# THE GENERA OF PEDALIACEAE IN THE SOUTHEASTERN UNITED STATES[1]

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## PEDALIACEAE R. Brown, Prodr. 519. 1810, "Pedalinae," nom. cons. (PEDALIUM, SESAMUM, or BENE FAMILY)

Annual or perennial herbs [sometimes with short, swollen stems and tuberous roots], [or small trees with swollen stems, or shrubs with or without swollen main branches], of disturbed areas such as dry fields and roadsides, sometimes near coasts. Stems erect [to prostrate], usually unbranched [or branched], unarmed [or less often spiny], usually

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pubescent and with usually stalked, 4-celled, grayish-white mucilage secreting glands. Leaves opposite, subopposite, or sometimes alternate [or subwhorled], exstipulate; blades simple or occasionally trifoliolate [or palmately compound]; if simple, entire to deeply 3 [or more] lobed, shape ovate, cordate, elliptical, obovate, [suborbicular, or lorate], sometimes varied within plants; if trifoliolate, leaflets obovate, elliptical, or ovate; margins sometimes crenate or irregularly lobed; apices acute to obtuse or rarely truncate [or emarginate]; bases acute, obtuse, cordate, cuneate, or rarely truncate; main lateral veins ca. 3–10; blades thinly to densely pubescent, with indumentum similar to that on stems, including mucilage secreting glands above and usually more densely below [rarely glabrous]; petioles also pubescent and with mucilage glands. Inflorescences axillary; flowers solitary or occasionally in few-flowered cymes, usually subhorizontally oriented [or suberect]; pedicels with indumentum similar to that of the stem, flowers sometimes subtended by 1 or 2 sometimes deciduous, rudimentary or ± subulate, linear, [or rarely subhemispherical] bract(s), reduced petiolate leaves, or rudimentary flower(s). Flowers perfect, perianth 5-merous. Calyx synsepalous, green, lobes usually at least slightly unequal, entire, narrowly triangular, narrowly ovate, [more broadly ovate or triangular], or rarely linear persistent or deciduous in fruit, with indumentum similar to leaves. Corolla sympetalous, pink, purple, white, [blue, or yellow], sometimes with darker lines [or other patterns], zygomorphic, bilabiate or nearly so [or the lobes subequal], the lower lobe(s) usually the longest, tube often curved at base [sometimes funnel shaped or cylindrical, often slightly gibbous adaxially, or rarely spurred at base], lobes valvate or nearly so, entire [rarely fringed]; sparsely to densely pubescent and glandular. Stamens 4, didynamous, alternate with corolla lobes, included in the corolla tube [or the longer two exserted]; adaxial staminode present or absent; filaments inserted on corolla tube near its base; anthers oblong to sagittate, dorsifixed [or pendent from apex of connective], thecae subparallel [or divergent], longitudinally dehiscent; pollen grains solitary [or in tetrads in *Sesamothamnus*], [5] 7–13 colpate, oblate, suboblate, prolate, or spheroidal. Gynoecium superior, syncarpous, carpels [1] 2–4, locules [1] 2–4, [if more than 1] separated by a septum [or septa], each locule [sometimes] divided into 2 compartments nearly from base to apex by a secondary partition; ovules [1–] numerous, anatropous, subhorizontal [to erect or pendent], [solitary or] in a longitudinal row in [1, 2, or] each of the compartments, placentation axile [basal in *Linariopsis*]; disk hypogynous, subannular [or asymmetrical]; style filiform, longer than staminal filaments; stigma usually bilobed. Fruits [spiny, ridged, winged, or barbed] subobconoidal to ellipsoidal or subcylindrical, [subovoid, subglobose, obovoid, or subdiscoidal and horizontally flattened] loculicidal capsules, with [or without] an apical beak or 2 or apparently 4 apical horns [or other appendages], dehiscent at least near apex along the secondary partitions [or indehiscent], suberect [to horizontal] in axils. Seeds slightly to strongly flattened [or nearly round in transverse section], unwinged [or with 1–3 wings], obovate, [oblong, elliptical, or suborbicular] in outline, glabrous, light brown to black [or white], outer seed coat surface smooth, rugose, or verrucose [or with other patterns]; endosperm thin and oily; embryo sac of Polygonum type; embryo development of Onagrad type. Base chromosome number 8, possibly 13. TYPE GENUS: *Pedalium* D. Royen ex L.

A relatively small Old World family of 13 genera and about 60 species, sometimes but not here united with the Martyniaceae (about 3 genera, 13 species) or Trapellaceae (1 genus, 2 species). Within the Pedaliaceae the genera are distinct, but species within a genus are usually less clearly defined. The family is most diverse in Africa (one genus, *Uncarina* (Baillon) Stapf, is endemic to the Malagasy Republic) and is represented in India, Sri Lanka (*Pedalium*, *Sesamum* L.), and Australia (*Josephinia* Vent.). The New World representatives of the family are introduced.

*Ceratotheca triloba* (Bernh.) Hooker f. and *Sesamum orientale* L., sesame, have spread from cultivation and are of sporadic occurrence in the southeastern United States. Although the number of independent introductions of *C. triloba* is unknown, introductions of sesame have been frequent. It is not known how long naturalized populations of either species persist, but some populations appear to be self seeding.

The family is characterized by the four-celled mucilage glands that occur on most organs. Abortive flowers subtending fully developed ones, fruit morphology, and pollen characters also distinguish most Pedaliaceae from members of related families. These distinguishing features are discussed in turn below.

The mucilage glands of Pedaliaceae consist of four- to occasionally eight-celled capitula (the cells of which are delimited by thick vertical walls) borne on short uniseriate and usually unicellular stalks. The capitular cells have walls arching outward from the stalk. The mucilage is the product of the breakdown of cellulose in these thick walls; the cell lumina are almost full of mucilage (Solereder). The plants become slimy when wet, at least partly as a result of the heads breaking off the stalks, thereby releasing mucilage. The function of the mucilage glands is not certain, although sesame plants with many glands have been shown to wilt less than others with few glands during a period of drought and also to be more resistant to high soil-water content during a period of excess rainfall (Langham, 1945a, see under *Sesamum*; includes photographs of mucilage glands). Mucilage glands of this type are unknown elsewhere in the plant kingdom (Ihlenfeldt, 1967b), although nonmucilage producing capitate or subcapitate trichomes with different configurations of cells occur in Trapellaceae, Martyniaceae, Gesneriaceae, Acanthaceae, and Bignoniaceae. The trichomes of Martyniaceae produce sticky secretions (Thieret, Thorne).

The basic inflorescence type in the Pedaliaceae is a simple dichasium. Typically, however, dichasia are reduced to single flowers that are sometimes accompanied by one or two rudimentary lateral flowers. These may be secretory or excretory and thus have been termed extrafloral nectaries. In some species all three flowers of the dichasium develop fully (rarely up to eight flowers have been reported in aberrant individuals of *Sesamum orientale*). Field observations reveal that insects visit the flowers but not the extrafloral nectaries, even though they contain small quantities of sugars (Monod). These abortive flowers develop to varying degrees. Their morphology and anatomy are thoroughly addressed by Monod, and their development is traced by Singh (1960b). Extrafloral nectaries in related families are often of types not homologous to those just described.

The nature of the fruits also serves both to distinguish Pedaliaceae from related families and to distinguish genera within the family. Mature fruits are nonfleshy. Those of some genera (e.g., *Ceratotheca* Endl. and *Sesamum*) are dehiscent, while those of others (e.g., *Dicerocaryum* Bojer and *Josephinia*) are indehiscent. Partial indehiscence is noted in some individuals of each of our species. Within this overall framework, great variation in fruit wall ornamentation has evolved in the family, e.g., terminal beaks (*Sesamum*), angular horns (*Ceratotheca*), monstrous barbs (*Harpagophytum* (Burch.) DC. ex Meisn., *Uncarina*), and wings (*Holubia* Oliver, *Pterodiscus* Hooker). Though the fruits of our genera are different enough to distinguish them easily, they are more similar to each other than are those of most other genera in the family. Pedaliaceous fruits have been placed in three groups according to the planes of symmetry of their ornamentation (Ihlenfeldt, 1965, 1976b): without emergences (*Sesamum* and *Sesamothamnus* Welw.); with emergences in the vertical plane perpendicular to the septum (*Ceratotheca* horns, *Dicerocaryum* spines); and with emergences in other vertical planes (other genera), whether these emergences are wings, spines, or barbs. The other vertical planes form a relatively large angle with the plane of the septum, as in the wings of *Pterodiscus* and barbs of *Harpagophytum*. In some genera the emergences sometimes also occur in planes at a relatively small angle with the plane of the septum, e.g., the spines of *Rogeria* Gay ex Delile and *Josephinia*. In *Linariopsis* Welw., the fruits do not fall neatly into the above classification because emergences occur in planes both perpendicular to the septum and elsewhere.

The secondary partitions of fruits also serve to distinguish Pedaliaceae from related families. Although not universally present, such partitions often are, as in fruits of species in both of our genera. These traverse the middle of each ovary locule, and in our representatives of the family the fruits dehisce loculicidally along them. When secondary partitions are absent in Pedaliaceae, this character state appears to be derived (Ihlenfeldt, 1965). Comparable fruits with locule partitions are not found in the related Bignoniaceae, Martyniaceae, Trapellaceae, or Scrophulariaceae.

Pollen grains in the family are five or more colpate, with the colpi typically not reaching the polar regions. Similar grains occur in many Bignoniaceae (as only one of several distinct types found there), but bignoniaceous pollen is typically tricolpate (Ihlenfeldt, 1967b). Pollen very similar to that of Pedaliaceae occurs in some Acanthaceae (Bremekamp), e.g., *Thomandersia* Baillon. Pollen of Martyniaceae (Ihlenfeldt, 1967b; Thieret; Alvarado; Bretting & Nilsson), Scrophulariaceae (Cronquist, 1981) and Trapellaceae (Ihlenfeldt, 1967b) differs from that of the Pedaliaceae, as discussed below. Though the Pedaliaceae are relatively stenopalynous, differences among genera can be distinguished, mainly the exine of the mesocolpi, which varies from thinner to thicker at the edges of colpi than in between. *Sesamum* and *Ceratotheca* are among the genera in which the mesocolpi contain a more or less amorphous layer between the nexine and sexine. Such a layer has not been detected in all genera of the family. Pollen differences (Straka; Straka & Ihlenfeldt) correspond approximately to the three tribes of the Pedaliaceae *sensu* Ihlenfeldt (1967b).

Early classifications of Pedaliaceae (e.g., Bureau) emphasized the distinctiveness of gynoecial and fruit characters and the closeness to Bignoniaceae and Martyniaceae in other respects, while differing in the ranks assigned to suprageneric taxa. The comprehensive treatment of the family by Bentham (Bentham & Hooker) established four tribes, one of which included genera now segregated as the Martyniaceae. The other tribes of Pedaliaceae *sensu* Bentham & Hooker were Pedalieae Meisn. (anther locules separate and subpendulous from the filament apex, ovaries two locular, the locules lacking secondary partitions (*Pedalium*, *Pterodiscus*, *Harpagophytum*)); Sesameae (Endl.) Meisn. (anther locules parallel or diverging at the base, ovaries two locular, the locules with a secondary partition, some locules with many seeds (*Rogeria*, *Sesamothamnus*, *Sesamum*, *Ceratotheca*)); and Pretreeae Bentham (anther locules parallel or diverging at the base, ovaries from one to four locular, the locules often with a secondary partition, and one or two seeds per locule (*Pretrea* = *Dicerocaryum*, *Linariopsis*, *Josephinia*)). Until revised by Ihlenfeldt (1967b), this classification has been followed by most workers, except for the removal of Martyniaceae as a separate family, as discussed below.

Recent work in the family by Ihlenfeldt and his associates has led to the current classification of Pedaliaceae, set forth most completely, along with a thorough review of earlier taxonomic treatments, by Ihlenfeldt (1967b). Subfamilies are not recognized, and Martyniaceae and Trapellaceae are excluded. Emphasizing stamen morphology, Ihlenfeldt divided the family into three tribes of somewhat different circumscription from Bentham: Sesamothamneae Ihl. (shrubs with stems succulent at the base, anthers dorsifixed, thecae parallel, pollen in tetrads (*Sesamothamnus*)); Sesameae (herbs or subshrubs, anthers dorsifixed, thecae parallel, pollen solitary (*Sesamum*, *Ceratotheca*, *Dicerocaryum*, *Linariopsis*, *Josephinia*)); and Pedalieae (subshrubs or annual or perennial herbs, anther thecae diverging toward the base and pendent from the tips of the filaments, pollen solitary (*Pedalium*, *Holubia*, *Harpagophytum*, *Pterodiscus*, *Uncarina*, *Rogeria*)). The most significant modification is the isolation of *Sesamothamnus*.

Oliver considered the bilocular ovary without secondary partitions to be primitive in the Pedaliaceae and unilocular ovaries or secondary partitions derived. Accordingly (in the context of Bentham's classification) he considered the Pedalieae basal in the family, despite their specialized fruits. He considered the Pretreeae (partitions originating from the septum of the fruit) derived from this group and the Sesameae (secondary partitions from the adaxial and abaxial walls of the fruit) derived from the Pedalieae through *Harpagophytum*, which is characterized by adaxial and abaxial ingrowths that do not however reach all the way to the placenta. He considered *Pedalium* the closest relative of *Trapella* Oliver (Trapellaceae), noting geographic proximity and similarities in seed arrangement and structure. Thus, Oliver based his phylogeny largely on a single character set, ovary structure. While his phylogenetic hypothesis has not been accepted by later workers in the family, his analysis should be taken seriously to the degree that ovary structure may be conservative and thus entitled to greater weight than other characters, such as the external ornamentation of fruits, which are seen to have potential coevolutionary significance.

Ihlenfeldt placed the three tribes in a phylogenetic sequence in which Pedalieae are separated first and the other tribes are separated very soon thereafter. Within the Sesameae, *Sesamum* is considered most primitive, with subsequent divergences involving *Josephinia*, *Linariopsis*, *Ceratotheca*, and *Dicerocaryum*. Support for the primitiveness and isolated position of *Sesamothamnus* is drawn from the shrubby habit, broadly winged seeds (like some in the Bignoniaceae), pollen in tetrads (like some Bignoniaceae), hawkmoth-pollinated-type flowers (corolla spurred, lobes subequal), leaves borne from spines that are alternately arranged along the stem, and racemelike inflorescences. Its closeness to *Sesamum* and *Ceratotheca* is inferred from the similarity of the anthers and fruits, although fruits of *Sesamothamnus* are laterally compressed.

Members of the Pedaliaceae commonly are found in warm, relatively dry habitats with well-drained soils, although these may be near seacoasts or other water bodies. They are typically able to survive periods of water shortage. Adaptations such as swollen stems (*Sesamothamnus*, *Pterodiscus*), tuberous roots (*Harpagophytum*, *Pterodiscus*), or subsucculent leaves (*Holubia*, *Pterodiscus*, *Pedalium*, *Harpagophytum*) may serve as water holding organs in some genera. Most are annuals. The monotypic *Holubia* is a facultative biennial, and in other genera (e.g., *Dicerocaryum*, *Ceratotheca*, and *Sesamum*) some species (including both of ours) can be either annuals or perennials. Sites with a high water table are unfavorable, as has been documented for sesame.

Flowers of southern African genera of the family have been classified by Vogel as melittophilous (*Dicerocaryum*, *Sesamum*, *Ceratotheca*) or sphingophilous (*Holubia*, *Sesamothamnus*). Nevertheless, the flowers of *Sesamum orientale* are normally self-pollinated in cultivation, although bee pollination occurs also.

Much of the chemical research in the family has been on *Sesamum orientale* and *Harpagophytum procumbens* (Burch.) DC. ex Meisn. (Hegnauer). Iridoid monoterpenes (Seigler), flavones (Gibbs), iridoid glycosides, lignans, phenolic compounds, and miscellaneous storage carbohydrates have been identified in Pedaliaceae. Aluminum accumulators are unknown. Ellagic acid and alkaloids are also unknown, but the phenolic glycoside orobanchin, accumulated in members of the Orobanchaceae, also a member of the Scrophulariales, is present (Gibbs). The presence of mucilage is in contrast to almost all Martyniaceae, Bignoniaceae, Acanthaceae, and Scrophulariaceae (Gibbs). Seco-iridoids are absent, as they are throughout the Scrophulariales; the iridoids identified to date are all 10-hydroxylated carboxylic iridoids, as in Martyniaceae but unlike those of the Acanthaceae. These and other types of iridoids are present in Bignoniaceae and Scrophulariaceae (Dahlgren *et al.*). Calcium oxalate crystals, when present, are usually small and either solitary or clustered (Solereder).

Characteristics of the wood anatomy of Pedaliaceae include simple vessel perforation plates, vessel pits with sometimes wide apertures (perhaps a reflection of habitats promoting high transpiration), circular to oval lateral wall pits, simple pits in imperforate tracheary elements, septate fibers, multiseriate rays at least as abundant as uniseriate ones, relatively few procumbent cells in rays, and apotracheal banded parenchyma. In general, wood of Pedaliaceae resembles that of Martyniaceae (Carlquist).

Anther-wall formation in species that have been investigated is of the commonest "dicotyledonous" type, in which the inner secondary parietal layer develops directly into the tapetum with suppression of periclinal division, and the outer secondary parietal layer gives rise to two layers, the outer one forming the endothecium and the inner the "middle layer" (Davis). The tapetum is glandular, and its cells become multinucleate. In *Pedalium Murex* L. these nuclei later fuse, resulting in polyploid nuclei (Davis).

Outgrowths on some pedaliaceous fruits are adaptations for animal seed dispersal (Cronquist, 1988), for example, the trample-burs of *Harpagophytum*, in which seeds are trampled out of the fruits and into the ground (Van der Pijl). In others the outgrowths are wings, and the fruits are wind dispersed. In our species of *Sesamum* and *Ceratotheca*, the terminal and sometimes complete basipetal dehiscence of the capsules allows local distribution of seeds. The seeds nearest the base appear least likely to come out quickly. In a minority of species of *Ceratotheca* and *Sesamum*, structural features of the fruits may exaggerate this tendency to retard dispersal of the basal seeds (Stopp; Ihlenfeldt, 1967a; Abels; Roth). These involve basal thickening of the fruit wall or the formation of swollen "seed pockets" near the bases of all or only two of the fruit compartments. These features, however, are not constant within species and may be pathological (Ihlenfeldt, 1967a); they apparently have not been reported in either of our species. No reports of endozoochorous dispersal of the seeds are known.

The Pedaliaceae are placed by Cronquist (1988) in the Scrophulariales, an order characterized by often bilabiate tubular corollas with fewer stamens than corolla lobes. All of the chemical and nonchemical characters surveyed by Dahlgren (1980) and Dahlgren *et al.* (1981) support this placement; all characters surveyed are shared with some or all other families in the order. The Pedaliaceae are placed by Thorne in the Bignoniales, an order nearly the same in its circumscription as the Scrophulariales *sensu* Cronquist. Differences in circumscription between Scrophulariales of Cronquist and Bignoniales of Thorne involve taxa relatively distant from the Pedaliaceae (Loganiaceae [Buddlejaceae], Oleaceae, Plantaginaceae).

Families most often cited as close relatives of Pedaliaceae include Trapellaceae and Martyniaceae (included in Pedaliaceae as a subfamily by Goldberg and without infrafamilial rank by Cronquist), Bignoniaceae (e.g., Bruce, 1953a), Scrophulariaceae (Baillon), and Acanthaceae (Bremekamp). The Pedaliaceae may be derived from the immediate ancestors of the Bignoniaceae (Takhtajan, Thorne). However, wood anatomy of the Pedaliaceae is not conclusively more similar to that of the Bignoniaceae than to that of any other members of the Scrophulariales (Carlquist). Ihlenfeldt (1967b) considered the Acanthaceae-Scrophulariaceae to be basal, and Bignoniaceae, Pedaliaceae, and Martyniaceae/Trapellaceae derived in that order. Relationships between Pedaliaceae and each of these families are outlined below.

The monotypic Trapellaceae are aquatic plants of Asia almost universally believed to be related to the Pedaliaceae, with authors differing, however, on the nature of the relationship. They are distinguished from Pedaliacae in having only two fertile stamens and an inferior ovary. They were included by Oliver (as a monotypic tribe) and Cronquist (without formal infrafamilial rank) within the Pedaliaceae. Li considered them a family linking the Pedaliaceae and Myoporaceae. Ihlenfeldt (1967b) placed them slightly closer to Martyniaceae than Pedaliaceae. Takhtajan considered them to be derived but separate from the Pedaliaceae.

Pedaliaceae have been termed the Old World analogue of the New World Martyniaceae (Thieret). The Martyniaceae are a family usually distinguished from the Pedaliaceae in having parietal rather than axile placentation, although some authors doubt that the distinction between these two types of placentation is sufficient for a familial differentiation (Singh, 1960b; Cronquist, 1981). There are several other features that distinguish the two families. In the Pedaliaceae pollen is five or more colpate with vertical colpi usually not reaching the polar regions, inflorescences are axillary (although racemelike on short shoots in *Sesamothamnus*), fruits are hard when mature, and $x = 8$ or 13, in contrast to pollen apolar and without vertical colpi, terminal racemes, fleshy mature fruits, and $x = 15$ or 16 in the Martyniaceae (Bretting & Nilsson, Bentham & Hooker, Thieret, Raven). The wood anatomy of Martyniaceae is similar to that of herbaceous Pedaliaceae (Carlquist).

The Pedaliaceae "can be interpreted as an Old World branch of the Bignoniaceae Juss. with specialized (e.g., anemochorous and zoochorous) fruits" (Ihlenfeldt & Grabow-Seidensticker; see under *Sesamum*). There are several other features that distinguish typical Pedaliaceae from typical Bignoniaceae (Bruce, 1953a; Ihlenfeldt, 1967b; Raven). Members of the Pedaliaceae are typically herbaceous, have four-celled mucilage glands, two-carpellate ovaries with locules often divided into two compartments by secondary partitions, simple leaves, unilateral disks, obliquely campanulate corollas, thin endosperm, wingless seeds, and $x = 8$ or 13. Bignoniaceae are typically woody, have several types of glands but not of the pedaliaceous type, two-loculate ovaries rarely subdivided by secondary partitions, compound leaves, symmetrical disks, large and variable corollas, no endosperm, winged seeds, and $x = 20$. There are some exceptions, however. For example, in our representatives of Pedaliaceae the disk is subannular.

The Scrophulariaceae normally have capsules with loculicidal to septicidal or rarely irregular or poricidal dehiscence, usually tricolporate pollen, and base chromosome numbers as low as six. The Pedaliaceae have loculicidal capsules or indehiscent fruits, polycolpate pollen, and a base chromosome number of eight or thirteen (Cronquist, 1981; Raven).

The chief proponent of a close relationship between Pedaliaceae and Acanthaceae was Bremekamp, in part on the basis of similarity between pollen of *Thomandersia* and that of Pedaliaceae. Several characters distinguish the two families: Acanthaceae typically have cystoliths, seeds with a retinaculum (persistent hooked funiculus), transverse ridges between leaf petioles, and, like all other families, lack four-celled mucilage glands of the pedaliaceous type. Those representatives of Acanthaceae not sharing the above characters are transitional to Scrophulariaceae rather than Pedaliaceae (Cronquist, 1981). Bremekamp's suggestion that *Thomandersia* be placed in the Pedaliaceae, whether or not the two families are joined, has not been followed.

Some genera of the family other than our two are also of economic importance (Uphof). For example, *Pedalium Murex* has been reported to have various traditional medicinal uses, and its leaves are edible. Fruits of *Harpagophytum* and other genera with hooked fruits become stuck on livestock (Metcalfe & Chalk, Pijl) and the tubers of *H. procumbens* are medicinal (Uphof). Synergistic effects of extracts from *Sesamum orientale* and other members of the family have been reported to increase insecticidal effectiveness. Extracts of *Pedalium Murex* have been reported to be effective mosquito larvicides (Kalyanasundaram & Das).

Because of the interest in improving sesame as a commercial crop, the research and literature on the family are dominated by studies on this species. These are summarized in the following treatment of *Sesamum*.

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## KEY TO THE GENERA OF PEDALIACEAE IN THE SOUTHEASTERN UNITED STATES

General characteristics: *Erect annual or perennial herbs with stalked, capitate 4-celled mucilage secreting glands and uniseriate glandular and nonglandular hairs on nearly all parts; leaves opposite, subopposite, or rarely alternate, exstipulate; inflorescences axillary, flowers usually solitary, but often with abortive flowers also at the pedicel bases (showing the flowers to be terminal members of reduced dichasia); perianth pentamerous; calyx synsepalous, lobes slightly unequal; corolla sympetalous, subbilabiate, usually subhorizontal, curved at the base; fertile stamens 4, inserted in corolla tube near base, included, didynamous or nearly so, anthers dorsifixed, thecae subparallel; gynoecium syncarpous, superior, each locule divided into 2 compartments nearly from base to apex by a secondary partition; style 1, included; stigma 1, bilamellate when open; ovules numerous, attached along the axis in a longitudinal row in each of the compartments; fruits suberect, subcylindrical loculicidal capsules, when mature usually more or less tetrangular with longitudinal grooves at the septum and secondary partitions, the whole or the distal portion dehiscing basipetally along secondary partitions; seeds obovate in outline, glabrous, unwinged.*

A. Fruit not or hardly subtruncate at apex, without angular horns but with a conspicuous terminal beak; flowers with a staminode; leaves ovate, oblong, or rarely obovate; lower leaves often 7 or more cm long or wide, sometimes deeply 3 lobed or occasionally trifoliolate, if less than 7 cm long, not broadly subcordate or shallowly 3 lobed .......... 1. *Sesamum.*

A. Fruit subtruncate at apex, with a subdeltoid to linear horn at each of the outer edges of the apex, terminal beak inconspicuous or absent; flowers without a staminode; leaves broadly ovate-subcordate to less often rotund, elliptical, or slightly obovate; lower leaves not exceeding 7 cm in length or width, sometimes broadly subcordate or only shallowly 3 lobed .......... 2. *Ceratotheca.*

1. **Sesamum** Linnaeus, Sp. Pl. **2:** 634. 1753; Gen. Pl. ed. 5. 282. 1754.

Annual or perennial herbs, often in dry, disturbed areas and along roadsides. Stems erect [to prostrate], usually unbranched [or branched], terete near bottom, becoming ± tetrangular. Leaves usually drying light green [or darker], slightly [to strongly] discolorous [or concolorous], opposite, subopposite, or rarely alternate; blades simple or occasionally trifoliolate [or palmately compound]; if simple, unlobed to deeply 3 [or more] lobed, shape ovate, elliptical, obovate, [suborbicular, or lorate], often varied within plants, if trifoliolate, leaflet shape obovate, elliptical, or ovate, sometimes asymmetrical; apices usually acute [or obtuse]; bases acute, obtuse, or rarely truncate, main lateral veins ca. [3–] 6–10; margins sometimes irregularly lobed or crenate; blades usually sparsely to densely pubescent [rarely glabrous]. Flowers solitary or rarely in simple few-flowered cymes; flowers usually subtended by 1 or 2 rudimentary or ± subulate, linear [or subhemispherical] bract(s), and sometimes by 1 or 2 rudimentary flower(s) in the axil(s) of the bract(s). Calyx lobes slightly unequal, narrowly triangular, valvate, usually persistent [or deciduous] in fruit. Corolla pink, white, purple, or blue, sometimes with dots or other patterns of contrasting hues including red, black, or yellow, subbilabiate, usually subhorizontal, the lower lip as long as or longer than the upper; lobes entire or nearly so. Staminode 1; pollen 7–13 colpate, oblate to prolate or spheroidal. Carpels 2 (4), locules 2 (4). Fruits elliptical to weakly obovate [or ovate] in outline, with apical beaks. Seeds slightly [to strongly] flattened [or nearly round in transverse section], with 2 inconspicuous fringes [or 1 or 2 prominent fringes] around the seed, unwinged [or with 3 wings, 1 apical and 2 basal-lateral, borne from seed fringe locations], surfaces smooth, light brown (to black or white), [foveolate, or otherwise patterned]; endosperm cellular; embryo straight. Chromosome number $n$ = 13, [16, or 32], base number (probably) 8. (Including *Simsimum* Bernh., *Gangila* Bernh., *Sesamopteris* DC., and *Volkameria* L. ex Kuntze.) LECTOTYPE SPECIES: *S. orientale* L.; see Seegeler. (Name of uncertain but ancient origin, apparently ultimately based on Near Eastern names for sesame (Bedigian & Harlan, 1986).) — SESAME, BENNE, BENNISEED; see Bedigian & Harlan (1986), Brown (1957), and Morton for extensive lists of other vernacular names in the Old World, the Philippines, and the New World, respectively; see Nicolson *et al.* for interpretation of vernacular names in Van Rheede's *Hortus Malabaricus.*

A genus of 21 species in four sections (Ihlenfeldt & Grabow-Seidensticker), largely restricted to tropical and subtropical Africa, but with some species in Asia. *Sesamum orientale*, sesame, has become naturalized in scattered locations from plants under cultivation, including coastal and other places from at least South Carolina to Texas (the largest number of herbarium specimens from Florida).[3]

The correct name for sesame has been a matter of uncertainty since its description by Linnaeus as two separate species, *Sesamum orientale* (entire, ovate-oblong leaves) and *S. indicum* L. (lower leaves three lobed). De Candolle (1829) treated only *S. indicum*, provided a list of pre-Linnaean and nonbinomial synonyms, and suggested that *S. orientale* should probably be combined with *S. indicum*. However, he did not unite the two species, as emphasized by Seegeler (see Nicolson *et al.* for a contrary conclusion). The two species were united by Roxburgh (1832), followed by Graham (1839), under the name *S. orientale.* The union of these species by De Candolle (1845) under the name *S. indicum* does not have priority, and the correct name is *S. orientale* unless an earlier combination under the name *S. indicum* is found. Nevertheless, although some later authors (e.g., Gandhi, Van Steenis, and Matthew & Rani) have used *S. orientale*, others have adopted *S. indicum.*

Much morphological variation occurs in *Sesamum orientale*, including the "wild gingelly of Malabar" (John *et al.*) and many cultivars. Although the variation is often geographically correlated, no subspecies or varieties are recognized formally. Factor, discriminant, and cluster analyses have been used to evaluate this intraspecific variation; although most of this variation appears continuous, those plants with tetracarpellate capsules formed a statistically discernible group, as did some geographically defined groups of plants to a lesser extent (Bedigian, Smyth, & Harlan).

Worldwide, *Sesamum orientale* now consists mostly of plants in or derived ultimately from cultivation. Cultivation is most extensive in Asia, especially in India and China. Large acreages also occur in Sudan, Mexico, and Myanmar (Burma). Sudan, however, has accounted for over half of world exports because less than 10 percent of the total acreage probably enters world trade (Weiss). Africa accounts for about 70 percent of world exports of sesame. In Mexico and Venezuela cultivation as a cash crop is also significant, unlike in the United States. Some attempts have been made to cultivate sesame nearly everywhere it will grow, including the southeastern United States, where historically significant efforts to cultivate it have been centered in South Carolina

[3]Extended observations are needed to assess the extent of persistence of individual populations of sesame outside of cultivation. Although it has not been included in several floristic treatments within our area (e.g., Clewell, Long & Lakela, MacRoberts, and Radford *et al.*), it has in others (e.g., Batson, Small (1913, 1933), Wunderlin, and Duncan & Kartesz). Since there are herbarium specimens of noncultivated plants that apparently occurred beyond places of former cultivation (e.g., *Arnold s. n.*, Gainesville, Alachua County, Florida (FLAS); *Ellis s. n.*, Miami, Dade County, Florida (FLAS); *Brumbach 9506*, Sanibel Island, Lee County, Florida (FTG, GA, NY); *Cuthbert s. n.*, St. Helena Island, Beaufort County, South Carolina (FLAS); *Deramus D970*, Dauphin Island, Mobile County, Alabama (UNA, NCU, MO)), it is considered part of the flora. There are other collections from South Carolina, Georgia, Florida, Alabama, Mississippi, and Louisiana that were not reported to be of cultivated plants. Some of these probably also represent naturalized populations.

(Kinman & Martin). It arrived in the United States through slave routes from Africa (Weiss). Areas suitable for sorghum and dry-land cotton in the United States are considered suitable for nonirrigated cultivation of sesame (Weiss). It has been cultivated also in the southwestern United States.

With the exception of a few 19th century authors who considered *Ceratotheca* a section of *Sesamum*, *Sesamum* has been and is treated as a genus separated from others in the family by its unappendaged, nonwoody capsules. Within *Sesamum*, species are distinguished by presence and nature of wings, fringes, or other outer seed coat emergences and their patterns (unwinged, inconspicuously fringed, and almost always otherwise unadorned in *S. orientale*), leaf shape (very variable in *S. orientale*), persistence of calyx in fruit (persisting in *S. orientale*), habit (erect in *S. orientale*), degree of prominence of the lower lip of the corolla (slight in specimens of *S. orientale* from the southeastern United States), degree of reduction of the bracts subtending extrafloral nectaries (not very reduced in *S. orientale*), indumentum, and size and shape of capsules. Bruce (1953a) reviewed the history of classification within *Sesamum* and other genera of Pedaliaceae and expressed doubt about the validity of the then existing arrangement of sections of *Sesamum*, foreshadowing the recent revision of the genus (Grabow-Seidensticker, 1973, 1988; Ihlenfeldt & Grabow-Seidensticker).

In the most recent revision (Ihlenfeldt & Grabow-Seidensticker), *Sesamum* is divided into four sections, sect. SESAMOPTERIS Endl. (pollen 6 colpate, seeds 3 winged, testa foveolate), including *S. alatum* Thonn., *S. capense* Burman f., *S. grandiflorum* Schinz, and other species; sect. CHAMAESESAMUM Bentham (pollen 9–11 colpate, seeds unwinged and obscurely fringed, testa reticulate-foveate), including only *S. prostratum* Retz.; sect. APTERA Seidenst. (pollen 7–9 colpate, seeds unwinged and doubly fringed, testa patterns various but never foveolate), including *S. angolense* Welw., *S. calycinum* Welw., *S. radiatum* Schum. & Thonn., and other species; and sect. SESAMUM (pollen 9–10 colpate, seeds unwinged and doubly fringed, testa reticulate to smooth), including *S. latifolium* J. Gillett, *S. orientale*, and other species.

Section SESAMOPTERIS, species of which have winged seeds, is purportedly the most primitive section. It occurs only in Africa, and $2n = 26$ (20 "short," 6 "long" chromosomes) in all species. Section CHAMAESESAMUM is limited to Asia, and $2n = 32$ (all "short" chromosomes) in the only species. Section APTERA is represented only in Africa; its species are $2n = 32$ or $64$ (all "short" chromosomes). Species of sect. SESAMUM occur in Africa and Asia; these species have $2n = 26$ or $32$ (all "short" chromosomes).

Ihlenfeldt & Grabow-Seidensticker noted close relationships among *Sesamum, Ceratotheca* Endl., and *Dicerocaryum* Bojer. Of these genera, only *Sesamum* is divided into sections. *Sesamum* sect. *Chamaesesamum* is portrayed as more closely related to *Dicerocaryum* than to the other three sections of *Sesamum*, with the suggestion that sect.

*Chamaesesamum* may merit generic rank. *Sesamum* sect. *Aptera* is portrayed as closely related to *Ceratotheca*. Their innovative scheme also proposes that *Sesamum* sect. *Sesamum* is probably approximately equally closely related to *Sesamum* sects. *Aptera* and *Sesamopteris*. Evidence of the close relationships among these genera includes 1) overall morphological similarity, 2) pollen in *Ceratotheca* species spans the range of variation between the *Ceratotheca* and *Sesamum* types (discussed under *Ceratotheca*), and 3) the production of a sterile hybrid between *C. sesamoides* Endl. and *S. orientale* (Van Rheenen). In this context Hooker's opinion that *Ceratotheca* is only a section of *Sesamum* is noteworthy. To broaden the perspective on these affinities, it may be noted that a sterile hybrid was earlier reported between an unidentified species of *Sesamum* (*S. orientale*?) and *Martynia annua* L. (Martyniaceae) (Srinivasan, p. 162).

The two *Sesamum* species that occur in all three areas of the distribution of the genus, *S. Schenckii* Ascherson (= *S. grandiflorum*?) and *S. capense*, are $2n = 26$, as is *S. orientale*. Attempts to cross *S. orientale* with *S. alatum* (= *S. capense*?), also $2n = 26$, and with *S. Schenckii* have sometimes produced viable $F_1$ progeny. Sterile hybrids have resulted from crosses between *S. orientale* and *S. prostratum* (Asian, $2n = 32$). The amphidiploid of this sterile hybrid, $n = 29$, obtained by colchicine treatment of the $F_1$, is stable and almost pure breeding (Tribe). It can be crossed with *Ceratotheca sesamoides*, yielding sterile progeny. Overall, about two-thirds of the attempted interspecific crosses in *Sesamum*, including crosses between species in different sections, have proved at least somewhat successful (Nayar).

Opinion is divided whether cultivated sesame originated in Africa or Asia. *Sesamum latifolium*, which Ihlenfeldt & Grabow-Seidensticker cited as the probable ancestor, occurs in Africa. The "wild gingelly of Malabar," a variant of *S. orientale* which Bedigian, Seigler, & Harlan cited as the probable ancestor, occurs in Asia, a secondary center of diversity of the genus. Other species put forth as possible contributors to the gene pool of cultivated sesame include *S. radiatum*, *S. prostratum*, *S. alatum*, and *Ceratotheca sesamoides*. The higher chromosome numbers ($2n = 32$ or 64) of all the above, except *S. alatum* and *S. orientale*, make them unlikely as progenitors (Nayar & Mehra). However, at least one Indian cultivar of *S. orientale* has six "B" chromosomes in addition to the normal complement of 26, and a loss of six chromosomes from earlier stock(s) may be involved in the domestication of cultivated sesame (Ihlenfeldt & Grabow-Seidensticker). It is possible that sesame was brought into cultivation independently from wild plants in both Africa and Asia. Although most *Sesamum* species occur in only one geographic region (e.g., Africa, Asia, or the East Indies), three species occur in both Africa and the East Indies, two in Africa, India, and the East Indies, and one in Africa and Sri Lanka (Nayar & Mehra).

A high frequency of secondary association of chromosomes occurs during metaphase I of meiosis in pollen mother cells of *Sesamum orientale* and other *Sesamum* species (Kobayashi & Shimamura, Ihlenfeldt & Grabow-Seidensticker, and others), suggesting a paleopolyploid origin for these species. The original ancestor of sesame has been postulated to have had $x = 7$, 8, or 9 (Nayar & Mehra), depending on particular patterns of secondary association.

The above findings, especially the "B" chromosomes reported by Ihlenfeldt & Grabow-Seidensticker, seem to suggest that the *Sesamum* species with $2n = 32$ are paleotetraploids of the base number 8, and those with $2n = 26$ may be derived from $2n = 32$ by reduction, rather than $2n = 2x = 26$ from a base number of 13. Although earlier literature indicated both eight and thirteen as base numbers in *Sesamum* (Nayar) and the Pedaliaceae (Raven), more recent detailed study led Ihlenfeldt & Grabow-Seidensticker to consider eight to be the only base chromosome number for Pedaliaceae.

*Sesamum* species tend to prefer relatively dry areas in the warm regions where they are indigenous, although *S. radiatum* has been reported to occupy more moist habitats than *S. orientale* in Sri Lanka (Theobald & Grupe). *Sesamum orientale* is usually grown in areas with ca. 500–1100 mm annual rainfall between 25° North and 25° South latitudes. Variants are often adapted to local conditions to the extent that they do not do well when planted elsewhere. Among commercial crops, sesame is relatively tolerant of drought and poor soils, but it is sensitive to high salt concentrations and to excess moisture, especially at the seedling stage, when it is also vulnerable to competition from weeds. Plant growth in sesame has been found to be stimulated by infection with vesicular-arbuscular mycorrhizal fungi, indicating that these associations are important in obtaining nutrients, at least in some cultivars (Sulochana *et al.*). Sesame is intolerant of acid soils (Tribe). Sesame is very sensitive to day length; both long- and short-day forms occur (Purseglove), although it is reported to be basically a short-day plant (Weiss). On the basis of herbarium label data, flowering of noncultivated plants in the southeastern United States occurs at least from July through October.

Floral anatomy and development have been investigated in *Sesamum orientale* (Baillon, 1862; Singh, 1960b) and *S. alatum* (Sundari *et al.*), and leaf and hair anatomy have been studied in *S. laciniatum* J. T. Klein ex Willd. (Sayeedud-Din). The floral vasculature is noteworthy in that the primary vascular traces do not divide into calyx, corolla, or androecial traces, and in that the patterns are different between species. In *S. orientale*, the vasculature of the androecium and that of the median calyx bundles have a common origin; the calyx laterals and corolla vasculature arise as common traces; and the vasculature to the disc is partly from the traces to the stamens. In *S. alatum*, neither the disc nor the calyx vasculature has a trace in common with that to the androecium, but the petal midrib traces and sepal laterals have a common origin. In the adjacent abortive flowers (extrafloral nectaries) of *S. orientale*, the vasculature is similar to but reduced from that of the fully developing flowers.

Pollen of *Sesamum orientale* usually has 9 or 10 colpi, but the number varies from 8 to 13. Other species tend to have fewer colpi and pollen that is either the same size or smaller (Straka & Ihlenfeldt). In *S. orientale*, the grains are normally trinucleate at anther dehiscence and have a papillose exine (Singh, 1960b).

*Sesamum orientale* is usually self pollinated (McGregor), although *Sesamum* flowers are of a type usually associated with bee pollination (Vogel). Significant but usually less than 10 percent cross pollination also occurs in cultivation. This is attributed to honey bees, which are often seen visiting sesame plants (Langham, 1944; McGregor). The bees alight on the lip of the flower, squeeze inside, and emerge with pollen on their bodies and in their pollen baskets. Small flies also occasionally visit sesame flowers. Despite sesame's being normally self-pollinated, heterosis has been reported repeatedly (Srivastava & Singh, Sodani & Bhatnagar, and earlier workers referenced in Brar & Ahuja). The flowers vary from white to pink or purple with various patterns of other colors, including dots, flakes, and smears, at various locations and intensities on the corolla (Langham, 1947a), all suggesting generalized attraction of insects. Pollen is usually shed from the longitudinally dehiscent anthers either before the flowers open (Purseglove) or shortly thereafter (Weiss). In early morning, when the flowers open, the bilobed stigma separates and is covered with pollen. After midday the flowers wilt and the corolla and stamens are usually shed in the evening of the same day. The stigma is receptive one day before flower opening or at least at the time of flower opening, and remains receptive for an additional day. Under experimental conditions, pollen germination begins 5 min after pollination and is mostly complete after 15 min. Pollen tubes begin to reach the base of the non-hollow style after 2 hours, the average rate of travel being 4.7 cm per hour. A small amount of germination and growth of pollen and tubes still goes on 24 hours after pollination (Yang & Chou). In the United States sesame usually flowers in midsummer when little else does, providing an opportunity to bee keepers. Sesame is often found as a relic of cultivation worldwide, and its tendency is to persist weakly in disturbed areas of the United States and elsewhere, including Madagascar (Humbert, 1962, 1971) and India (Gandhi). Perhaps paucity of reliable pollinators during time of flowering where it has been introduced explains this tendency in part.

Cleistogamy has been reported as a rare event in *Sesamum orientale*. Although such cleistogamous flowers were shown to be fertile when pollen from "sister plants" was used, some of the ovules in some of the resulting fruits were replaced by parenchymatous outgrowths bearing glandular hairs (Srivastava, 1954).

Embryogeny is of the Onagrad (Singh, 1960b) variation of the Crucifer type (Hanawa, 1953; Davis) in which the first division of the hypophysis initial takes place by a curved wall.

Endosperm is present in the seeds, contrary to statements in some of the early literature. It is cellular, oily, two to five cell layers thick, and terminal cells at both micropylar and chalazal ends are absorptive in function (Srinivasan, Davis). Oil drops are located in the cells of the cotyledons, as well as those of the endosperm (Vaughan). The endosperm is largely used up by the embryo in mature seeds. The embryo is straight and the cotyledons are prominent. The testa can be as thick as 16 cells. In mature seeds the outer epidermis is one layer thick. This layer bears clusters of calcium oxalate crystals in the outer half (*Sesamum orientale*) or inner half (*S. radiatum*). Ridges on seeds, when present, are caused by cell elongation.

The thin seed coat of *Sesamum orientale* has been selected for and represents a juvenile stage in seed ontogeny, although vestiges of patterns reminiscent of those of other species occasionally occur, including the specimen in which six "B" chromosomes were documented. Moreover, the light color of the seed coat reflects the absence of tannins normally deposited in the testa during late stages of seed ontogeny (Ihlenfeldt & Grabow-Seidensticker). In many species of *Sesamum*, seeds are darkly colored when ripe (Ihlenfeldt & Grabow-Seidensticker).

Miscellaneous compounds have been reported from *Sesamum*, including alcohols, sugars, flavones, furanoflavones, lignans, and others (Hegnauer, Gibbs). Sesame seeds contain the lignans sesamin and sesamolin, which have not been reported from other edible oils (Bedigian, Seigler, & Harlan). Although these compounds have also been found in various tissues of members of related families, they seem not to be present in either *S. alatum* or *S. capense* and are not always detected in members of related families. Sesamol, another lignan, has also been isolated from the seeds of *S. orientale*. Some compounds in the seed oil of *S. orientale* may be toxic or may cause tumors (Bedigian, Seigler, & Harlan). *Sesamum orientale* tested negative for cyanogenesis (Gibbs). Two new antifungal naphthoxirene derivatives and a new iridoid glucoside have been isolated recently from the root bark of *S. angolense* by Potterat *et al.* (1987, 1988).

Yields of sesame are traditionally low compared to other oilseed crops, but a potential of up to a ton per acre per year has been demonstrated (McGregor). In 1976 sesame was reported to rank ninth worldwide among vegetable oil crops (Nayar). World production has recently remained static, though commercial demand has declined (Weiss).

Much experimental work has been done in attempts to improve sesame as a commercial crop (reviewed in Brar & Ahuja, Weiss, and others), contributing basic as well as practical knowledge. It is a convenient organism for genetic research (Langham, 1948), and many mutants have been found that are phenotypically expressed. These mutants include tufts of hair, glabrosity, separate corolla lobes, double flowers or lips, and fused anthers (Langham, 1946a). Genetically based variations in flower color have been classified as basic factors (which themselves do not add color but rather inhibit expression of factors controlling "true" color factors); as color factors (the coloring visible if basic factors are present); as pattern factors (location of color); and as intensification factors (amount of coloring matter) (Langham, 1947a). Simple Mendelian ratios have been found for most vegetative, floral, fruit, and seed characters, but duplicate, modifying, and complementary factors, multiple alleles, and linkages have also been demonstrated. Controls of some phenotypic characters are provisionally assigned to genes on each of the 13 chromosome pairs by Nohara (1934). High heritability values and few controlling genes have been postulated for percentages of germ, protein, and oil in sesame seeds (Culp, 1959).

Cultivars with indehiscent capsules and cultivars with extra flowers per node or extra carpels (up to 12) per fruit have been developed and tested for commercial potential with some but not spectacular success, as have cultivars with fruits that mature simultaneously rather than acropetally on the plant. A single cultivated plant can produce several thousand seeds.

Tetraploid variants have been induced with colchicine and studied experimentally for possible commercial value. The embryo grows more slowly in early stages in tetraploid plants, but development later catches up with that of diploids (Hanawa, 1953). Flowering is slightly later in tetraploids. Although fertility is somewhat reduced in tetraploids, pollen fertility is still nearly equal to that in diploids. Sesame polyploids characteristically are more variable than diploids. They also have more branching, larger and thicker stems and leaves, simple rather than tripartite leaves, and larger but fewer stomata than diploids. Pollen grains, flowers, fruits, and seeds usually are larger, and there are more capsules than in diploids. However, there are fewer seeds per capsule and usually per plant in tetraploids, so oil yield is not increased (Kobayashi & Shimamura; Srivastava, 1956).

The economically most important product of *Sesamum orientale* is its seed oil, although seed rather than oil is traded in world markets. The oil is in demand because of its good taste, stability, and lack of tendency to become rancid even without refrigeration, owing to its resistance to oxidation. It is odorless. Seed oil content is usually ca. 50 percent, but it varies with the source of the plants. Palmitic, stearic, oleic (ca. 40 percent), and linoleic (ca. 40 percent) acids are reported to be the major fatty acids present. Linolenic acid is absent. About 14 percent of the acids are saturated. The oil from both raw and toasted seeds is used in cooking and on salads. Oil from raw seeds is also used in margarine, soap, and paints, and as a lubricant and illuminant. In India, sesame oil is used as a body oil, and in the Philippines, it is used as an antirheumatic in massage treatment. It is a solvent vehicle for pharmaceutical drugs, perfumes, shampoos, and cosmetics, and is a component of some liniments and ointments.

Whole seeds are also commercially important, although less so than the oil. These are used on bread products. The seeds are used in soups, other foods, and medicines, e.g., as a laxative, in India, Africa, and Latin America. Protein content is ca. 20–25 percent and water content ca. 5 percent. The protein chemistry of the seeds has been well studied (e.g., Rajendran & Prakash). Wide ranges in content of iron and other mineral constituents of sesame seeds have been reported (e.g., Brar & Ahuja; Friedlander; Khan *et al.*). A large percentage of the mineral content is in the hulls of the seeds, which are usually removed before commercial use.

Among Indian oilseed flours including soya (*Glycine* L.), groundnut (*Arachis* L.), and chickpea (*Cicer* L.), sesame contains above average quantities of fat, crude fiber, calcium, phosphorus, iron, and thiamine. Compared to soya, cottonseed (*Gossypium* L.), and groundnut flours, sesame flour is high in methionine and tryptophan (Weiss). Sesame meal and expressed cake are high in methionine (in which legumes are deficient) and are thus valuable food and feed supplements for humans and livestock. The expressed cake is also high in protein, though it may be low in lysine.

Sesame also is a main ingredient of halvah (a Middle Eastern confection) and tahini (sesame paste). Young leaves are used in soups. The leaves have various medicinal uses in Africa, including the use of the mucilage from sesame plants in the treatment of diarrhea and dysentery. The cake has been used as a hair dressing and in rituals in Sudan. Sesame meal is a meat substitute and filler. Sesamin, sesamol, and sesamolin from the seeds are synergists for pyrethrin insecticides. Antifungal activity has been demonstrated in extracts from leaves, fruits, and seeds of sesame at various plant ages (Pagnocca *et al.*). Cherokee Indians have used the seed oil as a cathartic and a decoction of the leaves and seeds as an antidiarrheal, gynecological, and pediatric aid (Hamel & Chiltoskey, Moerman). Sesame is sometimes grown in the United States for use as a component of birdseed.

Other species of *Sesamum* have been used in some of the same ways as *S. orientale* on a more local basis, most often in Africa but also in Asia and Latin America (Uphof). *Sesamum angolense* has several African traditional medicinal uses. One of the new antifungal naphthoxirene derivatives recently isolated from its root bark was toxic to human colon carcinoma cells (Potterat *et al.*, 1987).

Seedling shoot-tips with cotyledons can be multiplied through tissue culture in *Sesamum orientale*. This could be a first step toward creating useful variants of sesame by cell culture, which has already been accomplished in some other crops (George *et al.*).

*Sesamum orientale* is subject to attack by a number of insect pests, reducing yield worldwide by ca. 25 percent. Fungal and bacterial diseases are common, and viral and other diseases and malformations also occur (thorough review by Weiss). The problems are locally defined, but according to Purseglove the most serious diseases are leaf-spots and *Fusarium* wilt. Some pests eat seeds, some leaves. Attacks can occur in the field or in storage. Leaf-curl disease, caused by a virus, was found to reduce plant yield and seed oil content but, at least on a percentage basis, to increase seed protein content (Prasad *et al.*).

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growth reduced with increasing boron; yields reduced with 15 or more percent exchangeable sodium.]

2. **Ceratotheca** Endlicher, Linnaea **7:** 5. 1832.

Annual or perennial herbs [or small shrubs] in pinelands and disturbed areas such as dry fields or roadsides [or in other relatively open areas]. Stems erect [or semi-prostrate], [branched or] unbranched, terete below, becoming ± tetrangular, pubescent. Leaves usually drying light green or brown, and discolorous [or concolorous], opposite, subopposite, [or rarely alternate]; blades simple, unlobed to shallowly 3 lobed, shape broadly ovate-cordate to less often rounded, elliptical or slightly obovate, often varied within plants; apices acute to obtuse, bases cuneate, [truncate], rounded, or cordate, main lateral veins ca. 3–6 [–10]; margins usually crenate; blades [usually] pubescent. Flowers solitary, sometimes subtended by 1 or 2 rudimentary or linear bract(s), subcircular, reduced petiolate leaves, or rudimentary flower(s). Calyx lobes unequal, usually narrowly ovate, valvate or subvalvate, usually deciduous [or persistent] in fruit. Corolla [white, pink, or] purplish, lobes sometimes with darker stripes or lines of dark spots, subbilabiate, usually subhorizontal, the lowest lobe the longest; lobes entire. Staminode absent; pollen (6) 7–9 (10) colpate, suboblate to spheroidal, peroblate, or prolate. Carpels 2, locules 2. Fruits obovate, truncate or subtruncate at apex, with 2 usually subhorizontal [to suberect], narrowly triangular to linear horns at the outer edges of the apex, the horns early splitting in half longitudinally and then appearing to be 4. Seeds flattened, doubly [or singly] fringed, unwinged, tan to nearly black, flat surfaces [sometimes radially] rugose to verrucose. Endosperm cellular; embryo straight. Chromosome number $2n = 32$. (Including *Sporledera* Bernh. non Hampe.) TYPE SPECIES: *C. sesamoides* Endl. (Name from Greek *keratos*, horn, and *theke*, case, container, capsule, in reference to the fruit.)

A genus of five species of tropical and southern Africa. The southern African *Ceratotheca triloba* (Bernh.) Hooker f. has been introduced into the United States as a cultivated ornamental and has escaped to become naturalized in the high pinelands and roadsides of peninsular Florida (Small, 1933).[4] The natural range of *C. triloba* is eastern

[4]Field observations are needed to evaluate the extent of persistence of *C. triloba* outside of cultivation. It is not mentioned by Clewell, Duncan & Kartesz, Long & Lakela, MacRoberts, Small (1913), or Radford *et al.*, but is included in Batson, Small (1933), and Wunderlin. There are herbarium specimens collected in Florida at locations beyond previously cultivated areas in Highlands County (*Small & Mosier s. n.*, from scrub in hills about Lake Istokpoga [NY] and *Small, Mosier, & Matthaus s. n.*, from scrub near Lakes Damon and Pythias [NY]), and other reported collections from "high pinelands and roadsides" near Fruitland Park, Lake County (*C. R. Williams s. n.*, [US]) and from Polk County (Wunderlin). For the purposes of this treatment it is thus considered naturalized.

South Africa, Zimbabwe, southern Mozambique, eastern and southeastern Botswana, Malawi, and Lesotho (Abels; includes distribution maps).

*Ceratotheca*, distinguished by its truncate, four-horned capsules (actually two horns each splitting early during dehiscence to become four) and its fringed seeds, was described as a new genus in Endlicher's order Sesameae, which also included *Sesamum*. Although fringed seeds occur also in some species of *Sesamum*, the horned capsules continue to be a reliable diagnostic feature.

Bernhardi originally described *Ceratotheca triloba* in a new genus, *Sporledera*, even though he was aware of Endlicher's *Ceratotheca* and treated it in the same publication. Hooker reduced *Sporledera* to synonymy under *Ceratotheca* without maintaining even a separate section for it, an arrangement that has been universally followed since. Hooker's notes indicated that *C. triloba* was "closely allied to" *Sesamum orientale* but "differs from the older genus [*Sesamum*] in no important characters but the two-horned capsule, and might well be regarded as a section of it." This suggestion, which would result in the transfer of the species of *Ceratotheca* to *Sesamum*, has not generally been followed (however, cf. Baillon, 1887). More recent indications of affinity are numerous. These include the production of sterile intergeneric hybrids between species of *Ceratotheca* and *Sesamum* (Van Rheenen, 1970; Tribe); the occurrence of some fruits of *S. radiatum* Schum. & Thonn. (doubly beaked) and *C. sesamoides* (lacking horns) that are possibly transitional between *Sesamum* and *Ceratotheca* (Abels); and the postulates that *Ceratotheca* may have diverged from *Sesamum* later than some species of *Sesamum* did from each other (Abels; Ihlenfeldt & Grabow-Seidensticker) or that *Ceratotheca* may have possibly contributed to the ancestry of *Sesamum* sect. *Sesamum* in a reticulate manner (Ihlenfeldt & Grabow-Seidensticker). Evolutionary relationships between the two genera need further study.

*Ceratotheca triloba* has doubly fringed seeds and is distinguished from other species of *Ceratotheca* by the combination of its often trilobed leaves, corolla size (often longer than 2.5 cm), fruits obovate in outline, and fruit horns nearly horizontal (Abels). It has been reported to have a strong, unpleasant odor like that of *Hyoscyamus niger* L. (Stapf, 1906).

The other species of *Ceratotheca* are *C. sesamoides*, $2n = 32$, (fruits strongly compressed laterally [and in this feature transitional to *Sesamothamnus* Welw., which is possibly basal in the family], seeds with a single fringe all the way around, horns oblique or absent) from sub-Saharan and eastern Africa; *C. integribracteata* Engler (leaves ovate to elliptical, seeds with a single apical and a double basal fringe), from Angola and adjacent countries; *C. saxicola* E. A. Bruce (leaves and fruits smaller than those in the other species, seeds with a single fringe), from a small area in southern Africa at the edge of the ranges of *C. sesamoides* and *C. triloba*); and *C. reniformis* Abels (leaves usually kidney shaped, seeds with two fringes, fruits broader near the base than at the apex, and fruit horns often erect), from Angola and adjacent countries (Abels; Bruce *et al.*).

Abels's monograph of *Ceratotheca* and *Dicerocaryum* Bojer is the latest and most complete treatment of the genus. On the basis of comparative seed morphology, supported by fruit characters (horn length), Abels postulated that the ancestor of *C. sesamoides* was the first to separate from the ancestors of the other species in the genus. Among the other four species, the ancestor of *C. integribracteata/C. saxicola* is believed to have separated from that of *C. triloba/C. reniformis* next, followed later by separation of *C. integribracteata* from *C. saxicola* and *C. triloba* from *C. reniformis*. This hypothesis is reinforced by the geographic distributions of the species, which are explainable by climatic fluctuations causing alternating advances and retreats of forest and savanna habitats. The present wide geographical separations of *C. integribracteata* from *C. saxicola* and *C. triloba* from *C. reniformis* may have resulted from relatively recent fragmentation of previously continuous suitable habitats. Other characters, such as habit, seed number, fruit length, and leaf shape, do not fully support the hypothetical arrangement (Abels, pp. 233–235). The genus has not been subdivided.

*Ceratotheca triloba* tends to prefer relatively dry, warm areas in well-drained soils both in the United States and its natural range. Flowering in naturalized representatives in our area is from June through August. Flowers of *Ceratotheca*, like those of *Sesamum*, are structurally bee-pollinated (melittophilous; Vogel), but confirmation by field observations is needed.

Pollen of *Ceratotheca* is of the Sesameae type (an amorphous middle layer of exine present between the sexine and the nexine) (Straka). The pollen of the species of *Ceratotheca* differs within this type. Pollen of *C. sesamoides*, probably the most primitive member of the genus, is (6) 7–8 colpate and is of the *Sesamum* subtype (the sexine approximately as thick at the margins of the mesocolpi as between them). Pollen of *C. integribracteata* is (8) 9 (10) colpate and is of the *Dicerocaryum* subtype (the sexine tenuimarginate, i.e., thinner at the margins of the mesocolpi than between them). Pollen of *C. triloba* is (8) 9 (10) colpate and is transitional between the two subtypes. This reinforces the closeness of these three genera, despite their distinctive fruits, as reflected in Ihlenfeldt & Grabow-Seidensticker's classification.

The staminode representing a rudimentary fifth stamen in *Sesamum* and other genera of Pedaliaceae is usually reported to be absent in *Ceratotheca*. Observations during preparation of this treatment confirmed this. However, field observations of large numbers of flowers would help to confirm that this is always true. Bernhardi explicitly downgraded this character, partly because he had little material to work with, and it has occasionally been reported in passing that the staminode is present (e.g., Small, 1933).

As in *Sesamum*, there are both micropylar and chalazal endosperm haustoria in *Ceratotheca* (Schnarf).

Growth rings occur in stems over a year old in *Ceratotheca triloba*; latewood vessels are narrower than earlier ones. Vessels are mostly in groups. Perforation plates are simple. Lateral wall pits are mostly oval, with narrowly oval apertures in vessel-to-vessel contacts. Multiseriate rays are much more frequent than uniseriate ones. In both types, upright, square, and procumbent cells are common. These features, which place *Ceratotheca* close to *Sesamum*, are also typical of Pedaliaceae and the Scrophulariales (Carlquist).

Little is known of chemistry in *Ceratotheca*. However, leaves of *C. triloba* have been tested for saponins, leucoanthocyanins, cyanogenesis, and tannins, with a negative result for the first three and a doubtful positive one for the fourth (Gibbs). Seed oil of *C. sesamoides* does not contain sesamolin (Hegnauer).

*Ceratotheca sesamoides* is cultivated to some extent in Africa as an oilseed crop. Its seeds contain smaller percentages of oil than those of sesame. Both its leaves and seeds are also eaten there. Our *C. triloba* is cultivated as a garden ornamental and conservatory plant (Bailey) and has also been reported in cultivation in the United Kingdom (Hooker) and India (Cooke).

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