

# THE LINACEAE IN THE SOUTHEASTERN UNITED STATES<sup>1</sup>

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LINACEAE S. F. Gray, Nat. Arr. Brit. Pl. 2: 639. 1821, "Lineae"  
[A. P. de Candolle, Théorie Élem. Bot. 214. 1813, "Linées"],  
nom. cons

(FLAX FAMILY)

Herbs [shrubs, trees or woody climbers] with simple and mostly alternate (rarely all opposite or whorled) leaves; stipules present or absent. Inflorescences various, cymose, racemose, corymbose, or paniculate [rarely solitary]. Flowers perfect, regular, 5[4]-merous; sepals and petals free or slightly connate at the base, the sepals quincuncially imbricate, the petals contorted in aestivation and often clawed; disc absent; stamens equal in number to the petals and alternate with them or twice as numerous and in two whorls, filaments connate at the base with nectar glands usually on the outside of the tube, staminodia sometimes present; ovary superior, syncarpous, 5[2-4]-carpellate, sometimes partially or completely subdivided into 10 [4-8] locules by the intrusion of false septa, ovules 2 per carpel, epitropous; styles as many as the carpels, mostly free or sometimes partly to completely united; stigmas distinct, capitate to filiform. Fruit a septicidal capsule [or drupe]; seeds often with a mucilaginous epidermis, embryo straight [or slightly curved]. (Linaceae sensu Hutchinson, 1967; Linoideae of Winkler, excluding Nectaropetaleae, and of Scholz.) TYPE GENUS: *Linum* L.

About 13 genera and 275-350 species of worldwide distribution, but with relatively few species in the Southern Hemisphere. Four genera are represented in North America: *Linum*, with about 41 (including 4 or 5

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introduced) species primarily in the Southwest and on the Atlantic and Gulf coastal plains; *Radiola* J. Hill (*Millegrana* Adanson), with *R. linoides* Roth introduced and established in Nova Scotia; *Hesperolinon* (Gray) Small, with 12 species largely confined to California; and the monotypic *Sclerolinon* C. M. Rogers, with *S. digynum* (Gray) C. M. Rogers ranging from Washington south to California. *Reinwardtia* Dumort. has been introduced into the West Indies from India. These genera, plus the Asian *Anisadenia* Wall. and *Tirpitzia* Hallier f., comprise the tribe Lineae (mostly herbs or subshrubs, stamens the same number as the petals, fruits capsular), which is generally of temperate regions. The tribe Hugonieae Planchon (trees, shrubs or woody climbers, stamens twice the number of the petals, fruits drupaceous) is mostly tropical and contains six genera, including the South American *Hebepetalum* Benthham and *Roucheria* Planchon. The family is evidently not indigenous to southern Central America, adjacent northern South America, and most of the West Indies.

Closely related to the Linaceae, or sometimes included within it, are the Humiriaceae, Ctenolophonaceae, Ixonanthaceae, and Erythroxylaceae, which share the simple leaves; regular flowers; diplostemonous androecium or stamens in only 1 whorl, rarely numerous, with the filaments basally united; nectiferous disc absent or small; and superior ovary. The Geraniaceae, Oxalidaceae, Malpighiaceae, Zygophyllaceae, and Polygalaceae are also sometimes considered to be related to the Linaceae. The Linaceae have recently been placed in the Linales (Cronquist), the Geraniales (Winkler, Scholz, Thorne, and Takhtajan), and the Malpighiales (Hutchinson, in his Lignosae). Hallier placed the Linaceae in his Guttalles as a derivative of the Ochnaceae and considered it as the evolutionary center of origin for several lines, including the Passiflorales, Myrtales, Sapotales, Santalales, and some families of the Tubiflorae. Airy Shaw suggests that through *Anisadenia* the Linaceae are connected with the Plumbaginaceae, and Erdtman (1969) says that on palynological grounds these two families are close.

The floral anatomy and morphology of *Linum* and certain other genera have been the subject of numerous papers (cf. Sharsmith and Narayana). The stamens in the Lineae are monadelphous, with a cup from which the filaments arise. In some species and genera nonvascularized structures, usually called staminodia, alternate with the stamens. Sharsmith found in *Hesperolinon*, *Radiola*, and a few species of *Linum* that the petals arise from the cup in exactly the same position as the staminodia found in *Linum* and other genera. In other species of *Linum*, and in *Anisadenia* and *Reinwardtia*, the petals originate from the receptacle at the base or from the sides of the cup. In all cases the petals have but a single vascular strand, are only lightly attached to the cup or receptacle, and usually fall readily if disturbed. Collections of members of this family should be made early in the morning and be pressed immediately.

Reported chromosome numbers are *Hugonia* (3 spp.)  $2n = 12, 24, 26$ ; *Radiola linoides*,  $2n = 18$ ; *Reinwardtia trigyna*,  $2n = 20, 22$ ; *Sclerolinon*



*digynum*,  $2n = 16$ ; and *Linum*,  $2n = 12, 16, 18, 20, 24, 26, 28, 30, 32, 34, 36, 52, 54, 60, 62, 68, 72, 84$ .

Pollen grains of the Linaceae are diverse and of some taxonomic importance. The tribe Lineae has 3-, 4- or 6-colpate, pantocolpate, or pantoporate grains with a granular to baculate sexine, while the Hugonieae have mostly tricolporate grains with the sexine usually strongly baculate and often tegillate. The pollen of *Anisadenia pubescens* and *Reinwardtia indica* was reported as nonaperturate by Erdtman, but Saad describes both as pantoporate. Pollen morphology supports the removal of *Ctenolophon* and the Humirioideae from the Linaceae. Pollen of the woody members of the family is of a more advanced type than that of the herbaceous members. Saad and Erdtman have pointed out similarities between the Linaceae, especially *Hugonia*, and the *Plumbago* group of the Plumbaginaceae. Palynological similarities to the Geraniaceae and Oxalidaceae have also been noted.

Anatomical studies indicate that the Linaceae *sensu lato* is not a natural group and its division into several families is warranted. The Linaceae and Erythroxylaceae are considerably different anatomically, while the Linaceae and Humiriaceae have numerous similarities, with the wood of the latter family more primitive than the former and similar to *Ctenolophon*. Within the Linaceae, *Indorouchera* has the most primitive wood. There is no evidence from wood anatomy that the woody members of the family are derived from herbs.

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- 105; *Linum usitatissimum*, 258, 259; *L. hirsutum*, 294, 295; *L. alpinum*, 304, 305; *L. perenne*, 306, 307.]
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#### Tribe LINEAE [Eulineae Planchon]

##### 1. *Linum* Linnaeus, Sp. Pl. 1: 277. 1753; Gen. Pl. ed. 5. 135. 1754.

Perennial or annual herbs [or shrubs], sometimes woody at the base, with one or several  $\pm$  erect stems arising from a taproot or rootstock, usually unbranched below the inflorescence, stems mostly glabrous, infrequently scabrous [or pubescent], and often striate. Leaves simple and alternate, sometimes opposite below, infrequently all opposite [or whorled], ovate or obovate to linear, entire, denticulate or glandular toothed, mostly sessile with one midvein or several prominent parallel veins; stipules absent or paired and glandular. Inflorescences terminating the main stems, usually much branched and several to many flowered [rarely solitary], basically cymose but often appearing as scorpioid cymes, panicles, racemes or corymbs. Flowers yellow, blue [white or red]. Sepals 5, free or united at the base, lanceolate to ovate or obovate with acute to long attenuate apices, rarely obtuse,  $\pm$  equal or the inner shorter than the outer, [glabrous or] all or only the inner glandular toothed, sometimes ciliate, with 1 or 3 prominent veins, persistent or infrequently deciduous, quincuncial. Petals 5, free [or connate by the claws], the lower adaxial surfaces pubescent or glabrous, inserted at the base of or on the staminal tube, fugacious, contorted, the claws or adaxial petal appendages small or almost absent. Stamens 5, alternate with the petals, basally united to form a cup around the ovary, nectar glands often on the outside of the cup; nonvascularized staminodia alternating with stamens or absent; anthers introrse, 2-locular at anthesis, opening lengthwise. Stigmas 5, distinct, capitate or clavate [to filiform]; styles 5, free or partly to almost completely united, homostylous [or heterostylous]; ovary superior, syncarpous, 5-carpellate but becoming  $\pm$  10-locular by the intrusion of incomplete to complete false septa, the true septa sometimes ciliate, ovules 2 in each carpel, pendulous,



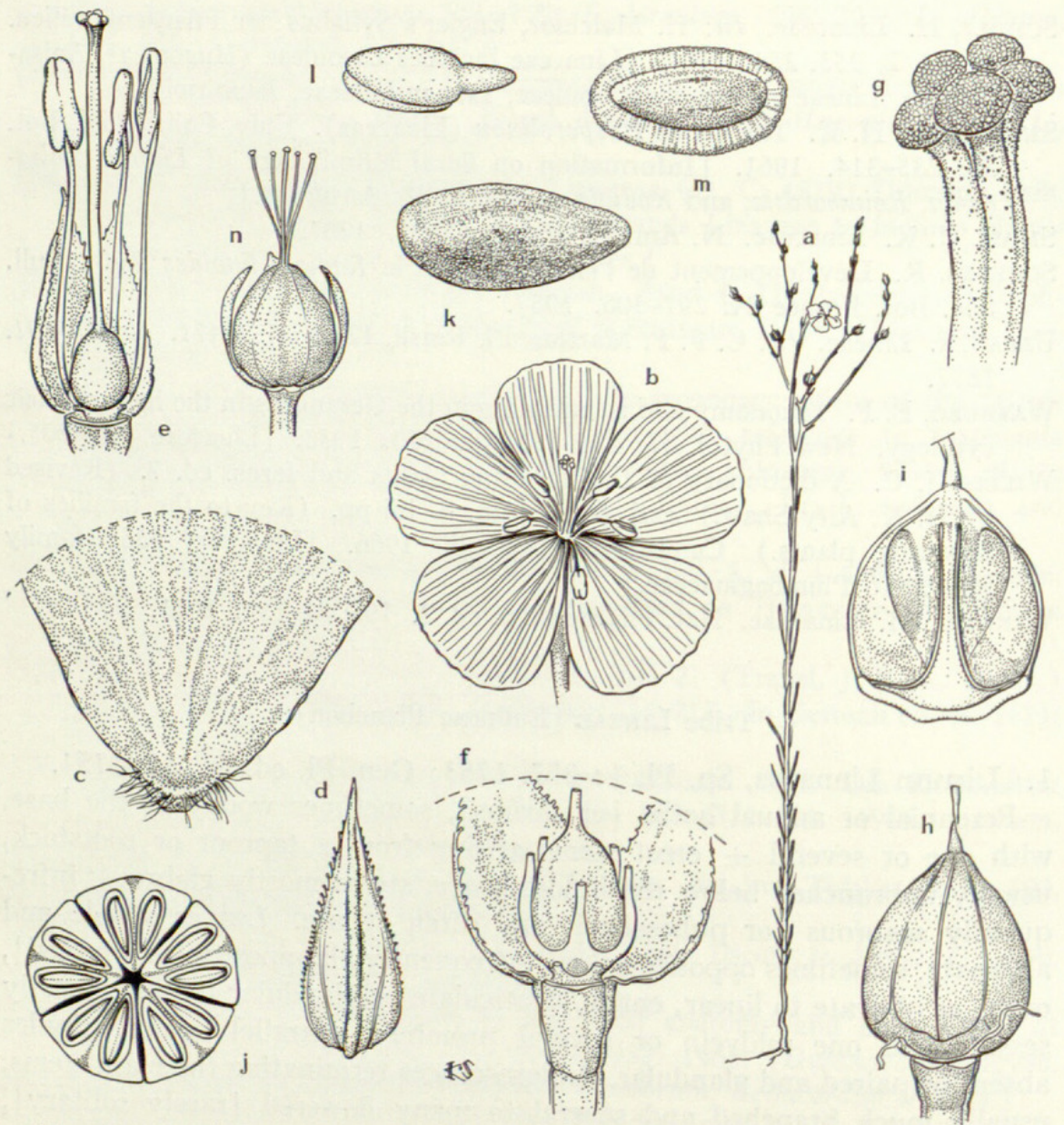


FIGURE 1. *Linum*. a-m, *L. Carteri* var. *Smallii*: a, plant with flower and immature capsules,  $\times 1/4$ ; b, flower,  $\times 2$ ; c, adaxial surface of petal base showing pubescent ligule with small abaxial pouches visible near margins,  $\times 12$ ; d, abaxial surface of outer sepal,  $\times 6$ ; e, flower (petals, three sepals and two stamens removed),  $\times 5$ ; f, flower (petals, three sepals and upper androecium and gynoecium parts removed) to show staminal cup and bases of filaments, two petal attachment points below, and nectar gland between petal attachment points,  $\times 10$ ; g, free capitate stigmas, upper part of style pubescent,  $\times 20$ ; h, capsule with persistent style and filaments (the sepals deciduous) — note basal cartilaginous plate,  $\times 5$ ; i, vertical section of capsule showing complete, partly cartilaginous and partly membranaceous false septa, two seeds visible through showing five 2-seeded segments which dehisce between the false septa (black),  $\times 6$ ; j, semidiagrammatic cross section of immature capsule showing five 2-seeded segments which dehisce between the false septa (black),  $\times 6$ ; k, seed, surface scalariform,  $\times 10$ ; l, embryo,  $\times 10$ ; m, moistened seed surrounded by striated mucilage,  $\times 6$ . n, *L. floridanum* var. *floridanum*: nearly mature capsule with persistent sepals (two removed) and distinct styles, a cartilaginous plate lacking,  $\times 6$ .

axile, epitropous. Fruit a septidial capsule, often beaked, dehiscing into 10 one-seeded or 5 two-seeded segments, the latter type with triangular



cartilaginous plates at the bases, usually dehiscing first between the false septa, rarely indehiscent; seeds sometimes retained within the capsule segments. Seeds compressed, smooth or slightly scalariform, mucilaginous when moistened; endosperm formation of the Helobial type, copious, scanty or absent in the mature seed; embryo straight. Embryo sac development of the Polygonum type, embryo development of the Solanad type. (Including *Cathartolinum* Reichenbach.) LECTOTYPE SPECIES: *Linum usitatissimum* L.; see J. K. SMALL, N. Am. Fl. 25: 67. 1907. (Ancient Latin name for flax and linen.) — FLAX.

A genus of 150–225 species widely distributed in temperate and subtropical regions, particularly in the Northern Hemisphere. Major centers of distribution are the Mediterranean region, the Balkan Mountains, Anatolia, the southwestern United States and Mexico, and the Coastal Plain province of the eastern United States. About 41 species occur in North America. In our area about fifteen species and seven varieties represent three major groups characterized by yellow, white, or blue flowers. The genus has not been examined on a world-wide basis since 1931, and the subgeneric classification is in need of re-evaluation, particularly the relationships between the North American species and those of South America, South Africa, and the Mediterranean region.

All species indigenous to our area belong to the “yellow-flowered” group, which is further characterized by small to medium-sized flowers, capitate stigmas, glands on all or the inner sepals, short pedicels, and all or at least the upper leaves alternate. These species are often placed in section CATHARTOLINUM (Reichenb.) Griseb., but are distinct and more closely related to the South American and Old World species referred to section LINASTRUM (Planchon) Reiche. These North American species, along with *Linum catharticum* L., were treated in the genus *Cathartolinum* Reichenb. by Small, who set up eight infrageneric units of undesignated rank, although some have considered them sections. Rogers and Harris have refined this scheme and recognize only five “species complexes” or “groups.”

The *Linum Schiedeanum* complex, characterized by perennial habit, usual presence of stipular glands, persistent and glandular-toothed sepals, staminodia alternating with petals, essentially distinct styles, and capsules separating into ten one-seeded segments, includes fifteen species, with the greatest diversity in east-central Mexico. One member of the complex, *L. arenicola* (Small) Winkler,  $2n = 36$ , distinguished from other species in our area by its separate styles and prominent stipular glands, is endemic to the pine woodlands southwest of Miami, Florida, and on the western Florida Keys. It is closely related to *L. rupestre* (Gray) Engelm. ex Gray,  $2n = 36$ , of Texas, Mexico, and Guatemala, and *L. scabrellum* Planchon,  $2n = 72$ , of central Mexico. *Linum bahamense* Northrop,  $2n = 68$ , known from five islands in the Bahamas, is evidently more closely related to a group of central Mexican species than to *L. arenicola*.



The perennial *Linum virginianum* complex, comprising seven species and distinguished by the capsule separating into 10 one-seeded segments, absence of staminodia, persistent sepals with glandular teeth present only on the inner sepals or absent, distinct styles, and absence of stipular glands, is largely confined to the eastern half of the United States. *Linum intercursum* Bickn.,  $2n = 36$ , with capsules ovoid and pointed at the apices, the septa ciliate, and the false septa clearly incomplete, occurs in the semishade of oak or pine woods along the Coastal Plain from Massachusetts south to the Carolinas and inland to Tennessee, northern Georgia, and Alabama; an isolated population is found in northwestern Indiana. Distinguished by subglobose capsules with rounded apices, nonciliate septa and inner sepal margins with conspicuous stalked glands, *L. medium* (Planchon) Britton var. *texanum* (Planchon) Fern. (*L. Curtissii* Small),  $2n = 36$ , is widespread in the East and also occurs in the Bahamas. The tautonymic variety,  $2n = 72$ , with thicker and wider leaves, is largely confined to the shores of the eastern Great Lakes. Particularly variable in southern Florida, this species needs further study. *Linum virginianum* L.,  $2n = 36$ , has small subglobose capsules with umbilicate apices, sparsely ciliate septa, complete false septa, early dehiscent capsules which leave many specimens without fruit, and sepals glandless or with inconspicuous sessile glands. It is widespread in open woods of the northern and eastern United States, becoming infrequent in the southern Atlantic Coastal Plain. Closely related to the two preceding species, *L. striatum* Walt.,  $2n = 36$ , is distinguished by its predominantly opposite leaves,  $\pm$  elongate paniculate inflorescences, nonciliate septa, and glandless sepals. Ranging from eastern Texas and northern Florida to southeastern Missouri and eastern Massachusetts, with several collections from western Michigan, *L. striatum* is largely restricted to unglaciated regions. Occurring on the Coastal Plain from North Carolina to Louisiana and Florida, *L. floridanum* (Planchon) Trel. has mostly alternate leaves and capsules to 3 mm. long with nonciliate septa. Varietas *floridanum* (*L. macrosepalum* (Small) Winkler, *L. jamaicensis* (Small) Fawcett & Rendle),  $2n = 36$ , has broadly ovoid capsules suffused with purple, and var. *chrysocarpum* C. M. Rogers,  $2n = 36$ , has yellowish ovate capsules. Questionably distinct from the latter variety, known only from the type locality near Mobile, Alabama, and possibly now extinct, *L. macrocarpum* C. M. Rogers is distinguished from *L. floridanum* by the larger capsules (to 3.8 mm. long) with sparsely and inconspicuously ciliate septa. *Linum Westii* C. M. Rogers,  $2n = 36$ , known only from two locations in northern Florida and one in northern Georgia, has predominantly opposite leaves and subglobose capsules with abruptly pointed apices and nonciliate septa.

The *Linum sulcatum* "complex" includes only *L. sulcatum* Riddell,  $2n = 30$ , a common annual species of prairies and fields in the central and eastern United States. It resembles plants of the *L. Schiedeanum* complex in fruit shape and structure, persistent sepals and floral pigmentation, while the thick-walled polyporate pollen and basic chromosome number



of 15 are characteristic of the *L. rigidum* complex. Rogers (1969) suggests that although "it is perhaps unlikely that *L. sulcatum* is on a direct line of evolution connecting the *L. Schiedeanum* and *L. rigidum* complexes, . . . plants resembling *L. sulcatum* may have served as the link between the otherwise very distinct *L. Schiedeanum* and *L. rigidum* complexes." In our area, only *L. sulcatum* has basally united styles and all five sepals glandular-toothed and persistent. Certain collections from the Southeast with dark herbage and racemose inflorescences are sometimes segregated as var. *Harperi* (Small) C. M. Rogers (*L. Harperi* Small).

Typical members of the annual *L. rigidum* complex have capsules separating into five 2-seeded segments, no staminodia, sepals deciduous and at least the inner glandular-toothed, and styles united nearly to the summit. The group is composed of ten species, mostly of the southwestern United States and northern Mexico; two tetraploid populations are endemic to southern Florida, and at least three species occur in the extreme western part of our area. The Florida populations have been considered to be either varieties of *L. rigidum* Pursh,  $2n = 30$ , or a distinct species. Rogers (1968a), drawing on the biosystematic work of Mosquin & Hayley, treated the populations with puberulent or scabrous stems, stipular glands, petals 9–11 mm. long, and found only in the pinelands southwest of Miami as *L. Carteri* Small var. *Carteri*,  $2n = 60$ . The other populations in Dade, Collier, and Monroe counties with  $\pm$  glabrous stems, stipular glands usually lacking, and petals 11.5–17 mm. long were identified as *L. Carteri* var. *Smallii* C. M. Rogers,  $2n = 60$ . *Linum Carteri* is most closely related to *L. rigidum* var. *Berlandieri* (Hooker) Torrey & Gray,  $2n = 30$ , with reddish pigment in the petals and thinner-walled capsules, occurring from southern Texas to eastern Colorado, northern Kansas, and western Arkansas and Louisiana. *Linum alatum* (Small) Winkler (*L. marginatum* Small),  $2n = 30$ , with unique glandular-toothed sepals with scarious margins, is largely confined to southern Texas and adjacent Tamaulipas, with one collection labeled "s.w. La." Another Texan species extending into our area in Louisiana is *L. imbricatum* (Raf.) Shinners (*L. multicaule* Hooker ex Torrey & Gray),  $2n = 30$ , with fringed glandless sepals and sparsely ciliate upper leaves.

The *Linum neo-mexicanum* complex is similar to the *L. Schiedeanum* complex, but staminodia are absent, and the base chromosome number is 13. None of the three species in this complex from the southwestern United States and northern Mexico approaches our area.

The "white-flowered" group, section CATHARTOLINUM (Reichenb.) Griseb., includes only *Linum catharticum* L.,  $2n = 16$ . This delicate annual has numerous features in common with the "yellow-flowered" group, but the observations of Rogers and Sharsmith indicate that it is not closely related to the flaxes indigenous to North America. This widely distributed European species is established in Nova Scotia and Newfoundland with scattered locations west to Michigan and south to Pennsylvania. No other species in the region has small white flowers and opposite leaves. S. F. Gray



placed *L. catharticum* in his CHAMAELINUM, but the subgeneric category of this taxon is uncertain (cf. Brizicky, Taxon 18: 650. 1969); the name predates Grisebach's sectional combination.

The predominantly European "blue-flowered" group, section LINUM (*Eulinum* Griseb.), with medium to large flowers, linear to capitate stigmas, glandless sepals, long pedicels, all leaves alternate, and stipular glands absent, has only one or two species indigenous to the New World. Widespread in western North America, *L. Lewisii* Pursh,  $2n = 18$ , is sometimes cultivated in the East and has been reported from Cave Mountain, West Virginia (Allard). Plants with sepals less than 5 mm. long are sometimes segregated as *L. pratense* (J. B. S. Norton) Small,  $2n = 18$ . This variable complex has been considered conspecific with the European *L. perenne* L.,  $2n = 18, 36$ , the only consistent difference between them being that *L. Lewisii*, like all the New World species, is homostylous, while *L. perenne* is heterostylous. The latter species is sometimes encountered as a garden escape. Other Old World species introduced to the eastern United States are the red- or pink-flowered *L. grandiflorum* Desf.,  $2n = 16$ , a native of Algeria, and *L. usitatissimum* L. (*L. humile* Mill.),  $2n = 30$ , flax. One of the oldest cultivated plants, flax is grown both for the fibers from which linen is made and for the seeds which yield linseed oil.

Section CLIOCOCCA (Bab.) Planchon contains only the South American *L. selaginoides* Lam., and is perhaps best regarded as a distinct genus. The Old World sections, SYLLINUM Griseb. and DASYLINUM (Planchon) Juz., do not occur in North America.

Rogers (1969) suggests a monophyletic origin for the North American yellow-flowered flaxes with the *L. Schiedeanum* complex, which includes the most primitive members of the group, giving rise to three lines — the *L. virginianum* complex, the *L. neo-mexicanum* complex, and the *L. sulcatum* and *L. rigidum* complexes. East-central Mexico, the center of distribution for the *L. Schiedeanum* complex, is postulated as the region of establishment and diversification of the North American yellow-flowered group. Rogers points out that some South African species are very similar to *L. Schiedeanum*, and preliminary evidence (personal communication) indicates similarities between the South American species and certain Mexican and African species.

A chemotaxonomic study of floral pigments in North American yellow-flowered Linums (Giannasi & Rogers) further emphasized the distinctness of the *L. rigidum* complex, since it possesses the  $\alpha$ -carotenoids leutin and its 5, 6-monoepoxide, while the other species complexes contain only the  $\beta$ -carotenoid violaxanthin. The distribution of the flavonoid pigments supports the presumed relationship between the *L. Schiedeanum* and *L. virginianum* complexes.

All species of *Linum* indigenous to North America are homostylous, while some Old World species are heterostylous. In some heterostylous species, such as *L. perenne*, both the filaments and styles are of different lengths while in others, such as *L. grandiflorum*, only the styles vary in length.



Charles Darwin first recognized that heterostyly is an out-breeding mechanism since the long-styled and short-styled forms are mostly self-sterile but cross-fertile; homostyled flowers are largely self-fertile. (See Baker's interesting paper for a misunderstanding between Darwin and Thomas Meehan, but also involving Asa Gray, about heterostyly and self-compatibility in *L. perenne* and *L. Lewisii*.)

The pollen morphology of *Linum* species is diverse. Aperture types are 3-, 4- or 6-colpate, pantocolpate and pantoporate. The tricolpate grains have been classified on the basis of aperture shape and size and the nature and texture of the nexine covering the colpi. The exine is thin, undulate or thick and bears surface processes that vary in size and shape. These processes may be monomorphic, dimorphic or polymorphic; in a few species the processes are united to form a tegillum which can bear suprategillar processes. The sexine shows a trend from a granular composition to the formation of distinct bacula. Ockendon found in the *L. perenne* group a correlation between aperture number and ploidy level, and between the morphology of the exine processes and the styler condition of the flower. Yermanos & Gill (1967) report that in eight species the pollen was 3-colpate in diploids and 4-colpate in their autotetraploids. To some extent pollen morphological trends follow the subgeneric classification of *Linum*. The thick-walled polyporate pollen of the *L. rigidum* and *L. sulcatum* complexes is evidently the most specialized in the genus.

The North American and European species of *Linum* are well known cytologically, and definite base numbers have been determined in certain sections and species complexes. Polyploidy and aneuploidy have occurred in most groups. Base numbers are: *Linum Schiedeanum* complex, 18, 31, 34; *L. virginianum* complex, 18; *L. neo-mexicanum* complex, 13; *L. sulcatum* and *L. rigidum* complexes, 15; section CATHARTOLINUM, 8; section LINUM, 9, 15; section LINASTRUM (Old World species) 8, 9, 10; section SYLLINUM, 14; section DASYLINUM, 6, 8; and *Linum monogynum* from New Zealand, reported as having  $2n = 84$ . Numerous older undocumented and doubtful counts have been excluded. The hybridization studies of Gill, Gill & Yermanos, and Mosquin & Hayley indicate that chromosomal rearrangements, particularly translocations, have played a major role in the evolution of *Linum* species.

Hybridization in nature is evidently rare, but has been reported in the *Linum rigidum* and *L. virginianum* complexes. Artificial hybrids have been produced in the *L. rigidum* complex and in both the *L. perenne* and *L. usitatissimum* groups of section LINUM.<sup>2</sup> Autotetraploids of the *L. perenne* group ( $2n = 36$ ) can hybridize with *L. usitatissimum* ( $2n = 30$ ). Haploid plants of the latter species have also been produced. There are numerous reports of unsuccessful hybridization attempts involving mostly Old World species.

<sup>2</sup> D. J. Ockendon (personal communication) has obtained a hybrid between *L. Lewisii* and *L. Leonii*, a homostylous member of the European *L. perenne* group, which did not flower.



One *Linum* hybrid cross is often used as an example of the requirement that the hybrid embryo, endosperm, and seed coat be mutually compatible. In the *L. perenne* ♀ × *L. austriacum* ♂ cross, the hybrid embryo develops normally but cannot sprout through the seed coat. If removed, it grows into a vigorous and fertile F<sub>1</sub> hybrid. In the reciprocal cross, the embryo is inhibited and will not develop unless dissected from the seed and placed in a nutrient solution.

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