uruguay (*Courbon s.n.*). Although Schulz (1924), Baehni and Macbride (1937), and Rollins (1943) discussed the species and its limits, none attempted to lectotypify it, though Schulz circumscribed the species (as *Halimolobos weddellii*) to be based on the two Bolivian collections above and assigned the two plants cited by Fournier from Argentina and Uruguay to *H. montanus*. We

designate *Weddell 3596* as the lectotype because it is the only collection annotated by Fournier as *S. weddellii* and because it precisely fits his description of the species. With the exception of *Mandon 907* (F, K, P), which clearly belongs to *Exhalimolobos hispidulus*, all collections we examined from Argentina, Bolivia, and Uruguay belong to one species recognized by Schulz (1924) and Rollins (1943) as *H. montanus*. Rollins did not examine any type material in this complex and reduced *H. weddellii* to a variety of *H. hispidulus*. *Exhalimolobos weddellii* (including *montanus*) is readily distinguished from *E. hispidulus* by the characters in the key above.

Plants of *Halimolobos boelckii* and *Exhalimolobos weddellii* are indistinguishable in every aspect of leaf, indumentum, flower, fruit, and seed. Martinez-Laborde (1992) indicated that the former has apetalous instead of petaliferous flowers, but this aspect is unreliable because the species is highly variable in petal size and some Argentinian collections of *E. weddellii* produce abortive or reduced petals towards the end of growing season.

8. *Exhalimolobos araboides* (Muschler) Al-Shehbaz and C.D. Bailey, comb. nov. *Greggia araboides* Muschler, Bot. Jahrb. Syst. 40: 274. 1908.—TYPE. PERU. Ancash: below Hacienda Cajomba, between Samanco and Garaz, 3000–3500 m, *A. Weberbauer 3157* (lectotype: here designated, B!).

Halimolobos weddellii O.E. Schulz var. *herreriae* O.E. Schulz, Notizbl. Bot. Gart. Berlin-Dahlem 11: 391. 1932; *Sisymbrium hispidulum* (DC.) Triana and Planch. var. *herreriae* (O.E. Schulz) J.F. Macbr., Publ. Field Mus. Nat. Hist., Bot. Ser. 8, 2(3): 977. 1938; *Halimolobos hispidulus* (DC.) O.E. Schulz var. *herreriae* (O.E. Schulz) Rollins, Contr. Dudley Herb. 3: 252. 1943.—TYPE: PERU. Valle de Urubamba, alrededores del pueblo de Zucay, 3000 m, Febr 1929, *F. L. Herrera 2245* (holotype: B, not seen).

Distribution. Peru (Ancash, Cuzco, Huancavelica, Junin, Lima, Puno).

Notes. Plants of *Exhalimolobos araboides* were variously annotated by Schulz as *Halimolobos weddellii* vars. *weddellii* and *herreriae* and by Rollins as *H. hispidula* var. *herreriae* and var. *longistyla*. The species is remarkably distinct from the remaining South American species of the genus by having larger flowers, longer styles, and wider, pendent to horizontal fruits.

9. *Exhalimolobos burkartii* (Romanczuk & Boelcke) Al-Shehbaz and C.D. Bailey, comb. nov.

Basionym: *Ploypsecadium burkartii* Romanczuk & Boelcke, Hickenia 1(56): 304. 1982—TYPE: ARGENTINA. Jujuy. Las Juntas, Sierra Santa Barbara, 7 Oct 1901, *R. E. Fries 286* (holotype: SI!; isotypes: MO!, S!).

Herbs annual, densely pubescent throughout except for fruits. Stems erect, often single from base, branched above, ca. 1 m tall, densely pubescent with 2–4-rayed trichomes 0.1–0.4 mm. Basal leaves not seen; middle and upper cauline leaves short petiolate, not auriculate or amplexicaul, oblong to lanceolate, 2–3.5 × 0.5–0.7 cm, densely pubescent with 2–4-rayed trichomes 0.1–0.4 mm, base cuneate, margin denticulate. Racemes elongated considerably in fruit; fruiting pedicels divaricate, pubescent, 3–8 mm long. Sepals oblong, purplish, sparsely pubescent, 2–2.5 × 0.5–0.7 mm; petals white, narrowly oblanceolate, 2–3 × 0.4–0.6 mm; filaments 1.5–2.5 mm long; anthers ovate, 0.4–0.6 mm long; ovules 140–150 per ovary. Fruits linear, 1.7–2.5 cm × ca. 1 mm; valves glabrescent; style ca. 0.1 mm long. Seeds oblong, subbiseriate, 0.4–0.5 × ca. 0.3 mm.

Notes. *Exhalimolobos burkartii*, which is known only from the type collection, resembles *E. hispidulus* in having glabrescent, narrow fruits ca. 1 mm wide and subbiseriate seeds. From the latter, which does not grow in Argentina, it is readily distinguished by lacking setose trichomes on the stem and by having non-auriculate cauline leaves cuneate at base, smaller seeds 0.4–0.5 mm long, and minute styles 0.1–0.2 mm long. By contrast, *E. hispidulus* has stems with setose trichomes to 1.5 mm long, auriculate to amplexicaul cauline leaves, larger seeds (0.6–)0.7–0.9(–1) mm long, and style 0.5–1.5 mm long.

MANCOA Wedd., Chloris Andina 2: t. 86d. 1859, nom. cons.—TYPE: *Mancoa hispida* Wedd.

Hartwegiella O.E. Schulz, Repert. Sp. Nov. Regni Veg. 33: 187. 1933.—TYPE: *H. nasturtioides* O.E. Schulz.

Annual or biennial herbs. Trichomes forked or dendritic, sometimes mixed with simple ones, rarely absent. Stems few to several from base, decumbent or ascending to erect, usually branched above. Basal leaves petiolate, often rosulate, 1- or 2-pinnatisect, very rarely simple, dentate or ultimate lobes subentire; cauline leaves sessile or short petiolate, auriculate or not, dentate to pinnately lobed. Sepals spreading or ascending, pubescent, base of lateral pair not saccate; petals white, obovate or spatulate, apex obtuse; stamens slightly tetradynamous, ascending or slightly spreading; filaments not dilated at base; anthers ovate or

oblong, obtuse at apex; nectar glands confluent, subtending bases of all stamens; ovules (30–)40–100 per ovary. Fruits dehiscent sicles, oblong to elliptic or ovate, strongly angustiseptate; valves obscurely veined, pubescent or glabrous, not torulose; style distinct or obsolete; stigma entire. Seeds biseriate, wingless; cotyledons incumbent. Basic chromosome number, $x = 8$.

Eight species: Argentina, Bolivia, Chile, Peru, Mexico.

Mancoa resembles *Exhalimolobos*, *Halimolobos* and *Pennellia* in having two distribution centers one each in North and South America. The genus

initially included two Andean species (Weddell 1859, 1864), but Schulz (1933, 1936) added two Mexican species, and Rollins (1941) accepted a total of seven in both continents. Three additional species were discovered from Mexico (Rollins 1976; Colderón de Rzedowski 1977) and a fourth from Argentina (Al-Shehbaz 1990a), to bring the total in the genus to 11 species. However, as shown by Bailey et al. (2002) and in the present study, *M. henricksonii* and *M. pubens* are nested within *Halimolobos*. Comparisons of morphological features suggest that *M. stylosa* also belongs to this lineage.

KEY TO THE SPECIES OF MANCOA

1. Fruit valves pubescent 2
 2. Annuals; cauline leaves auriculate; sepals caducous; Mexico 5. *M. mexicana*
 2. Biennials or perennials; cauline leaves not auriculate; sepals persistent; South America 3
 3. Stems decumbent or prostrate, 2–8 from base; leaf trichomes 2- or 3-rayed; fruit septum complete; styles 0.2–0.8 mm long; seeds 0.6–0.8 × 0.4–0.5 mm 7. *M. hispida*
 3. Stems erect, 1 or rarely 2; leaf trichomes (3 or) 4–8-rayed; fruit septum perforate or reduced to a rim; styles 0.8–1.5 mm long; seeds 1–1.4 × 0.6–0.9 mm 8. *M. venturii*
1. Fruit valves glabrous 4
 4. Stems glabrous; leaves not auriculate; sepals persistent; racemes ebracteate 6. *M. laevis*
 4. Stems pubescent; at least some leaves auriculate; sepals caducous; racemes bracteate at least basally 5
 5. Petals obsolete or to 1.2 mm long; plants prostrate; fruiting raceme 3–8 cm long 3. *M. rollinsiana*
 5. Petals distinct, (1.5–)2–4 mm long; plants erect to ascending or decumbent; fruiting raceme longer 6
 6. Fruits 3–4 mm long; fruiting pedicels 5–10 mm long 1. *M. bracteata*
 6. Fruits (5–)6–8 mm long; fruiting pedicels 1–3(–5) mm long 7
 7. Petals broadly spatulate, 3.5–4 × ca. 1.5 mm; fruiting pedicels pubescent; anthers oblong, 0.6–0.8 mm long; Mexico 2. *M. laxa*
 7. Petals oblanceolate, 1.5–2.5 × 0.4–0.6 mm; fruiting pedicels glabrous; anthers ovate, 0.2–0.3 mm long; Bolivia 3. *M. foliosa*

1. *MANCOA BRACTEATA* (S. Wats.) Rollins, Contr. Dudley Herb. 3: 193. 1941. *Nasturtium bracteatum* S. Wats., Proc. Amer. Acad. Arts 26: 131. 1891.—TYPE: MEXICO. Aguas Calientes, between Mexico City and Zacatecas, 1837, T. Hartweg 39 (holotype: GH!).

Distribution. Mexico (Durango, Zacatecas).

2. *MANCOA LAXA* Rollins, Rhodora 59: 68. 1957.—TYPE: MEXICO. Chihuahua: Rosario, east of La Junta, 14–15 Sept 1934, F. W. Pennell 1876 (holotype: GH!).

Distribution. Mexico (Chihuahua).

3. *MANCOA ROLLINSIANA* Calderón, Phytologia 36: 269. 1977.—TYPE: MEXICO. Hidalgo: Alrededores de la Presa Jaramillo, cerca de El Cerezo, municipio Pachuca, 22 June 1975, 2800, G. C. Rzedowski 33312 (holotype: ENCB; isotype: GH!).

Distribution. Mexico (Hidalgo).

4. *MANCOA FOLIOSA* (Wedd.) O.E. Schulz, Bot. Jahrb. Syst. 66: 98. 1933. *Hutchinsia foliosa* Wedd., Ann. Soc. Nat. Bot. V. 1: 284. 1864.—TYPE: BOLIVIA. [La Paz], Larecaja: vicinity of Sorata, Nov 1857, G. Mandon 919 (holotype: P!; isotypes: GH!, K!, 3P!).

Distribution. Bolivia (Cochabamba, La Paz).

5. *MANCOA MEXICANA* Gilg and Muschl., Bot. Jahrb. Syst. 42: 463. 1909.—TYPE: MEXICO. San Luis Potosí, 1876, J. G. Schaffner 147 (holotype: B!; isotype: GH!).

Capsella mexicana Hemsl., Diag. Pl. Nov. Mex. 19. 1879.—TYPE: MEXICO. San Luis Potosí: C. C. Parry and E. Palmer 19 (holotype: K!; isotypes: GH!, US!).

Distribution. Mexico (Jalisco, San Luis Potosí, and Zacatecas).

6. *MANCOA LAEVIS* Wedd., Ann. Soc. Nat. Bot. V. 1: 284. 1864.—TYPE: Bolivia. Potosí: near Potosí, D'Orbiguy 1491 (holotype: P!).

Distribution. Bolivia (Potosi).

Notes. Except for glabrous instead of densely pubescent stems, cauline leaves, pedicels, sepals, and fruit valves, *Mancoa laevis* is indistinguishable from *M. hispida*. Until recently, *M. laevis* was known only from the type specimen. A recent collection, Wood 14724 (K, MO), includes a mixed collection of the two species. It is possible that the *M. laevis* represents a glabrous form of *M. hispida*, but this needs to be confirmed experimentally.

7. *MANCOA HISPIDA* Wedd., *Chloris Andina* 2: t 86d. 1859.—TYPE: Southern Peru, Moho, 3900 m, 1848, *H. A. Weddell 4500* (lectotype: designated by Macbride (1938), P!).

Mancoa minima Rollins, *Contr. Dudley Herb.* 3: 194. 1941.—TYPE: CHILE. [Región I] Prov. Tarapacá: Depto: Tarapacá, Cord. Co. Columtusca, La Escalera, ca. 4200 m, Mar 1926, *E. Werdermann 1080* (holotype: GH!; isotypes: B!, F!, G!, K!, M!, MO!, US!).

Distribution. Argentina (Catamarca, Jujuy, Salta, Tucumán), Bolivia (La Paz, Oruro, Potosi), Chile (Antofagasta, Tarapacá), Peru (Ancash, Arequipa, Cusco, Lima, Moquegua, Tacna) .

Notes. Rollins (1941) distinguished *Mancoa minima* from *M. hispida* by the smaller size of the plant and flowers and by having a perforate rather than complete fruit septum. However, an examination of numerous collections of the latter reveals that none of the alleged differences hold, and *M. minima* is reduced herein to synonymy of *M. hispida*.

8. *MANCOA VENTURII* Al-Shehbaz, *Harvard Pap. Bot.* 2: 11. 1990.—TYPE: ARGENTINA. Jujuy: Dep. Tumbaya, Volcán, 16 Feb 1927, 2300 m, *S. Venturi 7253* (holotype: US!).

Distribution. Argentina (Jujuy).

PENNELLIA Nieuwl., *Amer. Midl. Naturalist* 5: 224. 1918.—TYPE: *Pennellia micrantha* (A. Gray) Nieuwl.

Perennial herbs. Trichomes simple mixed with stalked, forked or dendritic ones. Stems erect or ascending, often branched above. Basal leaves petiolate, rosulate, entire or dentate to sinuate or runcinate; cauline leaves short petiolate to sessile, not auriculate, entire or dentate to sinuate. Flowers cup shaped; sepals oblong to ovate, erect, caducous, pubescent or rarely glabrous, base of lateral pair slightly to strongly saccate; petals white throughout or lavender to purple at apex, spatulate to oblanceolate, apex obtuse; stamens slightly tetradynamous; filaments dilated at base; anthers ovate to oblong; nectar glands confluent, subtending bases of all stamens; ovules 40–250 per ovary. Fruits dehiscent siliques, linear, terete or latiseptate; valves with a conspicuous or obscure midvein, glabrous or pubescent; style distinct or obsolete; stigma entire. Seeds uniseriate or biseriate, wingless or winged; cotyledons incumbent or rarely oblique or accumbent. Basic chromosome number, $x = 8$.

Ten species: United States, Mexico, Costa Rica, Guatemala, Colombia, Bolivia, Chile, and Argentina.

Rollins (1980) recognized eight species of *Pennellia* in North America, Al-Shehbaz (1990a) added a South American species, and Price et al. (2001a) transferred two species originally placed by Rollins (1993) in *Arabis* L. Fuentes-Soriano (2004) delimited *Pennellia* to consist of only seven species. An eighth species has recently been added from Argentina (Beilstein and Al-Shehbaz 2005), and two more are transferred herein.

KEY TO THE SPECIES OF *PENNELLIA*

- 1. Fruits strongly latiseptate; seeds winged all around; cotyledons accumbent 2
- 2. Fruits 2–2.5 mm wide; seeds 2.4–2.8 mm, broadly winged; stem base with predominantly forked trichomes 5. *P. tricornuta*
- 2. Fruits 0.7–1.2 mm wide; seeds 0.9–1.1 mm, narrowly winged; stem base with dendritic trichomes 4. *P. microsperma*
- 1. Fruits terete or slightly latiseptate; seeds wingless; cotyledons incumbent 3
- 3. Racemes secund; fruiting pedicels arcuate, reflexed; fruit 5–10 cm, flattened; ovules/seeds 150–250 per ovary/fruit 3. *P. longifolia*
- 3. Racemes not secund; fruiting pedicels straight, erect or ascending; fruit (1.5–)2.2–5.8 cm, terete; ovules/seeds 140 or less per ovary/fruit 4
- 4. Basal leaves with malpighiaceus (sessile, medifixed, 2-rayed) trichomes 10. *P. lechleri*
- 4. Basal leaves with simple and stalked branched trichomes 5
- 5. Fruiting pedicels erect or nearly so, often appressed to rachis 6
- 6. Sepals, pedicels, and fruits glabrous; fruiting pedicels 3.5–8.5 mm long 1. *P. micrantha*
- 6. Sepals, pedicels, and fruits pubescent; fruiting pedicels 7.5–11.5 mm long 2. *P. lasiocalycina*
- 5. Fruiting pedicels horizontal, divaricate, to ascending, never appressed to rachis 7

7. Fruiting pedicels 3–6 mm long; fruits 0.6–0.8 mm wide; seeds 0.5–0.6 mm long; Mexico and Colombia 6. *P. patens*
7. Fruiting pedicels (7–)10–25 mm long; fruits 1–1.5 mm wide; seeds 0.7–1.6 mm long; Bolivia, Argentina, and Chile 8
8. Fruit compressed; seeds uniseriate, 24–32 per fruit, 1.2–1.6 mm long; lower stems with dendritic trichomes 0.05–0.1 mm long, considerably smaller than trichomes on basal leaves 9. *P. parvifolia*
8. Fruits terete; seeds subbiseriate, 50–108 per fruit; 0.7–1 mm long; lower stems glabrous or with simple and 2-rayed trichomes 0.2–0.4 mm long, about same size of trichomes on leaves 9
9. Fruits 1.3–1.8 cm long, 50–64-seeded; inflorescence corymbose; basal leaves with simple and 2-rayed trichomes 8. *P. brachycarpa*
9. Fruits (2–)2.5–3.5(–4.5) cm long; 76–108-seeded; inflorescences lax racemes; basal leaves with 2–7-rayed trichomes 7. *P. boliviensis*
1. *PENNELLIA MICRANTHA* (A. Gray) Nieuwl., Amer. Midl. Naturalist 5: 224. 1918. *Streptanthus micranthus* A. Gray, Mem. Amer. Acad. Arts 4: 7. 1849; *Heterothrix micrantha* (A. Gray) Rydb., Bull. Torrey Bot. Club 34: 435. 1907; *Thelypodium micranthum* (A. Gray) S. Wats., Proc. Amer. Acad. Arts 17: 321. 1882.—TYPE: U.S.A. New Mexico: Santa Fe Creek, July 1847, A. Fendler 23 (holotype: GH!; isotypes: GH!, MO!).
- Pennellia robinsonii* Rollins, Contr. Gray Herb. 210. 13. 1980.—TYPE: MEXICO. Chihuahua: 21 miles south of Chihuahua City, 15 Oct 1974, R. C. Rollins and K. W. Roby 74182 (holotype: GH!).
- Distribution.** United States (Arizona, New Mexico, Texas) and Mexico (Chihuahua, Coahuila, Distrito Federal, Estado de México, Durango, Michoacán, Querétaro, San Luis Potosí, Sonora).
2. *PENNELLIA LASIOCALYCINA* (O.E. Schulz) Rollins, Contr. Gray Herb. 210: 17. 1980. *Heterothrix micrantha* (A. Gray) Rydb. var. *lasiocalycina* O.E. Schulz, Pflanzenreich IV. 105(Heft 86): 296. 1924; *Pennellia micrantha* (A. Gray) Nieuwland var. *lasiocalycina* (O. E. Schulz) Rollins, Contr. Gray Herb. 206: 8. 1976.—TYPE: MEXICO. Coahuila: Sierra de Parras, July 1910, 8–9000 ft., C. A. Purpus 4604 (holotype: B!; isotypes: F!, GH!, MO!, UC!, US!).
- Distribution.** Mexico (Coahuila, Nuevo León).
3. *PENNELLIA LONGIFOLIA* (Benth.) Rollins, Rhodora 62: 16. 1960. *Streptanthus longifolius* Benth., Pl. Hartweg. 10. 1839; *Heterothrix longifolia* (Benth.) Rydb., Bull. Torrey Bot. Club 34: 435. 1907; *Lamprophragma longifolium* (Benth.) O.E. Schulz, Pflanzenreich IV. 105(Heft 86): 299. 1924; *Thelypodium longifolium* (Benth.) S. Wats., U.S. Geol. Explor. Fortieth Parallel (Bot.) 5: 25. 1871.—TYPE: MEXICO. Aguas Calientes, 1837, T. Hartweg 52 (holotype: K!; isotype: GH!).
- Pennellia hunnewellii* Rollins, Contr. Gray Herb. 210: 10. 1980.—TYPE: GUATEMALA. Sacatepéquez: Cumbre de Soledad, Volcán Acate-nango, 16 Feb 1937, 8,500 ft., F. W. Hunnewell 1482 (holotype: GH!).
- Pennellia mcvaughii* Rollins, Taxon 28: 24. 1979.—TYPE: MEXICO. Durango: near Mexican hwy 40, 26 miles E of El Salto, Sierra Madre Occidental, 21 Sep 1974, R. C. Rollins and K. W. Roby 7423 (holotype: GH!).
- Distribution.** United States (Arizona, New Mexico, Texas), Mexico (Chihuahua, Coahuila, Distrito Federal, Durango; Guanajuato, Hidalgo, Jalisco, Michoacán, Morelos, Nuevo León, Oaxaca, Puebla, Wueretaro, San Luis Potosí, Sinaloa, Sonora, Tamaulipas, Veracruz, Zacatecas), Costa Rica, Guatemala.
4. *PENNELLIA MICROSPERMA* (Rollins) R.A. Price, C.D. Bailey and Al-Shehbaz, Novon 11: 339. 2001. *Arabis microsperma* Rollins, Cruciferae Continental N. Amer. 176. 1993.—TYPE: MEXICO. Chihuahua, Nagogame, 28°30'N, 108°30'W, 1800 m, 10 Sep 1987, J. E. Laferriere 1069 (holotype: GH!).
- Distribution.** Mexico (Chihuahua).
5. *PENNELLIA TRICORNUTA* (Rollins) R.A. Price, C.D. Bailey and Al-Shehbaz, Novon 11: 339. 2001. *Arabis tricornuta* Rollins, in Kearney and Peebles, J. Wash. Acad. Sci. 29: 478. 1939.—TYPE: U.S.A. Arizona: Pima County, East-view, Rincon Mts., 13 Oct 1909, J. C. Blumer 3478 (holotype: GH!).
- Distribution.** United States (Arizona).
6. *PENNELLIA PATENS* (O.E. Schulz) Rollins, Rhodora 62: 15. 1960. *Heterothrix patens* O. E. Schulz, Pflanzenreich IV. 105(Heft 86): 296. 1924.—TYPE: MEXICO. Chiapas: District Comitán, 18 Aug 1898, C. and E. Seler 3038 (lectotype: GH!).

designated by Rollins (1980), B!; isoelectotype: GH!).

Heterothrix juncea O.E. Schulz, Pflanzenreich IV. 105(Heft 86): 297. 1924. *Pennellia juncea* (O.E. Schulz) Rollins, Contr. Gray Herb. 210. 19. 1980.—TYPE: MEXICO. Puebla: San Luis, 1908, C. A. Purpus 3486a (holotype: B!).

Distribution. Mexico (Aguascalientes, Chiapas, Distrito Federal, Durango, Michoacán, Oaxaca, Puebla, San Luis Potosí, Tlaxcala), Colombia.

7. *PENNELIA BOLIVIENSIS* (Muschl.) Al-Shehbaz, Harvard Pap. Bot. 2: 13. 1990. *Streptanthus boliviensis* Muschl., Bot. Jahrb. Syst. 40: 268. 1908.—TYPE: BOLIVIA. [Tarija]: Calderillo, 3200 m, 22 Mar 1904, K. Fiebrig 2788 (holotype: B!).

Distribution. Argentina (Córdoba, Jujuy, Salta, Tucumán), Bolivia (Chuquisaca, La Paz, Tarija).

8. *PENNELIA BRACHYCARPA* Beilstein and Al-Shehbaz, Novon 15: 267. 2005.—TYPE: Argentina. Jujuy: Abra Pampa, S of Abra Pampa City off route 9, among rocks on isolated hilltop, 3650 m, 22°49.352'S, 65°41.324'W, 10 Feb 2003, M. Beilstein, N. Whiteman & D. Eakman 03-148 (holotype: MO).

Distribution. Argentina.

9. *Pennellia parvifolia* (Phil.) Al-Shehbaz and C.D. Bailey, comb. nov. *Sisymbrium parvifolium* Phil., Linnaea 28: 667. 1856; *Stenodraba parvifolia* (Phil.) O.E. Schulz, Pflanzenreich IV. 105(Heft 86): 187. 1924; *Weberbaueria parvifolia* (Phil.) Al-Shehbaz, J. Arnold Arbor. 71: 248. 1990.—TYPE: Chile. Cordillera de Linares, Germain s.n. (holotype: SGO!).

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

Distribution. Argentina (Neuquén), Chile (Región Metropolitana, VII-Maule, VIII-Biobío).

10. *Pennellia lechleri* (E. Fourn.) Al-Shehbaz and C.D. Bailey, comb. nov. *Sisymbrium lechleri* E. Fourn., Rech. Crucif. 129. 1865; *Hesperis lechleri*

(E. Fourn.) Kuntze, Rev. Gen. Pl. 2: 934. 1891; *Stenodraba lechleri* (E. Fourn.) Ravenna, Nord. J. Bot. 1: 141. 1981.—TYPE: Chile. Terra Pehuénchorum, Dec. 1854, W. Lechler 3080 (holotype: P!, fragments BAA!; isotypes: 2G!, K!, 2P!).

Sisymbrium petraeum Phil., Linnaea 28: 668. 1856, non (L.) Delarbre, Fl. Auv. ed. 2: 349. 1800; *Hesperis petraea* Kuntze, Rev. Gen. Pl. 2: 935. 1891; *Heterothrix petraea* O.E. Schulz, Pflanzenr. IV. 105(Heft 86): 298. 1924; *Pennellia petraea* (O.E. Schulz) O.E. Schulz in Engler and Prantl, Nat. Pflanzenfam. 17B: 644. 1936; *Stenodraba glareosa* Ravenna, Nord. J. Bot. 1: 141. 1981.—TYPE: Chile. [Prov. Ñuble]: “in Andibus prope oppidum Chillán,” (holotype: SGO 49254).

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

Sisymbrium caespitosum Philippi, Anal. Univ. Chile 81: 184. 1892.—TYPE: Chile. En la Araucanía, entre Ercilla y Victoria, Nov. 1887, Philippi s.n. (holotype: SGO 71496).

Distribution. Argentina (Neuquén, Río Negro), Chile (Región Metropolitana, VIII-Biobío, IX-Araucanía, X-Los Lagos).

Notes. Both *Pennellia parvifolia* and *P. lechleri* were treated previously as species of *Weberbaueria* (Al-Shehbaz 1990b; Al-Shehbaz 2004). However, a recent examination of their types and the discovery of the related *P. brachycarpa* (Al-Shehbaz 1990b; Al-Shehbaz 2004; Beilstein and Al-Shehbaz 2005) support their placement in *Pennellia*. All species of *Pennellia* have cup-shaped flowers in which the petals hardly exceed the sepals, whereas species of *Weberbaueria* have open or elongated flowers in which the petals are distinctly longer than the sepals.

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

Cibotarium O.E. Schulz, Bot. Jahrb. Syst. 66: 91. 1933.—TYPE: *Cibotarium stellatum* (S. Wats.) O.E. Schulz.

Biennial or perennial herbs, sometimes subshrubs, with a woody caudex. Trichomes dendritic. Stems erect to ascending or decumbent. Leaves cauline, petiolate to sessile, entire or dentate. Sepals oblong, non-saccate; petals occasionally absent, generally white, narrowly oblanceolate to

spatulate; stamens slightly tetradynamous, exerted, filaments dilated at base; anthers ovate to oblong; nectar glands confluent at base; ovules 4–16 (–22) per ovary. Fruit dehiscent, moderately to densely pubescent, spherical to oblong, uncompressed to strongly angustiseptate; valves keeled or rounded, pubescent on both surfaces or only on exterior; styles 0.5–2 mm long; stigma entire or obscurely 2-lobed. Seeds uniseriate to biseriate, wingless; cotyledons incumbent.

Four species: Mexico (primarily in north-

central states from northern Coahuila to Puebla).

Sphaerocardamum was originally described as a monotypic genus by Schauer in 1847. However, Rollins (1984) had transferred to it seven additional species previously placed in *Cibotarium*, a monotypic genus originally described by Schulz (1933) and later expanded by Rollins (1941) to include six additional species. As currently delimited (Bailey 2001), *Sphaerocardamum* includes only four, exclusively Mexican, species.

KEY TO THE SPECIES OF *SPHAEROCARDAMUM*

1. Fruits uncompressed-globose; septum nearly circular in outline, 1–1.5 mm in diameter; seeds 4(–6) per fruit; styles 0.5–0.7 mm long 1. *S. nesliiforme*
1. Fruits not globose, elongate and terete to angustiseptate, septum elliptic to narrowly oblong, 2–6 × 0.6–2.2 mm; seeds 7–22 per fruit; styles 0.5–2.5 mm long 2
2. Petals 0.1–0.7 mm wide, at most subequal to the sepals; fruit obovate, about as long as wide; valves keeled dorsally; apical fruit notch present or absent; styles 0.2–1.1 mm long; seeds 0.4–1 mm long 2. *S. stellatum*
2. Petals 0.6–1.6 mm wide, clearly exceeding sepals; fruit oblong, at least twice as long as wide; valves keeled or rounded dorsally; apical fruit notch mostly absent; styles 0.5–2 mm; seeds 0.8–1.4 mm long 3
3. Fruit weakly angustiseptate; septum elliptic, length to width ratio 1.75–4.4; valves mostly rounded dorsally, pubescent on the interior 3. *S. divaricarpum*
3. Fruit strongly angustiseptate; septum narrowly oblong, length to width ratio 4.7–7.25; valves always keeled dorsally, glabrous on the interior 4. *S. compressum*

1. *SPHAEROCARDAMUM NESLIIFORME* S. Schauer, *Linnaea* 20: 720. 1847.—TYPE: MEXICO. Locality unknown, *Aschenborn 209* (holotype: B!).

Cibotarium microcarpum Rollins, *Rhodora* 59: 70. 1957.—TYPE: MEXICO. Hidalgo: District of Zimapán, dry rocky slopes of Barranca de Tolimán somewhat above the mines, 7.6 miles 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!).

Distribution. Mexico (Guerrero, Hidalgo).

2. *SPHAEROCARDAMUM STELLATUM* (S. Wats.) Rollins, *Contrib. Gray Herb.* 213: 14. 1984. *Capsella stellata* S. Wats., *Proc. Am. Acad.* 25: 142. 1890; *Cibotarium stellatum* (S. Wats.) O.E. Schulz, *Bot. Jahrb. Syst.* 66: 91. 1933.—TYPE: MEXICO. Coahuila: Limestone ledges on Carneros Pass, 9 Sep 1889, *Pringle 2844* (holotype: GH!).

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

Lepidium macrum Standl., *Publ. Field Mus. Nat. Hist., Bot. Ser.* 17: 248. 1937; *Cibotarium macrum* (Standl.) Rollins, *Contrib. Dudley Herb.* 3: 189. 1941; *Sphaerocardamum macrum* (Standl.) Roll-

ins, *Contrib. Gray Herb.* 213: 15. 1984.—TYPE: MEXICO. Neuvo 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. Neuvo León: Cerro Potosí, E slope, dry rocky open places between corn fields, 6050 ft, 9 July 1963, *MacGregor, Harms, Robinson, Rosaria and Segal 413* (holotype: GH!).

Distribution. Mexico (Aguascalientes, Coahuila, Neuvo León, San Luis Potosí, Zacatecas).

3. *SPHAEROCARDAMUM DIVARICATUM* (Rollins) Rollins, *Contrib. Gray Herb.* 213: 16. 1984. *Cibotarium divaricatum* Rollins, *Contrib. Dudley Herb.* 3: 189. 1941.—TYPE: MEXICO. Sierra de Parras, *Purpus 1027* (holotype: GH!; isotypes: NY!, UC!).

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

Distribution. Mexico (Coahuila, Hidalgo,

Neuvo León, Puebla, San Luis Potosí, Tamaulipas, Zacatecas).

4. *SPHAEROCARDAMUM COMPRESSUM* (Rollins) Rollins, *Contrib. Gray Herb.* 213: 15. 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!; iso-types: UC!, US!).

Distribution. Mexico (Coahuila).

ACKNOWLEDGMENTS. We are most grateful to Adriana Bertoli, David Boufford, Robert Cook, Norma Deginani, Jochen Heinrichs, Pete Lowry, Clodomiro Marticorena, Melica Muñoz, Pete Philipson, Roberto Tortosa, Robert Vogt, and Fernando Zuloaga for their help during the various stages of this study, especially in locating type collections. We thank Nicholas J. Turland and Kanchi Gandhi for nomenclatural advice, as well as the directors and curators of the herbaria cited in this paper. SEM work was conducted at the NMSU Electron Microscopy Facility and the authors are grateful to Soumitra Ghoshroy for his valuable assistance.

LITERATURE CITED

- AL-SHEHBAZ, I. A. 1973. The biosystematics of the genus *Thelypodium* (Cruciferae). *Contributions from the Gray Herbarium of Harvard University* 204: 3–148.
- . 1984. The tribes of Cruciferae (Brassicaceae) in the Southeastern United States. *Journal of the Arnold Arboretum* 65: 343–373.
- . 1990a. New or noteworthy species in the South American genera *Mancoa*, *Pennellia*, and *Sisymbrium*. *Harvard Papers in Botany* 2: 11–16.
- . 1990b. A revision of *Weberbaueria* (Brassicaceae). *Journal of the Arnold Arboretum* 7: 221–250.
- . 2004. A synopsis of the South American *Weberbaueria* (Brassicaceae). *Novon* 14: 258–268.
- and S. L. O'KANE, JR. 2003. *Transberingia*, a new generic name replacing the illegitimate *Beringia* (Brassicaceae). *Novon* 13: 396.
- , M. A. BEILSTEIN, and E. A. KELLOGG. 2006. Systematics and Phylogeny of the Brassicaceae (Cruciferae): an overview. *Plant Systematics and Evolution* 259: 89–120.
- APPEL, O. and I. AL-SHEHBAZ. 2003. Cruciferae. Pp. 75–174 in *Families and Genera of Vascular Plants*, ed. K. Kubitzki. Berlin: Springer-Verlag.
- BAEHNI, C. and J. F. MACBRIDE. 1937. Remarques sur les Cruciferae-Sisymbrieae. *Candollea* 7: 291–296.
- BAILEY, C. D. 2001. *Systematics of Sphaerocardamum* (Brassicaceae) and related genera. Ph.D. Dissertation. Ithica, NY: Cornell University.
- , R. A. PRICE, and J. J. DOYLE. 2002. Systematics of the Halimolobine Brassicaceae: evidence from three loci and morphology. *Systematic Botany* 27: 318–332.
- , M. KOCH, M. S. MAYER, K. MUMMENHOFF, S. L. O'KANE, JR., S. I. WARWICK, M. D. WINDHAM, and I. A. AL-SHEHBAZ. 2006. Toward a global phylogeny of the Brassicaceae. *Molecular Biology and Evolution* 23: 2142–2160.
- BEILSTEIN, M. A. and I. A. AL-SHEHBAZ. 2005. *Pennellia brachycarpa* (Brassicaceae), a new species from Jujuy, Argentina. *Novon* 15: 267–269.
- , ———, and E. A. KELLOGG. 2006. Brassicaceae phylogeny and trichome evolution. *American Journal of Botany* 93: 607–619.
- COLDERÓN DE RZEDOWSKI, G. 1977. *Mancoa rollinsiana*, una especie nueva de Cruciferae encontrada en el valle de Mexico. *Phytologia* 36: 269–273.
- DAVIS, J., M. P. SIMMONS, D. W. STEVENSON, and J. F. WENDEL. 1998. Data decisiveness, data quality and incongruence in phylogenetic analysis: an example from the monocotyledons using mitochondrial *atpA* sequences. *Systematic Botany* 47: 282–310.
- FOURNIER, E. 1865. Recherches anatomiques et taxonomiques sur la famille des Crucifères et sur le genre *Sisymbrium* en particulier. Doctorate, Faculty of Sciences, Paris.
- FUENTES-SORIANO, S. 2004. A taxonomic revision of *Pennellia* (Brassicaceae). *Harvard Papers in Botany* 8: 173–202.
- KOCH, M. 2003. Molecular phylogenetics, evolution and population biology in Brassicaceae. Pp. 1–35 in *Plant genome: biodiversity and evolution. Vol 1. Phanerogams*, eds. A. K. Sharma and A. Sharma. Enfield, New Hampshire: Science Publishers, Inc.
- , B. HAUBOLD, and T. MITCHELL-OLDS. 2000. Comparative evolutionary analysis of chalcone synthase and alcohol dehydrogenase loci in *Arabidopsis*, *Arabis*, and related genera (Brassicaceae). *Molecular Biology and Evolution* 17: 1483–1498.
- , ———, and ———. 2001a. Molecular systematics of the Brassicaceae: Evidence from coding plastidic *matK* and nuclear *Chs* sequences. *American Journal of Botany* 88: 534–544.
- , I. A. AL-SHEHBAZ, and K. MUMMENHOFF. 2003. Molecular systematics, evolution, and population biology in the mustard family (Brassicaceae). *Annals of the Missouri Botanical Garden* 90: 151–171.
- KOCH, M. A., B. WEISSHAAR, J. KROYMANN, B. HAUBOLD, and T. MITCHELL-OLDS. 2001b. Comparative genomics and regulatory evolution: Conservation and function of the *chs* and *Apetala3* promoters. *Molecular Biology and Evolution* 18: 1882–1891.
- MACBRIDE, J. F. 1938. Cruciferae. Pp. 937–983 in *Flora of Peru*, ed. J. F. Macbride, Publications of the Field Museum of Natural History, Bot. Ser. 2(3). Chicago: Field Museum of Natural History.
- MARTINEZ-LABORDE, J. B. 1992. Una nueva especie de *Halimolobos* (Cruciferae) de la Provincia de San Juan (Argentina). *Hickenia* 2: 63–65.
- MITCHELL-OLDS, T., I. A. AL-SHEHBAZ, M. A. KOCH, and T. F. SHARBEL. 2005. Crucifer evolution in the post-genomic era. Pp. 119–138 *Plant Diversity and Evolution: Genotypic and Phenotypic Variation in Higher Plants*, ed. R. J. Henry. Cambridge, Massachusetts: CABI Press.
- PRICE, R. A., C. D. BAILEY, and I. A. AL-SHEHBAZ. 2001a. Transfer of the cupulate-flowered *Arabis microsperma* and *A. tricornuta* (Brassicaceae) to *Pennellia*. *Novon* 11: 337–340.
- , I. A. AL-SHEHBAZ, and S. L. O'KANE, JR. 2001b. *Beringia* (Brassicaceae), a new genus of arabidopsoid affinities from Russia and North America. *Novon* 11: 332–336.
- ROLLINS, R. C. 1941. Some generic relatives of *Capsella*. *Contributions from the Dudley Herbarium* 3: 241–265.
- . 1943. Generic revisions in the Cruciferae: *Halimolobos*. *Contributions from the Dudley Herbarium* 3: 185–198.
- . 1959. The genus *Synthlipsis* (Cruciferae). *Rhodora* 61: 253–264.
- . 1976. Studies on Mexican Cruciferae. *Contributions from the Gray Herbarium of Harvard University* 206: 3–18.
- . 1980. The genus *Pennellia* (Cruciferae) in North America. *Contributions from the Gray Herbarium of Harvard University* 210: 5–21.

- . 1984. *Sphaerocardamum* (Cruciferae). *Contributions from the Gray Herbarium* 213: 11–17.
- . 1993. *The Cruciferae of Continental North America*. Stanford University Press, Palo Alto.
- and U. C. BANERJEE. 1979. Pollens of the Cruciferae. *The Bussey Institution of Harvard University* 1979: 33–64.
- SCHULZ, O. E. 1924. Cruciferae-Sisymbrieae. Pp. 1–388 in *Pflanzenreich IV*, ed. A. Engler. Leipzig: Verlag von Wilhelm Engelmann.
- . 1933. Kurze Notizen über neue Gattungen, Sektionen und Arten der Cruciferen. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 66: 91–102.
- . 1936. Cruciferae. Pp. 227–658 in *Die natürlichen Pflanzenfamilien*, eds. A. Engler and H. Harms. Leipzig: Verlag Von Wilhelm Engelmann.
- TAUSCH, I. F. 1836. Botanische Beobachtungen. *Flora* 19: 385–416.
- WARWICK, S. I., I. A. AL-SHEHBAB, R. A. PRICE, and C. SAUDER. 2002. Phylogeny of *Sisymbrium* (Brassicaceae) based on ITS sequences of nuclear ribosomal DNA. *Canadian Journal of Botany* 80: 1002–1017.
- WEDDELL, H. I. 1859. *Chloris Andina*. Vol 2. Paris: Bertrand.
- . 1864. Plantes inédites de Andes. *Annales des Sciences Naturelles Botaniques, Sér. 5* 1: 283–296.
- APPENDIX 1. Material Sampled for DNA and SEM work. With the exception of the newly generated sequences (see Materials and Methods), all GenBank accession numbers were presented in Bailey et al (2002). All samples used in the current study are listed list below by “Genus species (Collection number; Herbarium Acronym)”.
- Arabidopsis thaliana* (L.) Heynh. (C.D. Bailey 69; BH); *Boechera drummondii* (A. Gray) Á. Löve & D. Löve (Price C51; GA); *Capsella bursa-pastoris* (L.) Medikus (C.D. Bailey 1; BH); *Cusickiella douglasii* (A. Gray) Rollins (Price 1190; GA); *Halimolobos adpressa* O.E. Schulz (Jorgensen 1038; GH); *Halimolobos berlandieri* (Fourn.) O.E. Schulz (Bailey & Ochoterena 139; BH); *Halimolobos diffusa* (A. Gray) O.E. Schulz (Rusby 2; BH); *Halimolobos hispidiula* (D.C.) O.E. Schulz (Correll & Smith P737; TEX); *Halimolobos jaegeri* (Munz) Rollins (Tiehm & Moorefield 8542; BH); *Halimolobos lasioloba* (Link) O.E. Schulz (Rollins & Tryon 58251; TEX); *Halimolobos minutiflora* Rollins (Bailey & Ochoterena 145B; BH); *Halimolobos montana* O.E. Schulz (Burkart 7189; GH); *Halimolobos palmeri* O. E. Schulz (Bailey & Ochoterena 159; BH); *Halimolobos parryi* (Hemsley) Rollins (Rivas, Gonzalez, & Garcia 57; TEX); *Lepidium campsestre* (L.) Br. (C.D. Bailey 3; BH); *Mancoa bracteata* (S. Wats.) Rollins (Diaz & Worthington 10819; GH); *Mancoa foliosa* (Wedd.) O.E. Schulz (Jones 82–83; MO); *Mancoa henricksonii* Rollins (Henrickson 13471; MO); *Mancoa pubens* (A. Gray) Rollins (Correll 34172; GH); *Nerisyrenia linearifolia* (S. Wats.) E.L. Greene (C.D. Bailey 56; BH); *Physaria fendleri* (A. Gray) O’Kane & Al-Shehbaz (C.D. Bailey 43; BH); *Pennellia longifolia* (Benth.) Rollins (Bailey & Ochoterena 87; BH); *Pennellia micrantha* (A. Gray) Nieuwl. (Price 1391; GA); *Pennellia trichornuta* R.A. Price, C.D. Bailey, & Al-Shehbaz (Price 1396; GA); *Sphaerocardamum compressum* (Rollins) Rollins (Bailey & Ochoterena 115; BH); *Sphaerocardamum divaricatum* (Rollins) Rollins (Bailey & Ochoterena 102; BH); *Sphaerocardamum nesliiforme* Schauer (Bailey & Ochoterena 152; BH); *Sphaerocardamum stellatum* (S. Wats.) Rollins (Bailey & Ochoterena 125; BH) *Synthlipsis elata* Rollins (Correll & Johnston 20149, GH); *Synthlipsis greggii* A. Gray (McVaugh 7832, GH); *Transbergingia bursifolia* (D.C.) Al-Shehbaz & O’Kane (Price 1385; GA).