THE TRIBES OF CRUCIFERAE (BRASSICACEAE) IN THE SOUTHEASTERN UNITED STATES[1]

IHSAN A. AL-SHEHBAZ

The family Cruciferae is represented in the southeastern United States by 121 species in 43 genera assigned to seven tribes. The present account includes a family description, with general comments on the group as a whole; selected family references; a key to the tribes; an artificial key to 46 genera (including three known as escapes from cultivation to the west of this area); and brief descriptions of the tribes, each with a list of the representative genera in the Southeast.

When treating a family generally recognized as difficult for generic and tribal delimitation, one faces the problem of how genera should be arranged. An alphabetic sequence would definitely be incompatible with the scope of our flora. A few students of the family avoid recognizing tribes because they believe that tribal boundaries are usually artificial. However, these authors arrange the genera according to their nearest sister relatives—a disposition that often coincides so well with the tribal classification that ignoring or totally abandoning the tribes is unreasonable. Nearly half of the genera of Cruciferae occurring in our area belong to the tribes Thelypodieae, Brassiceae, and Lepidieae, which are widely recognized as natural groups. The majority of the remaining genera fall within the presumably well-defined centers of four other tribes. For these reasons I favor the use of tribes to provide a workable framework, even though

[1]Prepared for the Generic Flora of the Southeastern United States, a long-term project made possible by grants from the National Science Foundation and currently supported by BSR-8111520 (C. E. Wood, Jr., principal investigator), under which this research was done, and BSR-8303100 (N. G. Miller, principal investigator). This account, the 103rd in the series, follows the format established in the first paper (Jour. Arnold Arb. **39**: 296–346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of a family or genus in brackets [ ]. The two references that I have not verified are marked with an asterisk.

I am most grateful to Carroll Wood for his support, guidance, and help with many aspects of this paper, and particularly for his critical review of the manuscript. Reed C. Rollins, Norton G. Miller, George K. Rogers, and Elizabeth A. Shaw were helpful throughout this study, and I am indebted to Barbara Nimblett for her careful typing of the manuscript. I am grateful to Elizabeth B. Schmidt and Stephen A. Spongberg for their editorial help.

The illustrations were made by Karen Stoutsenberger (primarily under earlier grants), with the exception of FIGURES 1, s (by Rachel A. Wheeler) and 3, a–c (by the late Dorothy H. Marsh). Carroll Wood and/or Kenneth R. Robertson prepared the materials and supervised the illustrations. Fresh material was contributed by K. R. Robertson, R. C. Rollins, and C. E. Wood, and the fruits and seeds are largely from herbarium specimens of the Arnold Arboretum and the Gray Herbarium.

Journal of the Arnold Arboretum **65**: 343–373. July, 1984.

I fully admit that, when taken on a worldwide basis, some tribal boundaries become clearly artificial.

CRUCIFERAE A. L. de Jussieu, Gen. Pl. 237. 1789.
Nom. alt. BRASSICACEAE Burnett, Outlines Bot. 1123. 1835.

(MUSTARD FAMILY)

Annual, biennial, or perennial herbs [rarely vines, subshrubs, shrubs, or even small trees], with pungent, watery juice rich in glucosinolates (mustard-oil glucosides) and with idioblasts containing myrosinase; indumentum lacking or of simple, furcate, dendritic, or stellate unicellular, eglandular trichomes, very rarely with additional unicellular or multicellular glands. Leaves alternate [very rarely opposite], sometimes confined to a basal rosette, exstipulate, simple, very rarely pinnate or palmate, as in *Cardamine*; stomata typically anisocytic, rarely mixed with few of some other types. Inflorescences terminal (axillary in *Coronopus*), usually racemes, corymbs, or panicles, rarely solitary on long scapes (*Leavenworthia*), usually ebracteate (bracteate in *Selenia*). Flowers hypogynous, actinomorphic (zygomorphic in *Teesdalia*), perfect [very rarely imperfect]. Sepals 4, almost always free, in 2 decussate pairs, mostly deciduous; inner (lateral) pair often saccate [rarely spurred]. Petals 4, rarely absent, free, alternating with the sepals, usually clawed, arranged in the form of a cross (cruciform, hence the family name), imbricate or contorted [rarely circinate] in bud, entire [rarely lobed, pinnatifid, or fimbriate]. Stamens 6, tetradynamous (the outer 2 shorter than the inner 4), rarely equal in length (*Warea*) or in 3 pairs of unequal length (*Streptanthus*), sometimes 2 or 4 (*Lepidium*) [very rarely 8–24, as in *Megacarpaea polyandra*]; filaments filiform, sometimes winged or appendaged at the base, free [or those of the median pairs of stamens sometimes connate]; anthers 4-sporangiate, 2-loculate at anthesis; pollen grains tricolpate (5- to 7-colpate in *Lesquerella*) [or up to 10-colpate in *Dimorphocarpa*], usually oblate or prolate, reticulate, trinucleate when shed. Nectar glands receptacular in origin, highly diversified in shape, size, and disposition around the bases of filaments. Gynoecium 2-carpellate, syncarpous; style persistent, distinct or obsolete; stigma terminal, capitate or discoid, entire or 2-lobed, the lobes opposite the placenta (replum), rarely opposite the valves, sometimes decurrent and/or connate along entire length; ovary superior, usually sessile (long-stipitate in *Warea*), 2-loculate, rarely uniloculate, with a false septum connecting the 2 parietal (or rarely subapical) placentae; ovules anatropous or campylotropous, 2-integumented, crassinucellate or tenuinucellate, few to many (sometimes 1) per locule. Fruit typically a bivalvate capsule dehiscing longitudinally from below (commonly called a silique (siliqua) when more than 3 times longer than broad, or a silicle (silicula) when clearly shorter than 3 times the width, but such distinctions arbitrary and sometimes misleading), or fruit indehiscent and becoming lomentaceous or achenelike [or a nutlet, samara, schizocarp, or even a drupe], usually beakless, or having seedless or 1- to few-seeded beaks; replum (the framelike placenta) persistent; septum complete (incomplete or reduced to a rim in *Armoracia*), usually membranaceous [rarely thick and fibrous or

nerved]; gynophores generally lacking or very short (well developed in *Warea* and *Lunaria*). Seeds without endosperm, uniseriately or biseriately arranged, winged or wingless, mucilaginous or not when wet; megagametophyte (embryo sac) of the Polygonum type; embryogeny of the Onagrad type; embryo oily, occupying the entire seed, strongly curved (straight only in *Leavenworthia*) or folded in one of seven ways, most commonly notorrhizal (cotyledons incumbent—i.e., radicle lying on the back of 1 cotyledon), pleurorrhizal (cotyledons accumbent—radicle applied to the margin of both cotyledons), or orthoplocal (cotyledons conduplicate—folded longitudinally around the radicle) [or diplecolobal—cotyledons twice transversely folded]; germination epigeal. $x = 4–13$. (Including Raphanaceae Horan., Cruciaceae Dulac.) TYPE GENUS: *Brassica* L.

A large family of approximately 340 genera and more than 3350 species in some ten poorly defined tribes, distributed throughout the world, primarily in the temperate regions and most successfully in the arid areas (although a few species of *Draba* and of some other genera have penetrated well into the Arctic and to the subantarctic islands, while others grow at altitudes of up to 6000 meters (19,700 feet) in Kashmir and Tibet). The family is clearly most abundant in the Northern Hemisphere, with the major center of diversification and endemism in the Irano-Turranian region, where some 150 genera (62 endemic) and 900 species (530 endemic) are found, and a secondary center in the Mediterranean region, with more than 110 genera (21 endemic) and nearly 630 species (290 endemic). Most of the 37 endemic genera and more than 600 species native to North America are distributed primarily in the western United States and northern Mexico. In the Southern Hemisphere, there are 32 endemic genera and some 340 species native to South America (particularly along the Andes and in Patagonia), eight genera and 110 species in South Africa, and 19 genera and 114 species in Australia and New Zealand. Only two genera (*Romanschulzia* O. E. Schulz of Mexico and Central America and *Oreophyton* O. E. Schulz of eastern tropical Africa) are endemic to the high mountains of the tropics. Of all the genera in the family, only *Cardamine* L., *Lepidium* L., and *Rorippa* Scop. are represented by indigenous species on all continents but Antarctica. Of the 121 species occurring in the southeastern United States, 55 (falling in 27 genera) are naturalized weeds, most of which were originally introduced from Europe. The majority of our 66 native species occur elsewhere in eastern North America, but only 16 of them are endemic to the Southeast, and six others have their centers of distribution in our area. Only one genus (*Warea* Nutt.) is endemic, and another (*Leavenworthia* Torrey) has its center of diversity in the Southeast. Seven of the nine taxa of *Cakile* Miller native to North America occur in our area, but the genus apparently originated and has diversified in the Old World (southwestern Asia and Europe).

A very natural family easily distinguished by the cruciform corolla, the tetradynamous stamens, and the characteristic siliques (hereafter to include the silicle), the Cruciferae—whether placed in the order Capparales of recent authors or in the abandoned Englerian Rhoeadales (see Wettstein)—have always been closely associated with the Capparaceae. Systematists are now in agreement that the Rhoeadales represent two unrelated orders, the Capparales (containing glucosinolates, myrosin cells, and centrifugal stamens, and lacking

laticifers and benzylisoquinoline alkaloids) and the Papaverales (with benzylisoquinoline alkaloids, laticifers, and centripetal stamens, and lacking glucosinolates and myrosin cells) (see Gershenzon & Mabry; Rodman, 1981). The family has recently been considered to be a direct descendant from the capparaceous subfamily Cleomoideae via the cruciferous tribe Stanleyeae (= Thelypodieae) (Janchen; Takhtajan) or through the Hesperideae (Dvořák, 1973). Although the morphological evidence very strongly favors a connection through the Thelypodieae, none of the extant crucifers is truly archaic, and the palynological data (Al-Shehbaz, 1973) do not support such a direct link. It is, therefore, more reasonable to assume that the connection between the two families is through a common ancestor. Fossil evidence is of no help here, and the few scattered reports of cruciferous pollen from the Upper Miocene of France (Muller) and the Cretaceous of New Zealand (Couper), as well as the fossil siliques of *Thlaspi* L. from the Oligocene of Montana (Becker) and those of *Lepidium* and other genera (Schulz), only complicate the problem.

The tribal classification of the family has occasioned more controversy than any other aspect of its systematics, and none of the existing tribal systems comes close to satisfying all concerned. Although much criticized for its artificiality, Schulz's is the latest comprehensive monograph on the family, and despite its weaknesses, his system is the most widely followed. With the exception of the tribes Brassiceae, Lepidieae, and Thelypodieae (the Stanleyeae, Streptantheae, and Romanschulzieae of Schulz), all the other large tribes of his system fall short of being natural. Janchen reduced the 19 tribes of Schulz to 15, and his merging of the Matthioleae with the Hesperideae and of both the Drabeae and Lunarieae with the Alysseae is probably justified. The Cremolobeae R. Br. (two genera and 36 species of South America) and the Heliophileae DC. (four genera and 77 species of South Africa) are sufficiently distinct and probably merit recognition, but the tribal status of the Pringleeae Hayek and Chamireae Sonder, both unigeneric and monotypic, needs careful evaluation. On the other hand, the Stenopetaleae O. E. Schulz, an Australian unigeneric tribe with eight species, rest solely on the narrowly linear or filiform petals that are circinate in bud, a feature independently evolved in the unrelated Australian monotypic *Carinavalva* Ising and the North American *Lyrocarpa* Hooker & Harvey. The genera of the Schizopetaleae R. Br. ex Barn., *Schizopetalon* Sims (seven species, Chile), *Ornithocarpa* Rose (two species, Mexico), and *Dryopetalon* Gray (four species, northwestern Mexico and the adjacent United States), are united mainly by the divided petals. However, they are so different in their fruits, sepal orientation, indumentum, nectaries, stigmas, and cotyledons that they form a highly heterogeneous group of unrelated genera (see Rollins, 1969). In my opinion, each of these genera can be loosely associated with certain members of one of three other tribes.

Avetisian (1976, 1983) has recently reduced Schulz's tribes to three, Thelypodieae, Brassiceae, and Sisymbrieae, but such an action does not seem to be well founded. In the past, tribes have been erected on the basis of differences in a few characters such as cotyledonary position, type of pubescence, and fruit length and the type of its flattening, but this always leads to artificiality in the tribal classification. Perhaps a more realistic classification of the family can be

achieved by grouping the closely related genera and working upward to more natural infrafamilial taxa. The modified version of Janchen's system adopted here is only intended to provide a workable framework for infrafamilial subdivisions above the generic level, but even though it represents a major improvement over Schulz's system, it cannot be considered natural as far as the tribal limits of the Alysseae, Arabideae, Hesperideae, and Sisymbrieae are concerned. Generic boundaries in the family are often arbitrarily drawn, and the establishment of clear-cut intergeneric relationships is often difficult. Although there is an average of about ten species to a genus, the majority of genera (250) are oligotypic with five or fewer species, and 138 of these are monotypic. However, more than half of the species of the family belong to 12 large genera: *Draba* L. (340), *Erysimum* L. (180), *Cardamine* (175), *Lepidium* (175), *Alyssum* L. (170), *Arabis* L. (170), *Sisymbrium* L. (90), *Lesquerella* S. Watson (80), *Rorippa* (75), *Thlaspi* (75), *Heliophila* L. (72), and *Hesperis* L. (60). Unlike many of the small genera, the species are generally very distinct throughout the family. A few exceptions, however, do exist, and the most notable examples are the Old World genera *Isatis* L., *Aethionema* R. Br., and *Biscutella* L., in which hybridization, polyploidy, and apomixis, alone or together, may have played an important role in making species determination a very difficult task.

Chromosome numbers have been reported for more than 1400 species (41% of the family total) in 197 genera (author's compilation). A continuous series of base chromosome numbers from four to 13 exists, but a surprisingly high percentage (37%) of the species appear to be based on eight. The lowest chromosome number known for the family ($n = 4$) has been found so far only in two unrelated genera, the Australian *Stenopetalum* R. Br. ex DC. and the western North American *Physaria* (Nutt.) Gray, while the highest number reported ($n = 128$) is in *Cardamine laciniata* (Muhl. ex Willd.) Wood. Nearly 37 percent of the species are polyploid, and some of the genera such as *Crambe* L. (Brassiceae) and *Streptanthus* Nutt. (Thelypodieae) appear to be exclusively polyploid. Both genera are generally considered the most advanced in their respective tribes. However, Mukherjee believes that aneuploidy and diminution in chromosome size, rather than polyploidy, have played an important role in the evolution of the family. The tribes Alysseae and Arabideae have a base chromosome number of eight, which has been found in more than 60 percent of their species; only about 10–15 percent of their species are based on seven. On the other hand, the tribes Hesperideae, Lepidieae, and Sisymbrieae are based primarily on seven, which has been found in about 40–45 percent of their species, and secondarily on eight, encountered in about 20 percent of the species of each tribe. No single base chromosome number dominates in the Brassiceae, and with more than 77 percent of its species known cytologically, the base numbers 7, 8, 9, 10, 11, 12, and 15 occur with frequencies ranging from eight to 20 percent. Although the Thelypodieae have a continuous series of haploid chromosome numbers of ten to 15 (with nearly 46 percent of the species known cytologically), $n = 14$ occurs in more than 60 percent of the species and $n = 13$ in about 20 percent.

Many genera of the Cruciferae have been studied for their chemical con-

stituents, especially the glucosinolates (mustard-oil glucosides) and the seed fatty acids, both of which have been thoroughly surveyed in the economic species and their wild allies. The fatty-acid composition is known for at least 165 species in 70 genera; in this small sample, the linolenic or erucic acids are the most dominant constituents in the seeds of about 85 percent of the species surveyed. All Cruciferae appear to have glucosinolates, and of the approximately 85 types known, only methyl glucosinolate (typically characteristic of the Capparaceae) has not been found in any crucifer (see Hedge *et al.*). The distribution of these compounds has been shown to be a valuable tool in chemosystematic studies at the generic and specific levels (Rodman, 1981). In all, some 350 species in about 70 genera have been surveyed, but since most of the earlier reports have dealt only with the distribution of the major constituents, many of the species need to be reinvestigated in order to have a complete profile of their glucosinolates. It is agreed that the glucosinolates probably play the most important role in the chemical defense of crucifers against pathogens and herbivores. Research on the distribution of the fatty acids or the glucosinolates has so far failed to provide any meaningful support for the tribal classification of the family. The flavonoid chemistry in the family has not received the attention it deserves, and some of the recent works (Bacon) show that such compounds can be equally valuable in systematic studies in this family. Other secondary metabolites generally occur in negligible amounts, and they are often overlooked. However, relatively high concentrations of alkaloids (*Lunaria* L.), cucurbitacins (*Iberis* L.), and cardenolides (*Erysimum*) may be found, and the distribution of the last group of compounds may prove to be useful in solving some of the problems in taxonomically difficult genera such as *Erysimum*. Species of a few genera are known to accumulate high amounts of selenium (*Stanleya* Nutt.) or nickel (*Alyssum, Streptanthus*), but these capacities have no taxonomic value.

Floral anatomy in the Cruciferae has been studied in detail, mainly to resolve several controversial aspects of the gynoecial structure, such as the vasculature of the ovary, the number of carpels, the origin of the septum, the position of the stigmatic lobes, and the derivation of the placentae. The widely accepted bicarpellary hypothesis advocated by Arber, Zohary (1948b), Puri (1951), and Alexander states that the cruciferous gynoecium originated through the connation of the margins of two lateral carpels to form two median parietal placentae, each of which produces an outgrowth that fuses with the other in the center to form the false septum. This hypothesis, however, fails to provide an adequate explanation for the inverted position of the inner vascular bundles of the replum and for the frequent commissural position of the stigma lobes. The tetracarpellary views of Saunders, Eames & Wilson, Puri (1941), Merxmüller & Leins, and (more recently) Eigner agree that the cruciferous gynoecium is composed of four carpels, of which the median two are fertile and the lateral two are sterile. Despite the fact that these hypotheses provide sound interpretation for the vasculature of the stigma and replum, they do not adequately explain the origin of the false septum and the position of the ovules. Furthermore, as indicated by Zohary (1948b), in crucifers with dehiscent fruits, the lines of dehiscence appear only in the later stages of development and do not

correspond with carpel margins, as proposed by Saunders and others (see above). Although I support the bicarpellary interpretation and believe that the gynoecium of the Cruciferae is homologous to that of the closely related Capparaceae, both the bi- and tetracarpellary views fail to provide fully satisfactory answers for all the various aspects of the cruciferous gynoecium. The reader is advised to consult Maule and Roth for further details.

Flower colors of Cruciferae are predominantly yellow, white, and shades from lavender to purple; true blue or red flowers, if they occur at all, are indeed very rare. The remarkable constancy of floral architecture in the family has been very closely linked to pollination by insects, particularly various Hymenoptera, Diptera, Lepidoptera, and some Coleoptera. Wind pollination is extremely rare and is probably best known in *Pringlea antiscorbutica* R. Br., a species restricted to the small Kerguelen and Crozet islands of the southern Indian Ocean. Autogamy is common in many of the weedy species, while cleistogamy always occurs in the submersed plants of *Subularia aquatica* L. Unlike protogyny, protandry appears to be rare in the family (Al-Shehbaz, 1977), and except for very few examples, the flowers of the Cruciferae are almost always perfect. Dioecism is known in three species of *Lepidium* from New Zealand, while monoecism has been reported in *Megacarpaea megalocarpa* (Fischer ex DC.) Schischkin ex Fedtsch., of central Asia and southeastern Russia.

Fruits of the Cruciferae are so diverse that they are the most reliably used structures for the proper identification of genera and species. In plants with dehiscent siliques, seed dispersal—even if explosive, as in *Cardamine*—is confined to short distances from the parent plant. However, because of their small size, seeds of the family in general are easily washed farther away by rain or transported by strong winds in open habitats. The corky fruits of all but one of the taxa of *Cakile* and of some species of *Crambe* and *Raphanus* L. are transported by sea, while the winged seeds and samaroid and bladdery fruits that have independently evolved many times in the family are dispersed by wind. The dustlike seeds of certain Saharan species of *Diplotaxis* DC. may weigh as little as 0.05 mg and can therefore be transported by storms for several hundred miles. The remarkable rose of Jericho (tumbling or resurrection mustard), *Anastatica hierochuntica* L., is dispersed by the tumbling of the entire dry plant, and this species has a continuous distribution extending 8000 kilometers (5000 miles) in hot deserts from Mauretania to western Pakistan. Fruit dispersal by mammals is known for several genera having hooked hairs (*Tauscheria* Fischer ex DC.), glochidiate spines (*Clypeola* L.), and other adaptive features. Geocarpy has evolved independently in the Australian *Geococcus pusillus* Drumm. ex Harvey, in the South American *Cardamine chenopodiifolia* Pers., and in *Morisia monanthos* (Viv.) Ascherson, of Corsica and Sardinia.

The family is primarily herbaceous, and only some five percent of its species are typically woody; more than 62 percent are perennials. Growth forms, however, may vary from delicate annual herbs to the South American hummock-forming *Xerodraba pycnophylloides* (Spegaz.) Skottsb. and *Lithodraba mendociensis* (Spegaz.) Boelcke, the South African woody climber *Heliophila scandens* Harvey, the large shrubs *Foleyola* Maire of northern Africa and *Par-*

olinia Webb of the Canary Islands, or even the small tree *Farsetia somalensis* (Pax) Gilg & C. Benedict, of Somalia, Ethiopia, and Kenya. *Farsetia* Turra also contains a few annual or perennial herbs, which may be less than 10 cm high, as well as large shrubs that may exceed 2 m in height in eastern tropical Africa. Typical shrubs are found in about two percent of the total species of Cruciferae in at least 16 genera scattered in different tribes. The woody condition appears to be almost always a derived one, and it must have evolved independently many times within the family.

The family includes a number of important crop plants that are grown as food for humans or animals, as sources of condiments or edible and industrial oils, or as ornamentals. The family is also known for its more than 120 weedy species of local or cosmopolitan distribution that invade cultivated lands and occupy disturbed sites, roadsides, waste grounds, and the like. *Brassica* is the most important genus, for it contains several vegetable and salad plants such as cabbage, cauliflower, Brussels sprouts, kale, broccoli, kohlrabi (all considered to be varieties of *B. oleracea* L.), turnip and Chinese cabbage (*B. campestris* L.), rape (*B. napus* L.), Chinese or Indian mustard (*B. juncea* (L.) Czern.), and black mustard (*B. nigra* (L.) W. D. Koch). Other crops include the radish (*Raphanus sativus* L.), watercress (*Nasturtium officinale* R. Br.), and the common or garden cress (*Lepidium sativum* L.). Condiments are obtained from the fleshy roots of horseradish (*Armoracia rusticana* Gaertner, Meyer, & Scherb.), while table mustard is prepared from a mixture of the seeds of the white mustard (*Sinapis alba* L.) and those of either the black or the Indian mustard.

Oils from crucifer seeds, particularly from rape, rank fifth in terms of the world tonnage production, and most of it (except that used for making margarine in Europe and cooking oil in India) is utilized in the manufacture of numerous industrial products. The seed cake remaining after the expression of oil is rich in protein, and until recently it has been extensively used as feed for farm animals. It contains potentially harmful mustard oils, however, so this usage has become very limited, and most of the seed cake is now used as a fertilizer.

The most important ornamental crucifers include the wallflower (*Erysimum Cheiri* (L.) Crantz, rocket or dame's violet (*Hesperis matronalis* L.), candytuft (*Iberis* species), honesty or money plant (*Lunaria annua* L. and *L. rediviva* L.), sweet alyssum (*Lobularia maritima* (L.) Desv.), stock (*Matthiola incana* (L.) R. Br.), aubrietia (*Aubrieta deltoidea* (L.) DC.), rock cress (*Arabis* species), and some species of the genera *Aethionema, Alyssum, Brassica,* and *Draba.* The historic blue dye woad was obtained from the fermented ground leaves of *Isatis tinctoria* L.

REFERENCES:

The volume of literature dealing with the various aspects of the family is enormous. Most of the important literature published before 1936 is thoroughly covered by Schulz and has not been repeated here. Although the number of references given here may seem excessive, only about half of the literature consulted during the preparation of this paper has been included.

ALEXANDER, I. Entwicklungsstudien an Blüten von Cruciferen und Papaveraceen. Planta **41:** 125–144. 1952. [Floral development in *Arabis, Cheiranthus,* and *Hypecoum*; "homology" in floral diagram between Cruciferae and Fumariaceae.]

AL-SHEHBAZ, I. A. The biosystematics of the genus *Thelypodium* (Cruciferae). Contr. Gray Herb. **204:** 3–148. 1973. [Generic limits, keys, and evolutionary trends among members of the tribe Thelypodieae; pollen of selected Capparaceae; distribution of mustard oils.]

———. Protogyny in the Cruciferae. Syst. Bot. **2:** 327–333. 1977. [Report of protogyny in 21 species of 19 genera, and a compilation of that previously reported in 61 species of 32 genera.]

——— & M. M. AL-OMAR. *In:* A. LÖVE, ed., IOPB chromosome number reports LXXVI. Taxon **31:** 574–598. 1982. [Brassicaceae, 587–589, counts for 58 species in 38 genera.]

APPELQVIST, L.-A. Lipids in Cruciferae: VIII. The fatty acid composition of seeds of some wild or partially domesticated species. Jour. Am. Oil Chem. Soc. **48:** 740–744. 1971. [Fatty-acid composition of 29 species.]

———. Lipids in the Cruciferae. Pp. 221–277 *in* J. G. VAUGHAN *et al.*, eds., The biology and chemistry of the Cruciferae. London, New York, & San Francisco. 1976. [A review of fatty-acid composition, sterols, waxes, and other lipids; special emphasis on the cultivated species; *19 tables.*]

ARBER, A. Studies in floral morphology. I. On some structural features of the cruciferous flower. New Phytol. **30:** 11–41. 1931a. [The vascular supply of various floral parts; prefers the bicarpellary origin of gynoecium for descriptive purposes but questions the justification for treating the bi- or tetracarpellary hypotheses as true.]

———. Studies in floral morphology. II. On some normal and abnormal crucifers: with a discussion on teratology and atavism. *Ibid.* 172–203. 1931b. [*Alliaria, Brassica, Capsella, Crambe, Diplotaxis, Nasturtium,* and *Sinapis*; strong criticism of Saunders's assumptions that abnormalities represent reversionary ancestral conditions; see SAUNDERS.]

ARYAVAND, A. Contribution à l'étude cytotaxinomique de quelques Crucifères de l'Iran et de la Turquie. Bull. Soc. Neuchâteloise Sci. Nat. **98:** 43–58. 1975. [Counts for 33 species in 18 genera.]

AVETISIAN, V. E. Some modifications of the system of the family Brassicaceae. (In Russian; English summary.) Bot. Zhur. **61:** 1198–1203. 1976. [The six largest tribes reduced to two, Brassiceae and Sisymbrieae, the latter encompassing the Alysseae, Arabideae, Hesperideae, and Lepidieae; parallelism in most characters of these tribes.]

———. Some peculiarities in distribution of Brassicaceae in connection with their evolution. (In Russian.) *Ibid.* **65:** 825–829. 1980. [Lists the distributions of some 170 genera of the Brassiceae and the highly artificial Sisymbrieae in the North Temperate regions of the Old World.]

———. The system of the family Brassicaceae. (In Russian; English summary.) *Ibid.* **68:** 1297–1305. 1983. [Three tribes recognized: Thelypodieae (including Pringleeae and Cremolobeae), Brassiceae (including Chamireae and Heliophileae), and Sisymbrieae (including the remainder of the family).]

BACON, J. D. Taxonomy of *Nerisyrenia* (Cruciferae). Rhodora **80:** 159–227. 1978. [Extensive account of the cytology and flavonoid chemistry in the genus; nine species recognized.]

BAEZ MAYOR, A. Estudio cariológico de algunas crucíferas y su interpretación en la sistemática. Cavanillesia **6:** 59–103. 1934. [Basic number for family $x = 7$; counts for *Sisymbrium, Alliaria, Diplotaxis, Hirschfeldia, Eruca, Brassica, Moricandia, Rapistrum, Camelina.*]

BAILLON, H. Cruciferae. Hist. Pl. **3:** 181–292. 1871. [English translation by M. M. HARTOG, **3:** 179–291. 1874.]

BATEMAN, A. J. Self-incompatibility systems in angiosperms. III. Cruciferae. Heredity **9**: 53–68. 1955a. [A survey of 182 species in 80 genera, with particular emphasis on *Brassica, Capsella,* and *Cardamine.*]

———. Note on dioecy in the Cruciferae. *Ibid.* 415. 1955b. [*Lepidium sisymbrioides* of New Zealand is dioecious and may have evolved from inbreeding ancestors, or its sex-determining factor may have been derived from the S-gene.]

BAYER, A. Beiträge zur systematischen Gliederung der Cruciferen. Bot. Centralbl. **18**: 119–180. 1905. [Recognizes 15 tribes based primarily on differences in nectar-gland morphology.]

BECKER, H. F. Oligocene plants from the upper Ruby River Basin, southwestern Montana. Geol. Soc. Am. Mem. **82**: 1–127. 1961. [*Thlaspi primaevum,* n. sp., 69, *pl. 20, figs. 9–11*; excellent imprints of fruit.]

BEHNKE, H. D. Sieve-element characters. Nordic Jour. Bot. **1**: 381–400. 1981. [Sieve-tube plastids in Brassicaceae of the S-type in 22 species of 21 genera, and of the P-type in two species of one genus.]

——— & G. ESCHLBECK. Dilated cisternae in Capparales—an attempt towards the characterization of a specific endoplasmic reticulum. Protoplasma **97**: 351–363. 1978.

BENTHAM, G., & J. D. HOOKER. Cruciferae. Gen. Pl. **1**: 57–102. 1865. [Treatment by HOOKER.]

BERGGREN, G. Atlas of seeds and small fruits of northwest-European plant species with morphological descriptions. Part 3. 260 pp. Stockholm. 1981. [Cruciferae, 108–145, *pls. 70–105*; keys based on seed characters for 36 genera and 93 species; descriptions of fruits and seeds for genera and species.]

BERKUTENKO, A. N., & N. N. GURZENKOV. Chromosome numbers and distribution of Cruciferae in the south of the Magadan region. I. (In Russian.) Bot. Zhur. **61**: 1595–1603. 1976. [*Alyssum, Arabidopsis, Arabis, Cochlearia, Draba, Erysimum, Lesquerella*; counts for ten species; *10 maps.*]

BOLKHOVSKIKH, Z., V. GRIF, T. MATVEJEVA, & O. ZAKHAREVA. Chromosome numbers of flowering plants. A. A. FEDOROV, ed. (Russian and English prefaces.) 926 pp. Leningrad. 1969. [Brassicaceae, 162–179; chromosome counts through 1964.]

BOUMAN, F. Integument initiation and testa development in some Cruciferae. Bot. Jour. Linn. Soc. **70**: 213–229. 1975. [*Brassica, Capsella, Lunaria, Sinapis.*]

BREWBAKER, J. L. The distribution and phylogenetic significance of binucleate and trinucleate pollen grains in the angiosperms. Am. Jour. Bot. **54**: 1069–1083. 1967. [Cruciferae, 1078; pollen trinucleate when shed, 16 genera sampled.]

BRITTON, N. L., & A. BROWN. An illustrated flora of the northern United States, Canada and the British possessions. Vol. 2. iv + 735 pp. New York. 1897. [Cruciferae, 108–154; ed. 2, vol. 2, 146–196. 1913.]

BÜNNING, E. Über die Differenzierungsvoränge in der Cruciferenwurzel. Planta **39**: 126–153. 1951. [*Lepidium, Sinapis.*]

BUSCH, N. A., ed. Cruciferae. *In:* V. L. KOMAROV, ed., Fl. USSR **8**: 14–606. 1939. [English translation by R. LAVOOTT, **8**: 13–453, 471–490. Jerusalem. 1970.]

CAIUS, J. F. The medicinal and poisonous crucifers of India. Jour. Bombay Nat. Hist. Soc. **40**: 693–712. 1939. [Keys, common names, and use of 40 species in 22 genera.]

CALESTANI, V. Sulla classificazione delle Crocifere Italiane. Nuovo Giorn. Bot. Ital. **15**: 355–390. 1908.

———. Evoluzione e classificazione delle Crocifere. *Ibid.* **24**: 245–290. 1917. [Evolution in the flowers, fruits, and embryos; recognizes 16 subtribes and 14 tribes in the three "series," Orthorhizae, Siliculosae, and Siliquosae.]

CANDOLLE, A. P. DE. Cruciferae. Syst. Nat. **2**: 139–700. 1821. [95 genera in 21 tribes in five subfamilies (subordines) distinguished on the bases of fruit type and of cotyledonary position in relation to the radicle.]

———. Cruciferae. Prodr. **1**: 131–236. 1824.

CARLQUIST, S. Wood anatomy of Macaronesian and other Brassicaceae. Aliso **7**: 365–

384. 1971. [*Cheiranthus* (= *Erysimum*), *Crambe, Descurainia, Lepidium, Matthiola, Parolinia, Sinapidendron, Stanleya.*]

COLE, R. A. 1-cyanoepithioalkanes: major products of alkenylglucosinolate hydrolysis in certain Cruciferae. Phytochemistry **14:** 2293, 2294. 1975. [17 species in 11 genera.]

———. Isothiocyanates, nitriles, and thiocyanates as products of autolysis of glucosinolates in Cruciferae. *Ibid.* **15:** 759–762. 1976. [Quantitative determination of 22 glucosinolate products from seedlings of 74 species in 35 genera.]

CORBETT, G. A. New records for the West Virginia Cruciferae. Castanea **38:** 214–229. 1973. [61 species in 29 genera of Cruciferae in the state; eight new records; *20 maps.*]

COUPER, R. A. New Zealand Mesozoic and Cainozoic plant microfossils. New Zealand Geol. Surv. Paleont. Bull. **32:** 1–88. 1960. [Cruciferous pollen, 47, *pl. 7, figs. 1, 2*; from Haumurian (Maestrichtian) or ?Piripauan (Upper Senonian), found commonly throughout Cretaceous and Tertiary.]

CRISP, P. Trends in the breeding and cultivation of cruciferous crops. Pp. 69–118 *in* J. G. VAUGHAN *et al.*, eds., The biology and chemistry of the Cruciferae. London, New York, & San Francisco. 1976. [Economic importance, breeding systems, polyploidy, future trends; special emphasis on *Brassica.*]

CRONQUIST, A. An integrated system of classification of flowering plants. *Frontisp.* + xviii + 1262 pp. New York. 1981. [Capparales, 436–451; Brassicaceae, 446–449; suggests that the connection between the Brassicaceae and Capparaceae might be found among the Old World genera; fossils of family occur in Oligocene and more recent deposits.]

CROVELLO, T. J., & D. C. MILLER. Floristic similarities among 51 regions of the Soviet Union based on the Brassicaceae. Taxon **31:** 451–461. 1982. [Numerical study using principal components analysis of distributional data for 736 species of nine tribes.]

CURTIS, P. J., & P. M. MEADE. Cucurbitacins from the Cruciferae. Phytochemistry **10:** 3081–3083. 1971. [Compounds rare in Cruciferae, found in several *Iberis* species and in *Lepidium sativum.*]

DANIELAK, R., & B. BORKOWSKI. Biologically active compounds in seeds of crucifers. Part III. Chromatographical search for glucosynolates. Diss. Pharm. Pharmacol. **21:** 563–575. 1969. [Spot tests and R_f values for glucosinolates in 155 species.]

DAS, V. S. R., & K. N. RAO. Phytochemical phylogeny of the Brassicaceae (Cruciferae) from the Capparidaceae. Naturwissenschaften **62:** 577, 578. 1975. [Nine genera of Cruciferae and five of Capparaceae tested for 15 phenolic acids; data support the derivation of the former family from the latter.]

DAVIS, G. L. Systematic embryology of the angiosperms. x + 528 pp. New York. 1966. [Cruciferae, 97, 98.]

DAXENBICHLER, M. E., C. H. VAN ETTEN, F. S. BROWN, & Q. JONES. Oxazolidinethiones and volatile isothiocyanates in enzyme-treated seed meals from 65 species of Cruciferae. Agr. Food Chem. **12:** 127–130. 1964.

DVOŘÁK, F. On the evolutionary relationship in the family Brassicaceae. Feddes Repert. **82:** 357–372. 1971. [Relationships between *Macropodium, Lunaria, Christolea, Ermania,* and *Vvedenskyella* based on types of cellular pattern of the septum and on gynophore length; *table 1* compares floral and fruit characters.]

———. The importance of the indumentum for the investigation of evolutional relationship in the family Brassicaceae. Österr. Bot. Zeitschr. **121:** 155–164. 1973. [Multicellular glandular hairs occur in the Hesperideae and the ancestral Cleomoideae of Capparaceae, suggesting a possible link; unicellular glandular hairs only in *Descurainia.*]

EAMES, A. J., & C. L. WILSON. Carpel morphology in the Cruciferae. Am. Jour. Bot. **15:** 251–270. 1928. [Postulate that the cruciferous gynoecium evolved from four carpels (two outer ones that are sterile and two inner that are fertile but without locules and their ovules are placed in the locules of the sterile carpels); the septum represents an expansion of the ventral margins of solid carpels.]

——— & ———. Crucifer carpels. *Ibid.* **17:** 638–656. 1930. [Further arguments for their tetracarpellary hypothesis; vascular supply of the ovules is derived from inversely oriented ventral bundles.]

EASTERLY, N. W. Chromosome numbers of some northwestern Ohio Cruciferae. Castanea **28:** 39–42. 1963. [Counts for 21 species in 18 genera.]

———. Distribution patterns of Ohio Cruciferae. *Ibid.* **29:** 164–173. 1964. [*84 county distribution maps* for 78 species in 35 genera.]

———. An illustrated guide to the Cruciferae of Ohio. *Ibid.* **30:** 177–191. 1965. [Keys to genera and to species; *47 colored photos* of plants; photographs of seeds.]

EGGERS, O. Über die morphologische Bedeutung des Leitbundelverlaufes in den Blüten der Rhoeadalen und über das Diagramm der Cruciferen und Capparidaceen. Planta **24:** 14–58. 1935.

EIGNER, J. Zur Stempel- und Fruchtenwicklung ausgewählter Brassicaceae (= Cruciferae) unter neueren Gesichtspunkten der Blütenmorphologie und der Systematik. (English summary.) Beitr. Biol. Pflanzen **49:** 359–427. 1973 [1974]. [Gynoecium and fruit development of 34 species in 32 genera; support for the tetracarpellary hypothesis of gynoecium; trends in fruit evolution; modification of Janchen's system; see JANCHEN.]

ERDTMAN, G. Pollen morphology and plant taxonomy. Angiosperms. 539 pp. Stockholm. 1952. (Corrected reprint with addendum [pp. 541–553]. New York. 1971.) [Cruciferae, 133, 134; concludes from survey of 80 species in 55 genera that the family is ± stenopalynous, resembling the Capparaceae but differing from the Fumariaceae; see also AL-SHEHBAZ, 1973, and ROLLINS & BANERJEE, 1979.]

ETTLINGER, M. G., & A. KJAER. Sulfur compounds in plants. Pp. 59–144 *in* T. J. MABRY, R. E. ALSTON, & V. C. RUNECKLES, eds., Recent advances in phytochemistry. Vol. 1. New York. 1968.

FEENY, P. Defensive ecology of the Cruciferae. Ann. Missouri Bot. Gard. **64:** 221–234. 1977. [Role of glucosinolates in defending crucifers against bacteria, fungi, insects, and mammals; glucosinolates as attractants to adapted enemies.]

FERNALD, M. L. Gray's manual of botany. ed. 8. lxiv + 1632 pp. New York. 1950. [Cruciferae, 685–728.]

GERSHENZON, J., & T. J. MABRY. Secondary metabolites and the higher classification of angiosperms. Nordic Jour. Bot. **3:** 5–34. 1983. [Glucosinolates in Brassicaceae and other families, 14–16; *table 1* compares the systems of Cronquist, Takhtajan, Thorne, and Dahlgren with respect to the glucosinolate-containing families.]

GILG, E., & R. MUSCHLER. Aufzählung aller zur Zeit bekannten südamerikanischen Cruciferen. Bot. Jahrb. **42:** 437–487. 1909. [Enumeration of 287 species in 42 genera, four new genera, and 19 new species; numerous new combinations.]

GOERING, K. J., R. ESLICK, & D. L. BRELSFORD. A search for high erucic acid containing oils in the Cruciferae. Econ. Bot. **19:** 251–256. 1965. [Seeds of 35 species in 20 genera tested for percentages of erucic acid, C_{18} acids, oil, and protein.]

GÓMEZ-CAMPO, C. Studies on Cruciferae IV. Chorological notes. Anal. Inst. Bot. Cavanilles **34:** 485–496. 1978. [Notes on 32 taxa of 18 genera; traces the origin of two species of *Brassica* adventive to Australia and California.]

——— & L. DELGADO. Radioresistance in crucifers. Rad. Bot. **4:** 479–483. 1964. [More than half of 47 species in 38 genera showed high radioresistance; nuclear volume and chromosome size assumed as significant factors accounting for resistance.]

GÜNTHART, A. Beiträge zur Blüthenbiologie der Cruciferen, Crassulaceen und der Gattung *Saxifraga*. Bibliot. Bot. **11**(Heft 58). ix + 97 pp., *11 pls.* 1902. [Cruciferae, 3–38, *pls. 1–5*; detailed descriptions of the anthesis of 51 species in 14 genera.]

———. Über die Entwicklung und Entwicklungsmechanik der Cruciferenblüte und ihre Function unter natürlichen und künstlichen Bedingungen. Beih. Bot. Centralbl. **35**(Heft 1): 60–170. 1917.

GUYOT, M. Virescence et organisation de la fleur des Crucifères. Bull. Soc. Bot. France **109:** 170–176. 1962. [Theoretical floral diagram based on teratology.]

HANNIG, E. Untersuchungen über die Scheidwände der Cruciferenfrüchte. Bot. Zeit. **59:** 207–245. *pls. 8–10.* 1901. [Septum as an outgrowth from carpel margin, appearing at maturity of fruit as two epidermal layers firmly cohering but separating at regions of attachment to replum, where they carry stomata; the space between the two layers is filled with loose parenchyma; numerous examples.]

HARTWELL, J. L. Plants used against cancer. A survey. Lloydia **32:** 79–107. 1969. [Cruciferae, 79–92; some 40 species of 27 genera; a table of species, common names, medical preparations, disease conditions, comments, and old literature.]

HASAPIS, X., A. J. MACLEOD, & M. MOREAU. Glucosinolates of nine Cruciferae and two Capparaceae species. Phytochemistry **20:** 2355–2358. 1981. [*Alyssum, Arabis, Cardaria, Diplotaxis, Lobularia, Sinapis, Sisymbrium, Cleome, Gynandropsis.*]

HAYEK, A. VON. Entwurf eines Cruciferen-Systems auf phylogenetischer Grundlage. Beih. Bot. Centralbl. **27:** 127–335. *pls. 8–12.* 1911. [Recognizes ten tribes and 28 subtribes largely circumscribed on characteristics of myrosin cells and nectar glands; descriptions for 231 genera; phylogeny within tribes.]

HEBEL, M. The mustards and related plant families in eastern Tennessee. Jour. Tenn. Acad. Sci. **8:** 332–340, 382–417. 1933. [Phylogeny and taxonomy of Papaveraceae, Fumariaceae, Cruciferae, and Capparaceae; Cruciferae, 388–406.]

HEDGE, I. C. A systematic and geographical survey of the Old World Cruciferae. Pp. 1–45 *in* J. G. VAUGHAN *et al.*, eds., The biology and chemistry of the Cruciferae. London, New York, & San Francisco. 1976. [Evaluation of tribes, endemism and distributional patterns in Old World regions, primitive characters, and evolutionary trends; *6 tables, 8 figures*; tribal classification according to five systems.]

———, A. KJAER, & O. MALVER. *Dipterygium*—Cruciferae or Capparaceae? Notes Bot. Gard. Edinburgh **38:** 247–250. 1980. [Presence of methyl glucosinolate in *D. glaucum* supports the capparaceous disposition of the genus.]

——— & K. H. RECHINGER. Cruciferae. *In:* K. H. RECHINGER, ed., Fl. Iranica **57:** 1–372. *pls. 1–36.* 1968. [In Latin; area covers Iran, Afghanistan, and portions of Pakistan, Iraq, and USSR.]

HEGNAUER, R. Chemotaxonomie der Pflanzen. Vol. 3. 743 pp. Stuttgart. 1964. [Cruciferae, 586–607, 663–665, 674, 675.]

HEWSON, H. J. Brassicaceae. *In:* B. G. BRIGGS *et al.*, eds., Fl. Australia **8:** 231–357. 1982.

HEYWOOD, V. H., ed. Cruciferae. *In:* T. G. TUTIN *et al.*, eds., Fl. Europaea **1:** 260–346. 1964.

HILDEBRAND, F. Vergleichende Untersuchungen über die Saftdrüsen der Cruciferen. Jahrb. Wiss. Bot. **12:** 10–40. 1879. [Survey of nectar-gland morphology in 21 genera.]

HINATA, K., & T. NISHIO. Self-incompatibility in crucifers. Pp. 223–234 *in* S. TSUNODA *et al.*, eds., *Brassica* crops and wild allies. Tokyo. 1980. [Special emphasis on cultivated members.]

HOROVITZ, A., & Y. COHEN. Ultraviolet reflectance characteristics in flowers of crucifers. Am. Jour. Bot. **59:** 706–713. 1972. [UV patterns of 28 species in 24 genera; *21 figures.*]

INAMDAR, J. A., & N. V. RAO. Light and scanning electron microscopic studies on trichomes of some Brassicaceae. Feddes Repert. **94:** 183–190. 1983. [32 species in 20 genera; *1 SEM plate.*]

INGRAM, D. S., B. A. KNIGHTS, I. J. MCEVOY, & P. MCKAY. Studies in the Cruciferae. Changes in the composition of the sterol fraction following germination. Phytochemistry **7:** 1241–1245. 1968. [*Brassica, Cheiranthus, Raphanus, Sinapis.*]

IVERSEN, T.-H. The morphology, occurrence, and distribution of dilated cisternae of the endoplasmic reticulum in tissues of plants of the Cruciferae. Protoplasma **71:** 467–

477. 1970. [Dilated cisternae found in 35 species of Cruciferae but not in Resedaceae (four spp.) or Papaveraceae (20 spp.).]

——— & C. BAGGERUD. Myrosinase activity in differentiated and undifferentiated plants of Brassicaceae. Zeitschr. Pflanzenphysiol. **97:** 399–407. 1980. [Callus cultures of seven species.]

JAFRI, S. M. H. Brassicaceae. *In:* E. NASIR & S. I. ALI, eds., Fl. West Pakistan **55:** 1–308. 1973. [Some 250 species in 92 genera.]

JANCHEN, E. Das System der Cruciferen. Österr. Bot. Zeitschr. **91:** 1–28. 1942. [Criticism and modification of Schulz's system; 15 tribes and 41 subtribes recognized; see SCHULZ.]

JARETZKY, R. Untersuchungen über Chromosomen und Phylogenie bei einigen Cruciferen. Jahrb. Wiss. Bot. **68:** 1–45. 1928.

———. Beziehungen zwischen Chromosomenzahl und Systematik bei den Cruciferen. *Ibid.* **76:** 485–527. 1932. [Chromosome counts for 44 Old World genera.]

JART, A. The fatty acid composition of various cruciferous seeds. Jour. Am. Oil Chem. Soc. **55:** 873–875. 1978. [27 species of *Cardamine, Draba, Erysimum, Malcolmia,* and *Matthiola.*]

JONES, S. B., JR. Mississippi flora. III. Distribution and identification of the Brassicaceae. Castanea **40:** 238–252. 1975. [Keys and distribution maps for 39 species in 24 genera.]

JONSELL, B. Some tropical African Cruciferae. Chromosome numbers and taxonomic comments. Bot. Not. **129:** 123–130. 1976.

———. Cruciferae. *In:* R. M. POLHILL, ed., Fl. Trop. East Africa. 73 pp. Rotterdam. 1982. [Area covers Kenya, Tanzania, and Uganda; 21 genera and 53 species.]

JORGENSEN, L. B. Myrosin cells and dilated cisternae of the endoplasmic reticulum in the order Capparales. Nordic Jour. Bot. **1:** 433–445. 1981. [The ultrastructure of protein-rich cells, idioblastic myrosin cells, or cells of similar appearance supports the alignment of Gyrostemonaceae and Bataceae with the traditionally capparalean families Capparaceae, Brassicaceae, Tovariaceae, Resedaceae, and Moringaceae; 70 species investigated.]

KERBER, E. VON, & G. BUCHLOH. Sinapinfreie und sinapinhaltige Brassicaceae (= Cruciferen). Beitr. Biol. Pflanzen **55:** 377–384. 1981. [Seeds of 100 species in 45 genera analyzed for the presence of sinapine; 46 species in 25 genera contain this alkaloid.]

KINGSBURY, J. M. Poisonous plants of the United States and Canada. xiii + 626 pp. Englewood Cliffs, New Jersey. 1964. [Cruciferae, 28, 29, 158–171; 13 species of ten genera.]

KJAER, A. Naturally derived isothiocyanates (mustard oils) and their parent glucosides. Fortschr. Chem. Organ. Naturstoffe **18:** 122–176. 1960. [Structure and distribution of 30 mustard oils in some 150 species of 47 genera of Cruciferae and in 26 species of ten other families.]

———. Glucosinolates in the Cruciferae. Pp. 207–219 *in* J. G. VAUGHAN *et al.*, eds., The biology and chemistry of the Cruciferae. London, New York. & San Francisco. 1976.

KNIGHTS, B. A., & A. M. M. BERRIE. Chemosystematics: seed sterols in the Cruciferae. Phytochemistry **10:** 131–139. 1971. [Five classes of sterols surveyed in 55 taxa of 21 genera in nine tribes.]

KNOBLOCH, I. W. Intergeneric hybridization in flowering plants. Taxon **21:** 97–103. 1972. [Cruciferae, 100; 257 interspecific and intergeneric hybrids reported for the family, list of intergeneric hybrids incomplete.]

KNUTH, P. Handbook of flower pollination. (English translation by J. R. A. DAVIS.) Vol. 2. viii + 703 pp. Oxford. 1908. [Cruciferae, 74–128. In German ed., **2**(1): 17–130. 1898.]

KOLBE, K.-P. Serologischer Beiträge zur Systematik der Capparales. (English summary.) Bot. Jahrb. **99:** 468–489. 1978. [Capparales and Papaverales show no serological

relationships; proposes removal of Moringaceae from the Capparales, the latter consisting of Capparaceae, Brassicaceae, Tovariaceae, and Resedaceae only.]

———. Serological investigations to the structure of the Brassicaceae. (In German; English summary.) Pl. Syst. Evol. **140:** 39–55. 1982. [21 genera of eight tribes; serological support for tribal disposition of some genera but not others; realignment of the positions of some tribes.]

KROH, M. An electron microscopic study of the behavior of Cruciferae pollen after pollination. Pp. 221–224 *in* H. F. LINSKENS, ed., Pollen physiology and fertilization. Amsterdam. 1964. [*Brassica nigra.*]

KUMAR, P. R., & S. TSUNODA. Variation in oil content and fatty acid composition among seeds from the Cruciferae. Pp. 235–252 *in* S. TSUNODA *et al.*, eds., *Brassica* crops and wild allies. Tokyo. 1980. [A survey of 165 species (not 173 as listed by the authors) in 70 genera.]

LAPORTE, J. Semillas y plántulas de las Crucíferas cultivadas en la Argentina. 141 pp. Buenos Aires. 1959. [Keys, descriptions, and illustrations; species of 24 genera.]

LARSEN, P. O. Free amino acids in Cruciferae and Resedaceae. Danish Atomic Energy Commission. Risö Rep. no. 189. 155 pp. 1969. [Distribution of protein and non-protein free amino acids in 26 species of Cruciferae and 14 of Resedaceae; methods of analysis, structural determination, biosynthesis, biogenesis; bibliography of 285 references.]

LEMS, K., & C. HOLZAPFEL. Flora of the Canary Islands: the Cruciferae, the Crassulaceae and the ferns and their allies. Anal. Inst. Nac. Invest. Agrar. Ser. Prod. Veg. **4:** 165–273. 1974. [Cruciferae, 167–201.]

MACLEOD, A. J. Volatile flavour compounds of the Cruciferae. Pp. 307–330 *in* J. G. VAUGHAN *et al.*, eds., The biology and chemistry of the Cruciferae. London, New York, & San Francisco. 1976.

MAIRE, R. Cruciferae. Fl. Afrique du Nord **12:** 139–403. 1965; **13:** 5–365. 1967; **14:** 1–153. 1977.

MANTON, I. Introduction to the general cytology of the Cruciferae. Ann. Bot. II. **46:** 509–556. 1932. [Counts for 250 spp. in 80 genera, relationships among genera, significance of aneuploidy and polyploidy in the evolution of the family.]

MARAIS, W. Cruciferae. *In:* L. E. CODD, B. DE WINTER, D. J. B. KILLICK, & H. B. RYCROFT, eds., Fl. So. Africa **13:** 1–118. 1970.

MARKGRAF, F. Cruciferae. *In:* G. HEGI, Illus. Fl. Mittel-Europa, ed. 2. **4**(1): 73–514. 1963.

MAULE, A. F. An anomalous form of *Sinapis alba.* Bot. Tidsskr. **65:** 209–224. 1970. [Fruit with supernumerary carpels is due to a single recessive gene, heterozygotes are normal; discussion of the bi- and tetracarpellary views of crucifer gynoecium.]

MEDVE, R. J. The mycorrhizal status of the Cruciferae. Am. Midl. Nat. **109:** 406–408. 1983. [24 species in 15 genera examined; two were shown to be mycorrhizal, bringing the total of mycorrhizal crucifers to eight species in the genera *Brassica, Capsella, Lobularia, Lunaria, Raphanus,* and *Rorippa.*]

MERXMÜLLER, H., & P. LEINS. Die Verwandtschaftsbeziehungen der Kreuzblütler und Mohngewächse. (English summary.) Bot. Jahrb. **86:** 113–129. 1967. [Morphological support for dividing the Rhoeadales into Papaverales and Capparales; androecium of Cruciferae is diplostemonous and gynoecium is tetramerous.]

METCALFE, C. R., & L. CHALK. Anatomy of the dicotyledons. Vol. 1. lxiv + 724 pp. Oxford. 1950. [Cruciferae, 79–87.]

MILLER, R. W., F. R. EARLE, I. A. WOLFF, & Q. JONES. Search for new industrial oils. XIII. Oils from 102 species of Cruciferae. Jour. Am. Oil Chem. Soc. **42:** 817–821. 1965.

———, C. H. VAN ETTEN, C. MCGREW, I. A. WOLFF, & Q. JONES. Amino acid composition of seed meals from forty-one species of Cruciferae. Agr. Food Chem. **10:** 426–430. 1962. [Quantitative analysis for 14 protein amino acids.]

MUENSCHER, W. C. Weeds. ed. 2. xviii + 586 pp. Ithaca & London. 1980. [Cruciferae, 229–261, *figs. 44–57.*]

MUKHERJEE, P. Chromosome study as an aid in tracing the evolution of Cruciferae. Cytologia **40:** 727–734. 1975. [Counts for 20 species, karyotype analysis for seven species; proposes that the basic number for the tribes Arabideae and Brassiceae is six; aneuploidy and diminution in chromosome size played an important role in evolution within the family.]

MULLER, J. Fossil pollen records of extant angiosperms. Bot. Rev. **47:** 1–142. 1981. [Brassicaceae pollen from upper Miocene of France, 40.]

MULLIGAN, G. A. Chromosome numbers of Canadian weeds. I. Canad. Jour. Bot. **35:** 779–789. 1957. [*Berteroa, Camelina, Capsella, Erucastrum, Erysimum, Lepidium, Neslia, Sisymbrium, Thlaspi.*]

———. Chromosome numbers of the family Cruciferae. I. *Ibid.* **42:** 1509–1519. 1964. [Counts for 24 species in 11 genera.]

———. Chromosome numbers of the family Cruciferae. II. *Ibid.* **43:** 657–668. 1965. [Counts for three species of *Braya* and ten of *Cardamine.*]

———. Chromosome numbers of the family Cruciferae. III. *Ibid.* **44:** 309–319. 1966. [Counts for 13 species of *Draba* and seven of *Erysimum*; agamospermy is reported in *E. inconspicuum.*]

MURLEY, M. R. Seeds of the Cruciferae of northeastern North America. Am. Midl. Nat. **46:** 1–81. 1951. [Terminology, key to species based on seed characters, seed descriptions, and distributions for 118 species in 49 genera; *94 figures.*]

NETOLITZKY, F. Anatomie der Angiospermen-Samen. Handb. Pflanzenanat. II. Archegon. **10.** vi + 365 pp. 1926. [Cruciferae, 140–143.]

PALIWAL, G. S. Ontogeny of stomata in some Cruciferae. Canad. Jour. Bot. **45:** 495–500. 1967. [Subsidiary cells and guard cells originate from same protodermal cell following the syndetocheilic type of ontogeny; 12 species of eight genera.]

PANT, D. D., & P. F. KIDWAI. Development of stomata in some Cruciferae. Ann. Bot. II. **31:** 513–521. 1967. [Epidermal structure and ontogeny of stomata in ten taxa of *Brassica, Coronopus, Iberis, Lobularia, Nasturtium,* and *Raphanus*; anomalous or rare types of stomata.]

PATMAN, J. A checklist of Florida Cruciferae. Quart. Jour. Florida Acad. Sci. **25:** 192–200. 1962. [Key, common names, and county distributions of 32 native and naturalized taxa; list of 13 species of ornamentals and other cultigens.]

——— & H. H. ILTIS. Preliminary reports on the flora of Wisconsin. No. 44. Cruciferae — mustard family. Trans. Wisconsin Acad. Sci. Arts Lett. **50:** 17–73. 1961. [68 species, 40 introduced from the Old World, in 32 genera; keys, descriptions, distributions, *58 maps.*]

PERRY, L. M. Medicinal plants of East and Southeast Asia: attributed properties and uses. xii + 620 pp. Cambridge, Massachusetts. 1980. [Cruciferae, 110–113.]

POLATSCHEK, A. Chromosome numbers and remarks on systematics and distribution of some Brassicaceae from Europe, northern Africa, Asia, and Australia. (In German; English summary.) Phyton Austria **23:** 127–139. 1983. [Counts for 46 taxa of 27 genera; distribution, taxonomic notes, typification of certain taxa.]

PONZI, R. Presenza di cisterne dilatate del reticolo endoplasmico in alcune specie di Brassicaceae. (English summary.) Delpinoa **20:** 105–109. 1978. [Dilated cisternae in parenchyma of vascular bundles of five species of *Iberis, Lepidium, Lunaria, Nasturtium,* and *Rapistrum.*]

PRANTL, K. Cruciferae. *In:* A. ENGLER & K. PRANTL, Nat. Pflanzenfam. III. **2:** 145–206. 1891. [A system of classification based on pubescence divides the family into four tribes and 20 subtribes; brief descriptions for 208 genera; see SCHULZ for ed. 2.]

PRASAD, K. Development and organization of gametophytes in certain species of Cru-

ciferae. Acta Bot. Indica **3:** 147–154. 1975. [*Brassica, Coronopus, Farsetia, Lepidium, Malcolmia.*]

———. Seed coat structure and development in certain species of Cruciferae. New Botanist **3:** 95–103. 1976. [*Cakile, Capsella, Coronopus, Farsetia, Malcolmia, Thlaspi.*]

———. The development and structure of basal body in the ovule and seed of certain species of Cruciferae. Bot. Jahrb. **98:** 266–272. 1977. [*Brassica, Cakile, Capsella, Coronopus, Eruca, Farsetia, Lepidium, Malcolmia, Thlaspi.*]

———. Morphology and histochemistry of the nucellus and endosperm in certain species of Cruciferae. *Ibid.* **100:** 536–541. 1979. [Endosperm development is nuclear; nucellar tissue is persistent and closely associated with haustorial portion of endosperm at chalazal end; histochemical and structural changes; eight genera investigated.]

Puri, V. Studies in floral anatomy I. Gynaeceum constitution in the Cruciferae. Proc. Indian Acad. Sci. B. **14:** 166–187. 1941. [Four-carpellary gynoecium with axile placentation, fertile carpels solid; speculates that the origin of septum is receptacular in the basal region and placental in the upper.]

———. The role of floral anatomy in the solution of morphological problems. Bot. Rev. **17:** 471–553. 1951. [Crucifer carpels, 509, 510.]

Queiros, M. Contribuicão para o conhecimento citotaxonomico das spermatophyta de Portugal. IX. Cruciferae. Bol. Soc. Brot. **47:** 315–335. 1973. [Counts for 52 taxa in 30 genera.]

Radford, A. E., H. E. Ahles, & C. R. Bell. Manual of the vascular flora of the Carolinas. lxi + 1183 pp. Chapel Hill. 1968. [Cruciferae, 486–511.]

Rao, N. V., & J. A. Inamdar. Structure and development of normal and abnormal stomata in the seedlings of some Cruciferae. Proc. Indian Acad. Sci. Pl. Sci. **90:** 521–533. 1981. [Anisocytic, anomocytic, helicocytic, paracytic, and anomalous types found in 16 species of nine genera.]

——— & ———. Leaf architectural studies in the Brassicaceae. Bot. Mag. Tokyo **96:** 15–28. 1983. [Venation types of 35 selected species of 19 genera; tracheids and secondary veins show extraordinary variability.]

Rickett, H. W. Wild flowers of the United States. The southeastern states. Vol. 2, part 1. x + 322 pp. New York. 1967. [Cruciferae, 220–239, *pls. 81–85.*]

Rodman, J. E. Glucosinolates, methods of analysis and some chemosystematic problems. Phytochem. Bull. **11:** 6–31. 1978. [Isolation, separation, identification, and quantification; 176 references cited.]

———. Divergence, convergence, and parallelism in phytochemical characters: the glucosinolate-myrosinase system. Pp. 43–79 *in* D. A. Young & D. S. Seigler, eds., Phytochemistry and angiosperm phylogeny. New York. 1981. [Excellent review dealing with aspects of the chemistry, anatomy, genetics, and ecology of these compounds; critical evaluation of the taxonomic positions of the 12 glucosinolate-containing families within the systems of Cronquist, Dahlgren, and Thorne with respect to parallelism and convergence.]

——— & F. S. Chew. Phytochemical correlates of herbivory in a community of native and naturalized Cruciferae. Biochem. Syst. Ecol. **8:** 43–50. 1980. [Plant-specific glucosinolates as behavioral cues for oviposition and larval feeding of *Pieris*; *Arabis, Cardamine, Chorispora, Descurainia, Draba, Erysimum, Thlaspi.*]

Rollins, R. C. Chromosome numbers of Cruciferae. Contr. Gray Herb. **197:** 43–65. 1966. [Counts for 113 species in 29 genera; *10 figures in 3 plates.*]

———. A remarkable new crucifer from Mexico. *Ibid.* **198:** 3–8. 1969. [*Ornithocarpa torulosa,* sp. nov.; comments on the tribe Schizopetaleae.]

———. Weeds of the Cruciferae (Brassicaceae) in North America. Jour. Arnold Arb. **62:** 517–540. 1981. [Common names, habitats, distributions, and chromosome numbers for 95 introduced species in 48 genera and for 26 native species in 15 genera.]

——— & U. BANERJEE. Trichomes in studies of the Cruciferae. Pp. 145–166 *in* J. G. VAUGHAN *et al.*, eds., The biology and chemistry of the Cruciferae. London, New York, & San Francisco. 1976. [Comparative study of trichomes in 69 species of *Lesquerella; 36 SEM figures in 6 plates.*]

——— & ———. Pollens of the Cruciferae. Publ. Bussey Inst. Harvard Univ. **1979:** 33–64. 1979. [*14 SEM plates* of pollen of 35 species in 26 genera; see also ERDTMAN.]

——— & L. RÜDENBERG. Chromosome numbers of Cruciferae II. Contr. Gray Herb. **201:** 117–133. 1971. [Counts for 59 species in 20 genera; *28 figures in 5 plates.*]

——— & ———. Chromosome numbers of Cruciferae III. *Ibid.* **207:** 101–116. 1977. [Counts for 57 species in 29 genera; *18 figures in 4 plates.*]

——— & ———. Chromosome numbers of Cruciferae IV. Publ. Bussey Inst. Harvard Univ. **1979:** 79–92. 1979. [Counts for 34 species in 17 genera; *12 figures in 2 plates.*]

ROTH, I. Fruits of angiosperms. Encyclopedia of plant anatomy. Vol. 10, pt. 1. xvi + 675 pp. Berlin & Stuttgart. 1977. [Cruciferae, 218–225.]

SAMPSON, D. R. Intergeneric pollen-stigma incompatibility in the Cruciferae. Canad. Jour. Genet. Cytol. **4:** 38–49. 1962. [Pollen-tube inhibition on stigmas; 18 intergeneric pollinations between 13 species of ten genera.]

SATYANARAYANA, A., & S. K. SEN. A simple and efficient squash technique for somatic chromosomes of crucifers. *Ibid.* **15:** 369–371. 1973.

SAUNDERS, E. R. A reversionary character in the stock (*Matthiola incana*) and its significance in regard to the structure and evolution of the gynoecium in the Rhoeadales, the Orchidaceae, and other families. Ann. Bot. **37:** 451–482. 1923. [Cruciferous gynoecium typically composed of four carpels, but believes that some genera have as many as 50 carpels; evidence based on abnormally developed fruits.]

———. On a new view of the nature of the median carpels in the Cruciferae. Am. Jour. Bot. **16:** 122–137. 1929. [Criticism of the tetracarpellary gynoecium as interpreted by EAMES & WILSON (1928).]

SCHULZ, O. E. Cruciferae. *In:* A. ENGLER & K. PRANTL, Nat. Pflanzenfam. ed. 2. **17b:** 227–658. 1936. [The most comprehensive treatment of the family to date; 351 genera classified in 19 tribes and 30 subtribes with keys, descriptions, and *306 figures*; the basic reference for the earlier literature on the family.]

SCHWEIDLER, J. H. Über den Grundtypus und die systematische Bedeutung der Cruciferen-Nectarien I. Beih. Bot. Centralbl. **27:** 337–390. *pl. 13.* 1911.

SHAW, E. A. Taxonomic revision of some Australian endemic genera of Cruciferae. Trans. Proc. Roy. Soc. S. Austral. **89:** 145–253. 1965. [*Blennodia, Arabidella, Harmsiodoxa, Scambopus, Drabastrum, Pachymitus, Geococcus.*]

———. Revision of *Stenopetalum* (Cruciferae). Jour. Arnold Arb. **53:** 52–75. 1972. [Eight species endemic to Australia with haploid numbers of four or five.]

———. Revisions of some genera of Cruciferae native to Australia. Contr. Gray Herb. **205:** 147–162. 1974. [*Phlegmatospermum, Cuphonotus, Microlepidium, Ballantinia.*]

SHIVANNA, K. R., Y. HESLOP-HARRISON, & J. HESLOP-HARRISON. The pollen-stigma interaction: bud pollination in the Cruciferae. Acta Bot. Neerl. **27:** 107–119. 1978. [The involvement of the coating on the stigmatic papillae in the incompatibility reaction; *Raphanus, Cheiranthus, Sinapis.*]

SIMMONDS, N. W., ed. Evolution of crop plants. xii + 339 pp. London & New York. 1976. [*Brassica* spp., 45–59; *Sinapis,* 56–59; *Raphanus,* 60–62; *Nasturtium,* 62–64; *Armoracia,* 305, 306; *Lepidium,* 306.]

SMALL, J. K. Manual of the southeastern flora. xxii + 1554 pp. New York. 1933. [Brassicaceae, 551–575.]

SMITH, E. B. An atlas and annotated list of vascular plants in Arkansas. iv + 592 pp. Fayetteville, Arkansas. 1978. [Cruciferae, 123–136, 515, 528.]

SMITH, F. H. Some chromosome numbers in the Cruciferae. Am. Jour. Bot. **25:** 220, 221. 1938. [Counts for 12 species in eight genera.]

SPRATT, E. R. The gynoecium of the family Cruciferae. Jour. Bot. London **70:** 308–314. 1932. [On the basis of the anterior-posterior position of the stigma and the large size of the replum bundle that extends to the stigma, hypothesizes that the ovules are attached to the midribs of the carpels.]

STACE, C. A., ed. Hybridization and the flora of the British Isles. xiii + 626 pp. London, New York, & San Francisco. 1975. [Pp. 137–153, *Brassica, Diplotaxis, Raphanus, Cakile, Capsella, Cochlearia, Erophila, Cardamine, Barbarea, Arabis, Rorippa.*]

TAKHTAJAN, A. L. Outline of the classification of flowering plants (Magnoliophyta). Bot. Rev. **46:** 225–359. 1980. [Holds the view originally advanced in earlier versions of his system that the Cruciferae are derived from Capparaceae-Cleomoideae through the tribe Stanleyeae (Thelypodieae); Capparales includes five families placed in three suborders.]

THEOBALD, W. L., J. L. KRAHULIK, & R. C. ROLLINS. Trichome description and classification. Pp. 40–53, 190–198 *in* C. R. METCALFE & L. CHALK, Anatomy of the dicotyledons. ed. 2. Vol. 1. Oxford. 1979. [Numerous examples from Cruciferae.]

THORNE, R. F. Proposed new realignments in the angiosperms. Nordic Jour. Bot. **3:** 85–117. 1983. [Brassicaceae, 104, placed in the Capparales of the superorder Violiflorae; includes the capparaceous *Dipterygium* in the Brassicaceae.]

TSUNODA, S., K. HINATA, & C. GÓMEZ-CAMPO, eds. *Brassica* crops and wild allies. xviii + 354 pp. Tokyo. 1980. [Nineteen papers dealing with various aspects of the cultivated crucifers and their wild relatives.]

VALDES BERMEJO, E. Estudios citotaxonomicos en Cruciferas españolas. Ciencias Madrid **39:** 80–84. 1974.*

VAUGHAN, J. G. The preparation and staining of sections of cruciferous seed coats. Stain Tech. **35:** 229–231. 1960.

———, A. J. MACLEOD, & B. M. G. JONES, eds. The biology and chemistry of the Cruciferae. xvi + 355 pp. London, New York, & San Francisco. 1976. [Eleven papers dealing with various aspects of the family.]

———, J. R. PHELAN, & K. E. DENFORD. Seed studies in the Cruciferae. Pp. 119–144 *in* J. G. VAUGHAN *et al.*, eds., The biology and chemistry of the Cruciferae. London, New York, & San Francisco. 1976. [Seed structure, chemistry; particular emphasis on *Brassica.*]

——— & J. M. WHITEHOUSE. Seed structure and the taxonomy of the Cruciferae. Bot. Jour. Linn. Soc. **64:** 383–409. 1971. [Seeds of 200 species in 90 genera, *10 figures, 1 plate*; seed-coat characters do not support tribal divisions of the family.]

VIEGI, L., A. M. PAGNI, G. CORSI, & G. CELA RENZONI. Embryo suspensor in Cruciferae. I. Morphology and structure. (In Italian; English summary.) Giorn. Bot. Ital. **110:** 347–357. 1976. [Seven species of *Alyssum, Brassica, Capsella, Diplotaxis, Eruca, Lepidium,* and *Matthiola*; polyploidy with or without polyteny in suspensor cells.]

VILLANI, A. Sulla classificazione delle Crocifere. Ann. Bot. Roma **16:** 71–121. 1926. [Descriptions for 102 genera; 11 tribes recognized, the traditional Brassiceae divided into four.]

VOYTENKO, V. F. The forms of heterocarpy in the Brassicaceae Burn. family and the evaluation of their evolutionary significance. (In Russian; English summary.) Bot. Zhur. **53:** 1428–1439. 1968. [Heterocarpy and heterospermy; special emphasis on members of the Brassiceae.]

———. Experience in an ecological-geographical and phylogenetic analysis of heterocarpy (on the example of Cruciferae.) (In Russian; English summary.) Biul. Moskova Obshch. Isp. Pri. Biol. **75**(3): 77–84. 1970. [Occurrence of heterocarpy in 41 genera a derived feature restricted to advanced groups; adaptive significance.]

WALLACE, D. H., & M. E. NASRALLAH. Pollination and serological procedures for isolating incompatibility genotypes in the crucifers. Mem. Cornell Univ. Agr. Exper. Sta. **406:** 1–23. 1968.*

WALPOLE, B. A. Distribution of the Cruciferae in Michigan. Pap. Mich. Acad. Sci. Arts

Lett. **6:** 307–349. 1927. [Keys, distributions; 34 genera and 81 species, only 28 species indigenous.]

WELSH, S. L., & J. L. REVEAL. Utah flora: Brassicaceae (Cruciferae). Great Basin Nat. **37:** 279–365. 1977. [Keys, descriptions, distribution data, new taxa and combinations, index; 155 species, including 37 introduced weeds.]

WETTSTEIN, R. Handbuch der systematischen Botanik. ed. 4. x + 1152 pp. Leipzig & Vienna. 1935. [Rhoeadales, 716–728; Cruciferae, 722–727; recognizes 12 tribes.]

WILLIS, J. C. A dictionary of the flowering plants and ferns. ed. 8. (Revised by H. K. AIRY SHAW.) xxii + 1245 + lxvi pp. Cambridge, England. 1973. [Cruciferae, 307–309.]

YARNELL, S. H. Cytogenetics of the vegetable crops. II. Crucifers. Bot. Rev. **22:** 81–166. 1956. [*Armoracia, Brassica, Crambe, Eruca, Lepidium, Nasturtium, Raphanus, Sinapis*; special emphasis on *Brassica* and *Raphanus*; 288 references cited.]

YEN, C. On a new view of carpel morphology in *Brassica*. (In Chinese; English summary.) Acta Bot. Sinica **8:** 271–288. 1959. [The six-carpel hypothesis; normal and abnormal fruits of *B. napella* Choix.]

ZOHARY, M. Follicular dehiscence in Cruciferae. Lloydia **11:** 226–228. 1948a. [*Leptaleum filifolium*; fruit dehiscence from separation tissue restricted to the adaxial (posterior) side; such tissue lacking on the abaxial side.]

———. Carpological studies in Cruciferae. Palestine Jour. Bot. Jerusalem Ser. **4:** 158–165. 1948b. [Use of terms silique and silicle discarded; seven fruit types recognized—valvoid, folliculoid, nucamentoid, valvo-nucamentoid, valvo-lomentoid, lomentoid, and schizocarpoid; evolutionary trends in fruit; support for the bicarpellary origin of cruciferous gynoecium.]

KEYS TO THE TRIBES AND GENERA OF CRUCIFERAE IN THE SOUTHEASTERN UNITED STATES

General characters: *Mostly annual, biennial, or perennial herbs, rarely shrubs, glabrous or with simple or variously branched unicellular trichomes, rarely with multicellular glandular trichomes; leaves exstipulate, usually simple, alternate; inflorescences basically racemes or corymbs (flowers rarely solitary), usually ebracteate; flowers hypogynous, mostly actinomorphic, perfect; sepals 4, in 2 decussate pairs, erect or spreading, the lateral (inner) pair often saccate at the base; corolla cruciform, the petals 4, usually clawed, rarely absent; nectar glands receptacular, surrounding or subtending the bases of some or all filaments; androecium of 6 stamens (rarely 2, 4, or more than 6) in 2 whorls, the outer pair usually shorter than the 2 inner pairs (tetradynamous), rarely all equal in length; gynoecium of 2 united carpels; ovary superior, often 2-locular by a false septum connecting the 2 parietal placentae; style persistent, distinct or obsolete; stigma entire or 2-lobed; ovules 1 to many, anatropous or campylotropous; fruit basically a capsule (often called a silique), dehiscing longitudinally by 2 valves, sometimes indehiscent and modified to a loment, nutlet, samara, or schizocarp; seeds without endosperm, winged or wingless, mucilaginous or not when wet; embryos large, almost always folded or curved in one of several ways.*

Key to the Tribes

A. Fruits mostly beaked, sometimes transversely jointed and breaking at maturity into 2 or more seed-bearing segments; beak 1- or few-seeded, rarely seedless; cotyledons almost always conduplicate. ..... Tribe 2. BRASSICEAE.

A. Fruits beakless or very rarely with a seedless stylelike beak, never jointed; cotyledons accumbent or incumbent.

B. Fruits strongly compressed at right angles to the septum; replum much narrower than width of fruit. ..... Tribe 3. LEPIDIEAE.

B. Fruits terete, angular, inflated, or compressed parallel to the septum; replum equaling width of fruit.
  C. Fruits less than 3 times longer than broad (except in a few species of *Draba*); plants mostly with stellate or furcate trichomes, with or without unbranched ones. ..... Tribe 4. ALYSSEAE.
  C. Fruits mostly more than 3 times longer than broad, if less the plants (ours) glabrous; trichomes branched, unbranched, or absent.
    D. Stamens mostly exserted, equal in length, sometimes slightly tetradynamous, or in 3 pairs of unequal length; petals mostly crisped or channeled; gynophores (1–)2–30 mm long; trichomes simple or absent. ..... Tribe 1. THELYPODIEAE.
    D. Stamens included or slightly protruding, tetradynamous; petals usually neither crisped nor channeled; gynophores absent or rarely present, to 2 mm long; trichomes branched, simple, or lacking.
      E. Sepals erect, calyx closed at anthesis; multicellular glandular trichomes commonly present. ..... Tribe 6. HESPERIDEAE.
      E. Sepals spreading or ascending, calyx open at anthesis; multicellular glands always absent.
        F. Cotyledons accumbent. ..... Tribe 5. ARABIDEAE.
        F. Cotyledons incumbent. ..... Tribe 7. SISYMBRIEAE.

Key to the Genera

Several species of *Iberis* L. (candytuft), *Malcolmia* R. Br. (Virginian stock), and *Matthiola* R. Br. (stock) are cultivated in our area, but there are no records that any of them has become naturalized. *Malcolmia africana* (L.) R. Br. and *Matthiola longipetala* (Vent.) DC. are well-established weeds in Texas and some of the western states, but neither of them has been found in our area. These three genera are included in the following key, but they will not be dealt with further.

A. Fruits transversely jointed or lomentaceous, indehiscent, often breaking transversely at maturity into 1- or few-seeded segments.
  B. Plants with stalked, multicellular, glandular trichomes; fruits not transversely jointed; stigmas with strongly decurrent connate lobes. ..... 37. *Chorispora.*
  B. Plants eglandular, glabrous or with simple, unicellular trichomes only; fruits transversely jointed; stigmas entire or 2-lobed—if 2-lobed, lobes neither decurrent nor connate.
    C. Lower segment of fruit always seedless; upper segment several seeded, more than 10 times longer than the lower segment. ..... 9. *Raphanus.*
    C. Lower segment of fruit usually 1-seeded, rarely 3-seeded or seedless; upper segment 1- or rarely 2-seeded, equaling or up to 5 times longer than the lower segment.
      D. Petals yellow; fruits not corky, less than 1 cm long; cotyledons conduplicate; hirsute, nonfleshy weeds of waste grounds and cultivated land. ..... 10. *Rapistrum.*
      D. Petals white, or lavender to purple; fruits corky, often more than 1.5 cm long; cotyledons accumbent, rarely incumbent; glabrous, often fleshy plants of sandy shores or beaches. ..... 12. *Cakile.*

A. Fruits neither jointed nor lomentaceous, dehiscent or rarely indehiscent (*Calepina*), not breaking transversely into segments.
  E. Early flowers solitary, borne on scapes 3–10 cm long originating from center of a basal rosette; radicles straight or slightly curved, much shorter than cotyledons. ..... 30. *Leavenworthia.*
  E. All flowers borne in terminal or axillary racemes or corymbs; radicles strongly curved, about as long as the accumbent, incumbent, or conduplicate cotyledons.

F. Fruits less than 3 times longer than broad, broadly oblong or elliptic to globose, orbicular, triangular, or didymous.
G. Fruits strongly compressed at right angles to the septum; replum much narrower than width of fruit.
H. Flowers zygomorphic; outer petals markedly larger than inner.
I. Seed 1 in each locule; median filaments not appendaged. . . . . [*Iberis.*]
I. Seeds 2 in each locule; median filaments with a broad, scalelike appendage. . . . . 18. *Teesdalia.*
H. Flowers actinomorphic; petals equal in size, sometimes reduced or lacking.
J. Seeds 3 or more, rarely 2 per locule.
K. Fruits obcordate-triangular; basal leaves forming a rosette; plants with furcate and stellate trichomes. . . . . 19. *Capsella.*
K. Fruits orbicular or elliptic; basal leaves not in rosettes; plants glabrous or with unbranched trichomes only. . . . 17. *Thlaspi.*
J. Seed 1 per locule.
L. Fruits coarsely reticulate or verrucose, often didymous; inflorescence axillary; upper cauline leaves 1- or 2-pinnatisect. . . . . 15. *Coronopus.*
L. Fruits smooth; inflorescence terminal; upper cauline leaves entire, toothed, or pinnately lobed.
M. Fruits dehiscent, obtuse or cuneate at base, retuse or emarginate at apex; annuals, biennials, or nonstoloniferous perennials. . . . . 14. *Lepidium.*
M. Fruits indehiscent, cordate at base, cuneate at apex; stoloniferous perennials. . . . . 16. *Cardaria.*
G. Fruits inflated, globular, or compressed parallel to the septum; replum about as broad as width of fruit.
N. Plants glabrous or pubescent with unbranched trichomes only.
O. Fruits coarsely reticulate-rugose, ribbed, indehiscent, 1-seeded; petals unequal; cotyledons conduplicate. . . . . 11. *Calepina.*
O. Fruits smooth, not ribbed, dehiscent, many seeded; petals equal; cotyledons accumbent.
P. Fruits strongly compressed parallel to the septum; seeds compressed, broadly winged, 3–10 mm wide.
Q. Flowers purple, rarely white; inflorescence ebracteate; leaves dentate; fruits more than 1.5 cm broad; gynophores 1–3 cm long; funiculi united with the septum. . . 20. *Lunaria.*
Q. Flowers yellow; inflorescence bracteate throughout; leaves pinnatisect; fruits less than 1 cm broad; gynophores less than 0.5 cm long; funiculi free from the septum. . . . . 31. *Selenia.*
P. Fruits inflated; seeds plump, wingless, less than 1.5 mm wide.
R. Flowers white; septum rudimentary or incomplete; plants perennial. . . . . 36. *Armoracia.*
R. Flowers yellow; septum complete; plants annual or biennial, rarely perennial. . . . . 35. *Rorippa.*
N. Plants pubescent with furcate, branched, or stellate trichomes, and with or without unbranched ones.
S. All trichomes uniformly bifurcate, medifixed, appressed, sessile. . . . . 22. *Lobularia.*
S. Trichomes stellate, furcate, or branched, mixed with unbranched ones or not, stalked, sometimes sessile and appressed when stellate.

T. Petals deeply bilobed.
U. Plants scapose; fruits glabrous; filaments of lateral stamens not appendaged; styles obsolete. ..... 24. *Draba.*
U. Plants not scapose; fruits densely pubescent; filaments of lateral stamens appendaged; styles 1.5–4 mm long. ..... 23. *Berteroa.*
T. Petals entire or slightly emarginate.
V. Fruits orbicular or oblong to lanceolate, often strongly compressed.
W. Seeds wingless, biseriate, usually more than 4 per locule; fruits oblong or lanceolate. ..... 24. *Draba.*
W. Seeds winged or margined, uniseriate, 1–4 per locule; fruits orbicular or nearly so.
X. Cauline leaves cuneate, not auriculate; styles less than 1 mm long; seed 1 per locule, strongly mucilaginous when wet. ..... 21. *Alyssum.*
X. Cauline leaves auriculate; styles 1.5–3 mm long; seeds 2–4 per locule, not mucilaginous when wet. ..... 25. *Lesquerella.*
V. Fruits globose or pyriform, inflated.
Y. Fruits globose, not keeled, beakless; valve apex obtuse, ending at base of style; seeds usually orbicular; cotyledons accumbent. ..... 25. *Lesquerella.*
Y. Fruits pyriform, keeled at the replum, ending abruptly in a stylelike beak; valve apex acuminate, extending 0.5–1.5 mm into the beak area; seeds usually oblong; cotyledons incumbent. ..... 26. *Camelina.*

F. Fruits at least 4 times longer (often much more) than broad, linear or narrowly oblong.
a. Plants with forked, branched, dendritic, or stellate trichomes, sometimes mixed with unbranched ones.
b. Leaves 2- or 3-pinnatisect. ..... 43. *Descurainia.*
b. Leaves entire to pinnately lobed, never 2-pinnatisect.
c. Stigmas with strongly decurrent lobes.
d. Stigma lobes with a lateral horn or swelling in fruit. ..... [*Matthiola.*]
d. Stigma lobes without an outgrowth.
e. Annuals; stigma lobes connate along their entire length in fruit; fruits sharply pointed. ..... [*Malcolmia.*]
e. Biennials; stigma lobes free in mature fruits; fruits not pointed. ..... 38. *Hesperis.*
c. Stigmas capitate, entire or 2-lobed (if 2-lobed, lobes shallow, divergent, never decurrent).
f. Trichomes appressed, medifixed, bifurcate mixed with 3–5-furcate or stellate ones, never unbranched; fruits mostly quadrangular in section. ..... 39. *Erysimum.*
f. Trichomes a mixture of 2 kinds: unbranched and stalked furcate; fruits terete or flattened parallel to the septum.
g. Fruits terete; cotyledons incumbent. ..... 42. *Arabidopsis.*
g. Fruits flattened; cotyledons accumbent.
h. Plants scapose; fruits less than 2 cm long, less than 6 times longer than broad; seeds clearly biseriately arranged. ..... 24. *Draba.*
h. Plants not scapose; fruits mostly more than 2 cm long, more

than 10 times longer than broad; seeds uniseriately arranged, very rarely obscurely biseriate. ..... 32. *Arabis.*

a. Plants glabrous or with unbranched trichomes only.
  i. Stamens long-exserted, equal in length; sepals strongly reflexed; petal claws papillose near the base; gynophores (3–)5–14 mm long. ..... 1. *Warea.*
  i. Stamens included or slightly protruding, tetradynamous or in 3 pairs of unequal length; sepals erect or spreading, very rarely reflexed; petal claws glabrous; gynophores absent or very rarely present, to 3 mm long.
    j. Fruits with a strongly developed beak in addition to style, rarely obscurely beaked (*Diplotaxis* and *Erucastrum*); cotyledons always conduplicate.
      k. Valves with 1 prominent midnerve, with or without a few inconspicuous lateral veins.
        l. Inflorescence bracteate; fruits 4-angled. ..... 4. *Erucastrum.*
        l. Inflorescence ebracteate; fruits terete or flattened.
          m. Beaks strongly flattened, ensiform; stigma lobes decurrent; petals with dark brown or purple veins. ..... 8. *Eruca.*
          m. Beaks conical or stylelike; stigmas entire or with nondecurrent lobes; petal veins not darkly colored.
            n. Fruits flattened; seeds biseriately arranged, ovoid or oblong, up to 1.5 mm long. ..... 7. *Diplotaxis.*
            n. Fruits terete; seeds uniseriately arranged, globose, 1.5–2.5 mm in diameter. ..... 3. *Brassica.*
      k. Valves with 3–7 prominent nerves (these often more conspicuous on immature fruits).
        o. Sepals erect, saccate at the base; petal claws as long as or longer than the sepals. ..... 5. *Hutera.*
        o. Sepals widely spreading or reflexed, not saccate; petal claws shorter than the sepals. ..... 6. *Sinapis.*
    j. Fruits beakless; cotyledons accumbent or incumbent.
      p. Fruits flattened parallel to septum; petals never yellow.
        q. Valves dehiscing suddenly and elastically from the base, coiling circinately or spirally; replum flanged with remains of valve margin; seeds neither winged nor margined; plants perennials with tubers or rhizomes, sometimes annuals or biennials. ..... 27. *Cardamine.*
        q. Valves not dehiscing elastically, not coiling; replum margin not flanged; seeds winged or margined, very rarely wingless; plants (ours) annuals or biennials.
          r. Cauline leaves all pinnatisect or pinnatifid. ...33. *Sibara.*
          r. Cauline leaves entire or toothed.
            s. Petals showy, purple to magenta, rarely lavender, crisped, 1–2 cm long, differentiated at base into an oblanceolate claw; sepals colored; buds acute; fruits on gynophores 1–3 mm long. ..... 2. *Streptanthus.*
            s. Petals white or lavender, less than 1 cm long, not crisped, often gradually attenuate to a clawlike base; sepals greenish; buds obtuse; fruits sessile or nearly so. ..32. *Arabis.*
      p. Fruits terete or quadrangular, very rarely slightly flattened; petals commonly yellow, sometimes white or lavender.
        t. Leaves entire, cordate-amplexicaul; mature fruits strongly quadrangular; seeds readily releasing abundant mucilage when wet. ..... 13. *Conringia.*

t. Leaves (at least some of them) pinnately lobed or petiolate; fruits terete or obscurely 4-angled; seeds not mucilaginous (very rarely producing a thin coat of mucilage) when wet.
u. Valves of fruits nerveless or obscurely nerved; seeds biseriately or rarely uniseriately arranged; plants aquatic or of very wet habitats.
v. Flowers yellow; median nectaries present outside the inner stamens; leaves simple, sinuate or pinnately lobed; lower nodes usually lacking adventitious roots. ..... 35. *Rorippa.*
v. Flowers white or lavender; median nectaries lacking; leaves pinnate; lower nodes with adventitious roots. .. .. 34. *Nasturtium.*
u. Valves with a prominent midnerve; seeds uniseriately arranged; plants mostly terrestrial.
w. Lower leaves cordate or reniform, dentate, not auriculate; seeds longitudinally striate. ..... 40. *Alliaria.*
w. Lower leaves pinnate and/or auriculate; seeds reticulate.
x. Flowers white or lavender; inflorescence an elongated raceme; cauline leaves serrate or entire, cuneate. .. .. 29. *Iodanthus.*
x. Flowers yellow; inflorescence corymbose; cauline leaves pinnately lobed, the uppermost sometimes unlobed.
y. Valves 3-nerved; fruits terete; cotyledons incumbent; cauline leaves not auriculate. .... 41. *Sisymbrium.*
y. Valves 1-nerved; fruits slightly flattened or somewhat 4-angled; cotyledons accumbent; cauline leaves auriculate or amplexicaul. .. 28. *Barbarea.*

Full treatments of the tribes, including references, distributions, and aspects of their biology, will appear in separate papers as in the sequence below. The following brief accounts for the tribes are mainly intended to provide guidelines for the tribal limits and for the number of representative species and genera in the southeastern United States.

Tribe 1. **Thelypodieae** Prantl in Engler & Prantl, Nat. Pflanzenfam. III. **2:** 155. 1891.

Herbaceous annuals or biennials, rarely perennials, glabrous or with simple hairs only; sepals equal at base or sometimes slightly saccate, erect or spreading to reflexed, occasionally forming an urceolate or bilabiate calyx; petals often strongly differentiated into claw and blade, usually crisped or channeled; stamens exserted or slightly protruding, equal in length or somewhat tetradynamous, rarely in 3 unequal pairs, not appendaged; siliques dehiscent, linear, several to many times longer than broad, terete or flattened parallel to the septum, often borne on a distinct gynophore; seeds winged or wingless, not mucilaginous when wet; cotyledons accumbent or incumbent. (Including Stanleyeae Robinson, Romanschulzieae O. E. Schulz, Streptantheae O. E. Schulz.)
TYPE GENUS: *Thelypodium* Endl.

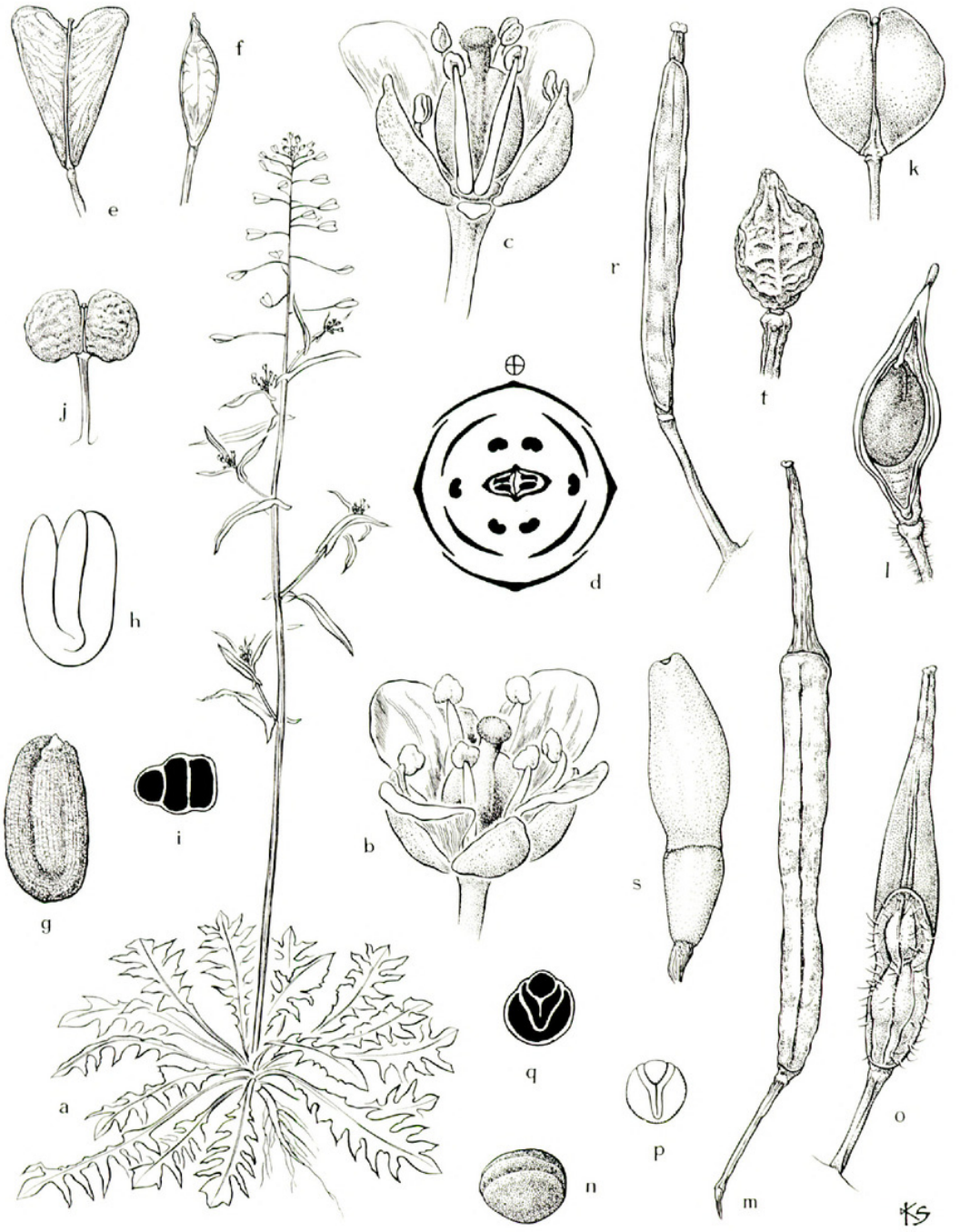

FIGURE 1. Tribes **Lepidieae** and **Brassiceae.** a–l, LEPIDIEAE. a–i, *Capsella bursa-pastoris:* a, plant with flowers and fruits, × ½; b, flower, × 12; c, flower with sepal and two petals removed, × 12; d, floral diagram; e, fruit, × 3; f, replum and septum, × 3; g, seed, × 25; h, embryo, oriented as in seed, × 25; i, diagrammatic cross section of seed showing incumbent cotyledons, × 25. j, *Coronopus didymus,* fruit, × 6. k, *Lepidium virginicum,* fruit, × 6. l, *L. campestre,* fruit after removal of valve—note apical attachment of seed, × 6. m–t, BRASSICEAE. m, n, *Brassica campestris:* m, fruit, × 2; n, seed, × 6. o–q, *Sinapis alba:* o, fruit, × 2; p, embryo, × 6; q, diagrammatic cross section of seed showing conduplicate cotyledons, × 6. r, *Diplotaxis muralis,* fruit, × 3. s, *Cakile edentula* subsp. *Harperi,* fruit—note transverse joint, × 1½. t, *Calepina irregularis,* fruit, × 6.

A natural tribe of 11 genera and some 110 species; represented in our area by seven indigenous species in two genera, *Warea* Nutt. and *Streptanthus* Nutt.

Tribe 2. **Brassiceae** DC. Syst. Nat. **2:** 152. 1821.

Annual, biennial, or perennial herbs, sometimes subshrubs or large shrubs, glabrous or with simple hairs only; sepals erect or spreading, often saccate at base; petals usually clawed; stamens tetradynamous, the filaments very rarely appendaged; siliques long or short, dehiscent or indehiscent, often clearly differentiated into valvular and stylar (beak) segments, 1 or both seed-bearing, or the fruits transversely jointed or lomentaceous and breaking into parts, terete, angular, or flattened; seeds mucilaginous or not when wet, winged or wingless; cotyledons almost always conduplicate (very rarely accumbent or incumbent). (Including Cakilineae DC., Calepineae Godron, Erucarieae DC., Psychineae DC., Raphaneae DC., Velleae DC., Zilleae DC.) TYPE GENUS: *Brassica* L.

A natural tribe of some 52 genera and about 230 species; represented in the Southeast by 21 species, all (except four of *Cakile* Miller) naturalized weeds belonging to 11 genera: *Brassica, Erucastrum* Presl, *Hutera* Porta, *Sinapis* L., *Diplotaxis* DC., *Eruca* Miller, *Raphanus* L., *Rapistrum* Crantz, *Cakile, Calepina* Adanson, and *Conringia* Heister ex Fabr.

Tribe 3. **Lepidieae** DC. Syst. Nat. **2:** 151. 1821.

Annual, biennial, or perennial herbs, sometimes subshrubs or shrubs, glabrous or usually pubescent with simple hairs only; sepals erect or spreading, rarely conspicuously saccate at base; petals often slightly differentiated into blade and claw; stamens 6, tetradynamous, or reduced to 4 or 2, the filaments frequently appendaged; siliques almost always shorter than 3 times their width, dehiscent or indehiscent, occasionally didymous and schizocarpic, always compressed at right angles to the septum (angustiseptate), replum much narrower than width of the fruit; seeds often mucilaginous when wet, winged or wingless; cotyledons accumbent or incumbent. (Including Brachycarpeae DC., Iberideae Godron, Isatideae DC., Senebiereae Godron, Subularieae DC., Thlaspideae DC.) TYPE GENUS: *Lepidium* L.

A natural tribe of over 60 genera and more than 600 species; represented in our area by *Lepidium, Coronopus* Zinn, *Cardaria* Desv., *Thlaspi* L., *Teesdalia* R. Br., and *Capsella* Medicus, and about 16 species, of which all (except four species of *Lepidium*) are introduced weeds.

Tribe 4. **Alysseae** Godron in Gren. & Godron, Fl. France **1:** 112. 1848.

Herbaceous annuals, biennials, or perennials, rarely subshrubs or shrubs, usually with branched or stellate trichomes, sometimes the trichomes simple or absent; sepals erect or spreading; petals attenuate at base or occasionally strongly clawed; stamens 6, tetradynamous, rarely 4, often with appendaged, toothed, or winged filaments, infrequently slender at base; siliques almost always shorter than 3 times their width, dehiscent or rarely indehiscent, spherical,

FIGURE 2. Tribes **Thelypodieae, Brassiceae, Lepidieae, Alysseae,** and **Arabideae.** a, b, THELYPODIEAE, *Warea Carteri:* a, infructescence, × 1; b, fruit—note gynophore, × 2. c–f, BRASSICEAE. c, *Raphanus Raphanistrum,* infructescence—note lomentaceous fruits, × ½. d, *R. sativus,* fruit—note aborted lower segment, × 2. e, f, *Eruca vesicaria* subsp. *sativa:* e, fruit—note beak, × 2; f, fruit after fall of valves. g–l, LEPIDIEAE. g–i, *Thlaspi arvense:* g, fruit, × 2; h, fruit after fall of valves, × 2; i, seed, × 6. j–l, *Teesdalia nudi-*

inflated, or commonly compressed parallel to the septum (latiseptate); seeds mucilaginous or not when wet, winged or wingless; cotyledons accumbent, very rarely incumbent. (Including Camelineae DC., Drabeae O. E. Schulz, Lunarieae O. E. Schulz, Physarieae Robinson.) TYPE GENUS: *Alyssum* L.

A tribe with poorly defined boundaries and comprising a heterogeneous assemblage of 41 genera and some 750 species; represented in our area by 20 species (13 indigenous) and seven genera: *Lunaria* L., *Alyssum, Lobularia* Desv., *Berteroa* DC., *Draba* L., *Lesquerella* S. Watson, and *Camelina* Crantz.

Tribe 5. **Arabideae** DC. Syst. Nat. **2**: 161. 1821.

Annual, biennial, or perennial herbs, rarely subshrubs, glabrous or with simple, furcate, or branched hairs; sepals often ascending or spreading, equal or saccate at base; stamens tetradynamous, with slender or very rarely toothed filament bases; stigmas entire or slightly 2-lobed; siliques dehiscent, narrowly linear, sometimes oblong, rarely subspherical, often compressed parallel to the septum, occasionally inflated; seeds winged, margined, or sometimes wingless; cotyledons accumbent. (Including Cardamineae Calestani.) TYPE GENUS: *Arabis* L.

A tribe with a natural core of large genera and their relatives (but with artificially drawn boundaries) consisting of more than 570 species in 36 genera; represented in the Southeast by 44 species, of which only nine are introduced weeds, and ten genera: *Cardamine* L., *Barbarea* R. Br., *Iodanthus* Torrey & Gray ex Steudel, *Leavenworthia* Torrey, *Selenia* Nutt., *Arabis, Sibara* Greene, *Nasturtium* R. Br., *Rorippa* Scop., and *Armoracia* Gaertner, Meyer, & Scherb.

Tribe 6. **Hesperideae** Prantl in Engler & Prantl, Nat. Pflanzenfam. III. **2**: 154. 1891.

Annual, biennial, or perennial herbs, rarely subshrubs or shrubs, glabrous or with simple, bifurcate, branched, or stellate trichomes, occasionally with multicellular glands; sepals erect, sometimes connivent; petals usually differentiated into blade and claw; stamens tetradynamous, filaments of the median pairs usually expanded at base or connate; stigma 2-lobed or very rarely entire, the lobes commonly decurrent; siliques long or short, dehiscent or rarely indehiscent, occasionally lomentaceous, infrequently beaked or appendaged; seeds often wingless; cotyledons incumbent or accumbent. (Including Anchonieae DC., Cheirantheae Villani, Erysimeae Reichenb., Matthioleae O. E. Schulz, Schizopetaleae R. Br. ex Barn.) TYPE GENUS: *Hesperis* L.

---

caulis: j, fruit, × 6; k, fruit after fall of valves, × 6; l, seed, × 12. m, n, ALYSSEAE, *Lobularia maritima:* m, fruit, × 6; n, replum and septum, × 6. o–r, ARABIDEAE, *Selenia aurea:* o, infructescence—note bracts, × 1; p, seed—note wing, × 6; q, embryo, × 6; r, diagrammatic cross section of seed showing accumbent cotyledons, × 6.

FIGURE 3. Tribes **Arabideae, Hesperideae,** and **Sisymbrieae.** a–h, ARABIDEAE. a–c, *Leavenworthia:* a, *L. stylosa,* plant with flowers—note single-flowered scapes from center of basal rosette, × ½; b, *L. uniflora,* fruit, × 1; c, *L. torulosa,* embryo—note straight radicle, × 6. d, *Sibara virginica,* fruit, × 3. e, f, *Nasturtium officinale:* e, replum and septum—note funiculi of biseriately arranged seeds, × 3; f, seed, × 12. g, *Arabis canadensis,* fruit, × 2. h, *Armoracia aquatica,* fruit, × 3. i, j, HESPERIDEAE: i, *Hesperis matronalis,* fruit, × 1; j, *Erysimum repandum,* fruit, × 2. k–p, SISYMBRIEAE. k–m, *Alliaria petiolata:* k, portion of plant with flowers, × ½; l, fruit, × 1; m, portion of fruit after removal of valve—note uniseriate arrangement of seeds, × 3. n–p, *Descurainia pinnata:* n, tripinnatisect leaf, × ½; o, fruit, × 6; p, seed, × 25.