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THE GENERA OF BRASSICEAE (CRUCIFERAE; BRASSICACEAE) IN THE SOUTHEASTERN UNITED STATES[1,2]

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Tribe **Brassiceae** [A. P. de Candolle, Syst. Nat. **2:** 152. 1821.]

Annual, biennial, or perennial herbs [sometimes subshrubs or shrubs], unarmed [rarely spiny], glabrous or with simple trichomes only. Inflorescence usually an ebracteate corymbose raceme, often greatly elongated in fruit; flowers few to many [rarely solitary]. Sepals erect or spreading, saccate at base or not. Petals usually obovate, clawed. Stamens 6; filaments without [very rarely with] a basal appendage. Median nectar glands present or absent. Stigmas entire or 2-lobed, the lobes sometimes decurrent. Siliques usually differentiated into lower (valvular) and upper (beak) segments, sometimes transversely jointed and breaking into parts, occasionally lomentaceous [or samaroid or nutlike],

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The illustrations were made by Karen Stoutsenberger (FIGURE 1) and Rachel A. Wheeler (FIGURE 2) under earlier grants.

[2] For an account 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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terete, angular, or flattened parallel [rarely perpendicular] to the septum, variable in length, shape, and size; lower segment dehiscent or indehiscent, 1- to many-seeded, rarely seedless and abortive or altogether lacking; upper segment indehiscent, 1- to several-seeded, rarely seedless and resembling the style or obsolete. Seeds mucilaginous or not when wet, wingless [or winged], uniseriately or biseriately arranged in each locule; cotyledons conduplicate, very rarely accumbent or incumbent, usually emarginate. Base chromosome numbers 6–13, 15, 17. (Including Cakilineae DC., Calepineae Godron, Erucarieae DC., Psychineae DC., Raphaneae DC., Velleae DC., Zilleae DC.) TYPE GENUS: *Brassica* L.

A natural tribe of 52 genera and about 230 species in six subtribes centered in the southwestern Mediterranean region, particularly Algeria, Morocco, and Spain (where some 41 genera are either endemic or exhibit maximum diversity), and extending eastward into India and Pakistan and southward into South Africa, with a poor representation in the New World. Three genera, *Conringia* Heister ex Fabr. (six species), *Enarthrocarpus* Labill. (five species), and *Erucaria* Gaertner (eight species), have diversified in the eastern Mediterranean, while *Physorrhynchus* Hooker (two species) and the monotypic *Chalcanthus* Boiss., *Douepia* Camb., *Fortuynia* Shuttlew., and *Pseudofortuynia* Hedge are endemic to parts of Iran, Afghanistan, and Pakistan. The tribe is represented in the southeastern United States by 11 genera and 21 species, of which only four of *Cakile* Miller are indigenous; the remainder are weeds most likely introduced from Europe or southwestern Asia.

The Brassiceae are the most distinctive and the most natural of all tribes of the Cruciferae. The great majority of members are characterized by having conduplicate cotyledons and/or two-segmented (occasionally called heterocarpic) siliques that contain seeds in one or both segments. These features are unknown elsewhere in the family. Segmented siliques are found in 32 genera of the tribe, and with the exception of *Ammosperma* Hooker f. (monotypic), *Pseuderucaria* (Boiss.) O. E. Schulz (three species), and *Conringia,* all of which have accumbent or incumbent cotyledons, the remaining genera with unsegmented siliques have conduplicate cotyledons. Nonconduplicate cotyledons characterize all species of *Cakile* and the closely related *Erucaria,* but these have strongly two-segmented siliques. *Calepina* Adanson (monotypic), *Orychophragmus* Bunge (monotypic; China), and *Sprygínia* Popov (six species; Central Asia) have traditionally been placed in the Brassiceae but have been excluded by Gómez-Campo (1980a) because they lack the typical features of the tribe. The removal of the last two genera is justified, but *Calepina* has somewhat conduplicate cotyledons (FIGURE 1o) and is without close relatives outside the tribe. It seems, therefore, more appropriate to retain it here.

Gómez-Campo (1980a) has proposed significant alterations to the comprehensive subtribal classification of Schulz (1919, 1923). Subtribes Zillinae (DC.) O. E. Schulz (four genera) and Vellinae Prantl (ten genera including those of the Savignyinae Hayek) are not represented in our flora. Subtribe Cakilinae (DC.) O. E. Schulz (cotyledons lanceolate or linear, accumbent or incumbent;

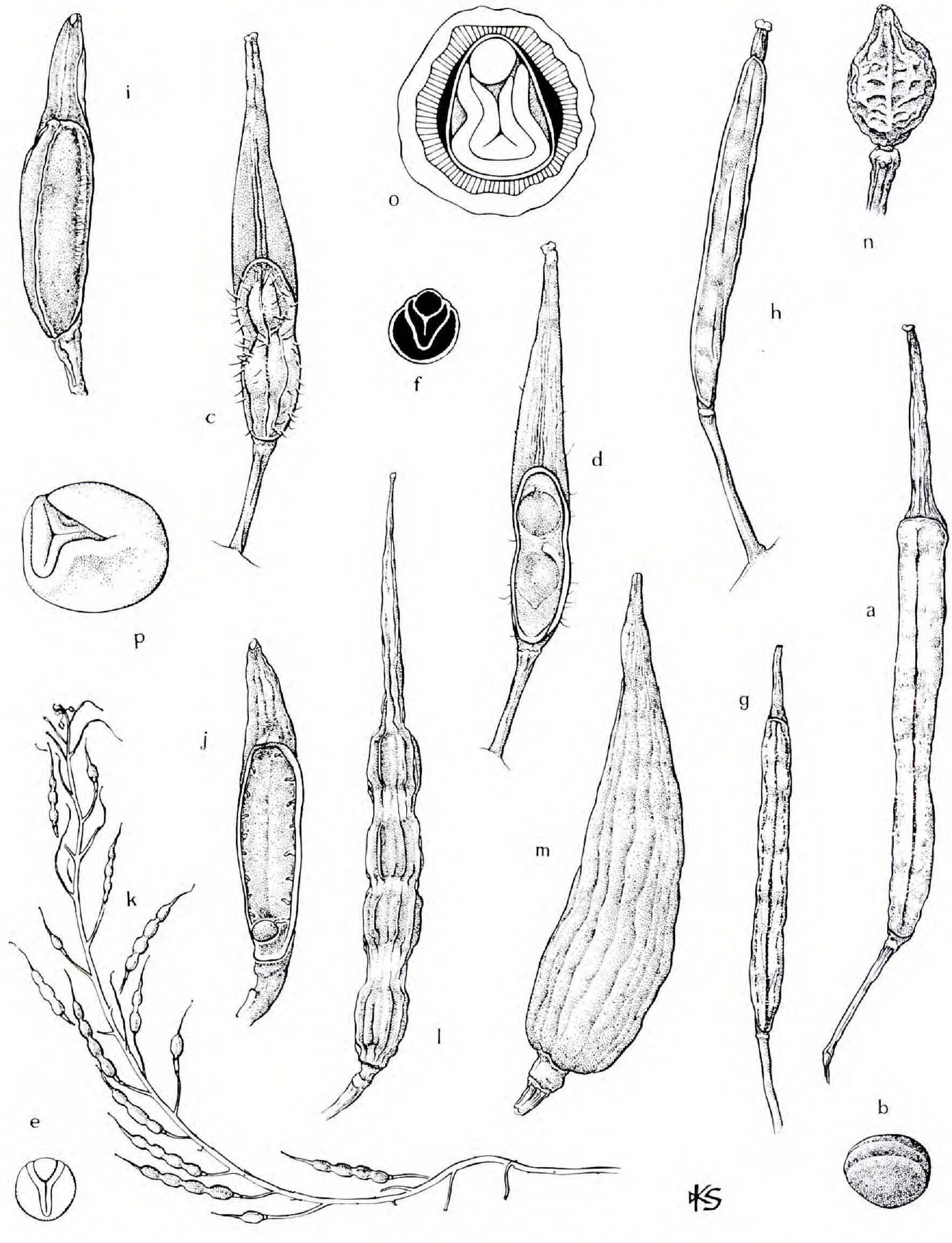

FIGURE 1. Fruits and seeds of selected Brassiceae. a, b, *Brassica campestris:* a, fruit, × 2; b, seed, × 6. c–f, *Sinapis alba:* c, fruit—note beak, × 2; d, fruit after removal of valve, × 2; e, embryo, × 6; f, diagrammatic cross section of seed showing conduplicate cotyledons, × 6. g, *S. arvensis,* fruit, × 2. h, *Diplotaxis muralis,* fruit, × 3. i, j, *Eruca vesicaria* subsp. *sativa:* i, fruit, × 2; j, fruit after fall of valve, × 2. k, l, *Raphanus Raphanistrum:* k, infructescence, × ½; l, fruit—note aborted lower segment and lomentaceous upper one, × 2. m, *R. sativus,* fruit, × 2. n–p, *Calepina irregularis:* n, fruit, × 6; o, diagrammatic cross section of fruit—note woody inner part (hatched) of fruit wall and seed with conduplicate cotyledons, × 12; p, embryo, × 12.

siliques strongly segmented, with one or few seeds in each segment) is a natural group including only *Cakile* and *Erucaria* and represented in the Southeast by five species of the former. The Moricandiinae Prantl (seven genera, including *Conringia*) are a heterogeneous assemblage of genera that have dehiscent, elongated fruits with seedless beaks and that lack median floral nectaries. Members of subtribe Brassicinae (eight genera) also have dehiscent, elongated fruits, but differ in having median nectaries and usually seeded beaks. However, the lines separating the two subtribes are undoubtedly artificial. The first six genera of the present treatment are considered typical of the Brassicinae. The Raphaninae Hayek (21 genera), probably the most heterogeneous of all six subtribes, have conduplicate cotyledons and indehiscent, usually strongly segmented fruits with seeds in both segments or in the upper one only. *Raphanus* L., *Rapistrum* Crantz, and *Calepina* represent this subtribe in the Southeast.

The Brassiceae are the best known cytologically of all tribes of the Cruciferae. Chromosome numbers have been reported for about 180 species (nearly 78 percent of the tribe) in 44 genera. The highest number ($n = 75$) has been found in *Crambe Gordjaginii* Sprygin & Popov (see Gómez-Campo & Hinata), while the lowest count ($n = 6$) was reported for *Erucaria cakiloidea* (DC.) O. E. Schulz (Al-Shehbaz, 1978). Polyploidy occurs in about 36 percent of the species and appears to be exclusive in all members of *Crambe* L., *Moricandia* DC., *Vella* L., *Boleum* Desv., *Zilla* Forsskål, and *Euzomodendron* Cosson. A continuous series from diploid to octoploid occurs in *Erucastrum* Presl. On the other hand, aneuploidy probably has played an important role in the evolution of *Diplotaxis* DC. and *Brassica*. The latter genus also exhibits the classic examples of amphiploidy that involve six cultivated species. No single base chromosome number is dominant in the Brassiceae, and the most common ones (7, 8, 9, and 15) occur in 14 to 18 percent of the species, while 10, 11, and 12 are found in 6 to 9 percent.

Natural intergeneric hybridization has been well documented between the northwestern African *Trachystoma Ballii* O. E. Schulz and *Ceratocnemum rapistroides* Cosson & Balansa, and between *Cordylocarpus muricatus* Desf. and *Rapistrum rugosum* (L.) All. Their hybrids are somewhat fertile and have been named ×*Trachycnemum mirabile* Maire & Samuels. and ×*Rapistrocarpus ramosissimus* (Pomel) Al-Shehbaz,[3] respectively. Artificial intergeneric hybrids have successfully been made on a large scale between various genera of the tribe, particularly members of subtribe Brassicinae (Harberd & McArthur, 1980). The classic intergeneric hybrid between the remotely related *Brassica* and *Raphanus*, ×*Raphanobrassica*, was produced by Karpechenko in 1924 (see *Raphanus*).

Many species of the Brassiceae, especially the economically important ones, have been surveyed extensively for glucosinolates, seed proteins, oil content, and fatty acids, and on a smaller scale for alkaloids, flavonoids, and mucilage.

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[3] ×*Rapistrocarpus* Al-Shehbaz, nothogen. nov. (*Rapistrum* Crantz × *Cordylocarpus* Desf.) — ×*Rapistrocarpus ramosissimus* (Pomel) Al-Shehbaz, comb. nov., which is based on ×*Rapistrella ramosissima* Pomel (Mat. Fl. Atlant. 11. 1860), should replace the latter because the nothogeneric name ×*Rapistrella* is not a condensed formula (see ICBN, Article H.6, p. 74. 1983).

The distribution of secondary constituents is not taxonomically useful at the subtribal level, and only in a few cases does it support the alliance of or the distinction between controversial genera. On the other hand, the distribution of glucosinolates is very useful within genera such as *Cakile* and *Brassica.*

Species of the Brassiceae occupy diverse habitats, but the majority show several adaptations to xeric environments in habit or in seed dispersal. The dustlike seeds of several species of *Diplotaxis,* the broadly winged seeds of *Savignya* DC. and *Oudneya* R. Br., and the samaras of *Fortuynia* are the most notable adaptations for dispersal by wind in desert plants. Seed mucilage is produced in at least 60 percent of the taxa with dehiscent fruits and apparently is lacking in 65 species of 18 genera with indehiscent fruits. Mucilage production may be an adaptation to anchor the seeds to the ground, as well as to enable them "to endure temporal droughts during the early stages of seed germination" (Gómez-Campo, 1980a, p. 8). Dispersal of corky fruit segments by sea water has probably evolved independently in *Crambe* (*C. maritima* L.), in *Raphanus* (two subspecies of *R. Raphanistrum* L.), and in *Cakile* (all taxa but one).

Members of 12 genera of the Brassiceae are either exclusively shrubs or herbs with a strongly woody base. In six others both herbaceous and woody taxa occur. All species of *Vella, Hemicrambe* Webb, *Boleum, Euzomodendron, Foleyola* Maire, and *Sinapidendron* Lowe, as well as the Canarian species of *Crambe,* are large shrubs or subshrubs. Carlquist, who studied the wood anatomy of the last two genera, believes that the woody condition in the family has almost always been derived from herbaceous ancestry, while Gómez-Campo (1980a) suggests that it is a primitive feature in the tribe.

The tribe includes the most economically important plants of the Cruciferae. *Brassica* and *Raphanus* provide many vegetables that are cultivated for their fleshy roots, swollen stems, leaves, buds, flowers, or young fruits. Edible and industrial oils are extracted from the seeds of *Brassica, Crambe,* and *Eruca* Miller, while condiments are obtained from seeds of *Sinapis* L. and *Brassica.* A few species are important fodder for livestock, and others of 13 genera (including the 11 treated here) are weeds naturalized throughout much of the world.

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KEY TO THE GENERA OF BRASSICEAE IN THE SOUTHEASTERN UNITED STATES

A. Fruits indehiscent, usually lomentaceous or transversely jointed, often breaking transversely at maturity into 1- or few-seeded segments; valves undifferentiated, reduced, or obsolete.
  B. Fruits transversely jointed, 2- to many-seeded, very rarely 1-seeded, more than 6 mm long; cauline leaves petiolate; petals equal.
    C. Style absent; cotyledons accumbent, rarely incumbent; glabrous and often fleshy plants of beaches or sandy shores. .... 12. *Cakile.*
    C. Style present; cotyledons conduplicate; usually pubescent and nonfleshy weeds of cultivated land, roadsides, or waste grounds.
      D. Fruits to 1 cm long; upper segment 1-seeded, ± equal to the 1-seeded (or rarely seedless) lower segment. .... 10. *Rapistrum.*
      D. Fruits more than 2 cm long; upper segment several seeded, more than 10 times longer than the lower, seedless segment. .... 9. *Raphanus.*
  B. Fruits not jointed, 1-seeded, 2–4 mm long; cauline leaves auriculate; petals unequal. .... 11. *Calepina.*
A. Fruits dehiscent, neither lomentaceous nor transversely jointed, never breaking at maturity into segments; valves well developed.
  E. Seeds biseriately arranged in each locule.

F. Beak strongly flattened, ensiform; stigma with decurrent lobes; petals with dark brown or purple veins. .... 8. *Eruca.*
F. Beak usually terete, stylelike; stigma entire or with nondecurrent lobes; petal veins not dark colored. .... 7. *Diplotaxis.*
E. Seeds uniseriately arranged in each locule.
G. Valves with 3–7 prominent nerves; beak usually ensiform.
H. Sepals erect, saccate at base; petal veins usually darker in color than the rest of blade. .... 5. *Hutera.*
H. Sepals reflexed or spreading, not saccate; petals uniform in color. .... 6. *Sinapis.*
G. Valves with 1 prominent midnerve, lateral nerves usually inconspicuous, sometimes evident and anastomosing; beak not ensiform.
I. Leaves entire, cordate-amplexicaul; fruits strongly 4-angled; cotyledons incumbent; seeds readily releasing abundant mucilage when wet. .... 13. *Conringia.*
I. Leaves (at least the lowermost ones) pinnately lobed or dentate, rarely upper ones auriculate or amplexicaul; fruits terete or flattened, sometimes slightly 4-angled; cotyledons conduplicate; seeds slightly or not at all mucilaginous when wet.
J. Inflorescence ebracteate; seeds globose; inner sepals saccate; fruits usually terete or flattened, rarely 4-angled. .... 3. *Brassica.*
J. Inflorescence (at least the lower part) bracteate; seeds oblong; inner sepals not saccate; fruits usually 4-angled. .... 4. *Erucastrum.*

3. **Brassica** Linnaeus, Sp. Pl. **2:** 666. 1753; Gen. Pl. ed. 5. 299. 1754.[4]

Herbaceous annuals [or perennials with woody base], rarely biennials, glaucous or not, glabrous or with simple trichomes. Stems erect, branching above [or below], leafy [very rarely leafless]. Lower leaves petiolate, usually forming a rosette, undivided or lyrately pinnatifid [or pinnatisect]; lateral lobes few [to many or absent], smaller than the terminal one. Upper leaves short petiolate or sessile, sometimes auriculate or amplexicaul, and entire, dentate, or lobed. Inflorescence an ebracteate, few- to many-flowered raceme, much elongated in fruit. Sepals erect or ascending, rarely spreading, oblong or ovate, green or yellow-green, glabrous [or pubescent]; outer pair sometimes slightly cucullate; inner pair usually saccate at base. Petals clawed, yellow [rarely white or pink], broadly [to narrowly] obovate [or rarely oblanceolate]. Lateral nectar glands flat, reniform or prismatic; median glands oval [or filiform or oblong, very rarely absent]. Stamens tetradynamous, not appendaged; anthers oblong or ovate. Ovary sessile [or borne on a gynophore], glabrous, many ovulate; style conspicuous; stigma capitate or 2-lobed. Siliques narrowly [to broadly] linear [or occasionally oblong], dehiscent, torulose [or not], terete or sometimes compressed parallel to the septum, rarely 4-angled, erect to spreading [or reflexed]; valves convex, thin or thick [very rarely woody], obtuse or emarginate at apex, prominently [or obscurely] 1-nerved, lateral veins usually inconspicuous, sometimes finely anastomosing; beak long or short, conical or cylindrical, seedless or 1 [to 3]-seeded, usually forming a stylelike distal portion. Seeds uniseriately [or very rarely biseriately] arranged, globose [rarely oblong or slightly flattened],

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[4] Genera are numbered as in the treatment of tribes of Cruciferae in the southeastern United States (Jour. Arnold Arb. **65:** 343–373. 1984). Genera 1 and 2 appeared in *ibid.* **66:** 95–111. 1985.

wingless, slightly mucilaginous or not when wet, yellow or light to dark brown or black, finely to coarsely reticulate; cotyledons conduplicate, usually emarginate at apex. Base chromosome numbers 7–11. (Including *Brassicaria* (Godron) Pomel, *Brassicastrum* Link, *Guenthera* Andrz. ex Besser, *Melanosinapis* Schimper & Spenner, *Rapa* Miller.) LECTOTYPE SPECIES: *B. oleracea* L.; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. **2:** 192. 1913. (Name from classical Latin for several kinds of cabbage; a few authors believe that it is from the Greek *brazo,* I cook, in reference to the vegetables of the genus.)—MUSTARD, COLE, TURNIP.

The largest genus of the Brassiceae, with some 35 species mostly centered in the Mediterranean region, particularly in southwestern Europe and northwestern Africa, extending eastward into southwestern Asia to Afghanistan, and southward into Ethiopia and Somalia. Although the native ranges of the weedy and the cultivated species are uncertain, it is unlikely that they have originated outside the Mediterranean region and western Asia. Of the eight species introduced to the United States, at least four are naturalized in the Southeast.

The sectional classification of *Brassica* is controversial, and the three highly artificial sections recognized by Schulz (1919) have recently been divided by Salmeen into nine largely natural ones. The boundaries of sect. MICROPODIUM DC. have been arbitrarily redrawn by Salmeen to include a few unrelated species that differ in chromosome numbers and in morphology. On the other hand, sect. BRASSICARIA (Godron) Cosson (three species; southwestern Europe and northwestern Africa) is morphologically distinct from the rest of the genus, and on the basis of seed anatomy (Bengoechea & Gómez-Campo), chromosome numbers (Gómez-Campo & Hinata), juvenile characters (Gómez-Campo & Tortosa), and glucosinolates (Horn & Vaughan), the section is somewhat anomalous in *Brassica* and closely resembles the Madeiran *Sinapidendron.* However, *B. Gravinae* Ten. of sect. BRASSICARIA is intermediate between the typical members of this section and the rest of *Brassica.* Most taxa (including the type species) of sect. LIGNOSAE Widler & Bocquet are very closely related to *B. oleracea* and should be placed with it in sect. BRASSICA as defined by Stork and colleagues.

Section MELANOSINAPIS (DC.) Boiss. (sect. *Sinapioides* Peterm.) (annuals, upper leaves petiolate, sepals spreading, petals long clawed, fruiting pedicels appressed to the rachis, siliques torulose and 4-angled, valves 5–27 mm long, beaks seedless, seeds 4–10) has been reduced by Salmeen to include only *Brassica nigra* (L.) W. D. Koch (*Sinapis nigra* L.), black mustard, charlock (Small), $2n = 16$. The species may be a native of the Middle East. It is a cosmopolitan weed that grows in fields, roadsides, orchards, and waste places throughout much of the United States. It is locally common in scattered counties in Alabama, Louisiana, Mississippi, and Tennessee and may occur in the remaining states of the Southeast as well.

Section RAPA (Miller) Salmeen ex Al-Shehbaz[5] (annuals or biennials, basal

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[5] *Brassica* sect. *Rapa* (Miller) Salmeen ex Al-Shehbaz, comb. nov. Based on *Rapa* Miller (Gard. Dict. abr. ed. 4. Vol. 3 (alph. ord.). 1754). The new combination was originally proposed by the late O. J. Salmeen in her Ph.D. dissertation (see references).

leaves not forming a rosette, cauline leaves auriculate, sepals erect or ascending, valves 2.5–8 cm long, beaks seedless or 1-seeded) is represented in our area by its two species that are both crop plants and naturalized weeds. *Brassica Rapa* L., turnip, turnip rape, bird's rape, field mustard, $2n = 20$, grows in waste places, cultivated fields, orchards, disturbed sites, and gardens, and on roadsides in all of the Southeastern States. The native range of the species is obscure, but both the Mediterranean region and eastern Afghanistan–Pakistan are considered the main centers for the origin of the cultivated forms (McNaughton, 1976a). Complete interfertility, similar chromosome numbers, and lack of sufficient morphological discontinuities between this species and *B. campestris* L. justify the reduction of the latter to varietal rank (*B. Rapa* var. *campestris* (L.) W. D. Koch).[6] The fleshy roots and the biennial habit of *B. Rapa* var. *Rapa* vs. the nonfleshy roots and annual habit of var. *campestris,* which are the only characters separating the two, become unreliable differences when plants of the former escape from cultivation. *Brassica Rapa* is characterized by bright yellow flowers that overtop the floral buds, ascending ("erect-spreading" of some authors) sepals, green and usually setose-ciliate lower leaves, auriculate cauline leaves, and short (6–10 mm) petals. The closely related *B. Napus* L. (*B. Napobrassica* (L.) Miller), rape, colza, swede, rutabaga, Swedish turnip, $2n = 38$, is an amphidiploid that originated in the Mediterranean region a few hundred years ago (McNaughton, 1976b) but does not presently occur in the wild state. It differs from *B. Rapa* in having creamy or pale-yellow flowers not overtopping the floral buds, longer (10–18 mm) petals, and glaucous and glabrous or sparsely pubescent lower leaves. Although *B. Napus* has been reported as a weed from nearly all of the Southeastern States, it is very likely that most reports represent misidentifications of plants of *B. Rapa.* It is very difficult to distinguish between the two species from specimens that lack flowers and lower leaves. Several authors (e.g., Jones, Radford *et al.,* and E. B. Smith) have listed one of the two species in the synonymy of the other, but it is obvious that they are morphologically and cytologically very distinct, and that overwhelming evidence (see below) supports the amphidiploid origin of *B. Napus* from *B. Rapa* and *B. oleracea.*

Brassica juncea (L.) Czern. (*Sinapis juncea* L., *B. juncea* var. *crispifolia* Bailey, *B. integrifolia* (West) O. E. Schulz, *B. cernua* (Thunb.) Forbes & Hemsley), Chinese or Indian mustard, brown mustard, leaf mustard, mustard greens, $2n = 36$, an amphidiploid species originated from *B. nigra* and *B. Rapa* somewhere in the Middle East or Central Asia, is widely distributed in all the states of the Southeast. It is an escape from cultivation and a weed of disturbed sites, roadsides, abandoned fields, and waste grounds elsewhere in North America, the West Indies, and Central and South America. The greatest diversity of forms occurs in India and China, where the species is grown as a vegetable or as an oil-seed crop. *Brassica juncea* has short-petiolate or sessile cauline leaves;

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[6] *Brassica Rapa* and *B. campestris* were simultaneously described by Linnaeus (Sp. Pl. **1:** 666. 1753). Metzger, who was the first to unite the two species, adopted *B. Rapa* for the combined species, and consequently this name has priority (see ICBN Article 57.2. 1983).

ascending sepals; spreading, torulose siliques 3–6 cm long; and seedless, slender beaks 5–10 mm long. Small listed *B. japonica* Sieb. from our area, but it is very likely that he was dealing with plants of *B. juncea* with narrower siliques and more divided leaves. The sectional disposition of *B. juncea* has not been adequately resolved. Salmeen assigned it to sect. MICROPODIUM but placed its parental diploid species in different sections. Other authors put *B. juncea* and *B. Rapa* in the same section.

Brassica oleracea L., $2n = 18$, has been listed as a weed in a few checklists covering parts of our area (e.g., Duncan & Kartesz, Lakela *et al.*, Rich & Thomas). However, I have not seen any specimens from the Southeast, and it is doubtful that the species is a successful weed there. Wild plants of *B. oleracea* are perennials that occupy sea cliffs in Europe, as do their relatives of sect. BRASSICA (sect. *Brassicotypus* Dumort., sect. *Pseudobrassica* Presl, sect. *Lignosae* Widler & Bocquet) that have erect sepals, large (15–30 mm long) petals, auriculate, somewhat fleshy cauline leaves, conical, seedless to two-seeded beaks, and a haploid chromosome number of nine.

Brassica carinata Braun, Abyssinian mustard, Ethiopian rape, $2n = 34$, has been cultivated in Florida as an experimental plant for seed-oil production but has not become naturalized in the United States. Both *B. Tournefortii* Gouan ($2n = 20$) and *B. elongata* Ehrh. ($2n = 22$) are widespread weeds in some of the Pacific and Mountain states, but neither one has reached the Southeast.

The generic limits of *Brassica* changed a great many times in the treatments of early authors. Most North American botanists follow Bailey (1922) and Wheeler in merging *Sinapis* with *Brassica*, while those elsewhere maintain both genera. The boundaries between *Brassica* and some of its nearest relatives (*Sinapidendron, Diplotaxis,* and *Erucastrum*) are not sharply defined. Section BRASSICARIA shows close ties with *Sinapidendron,* and according to Gómez-Campo & Tortosa, the ancestors of *Brassica* may have resembled plants of this section or may have evolved along an evolutionary line phenetically represented by the sequence *Diplotaxis-Erucastrum-Brassica. Brassica* is distinguished from these in being herbs with usually saccate inner sepals, obovate petals, terete or flattened siliques, one-nerved valves, and usually uniseriately arranged globose seeds. *Sinapidendron* differs from *Brassica* in its shrubby habit, basal rosette of leaves, narrowly oblong petals, and oblong seeds, while *Erucastrum* is distinguished by its oblong seeds, usually four-angled siliques, keeled valves, nonsaccate sepals, and sometimes bracteate inflorescences. *Diplotaxis* has biseriately arranged, small (usually less than 1 mm long), oblong to elliptic or oval seeds. All species of *Sinapis, Hirschfeldia* Moench, and *Hutera* Porta have valves with three to seven prominent nerves, while *Brassica* has one prominent midnerve and occasionally inconspicuous lateral ones (FIGURE 1a, c, g).

Nomenclatural instability and lack of agreement on the number and rank of recognizable taxa among the cultivated brassicas have created persistent taxonomic problems. Bailey (1922, 1930, 1940) recognized 22 species in cultivation, while Helm (1963a) accepted more than 40 varieties and forms within *Brassica oleracea* alone. However, it is generally agreed that all the cultivated forms with $n = 10$ belong to *B. Rapa* because they are completely interfertile (P. G. Smith & Welch) and differ only in leaf characters that may be controlled by a few genes (McNaughton, 1976a). Similarly, all the cultivated forms with n = 9 are interfertile and clearly belong to the *B. oleracea* complex.

Species of *Brassica* are pollinated by numerous kinds of insects (Knuth), but the most constant pollinators are various species of the bee genera *Apis, Andrena,* and *Halictus* (McGregor). The flowers of *B. nigra* and *B. oleracea* have highly patterned ultraviolet reflectance (Horovitz & Cohen) and usually secrete abundant nectar daily (estimated at 0.1 ml for each of three days). The sugar concentration in nectar varies among the cultivated species but usually reaches 50 percent, except in some cultivars of *B. Rapa,* where it may approach 69 percent. Protogyny, self-incompatibility, and male sterility are well known in several species. In male-sterile plants, pollen develops normally, but the anther wall fails to dehisce because of the formation of a thick, compact layer (Chowdhury & Das).

The cytogenetic relationships of the six crop species of *Brassica* have been thoroughly investigated (see the reviews of Prakash & Hinata and Yarnell). Three basic diploid species, *B. nigra* (n = 8, genome B), *B. oleracea* (n = 9, genome C), and *B. Rapa* (n = 10, genome A), are the immediate progenitors of the amphidiploids *B. carinata* (n = 17, genome BC), *B. juncea* (n = 18, genome AB), and *B. Napus* (n = 19, genome AC). The allotetraploid origin of the last three species was elucidated first cytologically by Morinaga and U. Extensive supporting evidence obtained from the artificial synthesis and breeding (U; Frandsen, 1943, 1947; Olsson, 1960b, d; Olsson & Ellerström; Prakash, 1973b), seed morphology and anatomy (Berggren, 1962; Mulligan & Bailey), karyotype analysis (Sikka), nuclear DNA content (Verma & Rees), chloroplast DNA (Palmer *et al.*, Erickson *et al.*), glucosinolate distribution (Ettlinger & Thompson; Vaughan, Hemingway, & Schofield; Röbbelen & Thies, 1980b), phenolics (Das & Nybom), and proteins (MacKenzie & Blakely; Robbins & Vaughan; Uchimiya & Wildman; Vaughan, 1977; Vaughan & Waite, 1967b; Vaughan, Denford, & Gordon; Vaughan, Phelan, & Denford; Yadava *et al.*) undoubtedly makes the cultivated brassicas the best-documented example of evolution through allotetraploidy. Contrary to the overwhelming evidence supporting the origin of *B. carinata* from *B. nigra* and *B. oleracea,* Yadava and colleagues have suggested that it is derived from *B. nigra* and *B. Rapa.*

Except in four amphidiploid species (the three above and *Brassica balearica* Pers.) polyploidy is uncommon and probably has not played a major role in the evolution of *Brassica.* Diploid and tetraploid infraspecific taxa are known in both *B. fruticulosa* Cyr. (x = 8) and *B. Gravinae* (x = 10), while plants of *B. dimorpha* Cosson & Durieu (n = 22) are exclusively tetraploids. The remaining species of *Brassica* are diploids with n = 7–11. On the basis of the maximum number of secondarily associated chromosomes during the first metaphase, Catcheside and Alam have speculated that the original base chromosome number for *Brassica* is six. Their hypothesis is supported by many cytological observations on chromosome homology within the genome of a given species (autosyndesis) or among genomes of different species (allosyndesis) in haploid, diploid, and polyploid plants and in hybrids. According to Röbbelen (1960a), balanced secondary polyploidy derived from x = 6 is found in the three diploid cultivated species that have six chromosome types recognizable by certain structural features (e.g., chromosome length, symmetry of arms, and especially shapes of the heterochromatin regions). However, no extant species of *Brassica* is based on six, and all earlier counts reported as having $n = 12$ belong to species of *Sinapis* and *Hutera.*

Although a large number of artificial interspecific and intergeneric hybrids have been obtained (Harberd, 1976; Harberd & McArthur), natural interspecific hybridization is very rare in *Brassica.* Hampered by hybrid sterility (caused by endosperm deficiency and embryo abortion), hybridization among the three cultivated diploid species is very difficult, and the original natural formations of the three cultivated amphidiploid species must have been extremely rare events. All diploids with $2n = 18$ (including *B. oleracea*) are interfertile and produce hybrids with normal meiosis, viable pollen, and good seed set (Snogerup, 1980). However, the species are geographically isolated, and their ranges rarely overlap. The intergeneric hybrid ×*Raphanobrassica* is discussed under *Raphanus.*

The chemistry of the cultivated species, particularly in relation to selection of cultivars high or low in oils, erucic acids, or glucosinolates, has been adequately covered in the reviews of Appelqvist (1976), Appelqvist & Ohlson, Josefsson (1970), and Röbbelen & Thies (1980a, b). The distribution of glucosinolates appears to be most useful taxonomically at the specific level. Chemical differences between *Brassica* and *Sinapis* are found, and the latter contains 4-hydroxybenzylglucosinolate, which is generally lacking in the former. However, Horn & Vaughan have found this compound in sect. BRASSICARIA; both the compound and the section are believed to be anomalous in *Brassica.* Other chemical differences between the two genera have been reviewed by Vaughan (1977). In *B. juncea* two chemical races are recognized: an Indian race with a preponderance of 3-butenylglucosinolate and without mucilage in the seed coat, and an oriental (eastern Asiatic–European) race rich in allylglucosinolate and with a mucilaginous seed coat (Vaughan, Hemingway, & Schofield). Vaughan & Gordon suggested that either *B. juncea* has evolved independently in the two regions (thus agreeing with Olsson (1960b) on the polyphyletic origin of the species) or, more likely, the Indian race has resulted from human selection for edible oil-producing cultivars that lack the toxic allyl isothiocyanate. The seed-protein data, however, do not support such racial distinctions (Denford). The types and amounts of glucosinolates in a given plant may be directly related to its allelochemic defense against certain herbivores or fungal pathogens. The susceptibility of many cultivated brassicas to several fungal diseases, such as the downy mildew (caused by *Peronospora parasitica* (Pers. & Fries) Fries), may have resulted from man's selective breeding for more tasty cultivars with lower concentrations of glucosinolates (Greenhalgh & Mitchell).

Wild cabbage (*Brassica oleracea* subsp. *oleracea*) and all of its relatives of sect. BRASSICA have isolated and spotty distributions along sea cliffs and rocky islets of the Mediterranean, western Europe, and the Canary Islands. Baker has indicated that *B. oleracea* escaping from cultivation has reverted to occupy sea-cliff habitats on the northern side of San Francisco's Golden Gate. Long-distance dispersal of seeds of sect. BRASSICA may be accomplished by sea birds. According to Mitchell & Richards (1979), the wild cabbage may perennate for

20 years and may produce as many as 70,000–100,000 seeds annually. Although it is not known how long these seeds remain viable, those of *B. nigra* included in the classic experiments of Beal (see Darlington) survived in the soil for 50 years.

Crops of *Brassica* are the most important economic plants of the Cruciferae. Probably the earliest known utilization of mustards dates from Sanskrit records in India to 3000 B.C. (Mehra). Some authors have suggested that the ancestral cabbage was cultivated in coastal northern Europe nearly 8000 years ago. Undoubtedly several brassicas of European origin were cultivated long before the Christian Era, but at least three (Brussels sprouts, kohlrabi, and rape) originated only a few hundred years ago.

The cultivated members with $n = 9$ have traditionally been treated as varieties of *Brassica oleracea* but were listed as groups without formal rank by Bailey and colleagues. The most common types grown in our area are Brussels sprouts (var. *gemmifera* Zenk), cabbage (var. *capitata* L.), cauliflower (var. *botrytis* L.), kohlrabi (var. *gongylodes* L.), kales and collards (var. *acephala* DC.), and sprouting broccoli (var. *italica* Plenck). Several authors have stated that the diversity among these varieties could not have evolved from the limited variation presently existing in the wild cabbage and have therefore suggested a multiple origin from more than one ancestral species.

A wide range of leafy forms has been selected in China from plants originally introduced from western or central Asia for seed oils. All of the Far Eastern forms except the Chinese kale (known as *B. alboglabra* Bailey but probably a form of *B. cretica* Lam.) belong to *B. Rapa* and *B. juncea*. The classification of these oriental forms is not settled, and various specific, subspecific, and varietal ranks have been assigned to them (Kitamura; McNaughton, 1976a; Nishi; Helm, 1961, 1963b). The Chinese mustard or pak-choi (*B. Rapa* var. *chinensis* (L.) Kitam.) and the Chinese cabbage or pe-tsai (*B. Rapa* var. *amplexicaulis* Tanaka & Ono), commonly known as *B. pekinensis* Rupr., have the same chromosome number as—and produce fully fertile hybrids with—*B. Rapa*, from which they differ in leaf characters only. Hakuran, a newly developed Japanese vegetable crop, is a leafy form of *B. Napus* that produces "heads" instead of fleshy roots and has been synthesized from crossing the Chinese cabbage with our common cabbage (Nishi).

Various fresh parts of *Brassica* crops are eaten raw, stewed, cooked, fermented in brine, or pickled in vinegar. Many are important fodder for farm animals, and some colorful cabbages and kales are ornamentals. The seeds contain 30–40 percent oil, which is the principal cooking oil in India and is also used as a substitute for olive oil and in the manufacture of margarine in Europe. The seed-cake remaining after the expression of oil contains 25–35 percent protein and is used as a fertilizer. Oil of *B. napus* ranks fifth in terms of the world tonnage of vegetable oil production. It is used in the manufacture of general-purpose grease, lubricants, varnishes, lacquers, soft soap, plastics, resins, vinyl stabilizers, synthetic flavors and odors, flotation agents, insect repellents, nylons, and pharmaceuticals (Ohlson). Table mustard is manufactured from the seeds of *Sinapis alba* L. (contributing the hot principle

4-hydroxybenzyl isothiocyanate) and *B. juncea* or *B. nigra* (providing the pungent principle allyl isothiocyanate). The seeds also are used as a spice in the preparation of pickles and in the seasoning of food items.

Seeds of *Brassica nigra* and *B. juncea* have been used extensively as laxatives, vesicants, stimulants, irritants, rubefacients, emetics, tonics, and antiseptics; employed as remedies for colds, stomach disorders, abscesses, rheumatism, and lumbago; and also used in the preparation of ointments to relieve neuralgia, bronchitis, arthritis, and pneumonia (Perry). Hartwell has listed several species employed in the preparation of plasters, poultices, and juices as remedies for indurations and tumors. Preparations from the vegetative parts are used in China and India as antiscorbutics, antidysenterics, resolvents, and depuratives, and for the treatment of diabetes, chronic coughs, and bronchial asthma. Plasters are applied to swellings or blistered surfaces to promote free discharge and are used to cure warts.

In addition to being obnoxious weeds, several species of *Brassica* are harmful or poisonous to humans and livestock. Some of the weedy and cultivated members cause photosensitization, goiter, pulmonary emphysema, and several serious disorders in the digestive, nervous, and urinary systems of cattle and sheep that may eventually lead to death.

REFERENCES:

Although the references listed below may appear excessive, they represent approximately 26 percent of those consulted during the preparation of this treatment! The wealth of literature dealing with the agronomic, industrial, pathological, physiological, pesticidal, and many related agricultural aspects of the cultivated species is irrelevant to this study and has not been surveyed here. The reader is advised to consult the indexes of the *Bibliography of Agriculture* for leads.

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4. **Erucastrum** K. B. Presl, Fl. Sicula **1:** 92. 1826.

Annual, biennial [or perennial] herbs [rarely subshrubs], usually with simple, appressed, retrorse [or spreading] trichomes [rarely glabrous]. Basal leaves in a rosette or not, petiolate, lyrately pinnatifid [sometimes pinnatisect, runcinate, or undivided]. Cauline leaves resembling the basal ones, usually less divided [rarely pectinate or pinnatisect], short petiolate [or sessile and sometimes auriculate at base]. Inflorescence a terminal, bracteate [or ebracteate], corymbose raceme, conspicuously elongated in fruit. Sepals erect [or spreading], oblong [or linear], not saccate; outer pair sometimes cucullate, narrower than the inner one. Petals yellow or white, short [or long] clawed, obovate [rarely oblanceolate or oblong]. Nectar glands 4; lateral pair flat, prismatic or reniform; median pair usually ovoid [sometimes oblong or cylindrical]. Stamens tetradynamous; filaments not appendaged; anthers oblong or linear, obtuse at apex, sagittate at base. Ovary many ovulate; style distinct; stigma capitate, entire [rarely 2-lobed]. Fruiting pedicels slender [or stout], spreading [sometimes erect and subappressed to rachis]. Siliques linear, quadrangular, rarely subterete, torulose, glabrous [sometimes sparsely pilose or retrorsely scabrous], subsessile [or occasionally borne on short gynophores]; valves somewhat keeled, with a prominent midnerve and slender, usually anastomosing lateral veins, obtuse or emarginate at apex; beak conspicuous [rarely obsolete], usually 3-nerved, seedless [or 1- or 2- (or 3-)seeded], slender, stylelike [sometimes conical]. Seeds uniseriately arranged in each locule, oblong or oval [very rarely globose], usually reticulate, wingless, brown, slightly mucilaginous [or not] when wet; cotyledons longitudinally conduplicate, usually emarginate at apex. Base chromosome numbers 7, 8, 9. (Including *Conirostrum* Dulac.) LECTOTYPE SPECIES: *Sinapis virgata* J. S. & K. B. Presl = *E. virgatum* (J. S. & K. B. Presl) K. B. Presl; see Maire, Fl. Afr. Nord **12:** 204. 1965. (Name from *Eruca,* a genus of the Cruciferae, and *astrum,* indicating an incomplete resemblance.)

A genus of about 20 species primarily distributed in the western Mediterranean region and in most of Africa (except the Sahara and the western part of the continent), with extensions into central and eastern Europe, the Canary Islands, and the Arabian peninsula. Many taxa are endemic to the Iberian peninsula and northwestern Africa, and a few species are indigenous to the Canaries (two), tropical East Africa (two), and South Africa (two). *Erucastrum arabicum* Fischer & Meyer, probably a native of Ethiopia, is a weed widely distributed in Africa, while *E. nasturtiifolium* (Poiret) O. E. Schulz and *E. gallicum* are native in southwestern Europe and naturalized in most of that continent. The last species was introduced to the New World about the turn of the century and has since become abundant in many parts of Canada and the United States.

Erucastrum gallicum (Willd.) O. E. Schulz (*Sisymbrium gallicum* Willd., *S. Irio* L. var. *gallicum* (Willd.) DC., *S. Erucastrum* Poll., *S. hirtum* Host, *E. Pollichii* Schimper & Spenner, *E. vulgare* Endl., *E. inodorum* Reichenb., *E. ochroleucum* Calestani), dog mustard, rocket weed, $2n = 30$, has been reported from several localities in Dade and Palm Beach counties in Florida (Wunderlin) and from Caddo Parish in Louisiana (MacRoberts). The first report of *E. gallicum* in North America was based on two independent introductions in Massachusetts and Wisconsin (Robinson). The species is naturalized in all the provinces of Canada and in many parts of the United States, particularly the Midwest, where it grows in fields, waste places, gardens, and orchards, on roadsides, and along railways. From the other crucifers of our area, *E. gallicum* is easily distinguished by having deeply pinnatifid basal leaves, retrorsely appressed trichomes on the stem, pale yellow flowers, bracteate racemes, torulose linear siliques, strongly one-nerved valves, and slender, seedless beaks.

Patman listed *Erucastrum abyssinicum* (Rich) O. E. Schulz as a cultigen in Florida, but it is very likely that the record is based on a misidentification of plants of *Brassica carinata* Braun that were collected by G. Killinger and E. West and distributed under the former name. The establishment of *E. nasturtiifolium* as a successful weed in North America needs confirmation.

Although several earlier authors have reduced *Erucastrum* to a subgenus or a section of *Brassica* (De Candolle, 1821, 1824; Bentham & Hooker) or *Hirschfeldia* (Von Hayek), recent students of the Cruciferae maintain it as a genus intermediate between these two but more closely related to the former. No sections have been recognized in *Erucastrum.* The genus is distinguished by having usually quadrangular siliques; somewhat keeled, prominently one-nerved valves; oblong or oval, uniseriately arranged seeds; nonsaccate sepals; and occasionally bracteate inflorescences. *Brassica* differs in having terete or flattened siliques, convex valves, globose seeds, ebracteate inflorescences, and usually saccate inner sepals. The boundaries between the two genera are not always clearly drawn, and the distinction between them may rest on a single character. *Hirschfeldia* can easily be confused with some species of *Erucastrum* that have swollen beaks and subappressed siliques, but it is recognized by its erect sepals and three-veined siliques. The venation of valves is a difficult character to assess in mature fruits of *Hirschfeldia*, and young siliques are more useful for this purpose.

Chromosome numbers are known for at least 14 species of *Erucastrum*, and more than half of the taxa are based on eight. Diploid ($2n = 16$) and tetraploid infraspecific taxa are found in *E. rifanum* (Emberger & Maire) Gómez-Campo, *E. nasturtiifolium*, and *E. leucanthemum* Cosson & Durieu, while diploids, tetraploids, and hexaploids (based on eight) occur in *E. littoreum* (Pau & Font Quer) Maire. Octoploidy has recently been reported in *E. meruense* Jonsell ($2n = 64$), a species endemic to Tanzania. Both *E. gallicum* and *E. elatum* (Ball) O. E. Schulz have $2n = 30$ and appear to be amphidiploids. Harberd & McArthur observed eight bivalents in the triploid hybrids obtained from crossing *E. gallicum* with diploid plants of *E. nasturtiifolium* and have suggested that the former is an allotetraploid that may have originated from a parent (with $n = 8$) very closely related to the latter and from another diploid, not yet determined, having $n = 7$. No experimental evidence supports the amphidiploid origin of *E. elatum*, but according to Gómez-Campo (1983), its putative parents probably are very close to *E. littoreum* ($n = 8$) and either *E. virgatum* or *Hirschfeldia incana* (L.) Lagrèze-Fossat (both with $n = 7$). *Erucastrum abyssinicum* ($n = 16$) apparently has unselective stigmas that allow foreign pollen from unrelated genera of the Brassiceae to germinate and penetrate the style (Harberd, 1976). The triploid hybrids, obtained from crossing this species with several unrelated diploids, always have eight bivalents in meiosis—an indication of the autotetraploid origin of *E. abyssinicum*. No diploid populations, however, have been found in this species, but the closely related *E. arabicum* and *E. pachypodum* (Chiov.) Jonsell are diploids.

Seeds of a few species have been analyzed for glucosinolates and fatty acids. Large amounts of allylglucosinolate and traces of three other compounds have been identified from *Erucastrum gallicum*, while 3-methylsulfinylpropyl and 3-methylthiopropyl glucosinolates are the major components in *E. abyssinicum*. Nearly 52 percent of the fatty-acid composition of *E. cardaminoides* (Webb) O. E. Schulz is erucic acid, which makes the species a potentially useful source of industrial oils.

Except for the three weedy species mentioned above, the genus has very little economic importance. *Erucastrum arabicum* is occasionally grown in Ethiopia for seed oils, and the leaves are used as a vegetable.

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5. **Hutera** Porta, Atti Imp. Regia Accad. Rovereto, II. **9:** 109. 1891.

Annual, biennial, or perennial herbs with well-developed taproots [or much-branched rhizomes], sparsely to densely hispid [or glabrous]. Stems erect [rarely procumbent], simple or branched at base. Basal leaves in a rosette [or not], usually long petiolate, pinnatipartite or pinnatisect, with 3–10 pairs of lateral lobes [rarely undivided], entire, repand, or dentate. Cauline leaves petiolate, with fewer and narrower lobes than the basal ones [or undivided]. Inflorescence an ebracteate, corymbose raceme, greatly elongated in fruit. Sepals erect, obtuse, setulose below the apex [or glabrous]; outer pair narrowly oblong; inner one broader, saccate at base. Petals long clawed, obovate [rarely oblong or elliptic], obtuse [rarely emarginate], yellow [or white], usually with dark brown or violet veins; claws slender, usually longer than the sepals. Lateral nectar glands flat, median ones cylindrical [or absent]. Stamens tetradynamous; anthers linear [or oblong], sagittate at base, usually recurved at apex. Ovary many ovulate; style very short; stigma capitate, 2-lobed. Siliques linear, subsessile, torulose [or not], 2-segmented [very rarely transversely jointed], spreading, erect, or reflexed; lower segment dehiscent, terete [or slightly 4-angled], usually many seeded, with 3- or 5-nerved valves; upper segment (beak) indehiscent, persistent, 1–6-seeded, as wide as [or wider] and shorter [or equaling to longer] than the lower segment, linear [or oblong or ovoid], smooth [or torulose to moniliform], ensiform [very rarely inflated and corky]. Seeds uniseriately arranged in each locule, globose, dark brown to black, reticulate, wingless, slightly mucilaginous [or usually not] when wet; cotyledons longitudinally conduplicate, emarginate. Base chromosome number 12. (Including *Brassicella* Fourr. ex O. E. Schulz, *Coincya* Rouy, *Rhynchosinapis* Hayek.) TYPE SPECIES: *H. rupestris* Porta. (Name honoring Rupert Huter, 1834–1919, an Austrian clergyman, amateur taxonomist, plant collector, and distributor of exsiccatae.)

A genus of 12 species distributed in southern and southwestern Europe, particularly the Iberian peninsula, with two species endemic to western and southwestern Britain, one to northern Greece, and one to northwestern Africa. The genus is represented in North America by the naturalized weed *Hutera Cheiranthos* (Vill.) Gómez-Campo (*Brassica Cheiranthos* Vill., *Rhynchosinapis Cheiranthos* (Vill.) Dandy, *Coincya Cheiranthos* (Vill.) Greuter & Burdet), $2n$ = 24, 48, a native of western Europe. It is extremely variable, with several subspecies recognized. The species was first recorded from the New World in 1880 (Brown). It is locally common in pastures and on roadsides in Jackson and Yancey counties, North Carolina (Ahles & Radford; Rollins, 1961) but has not yet been reported from the other states of the Southeast. It is easily distinguished from other crucifers of our area in having pubescent, pinnatisect basal leaves; erect sepals; long-clawed, dark-veined yellow petals; siliques 3–8 cm long; three-veined valves; and ensiform, one- to three-seeded beaks 8–22 mm long. Radford and colleagues have listed the species as *Brassica Erucastrum* L., but according to Pugsley, this name is based on immature plants of *Raphanus Raphanistrum* L.

Both *Hutera* and *Coincya* were published in October, 1891, but the former was published five days earlier (Lacaita, González-Albo). Heywood recognized both *Hutera* and *Rhynchosinapis* and separated them by their siliques, which are transversely jointed in the former but not so in the latter. However, the extensive morphological (Gómez-Campo, 1977a; Clemente & Hernández-Bermejo, 1980a–d; Gómez-Campo & Tortosa) and cytological (Harberd, 1972;

Harberd & McArthur, 1972) data strongly support merging *Rhynchosinapis* with *Hutera.*

Although *Hutera* has been associated with *Brassica, Erucastrum, Hirschfeldia,* and *Erucaria,* its nearest relative is probably *Sinapis,* which it resembles in having three- or five-veined valves, similar chromosome numbers ($x = 12$), globose seeds, and well-developed, usually ensiform, few-seeded beaks. From *Sinapis, Hutera* is easily distinguished by its erect, saccate sepals and its dark-veined petals. The relationship between *Hutera* and *Brassica* is somewhat remote. The latter has one-nerved valves, seedless or few-seeded, nonensiform beaks, and chromosome numbers that are never based on 12.

Little is known about the floral biology of *Hutera.* Knuth suggested that the flowers of *H. Cheiranthos* (listed as *Sinapis*) form long floral tubes (ca. 1 cm) by the close coherence of the sepals and petal claws and are therefore adapted to pollination by Lepidoptera, such as members of the butterfly genus *Anthocharis.* Cross-pollination occurs as the insect probes its proboscis between the anthers of the median stamens and touches the stigma before reaching the nectar that accumulates in the pouches of the lateral sepals. According to Knuth, the large median nectaries do not secrete nectar but the small lateral ones do.

Chromosome numbers have been reported for all species of *Hutera,* and all except *H. nivalis* (Boiss. & Heldr.) Gómez-Campo are diploids or tetraploids based on 12. Although this species has $2n = 20$ (Strid & Franzén), further counts are needed to establish whether or not such a number is constant for it. Tetraploidy is known in *H. Johnstonii* (Samp.) Gómez-Campo and in some subspecies of *H. pseudoerucastrum* (Brot.) Gómez-Campo and *H. Cheiranthos.* The last species was first known as a tetraploid, and on the basis of its forming 24 bivalents at meiosis, Sikka suggested that it is an allotetraploid derived from *H. Wrightii* (O. E. Schulz) Gómez-Campo and *H. monensis* (L.) Gómez-Campo. However, the discovery of diploid populations in *H. Cheiranthos* (Favarger, 1965) and bivalent-forming autotetraploids in *Hutera* (Harberd, 1976) do not support Sikka's hypothesis.

Although natural hybridization has not yet been reported in *Hutera,* artificial crossing between *H. Cheiranthos* and *H. monensis* and between each of these and *H. hispida* (Cav.) Gómez-Campo, *H. longirostra* (Boiss.) Gómez-Campo, and *H. leptocarpa* González-Albo show an almost complete bivalency in the hybrids (Harberd & McArthur, 1972). On the other hand, artificial intergeneric hybrids between *Hutera* and *Brassica* and between *Hutera* and *Diplotaxis* gave mean numbers of bivalents of 2.2–4.7 (Harberd & McArthur, 1980).

The chemistry of *Hutera* is poorly understood. A single glucosinolate (5-methylthiopentyl) has been identified from the seedlings of *H. monensis* (Cole, 1976), and the fatty-acid composition of the seeds of *H. Cheiranthos* (listed as *Brassicella Erucastrum*), *H. leptocarpa,* and *H. longirostra* show a preponderance of linolenic and erucic acids, with substantial amounts of palmitic acid in the last species (Appelqvist, 1971; Kumar & Tsunoda, 1980).

As in several genera of the Brassiceae, *Hutera* shows reductional trends in fruit length accompanied by elaboration of the beak. The ensiform beaks probably aid in dispersal by animals. Beaks can persist for a few years in the soil, and seed germination takes place only after their walls disintegrate or break open.

Except for the weedy *Hutera Cheiranthos,* the genus has no economic importance.

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6. **Sinapis** Linnaeus, Sp. Pl. **2:** 668. 1753; Gen. Pl. ed. 5. 299. 1754.

Annual [rarely perennial] herbs, glabrous or with simple, retrorse or spreading trichomes. Stems erect, leafy, often branched above. Basal leaves petiolate, usually not in a rosette, lyrate or pinnatifid to pinnatisect, rarely undivided [or bipinnatipartite], usually coarsely dentate; terminal lobe larger than the lateral ones. Upper cauline leaves short petiolate or sessile, entire or shallowly divided. Inflorescence an ebracteate, corymbose raceme, greatly elongated in fruit. Sepals yellowish, widely spreading, rarely reflexed, not saccate at base, oblong or linear, glabrous or sparsely [to densely] hispid or villous on the dorsal side. Petals yellow, obovate; claws nearly as long as the sepals. Nectar glands 4, the lateral ones prismatic, flat [rarely lobed], the median ones oval, usually not lobed. Stamens tetradynamous; filaments linear, not appendaged; anthers oblong, obtuse. Ovary sessile, glabrous or pubescent; style long; stigma large, 2-lobed. Fruiting pedicels slender or stout, straight [rarely curved], ascending to divaricate [sometimes erect or recurved and appressed to rachis]. Siliques strongly beaked, linear or oblong, terete or somewhat flattened or angled, glabrous or hispid [or villous] with long trichomes and with or without much shorter, retrorse ones; lower (valvular) segment dehiscent, few to many seeded, usually torulose; valves convex, with 3–7 prominent veins, thin or thick [rarely hardened and inconspicuously veined]; upper segment (beak) indehiscent, 0–2[–10]-seeded, straight [or recurved], terete or strongly compressed, ensiform or conical, thick [or corky], equaling or shorter [or much longer] than the lower segment, usually smooth [rarely torulose, ribbed, or tuberculate]. Seeds uniseriately arranged in each locule, globose [very rarely slightly flattened], wingless, mucilaginous or not when wet, pendulous in the valvular part, erect in the beak, yellow or brown, sometimes black, slightly to strongly reticulate or alveolate; cotyledons longitudinally conduplicate, much wider than long, emarginate, glabrous or pubescent. Base chromosome numbers 7, 9, 12. (Including *Agrosinapis* Fourr., *Bonannia* K. B. Presl, *Leucosinapis* Spach, *Rhamphospermum* Andrz. ex Besser, *Sinapistrum* Chev.) LECTOTYPE SPECIES: *S. alba* L.; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. **2:** 191. 1913. (Name from Greek *sinape* or *sinapi,* mustard, in reference to the flavor of the seeds.)—CHARLOCK, MUSTARD.

A genus of seven species, all except *Sinapis Aucheri* (Boiss.) O. E. Schulz, an endemic of western Iran and eastern Iraq, native to the Mediterranean region. Two species are indigenous to Egypt, and two others are restricted to southwestern Europe and northern Africa. Both *S. alba* and *S. arvensis* L. are weeds widely naturalized throughout the world. They occur in all the Southeastern States in gardens, grainfields, cultivated land, waste places, and disturbed grounds, on roadsides, and along railroad tracks.

Four well-defined sections have been recognized by Schulz (1919). Section SINAPIS (sect. *Leucosinapis* DC.) (annuals; siliques generally with long, spreading trichomes usually mixed with more numerous short, retrorse ones, rarely glabrescent; beaks ensiform; seeds mucilaginous when wet) contains *S. flexuosa* Poiret of southern Spain and northwestern Africa and *S. alba* L. (*Brassica alba* (L.) Rabenh., *B. hirta* Moench), white mustard, yellow mustard, $2n = 24$, probably native to the Mediterranean region and Crimea. The latter is distinguished by the sectional characters above and by its dissected lower leaves and short (2–4 cm) siliques with two- to four-seeded locules.

Section CERATOSINAPIS DC. (annuals; siliques glabrous, rarely sparsely hispid; beaks conical, straight, one- or two-seeded; seeds many, not mucilaginous when wet) includes the cosmopolitan weed *Sinapis arvensis* and the Egyptian endemics *S. Allionii* Jacq. and *S. turgida* (Pers.) Delile. *Sinapis arvensis* L. (*Brassica arvensis* (L.) Rabenh., *B. sinapistrum* Boiss., *S. orientalis* L., *S. Kaber* DC., *B. Kaber* (DC.) Wheeler, *S. Kaber* var. *pinnatifida* (Stokes) Wheeler), charlock, field kale (Muenscher), wild mustard (Small), less commonly known as field mustard, crunchweed, and California rape, $2n = 18$, is one of the most widely distributed weedy crucifers in our area. It can easily be recognized by its subsessile cauline leaves, spreading sepals, strongly three-nerved valves, and conical, one- or two-seeded beaks.

The two remaining sections are monotypic, and neither is represented in our flora. Section ERIOSINAPIS Cosson contains *Sinapis pubescens* L., $2n = 18$, indigenous to northern Africa, Italy, Sicily, and Sardinia and easily recognized by its perennial habit and villous siliques with recurved beaks. *Sinapis Aucheri* of sect. CHONDROSINAPIS O. E. Schulz is anomalous in the genus because of its long, torulose, corky, six- to ten-seeded beaks and its haploid chromosome number of seven.

Sinapis can be separated from its closest allies in the Brassiceae by its combination of nonsaccate sepals; uniformly colored yellow petals; and strongly beaked fruits with one- or two- (to ten-)seeded beaks, three- to seven-veined valves, and uniseriately arranged globose seeds. It is closely related to *Hutera*, from which it is distinguished by its spreading, nonsaccate sepals and its lack of dark venation in the petals. Recent North American authors follow Bailey and Wheeler by merging *Sinapis* with *Brassica*, while botanists elsewhere maintain both genera. The latter has one-nerved valves and erect to ascending (rarely spreading) sepals, with the lateral pair usually saccate. The two genera also differ in their mustard oils and seed proteins. However, in lipid content *S. arvensis* shows more affinity to *Brassica* than does *S. alba* (Appelqvist, 1976), and some authors (e.g., Takahata & Hinata, 1980) have suggested that *S. arvensis* may be the connecting link between the two genera.

Numerous infraspecific taxa have been recognized in *Sinapis pubescens*, *S. arvensis*, and *S. alba*, but the majority of them are based primarily on characters such as the amount of pubescence, the orientation of the fruits, the lobing of the lower leaves, and the color of the seeds, all of which exhibit continuous variation that may be encountered within the same population. Therefore, no subordinate taxa are recognized here for plants of the last two species.

Because the sepals are spreading, the nectar in *Sinapis* may appear to be accessible to insects from the side of the flower. However, the dense grouping of the flowers makes it more convenient for sizeable insects to approach the nectar from the top of the flower, thus effecting pollination. The flowers of *S. alba* and *S. arvensis* have highly patterned ultraviolet reflectance and differ in the shape of their nectar guides (Horovitz & Cohen). More than 60 species of bees, butterflies, flies, and wasps have been recorded by Fogg and Knuth as visitors of the latter species, which is a very important source of nectar and pollen for honey bees (*Apis mellifera*) in fields that it heavily infests. The flowers of *S. alba* are odoriferous and secrete abundant nectar with a sugar concentration of 60 percent (Free). These floral adaptations (including the ultraviolet pattern) clearly contradict Hemingway's suggestion of pollination by wind in *S. alba*.

The sectional classification of the genus is supported by data on chromosome numbers. Members of sect. SINAPIS have $n = 12$, and those of sects. ERIOSINAPIS and CERATOSINAPIS have $n = 9$, while sect. CHONDROSINAPIS has $n = 7$. Easterly (1963) has reported $n = 8$ and $n = 16$ for *Sinapis arvensis*, but the counts probably are erroneous and have not been reported again. Naturally occurring polyploids have not been found in the genus. Mukherjee described the karyotype of *S. alba* (as *Brassica alba*) as consisting of one pair of long chromosomes with two constrictions and 11 pairs of short chromosomes with median or submedian constrictions.

Both *Sinapis alba* and *S. arvensis* have been thoroughly surveyed for sterols, fatty acids, tycophenols, paraffins, mustard oils, alkaloids, flavonoids, and seed proteins, but the other species of the genus have received only minimal attention in chemical studies. The two species contain 4-hydroxybenzylglucosinolate, which has not been found in the typical members of *Brassica* (see the treatment of this genus). Smaller amounts of 3-butenyl and 2-phenylethyl glucosinolates are found in *Sinapis,* but these are more abundant in *Brassica.* Other chemical differences, particularly in seed proteins, support the maintenance of *Sinapis* as a genus distinct from *Brassica.*

In seed-coat anatomy *Sinapis arvensis* resembles several species of *Brassica* and *Hutera*: all have a nonmucilaginous epidermis followed by radially elongated palisade cells. In *S. alba* two layers of subepidermal collenchyma are located between the mucilaginous epidermis and the isodiametric palisade cells (Vaughan & Whitehouse). The seed coat is coarsely reticulate in *S. alba* and minutely so in *S. arvensis* (Mulligan & Bailey, 1976), although Murley listed the former as having alveolate seeds, and Berggren indicated that both have an indistinct reticulum.

Sinapis arvensis is one of the most obnoxious weeds, and it is notoriously difficult to eradicate from crop fields. Factors contributing to its success and persistence in arable land include the immense productivity (estimated at a maximum of 25,000 seeds per plant (Markgraf)), the seed longevity (up to 75 years (Vaughan & Hemingway)—exceedingly high for a crucifer), the enforced dormancy when the seeds are buried at depths of many centimeters, the rapid germination when the seeds are exposed to favorable conditions, and the high relative growth rates of its vegetative organs (Fogg). The ability of the seeds to remain viable in the droppings of birds that feed on them probably plays an important role in the natural dispersal of *S. arvensis.* The seeds contained in the beak of the fruit may not germinate until the beak has rotted.

Sinapis alba subsp. *dissecta* (Lag.) Bonnier, a weed of flax fields in the Mediterranean region and Crimea but not yet introduced to our area, differs from subsp. *alba* in having bipinnatifid leaves, slender growth, glabrous or very sparsely pubescent siliques and stems, and flattened, reddish brown seeds. All these features have their analogues among other flax weeds and, according to Hjelmqvist, may have evolved through the selection of flax characters. It is quite difficult to remove the seeds of *S. alba* subsp. *dissecta* from those of flax (*Linum usitatissimum* L.) by winnowing because of their similarity in shape, weight, and size (Malzev).

The seeds of *Sinapis alba* are used for the manufacture of table mustard (see *Brassica*) and for the production of oils for making soap and mayonnaise, lubrication, and cooking (Vaughan & Hemingway). The seed cake contains 25–35 percent protein, and because of its high nitrogen content it is used as a fertilizer. The seeds of *S. arvensis* are used in eastern Europe for making poor-quality table mustard, while the young green parts are eaten as a salad in some parts of the Caucasus. The whole plant also is used as a green fodder.

The seeds have been used as a carminative, a diuretic, an emetic, an expectorant, a stimulant, a rubefacient, and a diaphoretic; as a remedy for bronchitis and dyspepsia; and in the preparation of an ointment to relieve neuralgia, arthritis, and rheumatism (Perry, Rosengarten). Hartwell has listed *Sinapis* *alba* as a source for preparations to cure tumors, sarcoma, carcinoma, endothelioma, and indurations of the skin.

Sinapis arvensis reduces the yield of some cereals (and probably other crops) to 53–69 percent in heavily infested fields (Mulligan & Bailey, 1975). Feeding on *S. alba* and *S. arvensis* may cause gastroenteritis, diarrhea, and irritation of the upper digestive tract and mouth of cattle and sheep, and the two species have been suspected of evoking photodermatitis (Kingsbury; Mitchell & Rook). In addition to being obnoxious weeds, these species are hosts for viruses and fungi that also attack many cruciferous vegetable crops.

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7. **Diplotaxis** A. P. de Candolle, Syst. Nat. **2:** 628. 1821.

Annual or perennial herbs, sometimes woody at base, glabrous or with spreading or retrorse trichomes [rarely scabrous], sometimes glaucous. Stems erect or ascending [rarely procumbent]. Basal leaves petiolate, forming a rosette or not, pinnatifid to pinnatisect or lyrate to sinuate-dentate, rarely entire [or bipinnatipartite]. Cauline leaves present or absent, short petiolate or sessile [occasionally auriculate]. Inflorescence an ebracteate, corymbose raceme [rarely with lowermost flowers from axils of uppermost leaves], greatly elongated in fruit. Sepals oblong or linear, erect or spreading, obtuse or acute, sometimes scarious at margin, glabrous or with a subapical tuft of hairs [or hairy on entire abaxial side]; inner pair as wide as [or much wider than] outer pair, usually not [rarely strongly] saccate at base. Petals broadly [or narrowly] obovate, attenuate to short [or long] claws, usually yellow [sometimes violet, lilac, or white]. Nectar glands 4, the lateral pair flat, usually prismatic or reniform, the median pair filiform or oval [sometimes clavate], lobed or not. Stamens tetradynamous; filaments free, linear, not appendaged; anthers oblong, cordate or sagittate at base, all fertile [or rarely the lateral pair sterile], median ones introrse or extrorse. Ovary usually with very numerous (to 260) ovules; style short [or obsolete]; stigma capitate or conical, 2-lobed [sometimes the lobes decurrent]. Fruiting pedicels somewhat stout [or slender], erect-ascending to divaricate [or reflexed]. Siliques dehiscent, linear, torulose, compressed parallel to the septum [or terete], borne on short [or long] gynophores [or subsessile]; valves 1-nerved, glabrous, somewhat thick [or membranaceous], obtuse or emarginate at apex; beaks 3-veined, seedless [or 1- or 2-seeded], narrower than [or as wide as] the valves, slightly flattened [or terete], cylindrical [or conical or obconical, rarely obsolete]. Seeds biseriately arranged in each locule, slightly compressed, usually very small (0.4–0.7(–1) mm long), ovoid, elliptic, or oblong, light brown, minutely reticulate or smooth, wingless, not [or slightly] mucilaginous when wet; cotyledons longitudinally conduplicate. Base chromosome numbers 7, 8, 9, 10, 11, 13. (Including *Pendulina* Willk.) LECTOTYPE SPECIES: *Sisymbrium tenuifolium* L. = *Diplotaxis tenuifolia* (L.) DC.; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. **2**: 194. 1913. (Name from Greek, *diploös,* double, and *taxis,* row or arrangement, in reference to the two-rowed (biseriate) arrangement of seeds in each locule of the fruit.)—SAND ROCKET.

About 25 species distributed in central Europe and the Mediterranean region, particularly in northwestern Africa, and extending eastward to Pakistan and western India, with a group of five species endemic to the Cape Verde Islands (Rustan & Borgen). *Diplotaxis nepalensis* Hara (isotype at A!), recently described from the Karnali Valley in western Nepal, extends the range of the genus much farther to the east. In nearly all aspects of the plant, *D. nepalensis* can easily be treated as a minor variant of the highly polymorphic *D. Harra* (Forsskål) Boiss., a species distributed from Morocco to Pakistan. At least four species are weedy in much of Europe, western Asia, and northern Africa. Of these, three have been brought to the New World as ballast plants during the last third of the nineteenth century; two are naturalized and sporadically distributed in the southeastern United States.

The sectional classification of *Diplotaxis* has not been treated adequately. The four sections recognized by Schulz (1919) have been raised by Nègre (see Markgraf) to three subgenera, of which two are monotypic. Characters such as the number of ovules, the length of the gynophore, and the orientation of the sepals have been emphasized in recognizing infrageneric groups in *Diplotaxis,* but these may vary between the populations of a given species.

Section DIPLOTAXIS (sect. *Catocarpum* DC.) (perennials, rarely annuals; sepals spreading or ascending, not saccate at base; ovules (50–)80–150; gynophore (1–)2–8 mm long; beak obsolete, or seedless and to 2 mm long) is represented in our flora by *D. tenuifolia* (L.) DC. (*Sisymbrium tenuifolium* L., *Sinapis tenuifolia* (L.) R. Br., *Brassica tenuifolia* (L.) Fries), wall rocket, slim-leaf wall rocket, flixweed (Small), $2n = 22$, a species native to southern and central Europe but naturalized elsewhere on that continent and in North America. Although *D. tenuifolia* has been reported from ballast and waste places in Florida, Alabama, and Louisiana (Small, Mohr), it has not been included in any of the recent plant checklists covering these states. It may have been overlooked, or it may have failed to become a successful weed in the Southeast. Plants of *D. tenuifolia* can easily be recognized; they are suffruticose perennials with pinnatipartite, petiolate cauline leaves, yellow petals two to three times longer than the sepals, and ascending siliques with seedless beaks and short gynophores 1–3 mm long.

Section ANOCARPUM DC. (annuals, rarely perennials; sepals spreading or ascending, equal at base; ovules 20–60; gynophores absent or to 1 mm long; beak 1- or 2-seeded, rarely seedless, conical or cylindrical) is represented in the southeastern United States by *Diplotaxis muralis* (L.) DC. (*Sisymbrium murale* L., *Sinapis muralis* (L.) R. Br., *Brassica muralis* (L.) Boiss.), sand rocket, stinking wall rocket, cross weed (Small), $2n = 42$. A native of southern and central Europe, *D. muralis* is widely naturalized in Canada, the United States, and the West Indies, but is less so in Mexico and South America. It grows in disturbed sites, abandoned fields, waste places, and grasslands, and along beaches and roadsides. Smith has reported it from Arkansas (Howard County), but earlier records from Alabama, Florida, and Louisiana have been based on ballast plants that may have failed to persist. The record of *D. muralis* from North Carolina was based on misidentification of plants of *Hutera Cheiranthos* (under *Hutera* see Ahles & Radford). From the other crucifers of our area, *D. muralis* can be distinguished by its annual habit, its rosette-forming, lyrately lobed or sinuately dentate leaves, its leafless or few-leaved stems, its yellow flowers, and its usually sessile, erect-ascending siliques 15–45 mm long with seedless beaks.

Diplotaxis has been considered by Von Hayek and Rytz to be basal to the rest of the Brassiceae, and nearly all of the primitive characters suggested by Gómez-Campo (1980a) for the tribe are found in the genus. However, the relationships between *Diplotaxis* and its nearest relatives of subtribe Brassicinae have not been established adequately. The genus has biseriate, small (usually less than 1 mm long), oblong or oval seeds; siliques with gynophores and one-nerved flattened valves; and two-lobed stigmas. *Brassica* can be separated from *Diplotaxis* by its larger, globose, and uniseriately arranged seeds. The boundaries between the two, however, become less sharply defined if some northwestern African taxa with subbiseriate seeds are considered. *Sinapidendron* differs from *Diplotaxis* in its terete siliques, uniseriate seeds, and entire stigmas. The two species of sect. HESPERIDIUM O. E. Schulz (*D. acris* (Forsskål) Boiss., of northern Africa and Arabia, and *D. Griffithii* (Hooker & Thomas) Boiss., of the Punjab, Afghanistan, and western Pakistan) resemble *Moricandia* in nearly all aspects of the flower and in certain features of the fruit. However, *Moricandia* differs from *Diplotaxis* in lacking median nectaries and in having sessile, terete or tetragonal siliques and larger, usually margined or winged seeds.

Little is known about the breeding systems and pollination ecology of *Diplotaxis,* and the scant data indicate that a few species of flies, bees, butterflies, and beetles visit the flowers of *D. muralis* and *D. tenuifolia* (Knuth). The former is self-compatible, while the latter and *D. erucoides* (L.) DC. are usually self-incompatible. The last species was introduced to this country more than a century ago, but it appears to be restricted to a few places along the east coast north of our area. The median anthers of *D. tenuifolia* and *D. muralis* are extrorse, and in the latter they and the sepal tips reflect ultraviolet light, while the rest of the flower absorbs it (Markgraf). In *D. acris* the veins of the petals absorb UV light, but the rest of the blade reflects it (Horovitz & Cohen).

Chromosome numbers are known for at least 20 species, and with the exception of $n = 12$, which has not yet been found, a continuous series of haploid numbers from seven to 13 is present in *Diplotaxis.* Aneuploidy may have played an important role in the evolution of the genus. Species with $n = 13$

(*D. Harra*, its relatives, and the Cape Verdean species) are treated as diploids, and although Harberd (1976) agreed with that, he believed that they may have originated either by allotetraploidy between a species with $2n = 14$ and an unrecorded one with $2n = 12$, or by the aneuploid loss from tetraploids with $2n = 28$. However, there is no evidence to support either of these hypotheses. Earlier chromosome counts deviating from $2n = 42$ for *D. muralis* may have been erroneous. Harberd & McArthur (1972) have presented experimental evidence supporting the allotetraploid origin of this species from *D. tenuifolia* ($2n = 22$) and *D. viminea* (L.) DC. ($2n = 20$). Hybrids resulting from the cross *D. muralis* × *D. tenuifolia* almost always showed 11 bivalents and ten univalents at meiosis, while those obtained from *D. muralis* × *D. viminea* gave ten bivalents and 11 univalents. Furthermore, the occasional occurrence of reduced lateral stamens in *D. muralis* is most likely inherited from *D. viminea*—the only species in the genus with sterile and highly reduced lateral stamens.

Natural interspecific hybrids in *Diplotaxis* appear to be very rare. Schulz (1919) described *D.* ×*Schweinfurthii* from Egypt as a hybrid between *D. acris* and *D. Harra* and cited a few collections from Germany, Yugoslavia, and Sweden (see also Johansson) as hybrids between *D. muralis* and *D. tenuifolia*. Little experimental work has been conducted on interspecific hybridization in the genus, but extensive intergeneric crosses between *Diplotaxis* and *Brassica, Erucastrum, Hirschfeldia, Hutera, Sinapidendron,* and *Sinapis* have successfully been made by Harberd (1976) and Harberd & McArthur (1980).

Four species have been surveyed for glucosinolates. *Diplotaxis viminea* and *D. tenuifolia* have high concentrations of 4-methylthiobutylglucosinolate, but the latter also contains a few related nonvolatile compounds. Allylglucosinolate is the principal component in both *D. erucoides* and *D. muralis*. The scant chemical data show some differences between species. Analyses of the fatty-acid composition of ten species show that the pattern of *Diplotaxis* is distinct from that of the closely related *Brassica*. The latter has higher concentrations of erucic acid and usually lower amounts of linolenic and palmitic acids than does *Diplotaxis*.

Diplotaxis has the smallest and lightest seeds in the Brassiceae. They are usually less than a millimeter long and may weigh as little as 0.05 mg (*D. Harra*), which is less than one two-hundredth the seed weight of some species of *Cakile* and *Crambe* that have the heaviest (10–15 mg) seeds in the tribe. Plants of *D. acris* and *D. Harra* produce enormous numbers (more than 200 per silique) of dustlike seeds that can easily be transported by strong winds for several hundred miles. Both species are widely distributed in the Sahara and in Arabia, and the latter species has an almost continuous distribution extending more than 7400 km (4500 mi) from Morocco to western Pakistan.

No local uses have been reported for the genus, and except for the four weedy species mentioned above, *Diplotaxis* has no economic importance. Mitchell & Rook mentioned that *D. erucoides* and *D. tenuifolia* have irritant properties.

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8. **Eruca** Miller, Gard. Dict. abr. ed. 4. Vol. 1 (alph. ord.). 1754.

Annuals [or caespitose and rhizomatous perennials], hispid or pilose with simple, spreading or retrorse trichomes, sometimes glabrous. Stems leafy [or scapose]. Basal leaves petiolate, [forming or] not forming a distinct rosette, usually lyrately pinnatifid or pinnatipartite, rarely bipinnatisect or undivided. Cauline leaves (when present) sessile or short petiolate, divided or coarsely dentate to subentire. Inflorescence an ebracteate, many-flowered, corymbose raceme, greatly elongated in fruit. Sepals erect, oblong or linear, caducous [or persistent until fruit matures], green or violet, glabrous or with a subapical tuft of trichomes, sometimes pilose or setulose along abaxial side; outer [and inner] sepals cucullate, inner ones saccate at base. Petals broadly obovate [or oblanceolate], cream or yellow with dark brown or violet veins [or entire blade violet]; claws well developed, as long as or longer than the sepals. Nectar glands 4 [2], lateral pair prismatic, median pair ovoid or oblong [or absent]. Stamens tetradynamous, not appendaged; filaments linear; anthers oblong or linear, sagittate at base. Ovary many ovulate; style present; stigma 2-lobed, the lobes usually decurrent. Fruiting pedicels glabrous or pubescent, erect to ascending, subappressed to the rachis [rarely divaricate]. Siliques subsessile, dehiscent, linear or oblong to elliptic, inflated, terete or slightly tetragonal, glabrous or retrorsely hispid or scabrous; valves strongly 1-nerved, slightly keeled, convex, somewhat coriaceous; beaks seedless, prominently 1-nerved, occasionally with obscure lateral nerves, flattened [rarely tetragonal], ensiform, acute or acuminate, shorter to longer than the valves. Seeds biseriately arranged, oval, wingless, reticulate, slightly to copiously mucilaginous when wet, orange or brown; cotyledons longitudinally conduplicate, emarginate. Base chromosome number 11. (Including *Euzomum* Link, *Velleruca* Pomel.) LECTOTYPE SPECIES: *Eruca sativa* Miller (*Brassica Eruca* L.) = *E. vesicaria* (L.) Cav. subsp. *sativa* (Miller) Thell.; see Maire, Fl. Afr. Nord **12:** 303. 1965. (Name the classical Latin name for the above species, but its origin uncertain; most likely derived from *eructo* (or the Greek *ereugomai*), to belch or eruct, or from *uro,* to burn, in reference to the hot taste of the plant.)—GARDEN ROCKET, ROCKET SALAD.

Three species, of which *Eruca loncholoma* (Pomel) O. E. Schulz and *E. setulosa* Boiss. & Reuter are endemic to Algeria; the third, *E. vesicaria,* is probably a native of the Mediterranean region but is naturalized throughout Europe, in much of Asia and Africa, and sporadically in Australia and North and South America. The genus is represented in the southeastern United States by *E. vesicaria* (L.) Cav. subsp. *sativa* (Miller) Thell. (*Brassica Eruca* L., *E. sativa* Miller, *E. Eruca* (L.) Ascherson & Graebner, *Raphanus Eruca* (L.) Crantz), garden rocket, rocket salad (less commonly: rocket, edible rocket, and roquette), $2n = 22$, a weed of cultivated fields, roadsides, and waste places. Although I have not seen specimens of this taxon from the southeastern United States, there is no doubt that it occurs there. The species is found in all of the states bordering our area and is included in the treatments of Small and Rickett. *Eruca vesicaria* subsp. *sativa* is easily distinguished from the other crucifers of our flora by its yellow or cream-colored petals with dark brown or violet veins, erect sepals, appressed siliques, one-nerved valves, ensiform beaks, and biseriately arranged seeds. Subspecies *vesicaria,* which is endemic to Spain, the Balearic Islands, and northwestern Africa, differs from subsp. *sativa* in its cucullate inner sepals and its persistent calyx that remains attached until the fruits are nearly ripe.

Eruca is well defined by its erect sepals, biseriately arranged seeds, one-nerved valves, somewhat decurrent stigmas, and long, seedless, ensiform or tetragonal beaks. It is related to *Diplotaxis,* particularly to sect. HESPERIDIUM O. E. Schulz, from which it differs in the ensiform beaks of the siliques and in the larger and fewer seeds. Some authors (e.g., Von Hayek and Rytz) have suggested a direct relationship between *Eruca* and *Sinapis,* but the two should be loosely associated. The latter is readily distinguished from *Eruca* by its spreading sepals, uniseriately arranged seeds, and three- to seven-veined valves. Both *E. setulosa* and *E. loncholoma* resemble *Brassica* sect. BRASSICARIA, but the relationship between the two genera is not entirely clear.

The petals of *Eruca vesicaria* exhibit high absorbance of ultraviolet light in the blade and low reflectance in the claw (Horovitz & Cohen). More than 100 species of insects have been reported as visitors of the flowers, but the most common pollinators appear to be members of the bee genera *Apis, Andrena,* and *Halictus.* Self-incompatibility has been reported by many authors, but the expression of this character is not absolute, and selfing may lead to the formation of short siliques with few seeds. Unlike that of the rest of the Cruciferae, the incompatibility system in *E. vesicaria* is controlled by at least three pairs of complementary genes, each with several alleles (Verma *et al.,* Lewis).

Chromosome numbers are known only for *Eruca vesicaria.* Although 11 bivalents have usually been found, Wills observed quadrivalents and hexavalents, as well as frequent chromosomal bridges. Despite these meiotic irregularities, pollen stainability was nearly 99 percent. The karyotype consists of single pairs of long and short and nine pairs of medium-sized metacentric chromosomes, of which the long pair has median and subterminal constrictions and one medium-sized pair has satellites (Mukherjee).

Artificial intergeneric hybridization between certain members of the Brassiceae and *Eruca vesicaria* has been successful if the latter is used as the maternal plant and the crossing is done at the bud stage. The stigmas of *Eruca* are unselective for foreign pollen and allow germination of and style penetration by pollen tubes of members of several genera (Harberd, 1976; Sampson). On the other hand, the pollen of *Eruca* always fails to germinate on foreign stigmas.

The seeds of *Eruca vesicaria* yield 22–36 percent oil, and the plant is considered to be among the crucifers richest in erucic-acid content. The unsaponifiable matter contains sterols dominated by β-sitosterol (49 percent) and campesterol (32 percent). The seeds contain high concentrations of 4-methylthiobutylglucosinolate and an enzyme that converts the glucosinolates to thiocyanates (Schlüter & Gmelin).

The earliest cultivation of *Eruca vesicaria* dates back to the ancient Romans and Greeks. It is currently grown in Europe (and infrequently in North America) as a salad plant and is cultivated extensively in central and western Asia for seed oil. The oil is used in pickling and as an illuminant and a lubricant; in India it is used for massaging the body, applied to the hair, and employed in the treatment of vitiligo and as a vesicant. However, it is known to cause allergic dermatitis, photodermatitis, and persistent melanosis of the skin (Mitchell & Rook). The seed cake and the entire plant are used as fodder for domestic animals. In southern Europe the young leaves are used as a stimulant, an antiscorbutic, a diuretic, and a stomachic, but a strong dose may cause vomiting. In India the whole plant is considered to be an aphrodisiac (Caius), and electuary preparations have been used to cure indurations of the liver (Hartwell). Finally, the species is an obnoxious cosmopolitan weed and is a host for several fungi and viruses that also attack cruciferous crops.

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9. **Raphanus** Linnaeus, Sp. Pl. **2:** 669. 1753; Gen. Pl. ed. 5. 299. 1754.

Annual, biennial, or rarely short-lived perennial herbs, scabrous or hispid, with simple, spreading or appressed trichomes, sometimes glabrous. Roots slender or thick, slightly woody, usually fleshy and variable in size, shape, and color in the cultivated forms. Stems erect [or prostrate], simple or branched. Basal leaves petiolate, sometimes forming a rosette, lyrately lobed or pinnatifid to pinnatisect; lateral lobes in 2–20 pairs, distant or contiguous; terminal lobe broadly ovate to orbicular, much larger than the lateral ones. Upper cauline leaves short petiolate or subsessile, smaller and less lobed than the lower ones. Inflorescence an ebracteate, many-flowered, corymbose raceme, usually greatly elongated in fruit. Sepals erect, oblong or linear, glabrous or hispid; inner pair saccate at base. Petals long clawed, white, yellow, lilac, or violet, usually with dark veins, broadly obovate, obtuse or truncate at apex. Nectar glands 4, the lateral pair prismatic, the median pair filiform or cylindrical. Stamens tetradynamous; filaments slender, not appendaged; anthers oblong. Ovary sessile, 2- to many-ovulate; style slender; stigma capitate, slightly 2-lobed. Fruiting pedicels ascending to divaricate [or reflexed and subappressed to the rachis]. Siliques indehiscent, transversely jointed, 2-segmented, linear or oblong to oval, sometimes dagger-shaped, glabrous or antrorsely [or retrorsely] scabrous or hispid; lower segment seedless, very short [or obsolete], narrow and nearly as wide as the pedicel, obscurely valved; upper segment few to many seeded, terete or angled, thick, corky, torulose to strongly moniliform, sometimes not constricted between the seeds, usually lomentaceous and breaking up at maturity into 1-seeded segments, longitudinally ribbed or smooth. Seeds uniseriately arranged, pendulous, globose to slightly ovoid [or oblong], wingless, not mucilaginous when wet, brown, reticulate or nearly smooth; cotyledons longitudinally conduplicate, emarginate at apex. Base chromosome number 9. (Including *Dondisia* Scop., *Durandea* Delarbre, *Ormycarpus* Necker, *Quidproquo* Greuter & Burdet.) LECTOTYPE SPECIES: *R. sativus* L.; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. **2**: 194. 1913. (From the Greek name *raphanos,* used by Dioscorides and Theophrastus for radish; derived from Greek *ra,* quickly, and *phainomai,* to appear, alluding to the rapid germination of the seeds.)—RADISH.

A genus of three species probably native to the Mediterranean region, with one species a cosmopolitan weed, and another a crop plant and an escape from cultivation. The third, *Raphanus Boissieri* Al-Shehbaz, is endemic to southern Lebanon and northern Israel and belongs to the monotypic sect. HESPERIDOPSIS Boiss., which is characterized by its short (1–1.2 cm long) petals, reflexed fruiting pedicels, retrorse pubescence on the siliques, obsolete lower fruiting segments, and oblong seeds.

Section RAPHANUS (sect. *Raphanistrum* DC.) (petals 1.7–3 cm long, fruiting pedicels ascending to divaricate, siliques glabrous or with antrorsely appressed or spreading trichomes, lower segment evident, seeds globose or nearly so) includes two weedy species that are naturalized in almost all of the Southeastern States and grow in fields, cultivated land, roadsides, waste places, orchards, and disturbed areas. *Raphanus Raphanistrum* L., wild radish, jointed charlock, jointed radish, charlock, $2n = 18$, was first reported from North America in 1814 and from Tennessee in 1901 (Gattinger) but has only recently been reported from the other states of the Southeast (Ahles *et al.,* 1958; Jones, 1961; Pullen *et al.*; Thieret; Thorne). Although the species has not yet been reported from Arkansas, it probably grows there. Individuals of *R. Raphanistrum* have corky, ribbed, torulose or moniliform, lomentaceous fruits (FIGURE 1k, l) and white or yellow petals with brown veins. The species is highly variable in flower color, fruit width, and number of seeds per fruit. The five subspecies that have been recognized on the basis of differences in these characters are completely interfertile, and natural hybridization apparently occurs in the areas where their ranges overlap.

The second species, *Raphanus sativus* L., radish, common radish, wild radish, garden radish, $2n = 18$, a vegetable grown primarily for its fleshy roots, is a naturalized weed common in many parts of our area. It differs from the preceding by having inflated, nonlomentaceous, and usually smooth, nontorulose siliques (FIGURE 1m). Thellung treated *Raphanus* as a monotypic genus and reduced the cultivated radish to a subspecies of *R. Raphanistrum,* but such a disposition has not been accepted by recent authors.

The relationships of *Raphanus* are somewhat controversial. Several authors have suggested direct associations with *Cossonia* Durieu (= *Raffenaldia* Godron) or *Hemicrambe,* but these genera appear to be only remotely related. Perhaps a more acceptable connection is with *Enarthrocarpus* or with *Trachystoma* O. E. Schulz. As pointed out by Gómez-Campo (1980a), *Raphanus* shows some affinity to subtribe Brassicinae in cotyledon morphology and in the ability to cross with several of its genera, but the genus is apparently much closer to the last two genera than to members of this subtribe. *Raphanus* is easily distinguished by its ebracteate inflorescences, erect sepals, dark-veined petals, and 2-segmented fruits with an indehiscent, inflated or lomentaceous, (2–)4–15-seeded upper segment and a seedless, aborted lower segment.

Plants of *Raphanus* with yellow or violet flowers are visited by insects more often than the white-flowered form. The low attractiveness of the white flowers may be attributed to their low reflectance. The white-flowered form apparently differs from the other color forms by a single allele (Kay). Numerous insect genera, the most common of which are *Apis, Andrena, Pieris,* and *Eristalis,* have been reported as pollinators. Self-incompatibility occurs in *R. Raphanistrum* and *R. sativus,* and male sterility has been found in the latter (Shiga).

Some cultivars of *Raphanus sativus* show karyotypic differences in number of secondary constrictions, presence or absence of satellites, arm ratios, and chromosome size. Mukherjee (1979) has postulated that karyotype evolution within *Raphanus* probably proceeded toward reduction in chromosome size. On the basis of chromosome morphology, secondary associations at meiosis, and study of haploid plants, some authors (e.g., Kaneko) have argued that the base chromosome number for the genus is six.

Natural hybridization between *Raphanus Raphanistrum* and *R. sativus* has been known since 1788, and the hybrid has been named *R.* × *micranthus* (Uechtr.) O. E. Schulz. In artificial hybrids, Harberd & McArthur (1972) have observed seven bivalents and a quadrivalent as the most frequent meiotic configuration. The reduced pollen fertility (approximately 50 percent) in the hybrids is associated with a reciprocal-translocation heterozygotic condition. The transfer of some of the weedy characters from *R. Raphanistrum* to *R. sativus* through natural hybridization may have played a major role in converting the latter from a crop plant into a very successful weed near the coastal areas of central California (Panetsos & Baker).

The classic intergeneric hybrid × *Raphanobrassica* is an amphidiploid originally obtained by Karpechenko from *Raphanus sativus* and *Brassica oleracea* var. *capitata.* It is easily synthesized by crossing autotetraploid forms of the parental species. The cross is successful when radish is used as the maternal parent, and the failure of the reciprocal cross is caused by the inability of the pollen of *Raphanus* to penetrate the styles of *Brassica.* The fruits of × *Raphanobrassica* are intermediate between those of the parental species in that the lower segment resembles *Brassica,* and the upper one *Raphanus.* Most of the experimental work on × *Raphanobrassica* deals either with the transference to *Brassica* of the resistance to certain fungal diseases or with the production of forage or high oil-yielding crops. Even after successive crossings with either parent, × *Raphanobrassica* is still impaired by meiotic irregularities and low seed set caused by endosperm deficiency. It has been suggested that the reduced fertility results from genic imbalances or perhaps from the insufficient meiotic timing between the parental genomes. The literature on ×*Raphanobrassica* and other intergeneric hybrids is extensive; the papers of Harberd & McArthur (1980), Kato & Tokumasu, McNaughton, Olsson & Ellerström, and Yarnell should be consulted for further details.

The genus has been thoroughly surveyed for glucosinolates, fatty acids, flavonoids, and sterols, and the distribution of these constituents apparently has no taxonomic value. Sinapine is the major alkaloid in *Raphanus*, and β-sitosterol and campesterol are the dominant sterols. The pungent principle in the roots of *R. sativus* is 4-methylthio-3-butenyl isothiocyanate, but several other isothiocyanates have been characterized from the other parts of the plant and from *R. Raphanistrum*. Raphanin, a seed-germination inhibitor with antibacterial properties (Ivanovics & Horvath), may well be the 4-methylsulfinyl-3-butenylglucosinolate present in the two species above.

The upper part of the root and the hypocotyl (or the latter alone) become fleshy in *Raphanus sativus*. Root succulence is markedly reduced by long days, and this may account for the failure of naturalized radishes to develop fleshy roots. The vascular cambium in young roots appears as two opposite crescent-shaped layers outside the diarch primary xylem. After forming a complete cylinder, the cambium eventually produces enormous amounts of thin-walled xylem parenchyma and much smaller amounts of vascular elements that are slightly lignified. Subsequent transformation of some of this parenchyma into secondary cambium and the extensive formation of tertiary tissues by the latter, along with the initial activities of the primary cambium, account for the fleshiness of the hypocotyl-root axis.

The corky fruit wall of *Raphanus sativus* is attributed to numerous layers of loose and thin-walled parenchyma that become lignified in the weedy forms. The inner part of the fruit wall consists of several layers of tangentially elongated storage tracheids that are lined by a layer of subepidermal fibers followed by the inner epidermis. The vascular bundles are located in the parenchymatous region and are connected with the inner part of the wall by strands of radially elongated storage tracheids. The function of these tracheids is not entirely understood, but they may transport water to maintain some moisture around the seeds (Kaniewski).

The fruits of *Raphanus Raphanistrum* break into one-seeded segments that vary in size according to the subspecies. In the inland *R. Raphanistrum* subsp. *microcarpus* (Lange) Thell. the segments are not corky and are 1.5–2 mm wide, while in the maritime subsp. *rostratus* (DC.) Thell. and subsp. *maritimus* (Sm.) Thell. they are 5–10 mm in diameter, strongly corky, and usually dispersed by sea water. None of these subspecies has been introduced in the New World, and the sole representative there is subsp. *Raphanistrum*.

The inscriptions on the inner walls of the Egyptian pyramids and the remarks of Herodotus (Banga) indicate that *Raphanus sativus* has been cultivated since at least 2780 B.C. Truly indigenous radishes have not been found, and claims of their occurrence in the original wild state in eastern Asia are based on escapes from cultivation. The direct ancestors of the radish are unknown, and certain authors believe that it may have originated as a hybrid between *R. Raphanistrum* subsp. *landra* (Moretti ex DC.) Bonnier & Layens and subsp. *mari-*

timus. However, Lewis-Jones and associates, who studied many gene loci coding for different enzymes, have suggested that the radish is much closer to the former and that subsp. *maritimus* probably is not one of its direct ancestors. Others have suggested that the eastern Asiatic, Indian, and Mediterranean radishes have evolved from different progenitors. On the basis of morphology and ecology, *R. sativus* is more closely related to *R. Raphanistrum* subsp. *Raphanistrum* than to any other subspecies (Zohary).

Selection for size of different parts in *Raphanus sativus* has led to variation unparalleled in any other cultivated herb. The diameter of the rosette ranges from less than 10 cm (4 in) to more than 2 m (7 ft), and the root may be as small as the cherry (*Prunus Avium* L.) to as large as the gigantic Japanese 'Lew-Chew' and Indian 'Jaunpuri' radishes, which are up to 1 m long and 50–60 cm wide. The 'Sakurajima' mammoth globe radishes may weigh more than 100 pounds (nearly 50 kg). All these gigantic radishes belong to var. *longipinnatus* Bailey (var. *niger* (Miller) Pers., according to Helm). The fruits of the rat-tailed radishes of India and Malaysia (previously treated as *R. caudatus* L., but more appropriately as *R. sativus* var. *Mougri* Helm) may be 1 m long; they are less than 10 cm in other radishes.

The roots, leaves, flower tops, and young fruits of the radish are eaten as a salad, and in eastern Asia the roots are preserved by canning, drying, or pickling in brine and rice hulls. The edible seed oil is used for soap making, illuminating, and crayon manufacturing. The giant radishes are cultivated in South Africa as a fodder crop. The leaves of *Raphanus Raphanistrum* are eaten as a salad by the poor in Italy, and the seeds have occasionally been used as a substitute for mustard in England.

Caius and Perry have listed some 35 medicinal properties for the radish that range from the treatment of burns, fevers, pains, and coughs to remedies for cholera, tumors, and paralysis. Contact dermatitis caused by *Raphanus sativus* has been reported by Mitchell & Jordan, and gastroenteritis, pain, and bloody diarrhea in livestock may be caused by *R. Raphanistrum.*

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10. **Rapistrum** Crantz, Classis Crucif. Emend. 105. 1769, nom. cons.

Annual [biennial or perennial] herbs, sparsely to densely hispid, occasionally glabrous or glaucous. Lower leaves petiolate, lyrately pinnatifid [or pinnatisect], rarely undivided; terminal lobe suborbicular or ovate, larger than the oblong or ovate lateral ones. Upper leaves subsessile or short petiolate, simple or sinuately lobed, subentire or dentate. Inflorescence an ebracteate, densely flowered, corymbose raceme, much elongated in fruit. Sepals ascending, glabrous or with a subapical tuft of hairs, oblong or linear, inner pair slightly saccate at base. Petals yellow, obovate, clawed. Nectar glands 4, the lateral pair small, prismatic, the median pair conical. Stamens tetradynamous; filaments linear, not appendaged; anthers oblong, median ones introrse or extrorse. Ovary cylindrical, 2–4-ovulate, glabrous or pubescent; style filiform, persistent, glabrous; stigma capitate, 2-lobed. Fruiting pedicels slender to very thick, erect to ascending, usually appressed to rachis. Siliques sessile, transversely jointed, 2-segmented, slightly to strongly constricted at the joint, erect, hirsute or hispid, sometimes glabrous; lower segment dehiscent or indehiscent, persistent, usually 1- (or 2- or 3-)seeded, occasionally seedless and nearly as wide as the pedicel, elliptic or oblong, longitudinally striate or smooth, valves rigid, septum present or absent; upper segment indehiscent, 1-seeded or very rarely seedless, spherical or oval, wider than [or nearly as wide as] the lower segment, usually rugose, with (8–)12–16 longitudinal, usually well-developed ribs, caducous at maturity, abruptly [or gradually] tapering at apex; style slender [or thick], longer [or shorter] than the upper segment. Seeds oblong or oval, slightly compressed, not mucilaginous when wet, wingless, smooth, brown, pendulous and small in the lower segment, erect and larger in the upper one; cotyledons longitudinally conduplicate. Base chromosome number 8. (Including *Schrankia* Medicus.) TYPE SPECIES: *Rapistrum hispanicum* (L.) Crantz (*Myagrum hispanicum* L.), typ. cons.; see Int. Code Bot. Nomencl. 1983, p. 350. = *R. rugosum* (L.) All. subsp. *Linnaeanum* (Cosson) Rouy & Foucaud. (Name from Latin *rapa,* turnip, and *astrum,* incomplete resemblance.)—WILD TURNIP, TURNIP WEED.

A genus of two species native to southern and central Europe and adventive elsewhere on that continent, with one species naturalized throughout much of the world. Schulz (1919) recognized three species in two sections, but it is doubtful that his sectional classification is useful or necessary. Both species have been introduced to the New World, and one has been reported from the Southeast.

Rapistrum perenne (L.) All., $2n = 16$, is known from a few localities in Canada but apparently has not yet reached the United States. The highly polymorphic *R. rugosum* (L.) All. (*Myagrum rugosum* L.), wild turnip, turnip weed, $2n = 16$, grows in waste places, along roadsides, and in fields in scattered localities in the United States, and it has only recently been recorded for the Southeast from Louisiana (MacRoberts). The species was introduced to South America long before 1830 (Cambessèdes) and was first collected from the United States as a ballast plant in 1873. *Rapistrum rugosum* is extremely variable in the shape, pubescence, rugosity, and prominence of ribs of the upper fruit segment, and in the length and thickness of the fruiting pedicels. Three poorly defined subspecies have been recognized, but complete intergradation between them has been encountered in Europe and Turkey. In *R. rugosum* subsp. *rugosum* the upper segment of the fruit is ovoid, strongly ribbed, and rugose, and the fruiting pedicel is thick and nearly as long as the lower segment; in subsp. *orientale* (L.) Arcang. the upper segments are globose, rugose, and strongly ribbed, and the fruiting pedicels are one and a half to three times longer than the lower segments. In subsp. *Linnaeanum* (Cosson) Rouy & Foucaud the upper segments are slightly rugose and weakly ribbed, and the fruiting pedicels are slender and two to five times longer than the stalklike lower segment. All three subspecies and some of their intermediates have been found in the United States.

The affinities of this well-marked genus are somewhat controversial. *Rapistrum* resembles *Ceratocnemum* Cosson & Balansa, *Octocarpus* Durieu, *Guiraoa* Cosson, and *Cordylocarpus* Desf. in chromosome number and in having jointed siliques with one-seeded upper segments. Perhaps it is closest to the last genus, with which it produces natural hybrids in Algeria and Morocco. On the basis of fruit morphology, *Rapistrum* shows some affinity to *Didesmus* Desv., but the two genera probably are not closely related. *Rapistrum* is easily distinguished from the above genera of subtribe Raphaninae by its yellow flowers and its unappendaged, terete fruits that have usually one-seeded segments with the upper one ribbed.

Little is known about the floral biology of the genus. *Rapistrum rugosum* is self-incompatible, while *R. perenne* has not been tested for this character. Petals of the former exhibit high ultraviolet absorbance at the claws and veins and high reflectance at the intercostal areas. Variation has been found among populations in the shape and size of the nectar guide, but the genetic basis for this variation is unknown (Horovitz & Cohen).

Consistent chromosome counts of $2n = 16$ have been documented for all taxa. In only one case (Murín & Váchová) has a different number ($2n = 18$) been reported.

The natural hybrid between *Rapistrum rugosum* and *Cordylocarpus muricatus*, ×*Rapistrocarpus ramosissimus* (Pomel) Al-Shehbaz, resembles the former species in several aspects of the fruit but differs in having cylindrical, two- or three-seeded lower fruit segments characteristic of the latter (Maire, Solms). Madiot reported a sterile plant allegedly derived from hybridization between *Rapistrum* and *Sisymbrium* L., but the lack of experimental evidence and the extreme remoteness of the two genera cast doubts on the identity of the parents.

The major mustard-oil glucosides in the seeds of *Rapistrum perenne* and *R. rugosum* are 3-butenyl and 3-methylsulfonylpropyl glucosinolates, respectively, and traces of other compounds have also been found in the latter species. The seed-oil content in *R. rugosum* is the lowest (6 percent of dry weight) among the numerous crucifers analyzed (Kumar & Tsunoda).

The hypodermis in *Rapistrum rugosum* is much less developed in the lower segment of the fruit than in the upper. The differentiation of ribs starts with the collapse of the outer layers of hypodermis, followed by the radial elongation and strong lignification of the inner cells at certain areas that become ribs and alternate with large schizogenous intercellular spaces. These developments may have misled Saunders to suggest that the gynoecium of *Rapistrum* is composed of 40 to 50 carpels.

Dispersal in the genus is accomplished primarily by the upper segment of the fruit, which is indehiscent, one-seeded, and readily detached when mature. The lower segment is persistent in both species, but it usually dehisces in

Rapistrum rugosum. Seed size in this species is dimorphic, and it may be related to dispersal.

Although all members of *Rapistrum* are weeds, *R. rugosum* has become a very serious pest in several areas of Queensland, Australia, and it is one of the prime suspects as the cause of endemic goiter (Bachelard & Trikojus).

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11. **Calepina** Adanson, Fam. Pl. **2:** 423. 1763.

Annual, or rarely biennial, glabrous herbs. Basal leaves petiolate, sometimes forming a rosette, oblanceolate or spatulate, usually lyrately pinnatifid, sometimes dentate or subentire. Cauline leaves sessile, sagittate or auriculate at base, dentate or entire. Inflorescence an ebracteate, corymbose raceme, greatly elongated in fruit. Sepals spreading, ovate or oblong, obtuse, scarious at margin, not saccate at base. Petals obovate or oblanceolate, attenuate to a clawlike base, usually unequal, with the abaxial pair larger than the adaxial one, white, very rarely rose or lavender. Nectar glands 4, the median pair subglobose, the lateral pair oblong, usually 2-lobed. Stamens slightly tetradynamous; filaments usually broadly flattened, somewhat dilated at base, white; anthers oblong or ovate, slightly sagittate at base. Ovary 1-ovulate, glabrous; stigma capitate, subsessile. Fruiting pedicels erect or ascending, slender, usually curved, sometimes subappressed to the rachis. Fruits indehiscent, nutlike, 1-seeded, oval to obpyriform, borne on slender and very short gynophores; pericarp thick, hard, usually longitudinally 4-ribbed, reticulate-rugose; septum lacking; beak conical, slightly compressed, short, blunt. Seeds pendulous, wingless, not mucilaginous when wet, subglobose to oval, brown; seed coat thin; cotyledons conduplicate at the base, involute at the distal half. Base chromosome number 7. TYPE SPECIES: *Myagrum irregulare* Asso = *Calepina irregularis* (Asso) Thell. (Name of obscure origin, considered by many to be derived from *Haleb* [or wrongly *Chaleb*], the Arabic name for the Syrian city of Aleppo, but more likely from Greek *chalepaino,* a term used by Theophrastus, probably in connection with weedy plants. Since Adanson based the genus on Bauhin's *Myagrum monospermum minus,* which was collected from the vicinity of Montpellier, France, it is highly unlikely that the generic name stems from Aleppo.)

A monotypic genus probably native to the steppes north of the Caspian Sea and widely naturalized in southern, central, and western Europe, southwestern Asia, and northern Africa for many centuries. *Calepina irregularis* (Asso) Thell. (*Myagrum irregulare* Asso, *Crambe Corvinii* All., *Calepina Corvinii* (All.) Desv., *Bunias cochlearioides* Willd., *Calepina cochlearioides* (Willd.) Dumort.), $2n =$ 14, 28, 42, is known from a few localities in North Carolina (Buncombe County), Maryland, and Virginia, where it grows primarily in fields and on farms. It occupies highly diversified habitats in Europe, however (Gómez-Campo, 1978). Fruits of *C. irregularis* were encountered some 30–40 years ago in shipments of Canary grass (*Phalaris canariensis* L.) imported to the United States from Morocco and Turkey. Most of the plants observed in Virginia (Blake) and North Carolina (Hardin) shortly after the initial introduction of the species were removed by hand, and it is uncertain whether the species still exists in our area.

Calepina has traditionally been placed in the Brassiceae, but such a disposition has recently been questioned by Gómez-Campo (1980a), who suggested its removal from the tribe due to its slightly conduplicate cotyledons with involute margins and its unsegmented fruit. However, he did not assign *Calepina* to another tribe. The genus apparently has no relatives outside the Brassiceae, and despite its deviation from the typical members of this tribe, it has been retained here. *Calepina* may be considered as a highly evolved member of the tribe with fruits lacking the septum and the valvular segment (Gómez-Campo & Tortosa, Zohary). The nutlike fruits may be interpreted as consisting of the indehiscent upper segment only, with the lower segment represented by a tiny, gynophorelike structure. However, there is no anatomical evidence that supports this interpretation.

The generic relatives of *Calepina* are obscure. Several authors have suggested direct or close ties with *Zilla* (Von Hayek), *Muricaria* Desv. (Rytz), or *Crambe* (Schulz, 1919). However, these genera are unrelated to *Calepina* and differ in fruit morphology and chromosome numbers. *Zilla* ($n = 16$) and three other genera, all shrubs, form the natural subtribe Zillinae (DC.) O. E. Schulz, while *Crambe* ($x = 15$) and *Muricaria* ($n = 12$) probably belong to two different groups within the highly heterogeneous Raphaninae. *Calepina* may also be assigned to the latter subtribe, but its nearest relatives are unknown. *Calepina irregularis* can be easily distinguished from the other crucifers of our area by its white flowers, its unequal petals, its flattened filaments, and its indehiscent, one-seeded, four-ribbed, reticulate, oval, nutlike fruits (FIGURE 1n).

Calepina irregularis consists of diploid (Manton), tetraploid (Larsen & Lagaard, Al-Shehbaz & Al-Omar), and hexaploid (Jaretzky, 1929, 1932) populations. The cytogeography of the species, however, is far from adequately known, and information about hybridization between plants with different ploidy levels is lacking.

The seed coat is composed of an epidermis (with large and hollow columns of mucilage that is not exuded when the seeds are wet), followed by a subepidermis, a palisade layer with flatly thickened inner tangential walls, and pigmented, aleurone, and hyaline layers (Vaughan & Whitehouse).

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12. **Cakile** Miller, Gard. Dict. abr. ed. 4. Vol. 1 (alph. ord.). 1754.

Annual or very rarely short-lived perennial, glabrous [or pubescent], succulent herbs. Stems usually branched at base. Lower leaves petiolate, entire or crenate, sometimes sinuate or pinnatisect and with narrow lobes. Cauline leaves gradually reduced in size and lobing. Inflorescence an ebracteate, corymbose raceme, greatly elongated in fruit; rachis straight or slightly to strongly flexuous or geniculate. Sepals erect, glabrous or sparsely pubescent at apex, usually hyaline at margin; outer pair slightly cucullate; inner pair somewhat saccate at base. Petals showy, rarely reduced to bristles or altogether lacking, white or lavender [or purple or violet], obovate or spatulate, obtuse or emarginate at apex; claws distinct, short or long. Nectar glands 4, the lateral pair 2-lobed or flat, the median pair oval or conical. Stamens tetradynamous; filaments linear, not appendaged, free; anthers oblong, acute or obtuse at apex, cordate at base. Ovary glabrous, sessile, transversely jointed, with 1 (or 2 or 3) ovules in each segment; style absent; stigma capitate, entire or sometimes slightly 2-lobed. Fruiting pedicels divaricate, rarely ascending or recurved, as wide as or narrower than the rachis. Siliques transversely jointed, 2-segmented, indehiscent, somewhat fleshy when immature, becoming dry and corky later; segments terete or angled, usually 1-seeded, occasionally 2- or 3-seeded, sometimes the lower segment seedless; septum very thin, usually appressed to the seed; articulation surface of the lower segment with 2 (rarely with more or without) conical or broad teeth that fit into the pits of the articulation surface of the upper segment; lower segment persistent, sometimes with 2 lateral horns at apex; upper segment readily separating at maturity, as long as or 2 or 3 times longer than the lower segment, obscurely to strongly 3-veined on each side, sometimes ribbed and sulcate, usually terminating in a conical or ensiform beak, obtuse to acute or retuse at apex. Seeds large, oblong or ellipsoid, slightly flattened, not mucilaginous when wet, wingless, brown, smooth or minutely punctate, large and erect in the upper segment, smaller and pendulous in the lower one; cotyledons accumbent or obliquely incumbent, lanceolate or oblanceolate. Base chromosome number 9. LECTOTYPE SPECIES: *Bunias Cakile* L. = *Cakile maritima* Scop.; see Adanson, Fam. Pl. **2:** 423. 1763; Britton & Brown, Illus. Fl. No. U. S. ed. 2. **2:** 195. 1913. (Name probably derived from Arabic *qaqoulla* (also spelled *qaqulla* or *qaqulleh*) previously used in North Africa for *C. maritima,* although a few authors believe that the name was used originally for cardamom and other aromatic plants.)—SEA ROCKET.

A genus of seven species, all except one of maritime habitats; distributed along the sandy beaches and shores of the Great Lakes of North America, the North Atlantic Ocean, the Caribbean Sea, the Gulf of Mexico, and the Baltic, North, Barents, Black, and Mediterranean seas; introduced and widely naturalized along the Pacific coast of North America, eastern, southern, and western Australia, New Zealand, New Caledonia, Japan, Uruguay, and Argentina. The single inland species, *Cakile arabica* Velen. & Bornm., is endemic to the sandy deserts of Kuwait, southern Iraq, adjacent Saudi Arabia, and southwestern Iran. The genus is the only member of the Brassiceae with indigenous species in the New World. Seven of the nine native North American taxa in four species are distributed in the southeastern United States, and an additional alien species has been reported.

Pobedimova (1953, 1964) divided *Cakile* into four sections on the bases of the dissection of leaves and the nature of the articulation surfaces of the fruit segments. However, the variation in these characters can be continuous, and it is doubtful that her sectional classification improved the taxonomy of the genus. Hadač & Chrtek raised sect. *Eremocakile* Pobed. to subgenus, but this action is not justified here either. The present treatment follows the excellent monograph of Rodman (1974), in which sections are not recognized.

Cakile edentula, the most widely distributed of our native sea rockets, is easily distinguished by its sinuate or dentate leaves, reduced (rarely lacking) petals, long (1–2 dm) infructescences, slender fruiting pedicels, and broad ((3–)5–9 mm), four-angled or eight-ribbed fruits with retuse or blunt beaks. Both of its subspecies occur in our area, and one is represented by one variety. *Cakile edentula* (Bigelow) Hooker subsp. *edentula* var. *edentula* (*Bunias edentula* Bigelow, *C. americana* Nutt., *C. californica* Heller, *C. edentula* var. *californica* (Heller) Fern.), $2n = 18$, is known from several localities along the Outer Banks of North Carolina, but its native range extends northward along the Atlantic coast to Labrador. The variety has been introduced to Japan, Australia, New Zealand, the Azores, the Great Lakes of North America, and the Pacific coast from California to Alaska. It is recognized by its fruit: the beak is shorter than the seed portion of the broad (5–9 mm), four-angled upper segment, and the articulation surface of the lower segment has two teeth. The other variety, *C. edentula* subsp. *edentula* var. *lacustris* Fern., $2n = 18$, an endemic of the shores of the Great Lakes, has narrower siliques and longer beaks.

The distribution of *Cakile edentula* subsp. *Harperi* (Small) Rodman (*C. Harperi* Small), $2n = 18$, extends from the Outer Banks of North Carolina southward to northern Florida. The northernmost limits of the subspecies is Cape Hatteras, where the warm Gulf Stream that effects its northward migration is deflected eastward by the cold Labrador Current. In that area the ranges of *C. edentula* subsp. *edentula* and *C. edentula* subsp. *Harperi* overlap, and natural hybridization occurs in the zone of sympatry (Rodman, 1980). Subspecies *Harperi,* which has been replaced by *C. constricta* Rodman in parts of northern Florida, is characterized by fruit with conical, eight-ribbed upper segments 12–20 mm long and flat and toothless articulation surfaces on both segments.

Another native species, *Cakile lanceolata,* is represented in the Southeast by three of its four subspecies. It is characterized by having white (rarely lavender) petals; four-angled or terete siliques 13–31 mm long; pinnatifid to entire, not particularly succulent leaves; and linear infructescences that usually exceed 2 dm in length. *Cakile lanceolata* (Willd.) O. E. Schulz subsp. *lanceolata* (*Raphanus lanceolatus* Willd., *C. aequalis* L'Hér. ex DC., *C. maritima* Scop. var. *aequalis* (L'Hér. ex DC.) Chapman, *C. domingensis* Tussac, *C. cubensis* Kunth, *C. americana* Nutt. var. *cubensis* DC., *C. maritima* var. *cubensis* (DC.) Chapman), $2n = 18$, is narrowly distributed in our area in Dade, Martin, and Palm Beach counties, Florida, but is common throughout the West Indies, the Caribbean coast of Central America, Colombia, Venezuela, and the Yucatan

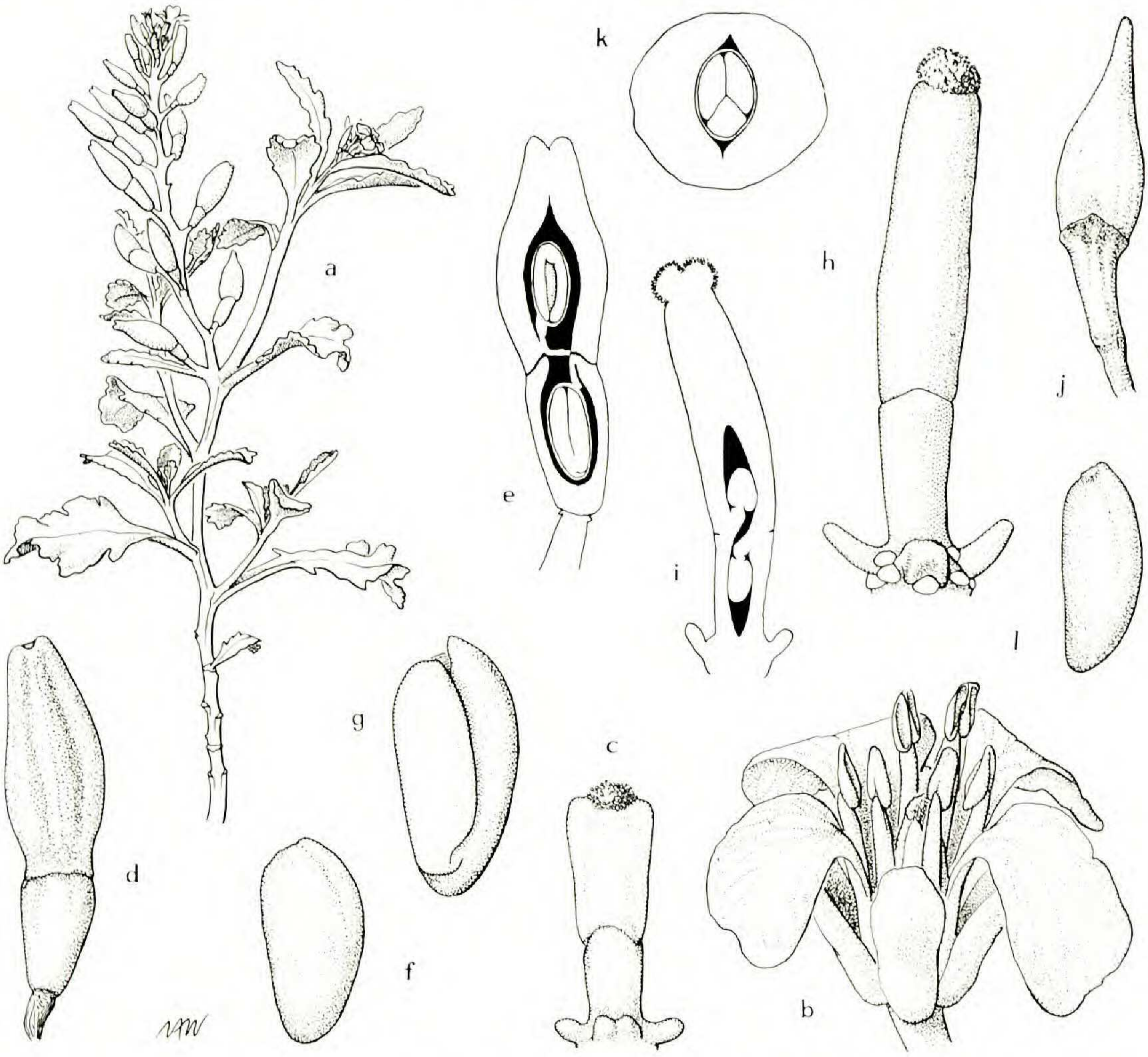

FIGURE 2. **Cakile.** a–g, *C. edentula* subsp. *Harperi:* a, portion of plant with flowers and fruits, × ½; b, flower, × 6; c, gynoecium—note transverse joint and nectar glands, × 10; d, fruit, × 1½; e, diagrammatic longitudinal section of fruit—note erect and pendulous seeds in upper and lower segments, respectively, × 1½; f, seed, × 5; g, embryo, × 6. h–l, *C. lanceolata* subsp. *fusiformis:* h, gynoecium—note cylindrical lateral nectar glands and prismatic median one, × 10; i, longitudinal section of gynoecium—note orientation of ovules, × 6; j, fruit, × 1½; k, diagrammatic cross section of upper segment of fruit—note thickness of fruit wall and accumbent cotyledons, × 4; l, seed, × 5.

peninsula of Mexico. The subspecies is easily recognized among our sea rockets by its entire or obscurely dentate leaves, narrowly lanceolate, long-beaked siliques, and short (5–10 mm) lower segments less than half the length of the upper ones.

The second subspecies, *Cakile lanceolata* subsp. *fusiformis* (Greene) Rodman (*C. fusiformis* Greene, *C. Chapmanii* Millsp.), $2n = 18$, is distributed along the coasts of the southern half of peninsular Florida and disjunctly in Honduras and the Yucatan peninsula. The frequently pinnatifid leaves and the characteristic fusiform, longitudinally four- or eight-sulcate (or -striate) siliques 16–26 mm long with lower segments 5–10 mm long easily separate this from other sea rockets. Rodman (1974) believed that the subspecies may have originated from hybridization between subsp. *lanceolata* and subsp. *alacranensis* (Millsp.) Rodman. The latter has turbinate siliques and is endemic to the Yucatan peninsula and neighboring islands.

Cakile lanceolata subsp. *pseudoconstricta* Rodman, $2n = 18$, occurs in Lee, Manatee, Sarasota, Pinellas, and Hillsborough counties on the west coast of peninsular Florida and disjunctly, possibly through recent introductions, at the southern tip of Texas and adjacent Tamaulipas, Mexico. Plants of this subspecies have finely dissected or pinnatifid leaves and narrowly lanceolate, terete or four-angled siliques with a distinct constriction at the articulation point. It resembles *C. constricta* in its fruits, but the latter has fleshy, entire to dentate (rarely sinuate) leaves and smaller flowers.

Cakile constricta Rodman, $2n = 18$, is morphologically intermediate between *C. edentula* and *C. lanceolata,* particularly in flower size, infructescence length, and leaf succulence, and according to Rodman (1974), it probably represents a link between these species. It extends along the Atlantic coast of Florida and along the beaches of the Gulf of Mexico from the Tampa Bay area northward and westward through Alabama, Mississippi, Louisiana, and southeastern Texas. It is separated from *C. edentula* by its petaliferous flowers and narrower (3–4 mm wide) siliques with acute beaks.

The most distinctive of our sea rockets is *Cakile geniculata* (Robinson) Millsp. (*C. maritima* var. *geniculata* Robinson, *C. lanceolata* var. *geniculata* (Robinson) Shinners), $2n = 18$, which extends along the Gulf of Mexico west of the Mississippi Delta in Louisiana westward along the coast of Texas and southward in Mexico to Veracruz. It is characterized by strongly geniculate infructescences, stout fruiting pedicels of the same width as the rachis, narrow (less than 2 mm wide) petals, and coarsely eight-ribbed, lanceolate siliques 20–27 mm long. Habitat instability, caused by the enormous amounts of silt and mud deposited at the Mississippi Delta as well as the repeated flooding of this area, may have been the main obstacles to the eastward migration of *C. geniculata.* Hybridization between this and *C. constricta* on the Grand Isle of Louisiana is suspected, and the heterogeneity of the populations there may have resulted from introgression (Rodman, 1974).

The alien *Cakile maritima* Scop. (*Bunias Cakile* L., *Cakile Cakile* (L.) Karsten; see Rodman (1974) for 45 additional synonyms), $2n = 18$, has been introduced in the Southeast as a ballast plant at least three different times. It has been found near Mobile, Alabama, and Wilmington, North Carolina, and in Florida (see Rodman, 1974; Small), but it has apparently failed to persist. Northward, it has only recently become naturalized in the Chesapeake Bay region of Maryland (Riefner). On the Pacific coast of North America, where it is now widespread, it was first recorded in 1936 (Rose). It has also become naturalized in Argentina, Uruguay, Australia, and New Caledonia. The native range of *C. maritima* extends along the shores of the Black and Aegean seas (subsp. *euxina* (Pobed.) E. I. Nyárády), the Baltic Sea (subsp. *baltica* (Rouy & Foucaud) P. W. Ball), and the North Sea, the European North Atlantic Ocean, and the Mediterranean Sea (subsp. *maritima*). Two characteristic lateral horns or triangular wedges on the top of the lower segment of the fruit and broad (3–6 mm wide) petals easily separate *C. maritima* from our native sea rockets.

Cakile is most closely related to *Erucaria* (Mediterranean region and southwestern Asia) and may represent an end point of an evolutionary line linked to an *Erucaria*-like ancestor by some inland species not very different from *C. arabica*. The original maritime species of *Cakile* may have inherited certain characters (e.g., annual habit, corky fruits, and succulent leaves) preadapting it to strand habitats. The range of this species probably expanded rapidly along the beaches of the Mediterranean Sea and the Atlantic coast of Europe. From the latter area, very rare successful immigrants reached North America to give rise to our present-day native sea rockets. The seed-glucosinolate evidence supports such an origin for the American *Cakile* (Rodman, 1974).

The genus is characterized by its lack of a style and by its fleshy leaves, its white to purple or violet flowers, its corky, two-segmented, jointed fruits, and its usually one-seeded upper segments. All taxa except *Cakile arabica* occupy strand habitats—an almost unique ecological specialization for the genus unknown elsewhere in the Cruciferae except for a species of *Crambe* and another of *Raphanus*. *Erucaria* differs from *Cakile* in having noncorky fruits, one- to six-seeded segments, slender styles, and nonfleshy leaves, and in occupying arid inland habitats.

The main source of taxonomic complexities in our native sea rockets is the enormous variation created by hybridization between taxa in zones of sympatry. The great dispersibility of fruits, the lack of reproductive isolation among species, and the overlap of distributional ranges are the main factors preventing the stabilization of populations in the Southeast. According to Rodman (1974, p. 115), "the southern and western Florida sea rockets present a nightmare of variation to the taxonomist."

Self-incompatibility is expressed strongly in *Cakile arabica* and weakly in the other Old World species (*C. arctica* Pobed. and *C. maritima*), while self-compatibility characterizes all the New World taxa. The shift in the breeding system toward autogamy in *C. edentula* has accompanied several changes in the flower (e.g., the total absence of petals or their reduction to bristles, the lack of scent, and the secretion of minimal nectar). The allogamous taxa exhibit variation in floral color that may be accompanied by differences in their ultraviolet absorption (Horovitz & Cohen). The apparent lack or rarity of natural hybridization between *C. edentula* and *C. maritima* in southern Australia and in California may be attributed to the breeding system. However, despite autogamy, *C. edentula* subsp. *edentula* and *C. edentula* subsp. *Harperi* produce a substantial number of hybrids (9–24 percent of the sample) in a narrow zone of sympatry on the Outer Banks of North Carolina (Rodman, 1980). The complex mixture of sea rockets along the coasts of Norway may have resulted from hybridization between *C. arctica* and two subspecies of *C. maritima* (Elven & Gjelsås). Although the potentiality for hybridization exists whenever sympatry occurs, only a few examples of natural hybridization have been carefully documented.

Uniform chromosome counts of $2n = 18$ have been reported for all taxa of *Cakile*. The single exception, which may be in error, is the tetraploid count of $2n = 36$ reported by Löve & Löve for *C. arctica*.

Cakile is the most thoroughly surveyed genus of Cruciferae for seed glucosinolates. Rodman (1974, 1976, 1980) has applied the distribution of these compounds in studies of migration, population variation, and hybridization. Sixteen glucosinolates have been identified in *Cakile*, and their overall profiles are usually taxon specific. The genus has been poorly surveyed for alkaloids, fatty acids, mucilage, and tannins. The seed-oil contents on a dry basis in *C. edentula* (49 percent) and *C. maritima* (46 percent) are the highest known for any crucifer (Kumar & Tsunoda).

The separation or articulation zone between the two segments of fruit is composed of transversely elongated small cells surrounded by larger ones that become lignified as the fruit matures. Soon after the lignification process is completed and due to a shortage of food and water, cells of the separation zone begin to degenerate, and their walls break at a stage when the mature fruit is still green. The vascular bundles in this zone consist of short tracheids instead of the vessels seen elsewhere in the fruit. These anatomical peculiarities are adaptations for the detachment of upper segments of fruit, and it is possible that they may be found in genera of the Brassiceae with articulated or lomentaceous fruits.

Cakile is remarkably adapted to long-distance dispersal by sea because of the buoyancy of the upper segment of the fruit, the inhibition of seed germination during flotation, and the maintenance of seed viability after exposure to sea water. Seed viability and fruit buoyancy decline drastically after prolonged periods of exposure to sea water. High levels of salt, particularly of sodium chloride, in the fruit wall and in the sand are the most important factors that inhibit seed germination in nature (Hocking). The naturalized range of *C. edentula* along the Pacific coast of North America has extended northward some 3200 km (2000 mi) from San Francisco Bay to Kodiak Island in a span of 50 years at the amazing migration rate of 64 km (40 mi) per year (Barbour & Rodman). Short-distance dispersal is accomplished by the tumbling of uprooted dead plants or by the rolling of upper segments of fruit along the beach during strong winds.

The green parts of *Cakile* are eaten as a salad or cooked as a potherb. In folk remedies the plants have been recommended for their antiscorbutic, purgative, and diuretic properties.

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13. **Conringia** Heister ex Fabricius, Enum. 160. 1759.

Annual or rarely perennial, glabrous and usually glaucous herbs. Stems erect, simple or branched at base. Basal leaves undivided, obovate or spatulate, subsessile, usually entire, slightly fleshy. Cauline leaves cordate-amplexicaul, rarely auriculate, oblong to elliptic or ovate [or suborbicular], entire, rarely crenulate. Inflorescence an ebracteate, corymbose raceme, usually elongated in fruit. Sepals erect or slightly ascending, obtuse; outer pair linear to narrowly oblong or lanceolate, sometimes cucullate; inner pair broader, slightly [to strongly] saccate [or not] at base. Petals yellow or white [rarely with purple veins], narrowly [to broadly] obovate, rarely oblanceolate, attenuate at base; claws usually as long as sepals. Median nectar glands usually absent, lateral ones lobed [or flat]. Stamens slightly tetradynamous; filaments not appendaged, linear, free; anthers oblong, slightly sagittate at base, equal in length [or the lateral pair 3–4 times longer than the 2 median pairs]. Ovary glabrous, many ovulate. Fruiting pedicels ascending to spreading [or erect], slender [or as thick as the fruit]. Siliques sessile, linear, dehiscent, quadrangular [or terete, 8-angled, or strongly compressed parallel to the septum], torulose [or not], beaked [or beakless], acuminate [or clavate] at apex; valves convex [or flat], somewhat keeled [or not], usually with a prominent midnerve and 2 obscure [or prominent] lateral nerves [or nerveless]; stigmas capitate, entire [or 2-lobed and the lobes sometimes decurrent]. Seeds uniseriately arranged, copiously [or not at all] mucilaginous when wet, wingless, oblong or elliptic, brown [or reddish or black], papillose [or smooth]; cotyledons incumbent [or subconduplicate]. Base chromosome numbers 7, 9. (Including *Goniolobium* Beck, *Gorinkia* J. & K. Presl.) LECTOTYPE SPECIES: *Brassica orientalis* L. = *Conringia orientalis* (L.) Dumort.; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. **2:** 174. 1913. (Name honoring Hermann Conring, 1606–1681, German professor of medicine, philosophy, and jurisprudence at Helmstedt University.)—HARE'S-EAR MUSTARD.

A well-defined genus of six species centered in the eastern Mediterranean, particularly in Turkey (where all species occur), and extending eastward to Afghanistan and western Pakistan. Two species are widely distributed in southern and central Europe, and one (*Conringia grandiflora* Boiss. & Heldr.) is a narrow endemic known only from a few localities in Antalya Vilayet, a province in southwestern Turkey. The genus is represented in North America by the alien weed *C. orientalis* (L.) Dumort., hare's-ear mustard, rabbit's-ear, treacle mustard, $2n = 14$, which grows in cultivated land, disturbed sites, abandoned fields, and waste places, and along roadsides. It is most common in the plains states of the United States and in the plains and prairie provinces of Canada (Rollins). It has been recorded from all the Southeastern States except Louisiana and South Carolina, but it probably grows there as well. *Conringia orientalis,* easily distinguished from the other mustards of our area, is a glabrous annual with deeply cordate-amplexicaul cauline leaves, white or yellow flowers, tetragonal siliques 6–15 cm long, and incumbent cotyledons.

Conringia has often been associated with *Moricandia* of subtribe Moricandiinae Hayek, but Botschantzev has questioned its disposition in the Brassiceae without adequately placing it in another tribe. Features such as the conduplicate cotyledons and/or segmented siliques, typical of most members of the Brassiceae, are not found in *Conringia, Ammosperma,* and *Pseuderucaria.* The last two genera have always been associated with *Moricandia,* and there are no solid grounds for not placing *Conringia* with them. In one species, *C. planisiliqua* Fischer & Meyer, the cotyledons are nearly conduplicate, and this may support retaining the genus in the Brassiceae.

Hardly anything is known about the floral biology of *Conringia.* The diversity in flower size among species is very striking. The flowers of *C. persica* Boiss., the smallest in the genus, are only 0.5 cm long and have nonsaccate sepals, while those of *C. grandiflora* exceed 2 cm in length and have strongly saccate inner sepals with pouches usually longer than 1 mm. All anthers of *C. grandiflora* are polliniferous, but those of the lateral pair of stamens are nearly four times longer than those of the median ones. To my knowledge, such anthers have not been encountered elsewhere in the Cruciferae, except in flowers of some species of *Streptanthus* Nutt. that have aborted median ones. Unfortunately nothing is known about the pollinators of *C. grandiflora.*

Chromosome numbers are known for all species except *Conringia grandiflora.* One species, *C. austriaca* (Jacq.) Sweet, is a tetraploid based on seven. The haploid number for *C. persica* is seven, but counts of $n = 7$ and $n = 9$ have been reported for both *C. planisiliqua* and *C. clavata* Boiss. (= *C. perfoliata* (C. A. Meyer) N. Busch).

A few cardenolides (erysimosid, erycorchosid, and helveticosid) have been found in *Conringia orientalis* (Kowalewski), but it is not known whether cardiac glycosides are present throughout the genus. In *C. planisiliqua* allylglucosinolate has been identified, and in *C. orientalis* 2-hydroxy-2-methylpropyl and 2-methylpropyl glucosinolates are the dominant pungent constituents. It has been suggested that *C. orientalis* may be a potentially new oil-seed crop because of its high ratio of linoleic to linolenic acid, but the presence of cardenolides may be an obstacle to such utilization.

The seeds of *Conringia orientalis* exude abundant mucilage immediately after soaking in water. The mucilage forms series of stiff separate conical masses, each with a cap representing the outer wall of the epidermal cell that exuded it. Other species contain very little or no seed mucilage.

Except for the weedy *Conringia orientalis,* the genus has no economic importance. Young plants of this species are said to make a good salad.

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