

THE GENERA OF SISYMBRIEAE
(CRUCIFERAE; BRASSICACEAE) IN THE
SOUTHEASTERN UNITED STATES^{1,2}

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Tribe *Sisymbrieae* A. P. de Candolle, Syst. Nat. 2: 150, 438. 1821.

Annual, biennial [or perennial] herbs [rarely shrubs]; glabrous or with unbranched, dendritic [furcate, malpighiaceus, or stellate] trichomes, these rarely mixed with unicellular, glandular, subclavate ones. Inflorescences ebracteate [or bracteate], corymbose racemes or panicles, usually elongated in fruit; flowers few to many [sometimes solitary on scapes arising from basal rosettes]. Sepals erect [to widely spreading], usually not conspicuously saccate at base, caducous [or persistent]. Stamens 6, usually tetradynamous; filaments free, not appendaged. Fruits linear, subclavate [oblong or rarely ovate], dehiscent [rarely indehiscent], terete [or conspicuously flattened parallel to the septum]; septum complete [rarely incomplete]; stigmas entire or 2-lobed. Seeds numerous [rarely few], uniseriately or biseriately arranged in each locule, wingless [or rarely winged], mucilaginous or not when wet; cotyledons incumbent. TYPE GENUS: *Sisymbrium* L.

The *Sisymbrieae* comprise a heterogeneous assemblage of some 70 genera (25 monotypic; about 30 with two to four species each) and approximately 400

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The figure was drawn by Karen Stoutsenberger under earlier grants. Carroll Wood prepared the material and supervised the illustration. The fruits and seeds are from specimens in the herbaria of the Arnold Arboretum and the Gray Herbarium.

²This is the eighth and final account of the Cruciferae. For treatment of the family and its tribes, see Al-Shehbaz, The Tribes of Cruciferae (Brassicaceae) in the Southeastern United States (Jour. Arnold Arb. 65: 343-373. 1984).

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species. It is represented in the Southeastern United States by four genera and seven species, one of which is indigenous. Although the Sisymbrieae are distributed on all continents except Antarctica, the tribe is most highly diversified in southern and western South America, where 24 genera (20 endemic) and ca. 130 species are found. That area is also the center of highest endemism for *Sisymbrium* L. (90 species) and *Descurainia* Webb & Berth. (40 species), the largest genera of the tribe. Nearly half of the species in these genera are South American. Another important center for the tribe comprises the Irano-Turanian (parts of central and southwestern Asia) and Himalayan regions. It has 22 genera (15 endemic) and about 100 species. The tribe is represented in North America by seven genera (none endemic) and approximately 50 species, and in Australia and New Zealand by 11 genera (all endemic) and 26 species.

As delimited by Schulz (1924, 1936), the boundaries of the tribe are highly artificial, and many genera should be associated with those that he placed in other tribes. Schulz overemphasized the importance of cotyledonary position and sepal orientation in defining what he recognized as four tribes. He distinguished the Sisymbrieae from the Arabideae DC. mainly on the basis of incumbent versus accumbent cotyledons, and from the Anchonieae DC. (as Hesperideae Prantl and Matthioleae O. E. Schulz) on open instead of closed calyces. It is evident, however, that these characters can be unreliable, and that there are many genera both in the tribe and elsewhere in the Cruciferae with more than one type of cotyledonary position or sepal orientation. Avetisian is probably justified in uniting the four tribes above in one (as Sisymbrieae), but her inclusion of the Alysseae DC. and the Lepidieae DC. in this tribe is unwarranted. In my opinion, neither Schulz's nor Avetisian's delimitation of the Sisymbrieae is satisfactory, and the complex needs thorough study on a world-wide basis.

Two of the six subtribes that Schulz (1924, 1936) recognized in the Sisymbrieae have somewhat natural boundaries. Subtribes Alliariinae (Prantl) O. E. Schulz (basal leaves undivided, long petiolate, cordate or reniform to orbicular; stigmas entire; petals white; seeds large, oblong) and Descurainiinae O. E. Schulz (leaves highly dissected, trichomes dendritic, seeds mucilaginous) include five and six genera, respectively. The remaining subtribes are artificially delimited because they are based primarily on characters (e.g., presence vs. absence of mucilage on seeds, fruit length in relation to width, separation vs. connation of the median and lateral nectaries) that are not useful at or above the generic level. It is beyond the scope of this flora either to revise the subtribal classification or to delimit the boundaries of the Sisymbrieae.

Chromosome numbers are known for slightly more than 100 species (ca. 25 percent of the tribe) and 25 genera. In about 68 percent of the species surveyed, the numbers are based on seven, while in only 19 percent they are based on eight. Nearly 70 percent of the species are diploid (author's compilation). Although most genera are uniformly based on one chromosome number, a few others (e.g., *Arabidopsis* (DC.) Heynh., *Sisymbrium*) have diploid and polyploid taxa with several base numbers. Polyploidy apparently characterizes most, if not all, species of the South American genus *Weberbaueria* Gilg & Muschler (four species) and the circumboreal *Braya* Sternb. & Hoppe (16 species). All

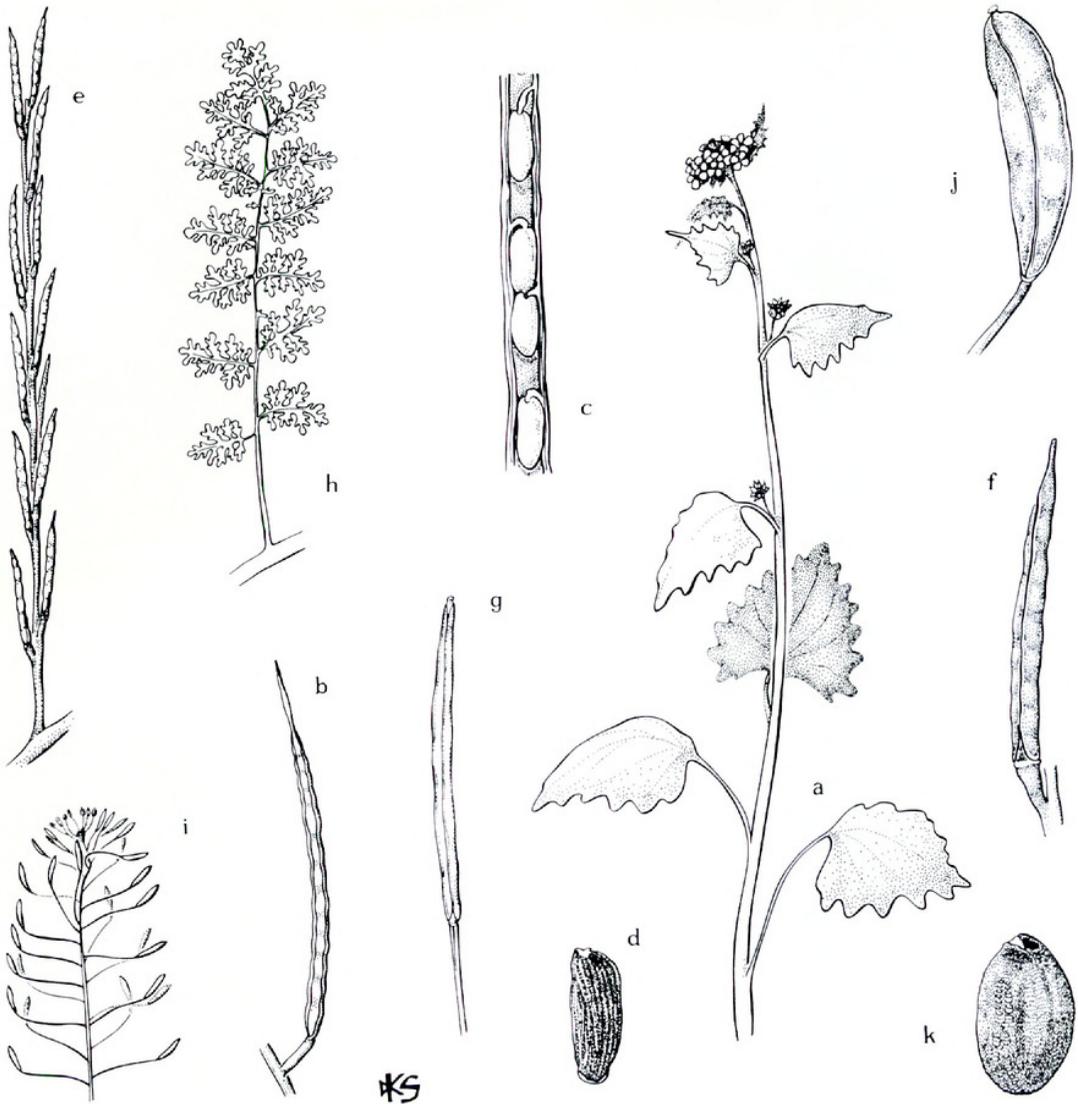


FIGURE 1. Selected representatives of tribe Sisymbrieae. a-d, *Alliaria petiolata*: a, portion of plant with flowers, $\times \frac{1}{2}$; b, fruit, $\times 1$; c, portion of fruit after removal of 1 valve, $\times 3$ —note uniseriate arrangement of seeds; d, seed, $\times 6$. e, f, *Sisymbrium officinale*: e, portion of infructescence, $\times 1$; f, fruit $\times 3$. g, *Arabidopsis thaliana*, fruit, $\times 3$. h-k, *Descurainia pinnata*: h, tripinnatisect leaf, $\times \frac{1}{2}$; i, portion of infructescence, $\times 1$; j, fruit, $\times 6$; k, seed, $\times 25$.

13 species of the latter that have been surveyed cytologically (Harris) are polyploids based on seven ($2n = 28, 42, 56, 70$). Numbers in *Smelowskia* C. A. Meyer, which includes 11 alpine species (five in Alaska and the Mountain and Pacific states (Drury & Rollins) and six in central and eastern Asia (Botschantsev)), are apparently based on six. In *S. calycina* (Willd.) C. A. Meyer, diploids ($2n = 12$), tetraploids ($2n = 24$), and aneuploid derivatives of tetraploids ($2n = 22$) characterize the various infraspecific taxa.

The chemical data on the Sisymbrieae are so scant that no meaningful conclusions can be reached. However, the presence of cardenolides (otherwise very rare in the Cruciferae) in both *Erysimum* L. and *Sisymbrium* rather strongly

supports a closer association between the two genera. Schulz (1936) placed the former in tribe Hesperideae, but as was indicated earlier (Al-Shehbaz, 1984, 1988), the status of these tribes needs careful evaluation.

Seed-dispersal mechanisms in the majority of Sisymbrieae are similar to those of other tribes. In *Geococcus* J. Drumm. ex Harvey (monotypic; Australia) the fruiting pedicels almost always become strongly recurved and bury the fruit in the vicinity of the mother plant (Shaw). Geocarpy has evolved independently in the Cruciferae, as is evidenced by its occurrence also in the South American *Cardamine chenopodiifolia* Pers. and in *Morisia monanthos* (Viv.) Ascherson, of Sardinia and Corsica. The strong curvature of fruits into loops or hooks in some species of *Neotorularia* Hedge & Léonard (11 species; southwestern and central Asia) may be an adaptation to dispersal by clinging to the fur of animals.

Except for the many weedy species, particularly of the genera *Alliaria* Scopoli, *Descurainia*, and *Sisymbrium*, the tribe has no economic importance. *Arabidopsis thaliana* (L.) Heynh. is the most widely used higher plant in biochemistry, genetics, molecular biology, and physiology.

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KEY TO THE GENERA OF SISYMBRIEAE IN THE
SOUTHEASTERN UNITED STATES⁴

- A. Leaves 2- or 3-pinnatisect, plants with dendritic trichomes. . . . 43. *Descurainia*.
 A. Leaves entire, toothed, or pinnately lobed, never 2- or 3-pinnatisect; plants glabrous
 or with unbranched or furcate trichomes.
 B. Lower leaves reniform or cordate, usually dentate; seeds longitudinally striate.
 40. *Alliaria*.
 B. Lower leaves oblong to lanceolate or oblanceolate, entire or pinnate; seeds smooth
 or reticulate.
 C. Plants short, up to 20 cm long; leaves entire; at least some trichomes furcate.
 42. *Arabidopsis*.
 C. Plants taller; leaves pinnate; all trichomes unbranched. . . 41. *Sisymbrium*.

40. *Alliaria* Heister ex Fabricius, Enum. Meth. Pl. 161. 1759.⁵

Annual or biennial herbs with unbranched trichomes. Stems simple or branched at base, up to 1.3 m high. Lower leaves long petiolate, not forming rosettes, undivided, reniform, cordate, or rarely deltoid, sinuate-dentate or sometimes crenate to repand; upper leaves short petiolate, cordate, deltoid [oblong or obovate]. Inflorescences corymbose racemes, ebracteate [or bracteate throughout], elongated in fruit; fruiting pedicels divaricately ascending [or subappressed to rachis], nearly as thick as the fruit. Sepals erect-ascending, oblong, equal and not saccate at base, caducous. Petals white, obovate, short clawed. Lateral nectar glands ringlike; median ones connate with the lateral, subtending the bases of paired stamens. Stamens 6, tetradynamous; filaments free, erect, unappendaged; anthers obtuse. Fruits linear, acute [or acuminate], torulose or smooth, subterete or somewhat 4-angled, dehiscent; valves keeled, strongly 3-nerved, glabrous [or scabrous]; septum hyaline, complete; styles slender, 1–3[–6] mm long; stigmas entire or rarely slightly 2-lobed. Seeds numerous [or few], oblong, dark brown to black, longitudinally striate, wingless, uniseriately arranged in each locule, nonmucilaginous when wet; cotyledons accumbent. Base chromosome number 7. (Including *Pallavicinia* Cocconi (1893), non Gray (1821), non De Not. (1847); *Raphanobus* Rupr.) TYPE SPECIES: *Erysimum Alliaria* L. = *A. petiolata* (Bieb.) Cavara & Grande. (Name from *Allium* L., onion or garlic, referring to the garliclike smell of the plant when crushed.)—GARLIC MUSTARD.

A genus of two species, one of which, *Alliaria brachycarpa* Bieb., is a narrow endemic of the Caucasus and the other is a Eurasian weed now naturalized in many parts of the world. *Alliaria petiolata* (Bieb.) Cavara & Grande (*Arabis*

⁴The genera are numbered as in the treatment of the tribes of Cruciferae in the southeastern United States (Jour. Arnold Arb. 65: 343–373. 1984). Genera 1 and 2 (Thelypodieae) appeared in *ibid.* 66: 95–111. 1985; genera 3–13 (Brassicaceae) in *ibid.* 279–351; genera 14–19 (Lepidieae) in *ibid.* 67: 265–311. 1986; genera 20–26 (Alysseae) in *ibid.* 68: 185–240. 1987; genera 27–36 (Arabideae) in *ibid.* 69: 85–166. 1988; and genera 37–39 (Anchonieae) in *ibid.* 193–212.

⁵Almost all recent floras cite Scopoli (Fl. Carniol. ed. 1. 515. 1760) as the author of *Alliaria*. As shown by Dandy (Regnum Veg. 51: 12, 13, 25. 1967), however, the genus should be attributed to Heister ex Fabricius.

petiolata Bieb., *Erysimum Alliaria* L., *Sisymbrium Alliaria* (L.) Scop., *Alliaria Alliaria* (L.) Britton, *Alliaria officinalis* Andrz.), garlic mustard, hedge garlic, $2n = 42$, is a weed of fields, alluvial woods, waste places, roadsides, and riverbanks. It is sporadic in North America (Rollins) and has been reported in our area from North Carolina, Tennessee, and Arkansas.

Schulz (1924) and Markgraf have recognized many varieties and forms in *Alliaria petiolata* on the basis of minor differences in flowers, fruits, and leaves. In my opinion, none of these infraspecific taxa merits recognition.

Schulz (1924, 1936) placed each of the two species of *Alliaria* in its own section. It is doubtful, however, that such sectional classification is useful. *Alliaria* is easily distinguished from all Cruciferae of the Southeastern States by its linear, somewhat quadrangular fruits, three-veined valves, oblong, black or dark brown, striate seeds, and reniform to cordate, sinuate-dentate (rarely crenate or repand) lower leaves with long petioles.

Although Von Hayek, Prantl, and Schulz (1924, 1936) placed *Alliaria* in three different tribes, they all associated the genus closely with *Eutrema* R. Br. (including *Wasabia* Matsum.), *Taphrospermum* C. A. Meyer (two species; central Asia), *Parlatoria* Boiss. (two species; Iran to southeastern Turkey), and *Sobolewschia* Bieb. (four species; Caucasus, Crimea, and Turkey). Von Hayek placed the first three genera in subtribe Arabidinae Hayek and the last two in subtribe Parlatoriinae Hayek, while Prantl and Schulz treated all five in subtribe Alliariinae. I concur with the last two authors. Subtribe Alliariinae has long-petiolate, undivided, reniform to cordate or orbicular basal leaves and usually large, oblong seeds.

The numerous chromosome counts for *Alliaria petiolata* suggest that the species is a hexaploid based on seven. Other counts of $n = 7$ (Naqshi & Javeid), $n = 18$ (Baez Mayor), and $2n = 36$ (Gadella & Kliphuis) have been reported. No chromosome counts are available for *A. brachycarpa*.

Alliaria petiolata is a self-compatible species with small, protogynous flowers that are frequently visited by bees, midges, and flies (Cavers *et al.*). Its seeds have a strong dormancy that can be broken artificially by scarification or by the application of gibberellic acid.

The seeds of *Alliaria petiolata* contain high concentrations of allylglucosinolate and only traces of benzylglucosinolate (Al-Shehbaz & Al-Shammari; Kjaer; Nielsen *et al.*). They are also rich in erucic (47 percent) and linoleic (22 percent) acids and have smaller amounts (four to seven percent each) of eicosenoic, linolenic, oleic, and palmitic acids (Miller *et al.*). *Alliaria brachycarpa* has not been surveyed for any secondary constituents.

The seed coat of *Alliaria petiolata* has flattened, nonmucilaginous epidermal cells with somewhat crystalline granules, and palisade cells with evenly thickened inner tangential walls (Vaughan & Whitehouse).

Alliaria petiolata has been used extensively in Europe and North America as a potherb, a source of fatty oils, a substitute for garlic (Busch), a medicinal plant, and a salad green. The plant has also been employed as a diuretic, a diaphoretic, and an expectorant and has been used in the treatments of asthma and dropsy. It has been said that the leaves of *A. petiolata* have higher amounts of vitamin C per weight than does the orange, and that their levels of vitamin

Are higher than those of spinach, the vegetable richest in this vitamin (Cavers *et al.*). The species is a host for certain mosaic viruses that attack several cultivated plants. Cows that feed on *A. petiolata* produce milk with a disagreeable taste.

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41. **Sisymbrium** Linnaeus, *Sp. Pl.* **2**: 657. 1753; *Gen. Pl.* ed. 5. 296. 1754.

Annual, biennial [or perennial] herbs [rarely subshrubs], glabrous or variously pubescent with unbranched [or branched] trichomes. Stems erect [rarely prostrate or decumbent], usually branched above. Basal leaves rosette forming or not, petiolate, lyrate, pinnatifid [runcinate, sinuate, or entire]; cauline leaves usually similar to the basal [sometimes sessile and auriculate to amplexicaul at base]. Inflorescences many-flowered, corymbose racemes, ebracteate [rarely bracteate and the flowers solitary or in fascicles], usually elongated in fruit; fruiting pedicels erect and appressed to rachis or ascending, divaricate [or reflexed], slender or stout and nearly as wide as the fruit. Sepals erect [or spreading], glabrous or pubescent, the inner pair slightly or not saccate at base, the outer pair sometimes cucullate. Petals yellow [white, pink, or purple], oblong to obovate, spatulate [or orbicular], usually differentiated into blades and claws. Nectar glands ringlike, usually surrounding the bases of lateral stamens and subtending those of the median ones. Stamens 6, tetradynamous; filaments free, unappendaged; anthers oblong, usually obtuse at apex. Fruits linear or subulate, terete [rarely flattened parallel to the septum], dehiscent, sessile, many seeded; valves smooth or torulose, glabrous or pubescent, usually with a prominent midvein and 2 less-conspicuous lateral veins; styles cylindrical to subconical [sometimes obsolete]; stigmas capitate or discoid, 2-lobed [rarely subentire]. Seeds numerous, oblong to elliptic, brown, papillose [reticulate or rarely striate], wingless [or marginate], uniseriately arranged in each locule, usually nonmucilaginous when wet; cotyledons incumbent or obliquely so [very rarely folded longitudinally]. Base chromosome numbers 7 [9, 10, 13]. (Including *Chamaeplium* Wallr.; *Chilocardamum* O. E. Schulz; *Coelophragmus* O. E. Schulz (in part); *Dimitria* Ravenna; *Irio* (DC.) Fourr.; *Kibera* Adanson; *Lepotocarpa* DC.; *Mostacillastrum* O. E. Schulz; *Norta* Adanson; *Pachypodium* Webb & Berth. (1836), non Lindley (1830), non Nutt. ex Torrey & A. Gray (1838); *Schoenocrambe* Greene; *Tonguea* Endl.; *Tricholobos* Turcz. (1854), non Blume (1850); *Valarum* Schur; *Vandalea* (Fourn.) Fourr.; *Velarum* Reichenb.)

LECTOTYPE SPECIES: *S. altissimum* L.; see Payson.⁶ (Name Latinized from an

⁶Britton & Brown arbitrarily lectotypified *Sisymbrium* by considering the watercress (*S. Nasturtium-aquaticum* L.), which was the first of 16 species recognized by Linnaeus (*Sp. Pl.* **2**: 657. 1753), as its type. Payson clearly demonstrated that such lectotypification is unacceptable and appropriately selected *S. altissimum* as the generic type. The watercress is now known as *Rorippa Nasturtium-aquaticum* (L.) Hayek.

ancient Greek name used by Dioscorides and Pliny for various mustards.)
—HEDGE MUSTARD, ROCKET.

A heterogeneous genus of about 90 species distributed primarily in temperate areas, with the center of greatest diversity being South America, where ca. 40–45 species grow. In addition, there are 14 species indigenous to Asia, nine to Europe, five to southern Africa, two to northwestern Africa, and about three or four to North America and the West Indies, as well as 11 weedy species of cosmopolitan or wide distribution. *Sisymbrium* is represented in the southeastern United States by three naturalized Eurasian weeds.

Schulz's (1924) sectional classification of *Sisymbrium*, which is the latest and most comprehensive, is controversial and unsatisfactory. Several of his 14 sections are artificially delimited; they include unrelated species and/or elements now believed to belong to other genera. Because of the inadequate infrageneric classification of the genus, I prefer not to recognize any sections here.

Sisymbrium altissimum L. (*Norta altissima* (L.) Britton, *S. sinapistrum* Crantz, *S. pannonicum* Jacq.), tumble mustard, Jim Hill mustard, $2n = 14$, is sporadically distributed in the Southeastern States. It has been reported from North Carolina, Georgia, Florida, Tennessee, Arkansas, and Louisiana, where it grows in fields, waste places, prairies, and disturbed areas, as well as along roadsides and railroad tracks. It is a tall (to 1 m high) annual with sinuate-pinnatifid lower leaves, pinnatisect upper leaves with narrowly linear segments, yellow petals 5–10 mm long, and stout fruiting pedicels nearly as wide as the rigid, terete fruits 4–10 cm long. It produces a very high number of seeds estimated by Muenscher (p. 4) at 511,208 for one plant. *Sisymbrium altissimum* is easily distinguished from the related Eurasian *S. orientale* L. ($2n = 14$), which is sporadic in western North America and adjacent Mexico, by its cucullate outer sepals and its cauline leaves with a linear terminal lobe. In *S. orientale* the outer sepals are not cucullate, and the terminal leaf lobe is ovate to lanceolate, usually with a hastate base.

Sisymbrium officinale (L.) Scop. (*Erysimum officinale* L.), hedge mustard, $2n = 14$, is easily distinguished from other Cruciferae of the Southeast by its pinnatisect lower leaves with large terminal lobes, yellow petals 2–4 mm long, short (1–2 mm), stout fruiting pedicels as wide as the fruits, and short (8–20 mm), subulate fruits closely appressed to the rachis. It is widely distributed in North America and has been reported from all of the Southeastern States. Robinson and most subsequent North American authors (e.g., Fernald; Radford *et al.*) have recognized two varieties in *S. officinale* on the basis of pubescent (var. *officinale*) or glabrous (var. *leiocarpum* DC.) fruits. However, the amount of pubescence on the upper parts of the plant can vary considerably within a given population. Most of the populations of *S. officinale* that I have examined in Southwest Asia, West Europe, and North America include plants with both glabrous and pubescent fruits. Evidently, these varieties do not merit recognition.

The third Eurasian weed is *Sisymbrium Irio* L. (*Norta Irio* (L.) Britton, *Descurainia Irio* (L.) Webb & Berth., *S. erysimastrum* Lam., *S. heteromallum*

Fourn., *S. latifolium* Gray), London rocket, $2n = 14, 28$. Despite its abundance in the southwestern United States and Mexico, *S. Irio* is rare in the Southeast, where it has been reported only from Florida (Long & Lakela) and Louisiana (MacRoberts). Except for a few counts, *S. Irio* is diploid throughout most of its native and naturalized ranges. Amin and Podlech & Dieterle have reported tetraploid counts from Egypt and West Pakistan, respectively, while Khoshoo (1959a) found diploid, triploid, tetraploid, hexaploid, and octoploid plants occurring naturally in India.

The Eurasian *Sisymbrium Loeselii* L., tall hedge mustard, $2n = 14$, and the South African *S. Turczaninowii* Sonder have both been reported from South Carolina (Berkeley and Florence counties) as weeds of waste grounds around wool-combing mills (Al-Shehbaz, 1986). They are not known elsewhere in the Southeast. *Sisymbrium Loeselii* has been recorded only recently from Kentucky (Cranfill & Thieret), but it is widespread in the plains region of the United States and Canada (Rollins, tribal reference).

Schulz's (1924) circumscription of *Sisymbrium* has been followed by most subsequent workers. However, many of the North American species have since been transferred to other genera (Rollins, 1982), while some of his generic segregates are now retained in *Sisymbrium* (Romanczuk, 1982). At least three or four North American species are good members of the genus. Schulz segregated *S. auriculatum* A. Gray and *Dryopetalon runcinatum* A. Gray (as *S. umbrosum* Robinson), both endemic to the Southwestern States and northern Mexico, to *Coelophragmus*. The latter was said to differ from *Sisymbrium* in having slender styles, seeds <0.5 mm long, and deeply pitted septa, instead of stout styles, longer seeds, and nonpitted septa. However, these alleged differences are unrealistic, and many species of *Sisymbrium* have most or all the features said to be unique to *Coelophragmus*. Payson's conclusion (p. 25) that "*Sisymbrium auriculatum* is strikingly reminiscent of certain European members of the genus—notably *S. Irio*, *S. Loeselii* and even *S. altissimum*" is perfectly valid. In my opinion, *S. auriculatum* and a few other North American species should be retained in the genus. As far as the South American members are concerned, the genus needs a comprehensive study—neither Schulz (1924) nor Romanczuk (1982) adequately solved the problem of its limits.

The generic boundaries of *Sisymbrium* are difficult to define. Although the majority of species have pinnately divided lower leaves, yellow or white flowers, terete, linear fruits, usually three-veined valves, prominently two-lobed stigmas, uniseriately arranged seeds, and incumbent cotyledons, many others do not have this combination of characters. Furthermore, several generic relatives of *Sisymbrium* have the same features and differ only in a few technical characters.

The reproductive biology of the genus is poorly studied. All of the weedy species are self-compatible and predominantly autogamous. In three of these (*S. Irio*, *S. officinale*, and *S. orientale*), however, the flowers are nearly always protogynous (Al-Shehbaz, 1977; Khoshoo, 1959c).

Chromosome numbers have been reported for 27 species; all but six are diploid. *Sisymbrium elongatum* (O. E. Schulz) Romanczuk (Argentina, Bolivia), *S. luteum* (Maxim.) O. E. Schulz (eastern Asia), *S. polyceratium* L.

(southern Europe and northwestern Africa), and *S. strictissimum* L. (Europe) are all tetraploid ($2n = 28$), while *S. runcinatum* L. (Eurasia) and *S. supinum* L. (Europe) are hexaploid ($2n = 42$). Except for four South American species, the genus is based primarily on seven. Two species, *S. Gilliesii* Romanczuk (Argentina) and *S. littorale* Phil. (Chile), have $2n = 26$, while *S. magellanicum* (Juss. & Pers.) J. D. Hooker (Patagonia) and *S. subscandens* Spegaz. (Argentina) have $2n = 18$ and $2n = 20$, respectively (Carrique & Martínez; Moore; Tschischow).

Due to the presence of the cardenolides helveticoside and corchoroside in *Sisymbrium Loeselii*, *S. officinale*, and ten species of *Erysimum* L., Latowski and colleagues have suggested that the two genera should be placed in the same tribe. Because of the extreme rarity of these compounds in the Cruciferae, they are potentially useful in assessing generic relationships. However, neither the two genera nor their close relatives have been surveyed adequately for cardenolides. Del Pero de Martínez & Aguinagalde have suggested that the distribution of leaf flavonoids is useful chemotaxonomically, but they studied only four species, and many more need to be surveyed before any meaningful conclusions can be reached.

The seeds of nine species have been analyzed for fatty acids (Appelqvist; Miller *et al.*). All have high concentrations (33–43 percent) of linolenic acid and moderate amounts of erucic (10–23 percent) and linoleic (10–19 percent) acids. *Sisymbrium erysimoides* Desf. has the second highest content (14 percent) of palmitic acid among the 172 species of Cruciferae surveyed thus far (Kumar & Tsunoda).

Glucosinolate profiles are known for at least eight species. In *Sisymbrium Irio* and *S. officinale* high concentrations (86–96 percent) of isopropylglucosinolate and smaller amounts (4–14 percent) of 2-butylglucosinolate have been found (Al-Shehbaz & Al-Shammary). The two compounds are also present in *S. strictissimum* L. In *S. orientale* the major constituent (82 percent) is 3-butenylglucosinolate, and the minor ones are phenylethyl (14 percent) and benzyl (4 percent) glucosinolates (Hasapis *et al.*). A complex chemical profile has been found in *S. austriacum* Jacq.; it has 1-hydroxy-2-propyl and 1-hydroxy-2-butyl glucosinolates, as well as their corresponding benzoate glucosinolates that are very rare in the Cruciferae (Kjaer & Christensen).

Large crystals of calcium oxalate have been found in *Sisymbrium altissimum*. They are seldom found elsewhere in the Cruciferae (Metcalf & Chalk).

The green parts of certain species of *Sisymbrium* are eaten raw in salads or cooked as a vegetable, while the seeds are used as a condiment (Crisp). Many medicinal properties have been attributed to various species, particularly *S. officinale*, the specific epithet of which means *of the shops*, from its former repute in medicine. This and other sisymbriums were said to be useful as antiscorbutics, diuretics, expectorants, rubefacients, and stimulants, and they were employed in the preparation of remedies for asthma, hoarseness, indurations, and swellings. Some species (e.g., *S. altissimum*, *S. Irio*, *S. officinale*, *S. orientale*) are noxious cosmopolitan weeds that are also hosts for certain viruses of crops.

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42. **Arabidopsis** (DC.) Heynhold in Holl & Heynhold, *Fl. Sachsen* **1**: 538. 1842.

Annual [biennial or perennial] herbs; trichomes furcate or stellate, usually mixed with unbranched ones, rarely absent. Lower leaves petiolate, entire [dentate or rarely pinnatifid]; upper leaves short petiolate [or sessile and auriculate to amplexicaul]. Inflorescences ebracteate [or bracteate] racemes, greatly elongated in fruit; fruiting pedicels slender, divaricate [to erect-ascending]. Sepals oblong, erect to ascending, equal and not saccate at base. Petals present [rarely absent], white, lilac [or yellow], obovate to spatulate, obtuse to truncate at apex. Nectar glands ringlike, usually subtending the bases of all filaments [sometimes toothlike, separated, 1 on each side of a lateral filament]. Stamens 6 and slightly tetradynamous [rarely 4]; filaments free, unappendaged; anthers ovate to oblong. Fruits linear, terete [or slightly flattened parallel to the septum], dehiscent, smooth [or slightly torulose]; valves 1-nerved, glabrous [or pubescent]; septum hyaline, usually 1-nerved, complete [rarely absent]; styles short, thick or slender; stigmas entire [or slightly 2-lobed]. Seeds ovate, smooth, uniseriately [rarely biseriately] arranged in each locule, wingless, mucilaginous [or nonmucilaginous] when wet; cotyledons incumbent. Base chromosome numbers 5–8. (Including *Hylandra* Á. Löve, *Pilosella* Kostel., *Stenophragma* Čelak., *Thellungiella* O. E. Schulz.) TYPE SPECIES: *Arabis Thaliana* L. = *Ara-*

bidopsis Thaliana (L.) Heynh.⁷ (Name from *Arabis*, a genus of the Cruciferae, and the Greek *opsis*, aspect, from a resemblance to *Arabis*.)—MOUSE-EAR CRESS.

A poorly defined genus of 15 to 20 species, the majority of which occur in the Himalayan region and in central and southwestern Asia. *Arabidopsis suecica* (Fries) Norrlin is widespread in subarctic Europe, whereas *A. salsuginea* (Pallas) Busch grows in northern North America (Canada; Colorado, Montana), Siberia, and central Asia. *Arabidopsis Thaliana* (L.) Heynh. (*Arabis Thaliana* L., *Sisymbrium Thalianum* (L.) Gay & Monnard, *Stenophragma Thaliana* (L.) Čelak.), mouse-ear cress, $2n = 10$, is naturalized throughout most of North America and has been reported from all of the Southeastern States. It grows on sandy soil in waste places, gardens, old fields, and river bottoms, as well as along roadsides (Rollins).

The generic limits of *Arabidopsis* are highly artificial, and careful evaluation of these and of the related Asiatic *Drabopsis* C. Koch, *Microsisymbrium* O. E. Schulz, and *Neotorularia*, the European *Cardaminopsis* (C. A. Meyer) Hayek, and the American *Halimolobos* Tausch are needed. Schulz (1924, 1936) and subsequent authors have distinguished *Arabidopsis* from these genera by cotyledonary position (incumbent vs. accumbent), presence or absence of seed mucilage or median nectaries, and nature of the style (slender vs. thick). These characters alone are doubtfully useful in generic delimitation. In my opinion, a few species of *Arabidopsis* can easily be accommodated in *Halimolobos* or the Asiatic relatives above, while a few species of the other genera are more appropriately placed in *Arabidopsis*. *Arabidopsis* includes delicate annuals with undivided, rosette-forming lower leaves, furcate trichomes, narrowly linear, terete fruits, slender fruiting pedicels, uniseriate, mucilaginous seeds, and incumbent cotyledons. A thorough study of the whole complex is needed.

Autogamy is apparently widespread in *Arabidopsis*, as is suggested in *A. parvula* (Schrenk) O. E. Schulz by the lack of petals, in *A. esepitata* Hedge by the reduction of stamen number to four, and in several others by the reduction in flower size. Although *A. Thaliana* is obligately autogamous if grown under

⁷When Heynhold (see above) raised *Sisymbrium* L. sect. *Arabidopsis* DC. to generic rank, he listed a single species, *A. Thaliana*. Many workers have considered this to be the generic type. However, such typification is incorrect because *A. Thaliana* was not one of the original species that De Candolle (1821) placed in sect. *Arabidopsis*. According to Article 7.10 of the Code (ICBN, 1983), the genus must be typified by the type of the basionym sect. *Arabidopsis*. However, none of the seven species originally assigned to this section (De Candolle, 1821) is now retained in *Arabidopsis*. They are placed in *Ammosperma* J. D. Hooker, *Murbeckiella* Rothm., *Neotorularia* Hedge & J. Léonard, *Sisymbrella* Spach, and *Sisymbrium*. Section *Arabidopsis* was first lectotypified by Čelakovsky, who retained only one of its original De Candollean species, *Sisymbrium bursifolium* L. (as *A. bursifolia* (L.) Čelak.) and treated the others in different genera. This species is now recognized as *Sisymbrella dentata* (L.) O. E. Schulz. Acceptance of Čelakovsky's lectotypification would imply that *Arabidopsis* should be reduced to a synonym of the earlier-published *Sisymbrella*. Furthermore, the choice of any of the remaining De Candollean species as the type of *Arabidopsis* would necessitate either the union of this genus with the earlier-published *Sisymbrium* or the reduction of the later-published *Ammosperma* (1862), *Murbeckiella* (1939), or *Neotorularia* (1986) to synonym of *Arabidopsis*. Štěpánek has suggested that the generic name *Arabidopsis* be either conserved or replaced by *Stenophragma*, its earliest generic synonym. I concur with him in conserving *Arabidopsis* because the name is well recognized among biologists.

insect-free conditions, some outcrossing does take place in open habitats. Using genetic markers, Lawrence & Snape have estimated that about 1.2–2.2 percent outcrossing has resulted from insect (e.g., hoverflies, Syrphidae) visitation. Müller's photographic evidence of protogyny in *A. Thaliana* confirms Kerner's (see Al-Shehbaz) original observations that were reported as early as 1895.

Chromosome numbers are known for at least ten species, of which all except *Arabidopsis Korshinskyi* Botsch., which is a hexaploid ($2n = 48$), are diploid. *Arabidopsis pumila* (Stephan) N. Busch (including *A. Griffithiana* (Boiss.) N. Busch) has diploid and tetraploid populations with chromosome numbers based on eight. Six other species are diploids based on eight, while *A. toxophylla* (Bieb.) N. Busch and *A. Thaliana* are diploids based on six and five, respectively. Further studies are needed for *A. Wallichii* (J. D. Hooker & Thomson) N. Busch, which has variously been reported to have $2n = 14$ (Polatschek, 1968), $2n = 16$ (Ginter & Ivanov; Podlech & Bader), and $2n = 18$ (Naqshi & Javeid, 1976). The karyotype of *A. Thaliana* consists of a small pair of subtelocentric chromosomes and four metacentric pairs, one of which has satellites (Ambros & Schweizer).

Several workers have been successful in crossing *Arabidopsis Thaliana* with certain species of *Cardaminopsis*. Although Berger, Hylander, and Löve have suggested that *A. suecica* ($2n = 26$) is an allotetraploid derived from *A. Thaliana* and *C. arenosa* (L.) Hayek ($2n = 32$), Laibach (1958), Měsíček, and Rédei (1974) have demonstrated that the experimental evidence does not support such an origin. Löve has segregated *A. suecica* to the monotypic *Hylandra*, but the overall morphology supports its retention in *Arabidopsis* (Ball).

Arabidopsis has been poorly surveyed for secondary constituents. High concentrations of isopropylglucosinolate and smaller amounts of allylglucosinolate are found in the seedlings of *A. Thaliana* (Cole). The seeds of *A. suecica* and *A. Thaliana* have comparable amounts of oleic (13–18 percent), linoleic (26–32 percent), and linolenic (18–25 percent) acids, but the eicosenoic acid is much higher in *A. Thaliana* (24–26 percent) than in *A. suecica* (11 percent) (Kerber & Buchloh; Miller *et al.*).

Arabidopsis Thaliana is the most widely studied of all flowering plants in biochemistry, molecular genetics, morphogenesis, and physiology. It is an excellent experimental plant because of its small size, brief generation time, low chromosome number ($n = 5$), low DNA content, and predominantly autogamous breeding system (Lawrence; Meyerowitz & Pruitt). Under favorable conditions, certain races flower within three weeks from the date of sowing. The species has the lowest nuclear DNA content reported so far in flowering plants. Its haploid genome, which has about 7×10^7 base pairs (Meyerowitz & Pruitt), is about five times larger than that of the yeast and about 50 times that of *Escherichia coli*.

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Under tribal references see AL-SHEHBAZ (1977); BOLKHOVSKIKH *et al.*; COLE; DUNCAN & KARTESZ; GOLDBLATT (1981, 1984, 1985); HEDGE; JONES; LÉONARD; MACROBERTS; MILLER *et al.*; MOORE; MUENSCHER; RADFORD *et al.*; ROLLINS; SCHULZ (1924, 1936); SHARP *et al.*; SMALL (1903, 1933); SMITH.

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43. *Descurainia* Webb & Berthelot, *Hist. Nat. Îles Canaries*, III. **1**: 72. 1836, nom. cons.

Annual, biennial [or perennial] herbs [or shrubs to 1.5 m high]; stems branched above [or at base], erect to ascending [or prostrate]; trichomes unicellular, dendritically branched or rarely unbranched, usually mixed with clavate [to capitate] glandular ones. Basal leaves petiolate, 2- or 3-pinnatisect [rarely once pinnate], usually forming rosettes early in the season, often withering before fruit maturity, pubescent with dendritic [and/or glandular] trichomes. Cauline leaves resembling the basal ones, progressively smaller and less divided upward. Inflorescences densely flowered, ebracteate [rarely bracteate], corymbose racemes, elongated [or not] in fruit; fruiting pedicels divaricate [rarely erect and

appressed to rachis]. Sepals green [or violet], erect to ascending [rarely spreading], oblong, obtuse at apex, not saccate at base. Petals yellow [rarely white], spatulate, obovate [ovate or oblong], short clawed, usually <3 [or to 6] mm long. Nectar glands ringlike, subtending the bases of all filaments or occasionally surrounding those of the lateral ones. Stamens 6, somewhat tetradynamous, included or slightly exerted; filaments free, not appendaged; anthers oblong, obtuse, yellow [or purplish]. Fruits narrowly linear, subclavate [oblong or elliptic], usually terete, dehiscent from the base upward [or from the apex downward], smooth [rarely torulose]; valves glabrous [or pubescent], with a prominent midvein and usually obscure, somewhat anastomosing lateral veins; septum membranaceous, complete [or reduced to a narrow rim], veinless or 1- to 3-veined; styles obsolete or rarely conspicuous; stigmas discoid to capitate, entire. Seeds oblong to elliptic, reddish brown to yellowish, wingless, uniseriately or biseriately arranged in each locule, usually mucilaginous when wet; cotyledons incumbent. Base chromosome number 7. (Including *Discurea* (C. A. Meyer ex Ledeb.) Schur; *Sophia* Adanson (1763), non Linnaeus (1775).) TYPE SPECIES: *Sisymbrium Sophia* L. = *D. Sophia* (L.) Webb ex Prantl, typ. cons.; see ICBN, p. 351. 1983. (Name commemorating François Descurain, 1658–1740, pharmacist at Étampes, France.)—TANSY MUSTARD.

A well-defined and taxonomically complex genus of about 40 species distributed primarily in three centers: the Canary Islands (seven species), North America (11), and South America (19). Two of the North American species also grow in South America. One, *Descurainia Kochii* (Petri) O. E. Schulz, is endemic to Turkey, Armenia, and the Caucasus, while *D. sophioides* (Fischer) O. E. Schulz is widespread in arctic North America and Asia. The genus is represented in the southeastern United States by two species, of which one is a Eurasian weed and the other is indigenous.

Schulz (1924) divided *Descurainia* into two well-marked sections. The Canarian sect. SISYMBRIODENDRON (Christ) O. E. Schulz (shrubs; lower leaves with axillary fascicles; petals oblong to ovate, 3–6 mm long; seeds striate-granular, often with a distal wing) has seven species, while the cosmopolitan sect. DESCURAINIA (sect. *Seriphium* O. E. Schulz) (herbs; lower leaves without axillary fascicles; petals spatulate, 0.5–3 mm long; seeds smooth or obscurely reticulate, wingless) includes the remaining species of the genus.

Descurainia pinnata (Walter) Britton (*Erysimum pinnatum* Walter; *Sisymbrium pinnatum* (Walter) Greene; *Sophia pinnata* (Walter) Howell; *Cardamine multifida* Pursh (1814), non *C. multifida* (Muhl. ex Ell.) Wood (1870); *D. multifida* (Pursh) O. E. Schulz; *Sisymbrium canescens* Nutt. (1818), non Bentham (1839), Griseb. (1874); *Sophia myriophylla* Rydb.; *D. multifoliata* Cory), tansy mustard, $2n = 14, 28, 42$, is the most variable species in the genus. Schulz (1924) recognized five species and six varieties in this complex, while Detling accepted a highly polymorphic species with 11 subspecies. Although Detling's account of the *D. pinnata* complex is evidently superior to Schulz's, the species limits were expanded to include elements now believed to belong to other species. Due to the lack of thorough experimental and field studies on the North American taxa, Detling's treatment is closely followed here.

Descurainia pinnata subsp. *pinnata* is widely distributed throughout the Southeastern States, where it grows in fields, prairies, woodlands, desert plains, and waste places, on sandy hummocks, hillsides, and banks, and along streams and roadsides. Because of its sporadic introduction to many parts of North America, the native range of the subspecies has been obscured. However, the subspecies is probably indigenous to most, if not all, of the Southeast. Diploid, tetraploid, and hexaploid counts have been reported, but very little is known about the cyto geography and fertility relationships among the three cytotypes.

The two other subspecies reported by Detling from the Southeastern States are less common. *Descurainia pinnata* subsp. *halictorum* (Cockerell) Detling (*Sophia halictorum* Cockerell, *D. halictorum* (Cockerell) O. E. Schulz, *D. pinnata* var. *halictorum* (Cockerell) M. E. Peck, *S. andrenarum* Cockerell, *D. andrenarum* (Cockerell) Cory, *D. halictorum* var. *andrenarum* (Cockerell) O. E. Schulz), $2n = 14, 28, 42$, has been reported only from Hempstead County, Arkansas. Its range outside the Southeast extends to northern Mexico, the Southwest, and most of the Pacific and Mountain states.

Descurainia pinnata subsp. *brachycarpa* (Richardson) Detling (*Sisymbrium brachycarpum* Richardson, *S. canescens* Nutt. var. *brachycarpum* (Richardson) S. Watson, *D. brachycarpa* (Richardson) O. E. Schulz, *D. pinnata* var. *brachycarpa* (Richardson) Fern.), $2n = 14, 28$, is sporadic in North Carolina, Georgia, and Tennessee, where it may be introduced, and widespread in Arkansas. It is distributed from the Southeastern States north to Quebec, west through subarctic Canada to southwestern Mackenzie District, and south through Washington to Texas.

Descurainia pinnata is easily distinguished from all of the North American species of the genus by its obtuse, clavate to subclavate fruits (4–)5–11(–13) mm long, obsolete styles, biserially arranged seeds, and divaricate fruiting pedicels. Differences between the three subspecies that grow in the Southeast are not very pronounced. Detling has distinguished subsp. *brachycarpa* from the other two on the basis of its fruiting pedicels spreading at angles of 45 (30–70) (vs. 75 (60–90)) degrees and its noncanescent (vs. canescent) herbage. Subspecies *pinnata* is separated from subsp. *halictorum* by its ovate to oblanceolate (vs. narrowly oblong to linear) leaf segments. It is evident, however, that the boundaries between these subspecies are somewhat artificially delimited, and that the orientation of the fruiting pedicels, the shape of the ultimate leaf segments, and the pubescence of the leaves all show continuous variation.

Small (1903, 1933) reported *Sophia intermedia* Rydb. from the Blue Ridge area of Tennessee. Detling, however, treated this taxon as *Descurainia pinnata* subsp. *intermedia* (Rydb.) Detling and indicated that it is distributed from southern British Columbia and Alberta to southern Colorado, western Nevada, and northeastern California.

The Eurasian *Descurainia Sophia* (L.) Webb ex Prantl (*Sisymbrium Sophia* L., *Sophia Sophia* (L.) Britton, *Hesperis Sophia* (L.) Kuntze, *Sisymbrium parviflorum* Lam., *Sophia parviflora* (Lam.) Standley), flixweed, tansy mustard, $2n = 14, 28$, is a weed of roadsides, waste places, disturbed sites, and fields. It has been reported from North Carolina, Georgia, Tennessee, Arkansas, and Louisiana and is likely to be found in the other Southeastern States. It is easily

distinguished from *D. pinnata* by its narrowly linear fruits, uniseriately arranged seeds, conspicuously two- or three-veined septa, and lack of glandular trichomes. None of the six varieties and eight forms recognized by Schulz (1924) in *D. Sophia* has any taxonomic value.

Descurainia is a sharply defined genus easily distinguished by its fine dendritic trichomes that are often mixed with glandular, subclavate ones, usually bi- or tripinnatisect lower leaves, filiform fruiting pedicels, and small seeds that are often mucilaginous when wet. The nearest relatives of *Descurainia* are *Sophiopsis* O. E. Schulz (four species; central Asia), *Hugueninia* Reichenb. (two species; central Europe and Mallorca, Spain), *Robeshia* Hochst. (monotypic; the Middle East), *Redowskia* Cham. & Schlecht. (monotypic; Siberia), and *Smelowskia*. As was indicated earlier, Schulz (1924, 1936) placed all six genera in subtribe Descurainiinae, a group with somewhat natural boundaries.

The reproductive biology of *Descurainia* has not been studied adequately. The Canarian species, all with large flowers and conspicuous nectaries, are self-incompatible (Bramwell), while the weedy *D. Sophia* is autogamous and protogynous (Al-Shehbaz; Best). Individual plants of the species produce an average of 75,650 seeds that are easily transported by wind because of their light weight (ca. 0.12 mg each) and by animals and farm equipment because of their mucilage (Best).

Chromosome numbers are known for 18 species; all are based on seven or 13 and are exclusively diploid. The Mexican *Descurainia Virletii* (Fourn.) O. E. Schulz is tetraploid, *D. Sophia* and the North American *D. obtusa* (Greene) O. E. Schulz have both diploid and tetraploid populations, and *D. pinnata* and *D. Richardsonii* (Sweet) O. E. Schulz have diploid, tetraploid, and hexaploid plants. The report of $2n = 12$ for *D. Sophia* (Saidabadi & Gorenflot) does not agree with 30 counts of $2n = 14$ and 28 from Asia, Europe, and North America.

Only *Descurainia Richardsonii* and *D. Sophia* have been surveyed thoroughly for glucosinolates. The former, which contains nine compounds in the leaves, has a predominance (89–99 percent) of 3-butenylglucosinolate and traces of allyl, 2-butyl, 4-pentenyl, and benzyl glucosinolates (Rodman & Chew). *Descurainia Sophia* also has 3-butenyl and allyl glucosinolates as the major and minor constituents, respectively, but it has traces of 4-methylthiobutyl and 2-phenylethyl glucosinolates (Lockwood & Afsharypuor). The seeds of *D. Bourgaeana* Webb ex O. E. Schulz, *D. pinnata*, and *D. Sophia* have fatty-acid profiles characterized by moderate amounts (28–37 percent) of linolenic acid, smaller ones (17–20 percent) of linoleic acid, and comparable concentrations (9–14 percent each) of eicosenoic, erucic, and oleic acids (Kumar & Tsunoda).

The seed-coat anatomy of *Descurainia Richardsonii* and *D. Sophia* was studied by Vaughan & Whitehouse. They showed that the epidermal cells contain large, solid columns protruding from the inner tangential walls into the cell lumen. The palisade cells are tangentially elongated, and their radial and inner tangential walls are conspicuously thickened.

Descurainia Sophia was used externally for treating indolent ulcers and internally to eradicate intestinal worms. The plant is said to be antiscorbutic and astringent, and the seeds are reputed to cure fevers, bronchitis, and dysentery. The seeds are also used as a substitute for mustard in the Caucasus (Busch).

Cattle feeding on large quantities of *D. pinnata* become blind and unable to swallow food (Kingsbury).

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