

THE GENERA OF PORTULACACEAE AND BASELLACEAE
IN THE SOUTHEASTERN UNITED STATES ¹

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PORTULACACEAE A. L. de Jussieu, Gen. Pl. 312. 1789, "Portulaceae,"
nom. cons. (PURSLANE FAMILY)

Fleshy or succulent herbs or subshrubs [shrubs or rarely small trees], with erect to procumbent branches, reproducing vegetatively by means of rhizomes, stolons, or axillary bulblets. Roots fleshy, basal or adventitious, fibrous, tuberous, cormose, or plant with a simple to branched taproot. Leaves alternate, opposite, or in basal rosettes, the blades entire, cylindrical (or nearly so) to flat; stipules scarious, fimbriate, of tufted hairs, or absent. Inflorescence terminal or lateral, basically cymose but often appearing racemose or paniculiform, or flowers solitary in the axils. Flowers perfect, regular, inconspicuous or often showy, erect, spreading or nodding. Perianth biseriate (or uniseriate). Sepals (involucral bracts?) 2 [4-8], imbricate, \pm equal, free or basally connate, deciduous or persistent. Petals (tepals?) 4-6 (sometimes 2 or 3), free or basally connate, hypogynous or perigynous, often ephemeral. Stamens few to many, alternate with and/or opposite the petals, free or inserted on the corolla base; filaments filiform; anthers 2-loculate, dehiscing longitudinally and introrsely. Gynoecium 2-9-carpellate, syncarpous; styles as many as the carpels, \pm united, rarely simple, with linear to capitate stigmas; ovary superior to half-inferior, or inferior, unilocular; ovules many to few [-1], sometimes on long, ascending funiculi, anatropous or amphitropous; placentation free-central or basal, the placenta 2-9-parted or 1. Fruit a pyxis or capsule [rarely an achene], dehiscence

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circumscissile, or by 3 longitudinal valves. Seeds one to many, \pm round-reniform, flattened. Seed coat often crustaceous, sometimes arillate, smooth or variously sculptured (rugulate, granulate, muricate, tuberculate). Embryo curved to annular, enclosing the abundant mealy endosperm; cotyledons (1-)2 [rarely 4]. TYPE GENUS: *Portulaca* L.

A small family of 15 to 31 genera with centers of distribution in western North America, southern South America, and South Africa, but extending to eastern Siberia, Australia, New Zealand, and Madagascar. Many of the genera are small or monotypic and restricted in distribution. Only a few have more than about a dozen species (*Anacampseros*, *Calandrinia*, *Claytonia*, *Montia* sensu lato, *Portulaca*, *Talinum*). Interesting patterns of distribution are evident in several genera: *Portulaca* and *Talinum* have attained wide distributions in the tropics and subtropics of both hemispheres; *Calandrinia* has centers of development in western North America, South America (Chile), and Australia; and *Montia*, which is principally boreal in range, is represented in far flung areas of the Southern Hemisphere.

De Candolle and Bentham & Hooker viewed the family in a narrow sense, essentially as it is regarded today, including 12-15 genera but no subfamilial categories, while Fenzl (followed by Endlicher) took a much broader view of the family, recognizing seven tribes and including many genera now placed in such related families as Basellaceae, Aizoaceae, and Molluginaceae. Similarly Baillon established three series within his Portulacaceae: Portulaceae, Aizoideae, and Mollugineae.

The system of the family established by Franz, which was based on a wide range of morphological and anatomical characteristics, has been followed with modification by Pax & Hoffman and by Eckardt. The genera of Basellaceae originally included by Franz were removed, as were some of doubtful affinity (*Hectorella* Hook. f., and *Lyallia* Hook. f. which have recently been established as a family Hectorellaceae). Of the two subfamilies now recognized in the Portulacaceae, the smaller Montioideae Franz includes only *Montia* L., *Claytonia* L., and the monotypic Chilean *Wangerinia* Franz. Rydberg and, more recently, Nilsson have split eight segregate genera out of the *Claytonia-Montia* complex, but these are not universally recognized. The large subfamily Portulacoideae consists of about 13 genera arranged in two tribes, each with two subtribes. Of primary interest in our area are tribe Portulaceae, subtribe Portulacinae, containing only *Portulaca* L., and tribe Calandrinieae, subtribe Calandrininae, containing *Talinum* Juss. and four related genera.

The Portulacaceae share several features with other Centrospermae, including the presence of betacyanins (betalains) in place of anthocyanins, curved to annular peripheral embryos, and basal placentation in a compound ovary. The family is considered closely related and possibly ancestral to the Basellaceae through such features as intraxylary phloem (weakly developed in some Montioideae), uniovulate ovaries in ad-

vanced genera, a tendency toward unisexual flowers, and similar floral plans. Relationships to the Caryophyllaceae, Chenopodiaceae, and Amaranthaceae are seen in the morphology and anatomy of the seeds, and to the Aizoaceae (through *Sesuvium*), from which the Portulacaceae differ principally in characteristics of floral organization and the lack of well-developed anomalous secondary growth. A relationship to the Primulaceae, advanced particularly on embryological evidence (Guignard, cf. *Talinum*), has found little support.

Embryological studies in a few of the better known genera reveal anatropous to amphitropous, crassinucellar ovules in which the inner of the two integuments forms the micropyle. A Polygonum-type embryo sac is formed from the chalazal cell of a linear tetrad. Endosperm formation is initially nuclear, later becoming entirely cellular (or only partially so in *Portulaca oleracea*). Both solanad (in *Portulaca*) and caryophyllad (in *Claytonia*) types of embryo development occur in the family, and polyembryony is reported in *Portulaca oleracea*. Anthers are tetrasporangiate, and pollen grains are generally three celled (rarely two celled) when shed. Embryos with only one cotyledon are reported in *Claytonia virginica* L., while four cotyledons have been found in *Anacampseros lanceolata* (Haw.) Sweet.

The pollen morphology of the family is diverse, ranging from tricolpate to rugate (with several to many colpi distributed evenly over the surface), to forate (with many evenly distributed round pores). The surfaces of the grains usually bear small spines (Erdtman, Franz).

On the basis of studies of floral development and anatomy the perianth and androecium in the family have been variously interpreted as biseriate or uniseriate, while the pentamerous floral plan evident in many genera has been considered as either basic, or derived from a basically trimerous (Payer, Eichler) or bimerous (Sharma) pattern. Thus the two (to several) sepals are considered by some as involucral bracts, and the petals as tepals (cf. Pax & Hoffman, 237, 238). In the light of conflicting interpretations, as well as for taxonomic convenience, the traditional terms sepal (calyx) and petal (corolla) are used here.

The ovary has been shown in several genera (*Anacampseros*, *Calandrinia*, *Montia*, *Portulaca*) to be septate early in ontogeny. The septa are lost as the ovary develops, resulting in free-central or basal placentation, with the ovules arranged in one to several groups, each group presumably representing a lost locule. Anatomical data for the family are fragmentary and not particularly distinctive. The intraxylary phloem reported to occur in *Montia* and its allies is not always well defined. A petiolar vascular supply of a single bundle has been reported in species of *Portulaca* and illustrated in the monotypic genera *Mona* O. Nilss. and *Neopaxia* O. Nilss.

Chromosome counts available for some of the better known genera (*Calandrinia*, *Claytonia*, *Lewisia*, *Montia*, *Oreobroma*, *Portulaca*, *Talinum*) show diploid numbers ranging from $2n = 8$ to ca. 191, in either dysploid or euploid series, suggesting a rather complex evolution through

the development of polyploidy followed by the formation of aneuploids.

The family is of only minor economic importance. Species of *Anacampseros*, *Calandrinia*, *Lewisia*, *Montia*, *Portulaca*, and *Talinum* are grown as ornamentals. A few species are used as vegetable or salad "greens" or in folk medicine for various internal complaints. Species of *Portulaca* and *Calandrinia* have proven poisonous to livestock in the southwestern United States and Australia due to high concentrations of oxalic acid.

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KEY TO THE GENERA OF PORTULACACEAE

General characters: low, succulent to suffrutescent herbs with simple, fleshy, flat to terete, alternate, opposite, or basal leaves; stipules scarious, or of tufted hairs, or absent; stems erect to procumbent; inflorescence axillary, terminal, or scapose, diffuse to congested, basically cymose but often appearing racemose or paniculate; flowers complete, small to large, regular, hypogynous to epigynous; sepals 2; petals usually 5 (4–6); stamens 5–100, alternate or opposite the petals, free or fasciculate; ovary 2–9-carpellate, unilocular, with basal placentation; ovules few to numerous, ascending; fruit a 3- to many-seeded capsule, circumscissile or valvate.

- A. Stipules present, scarious or lacinate, or of tufts of hair; inflorescence a terminal head or congested helicoid cyme, usually surrounded by a whorl of leaves; ovary half-inferior to inferior; stamens few to many, perigynous; fruit a circumscissile capsule; ovules and seeds numerous, stalked. 1. *Portulaca*.
- A. Stipules absent; ovary superior; fruit a 3-valved capsule.
 - B. Leaves cauline or basally tufted on stems from tuberous roots or rhizomes; inflorescence a terminal peduncled cyme, or flowers axillary, solitary; stamens 5–100, alternate with or opposite the petals; ovules and seeds numerous. 2. *Talinum*.

- B. Leaves few to many from a deep-seated corm; flowering stem scapose, bearing a single pair of opposite leaves; inflorescence a loose raceme; stamens 5, opposite the petals; ovules and seeds (3-)6. . . 3. *Claytonia*.

Subfamily PORTULACOIDEAE [Franz]

Tribe PORTULACEAE [Franz]

Subtribe *Portulacinae* [Franz]

1. *Portulaca* Linnaeus, Sp. Pl. 1: 445. 1753; Gen. Pl. ed. 5. 204. 1754.

Low, annual or perennial herbs with erect, ascending or procumbent, fleshy or suffrutescent, sometimes reddish stems from fleshy or fibrous roots. Leaves alternate to subopposite, terete, subterete, or flat, entire, often congested in an involucre about the flowers. Stipules scarious or reduced to tufts of hairs, rarely absent. Flowers erect, sessile to subsessile, solitary and axillary or few in terminal heads or compact helicoid cymes. Sepals 2, opposite, the abaxial larger than the adaxial, united below. Petals 4-6, free or basally connate, gelatinous-deliquescent after flowering. Stamens 6-40 [4-100], inserted perigynously; filaments usually pubescent below; pollen polyrugate. Carpels as many as the style branches; styles short, 2-9-parted [rarely simple]; ovary semi-inferior to inferior, globose to obovate, plurilocular below to unilocular above; ovules numerous, amphitropous, on a simple or branched free-central placenta. Capsule membranaceous, chartaceous, circumscissile. Seeds numerous, reniform to cochleate; seed coat smooth or variously sculptured, in ours granular to stellate-tubercular or -echinate, brown to black or gray. Embryo peripheral, annular, surrounding the endosperm. (Including *Portulacca* Haw.). LECTOTYPE SPECIES: *P. oleracea* L.; see Britton & Brown, Illus. Fl. No. U.S. ed. 2. 2: 39. 1913. (Name probably derived from Latin, *portula*, a small gate or door, in reference to the calyptra of the capsule.) — PURSLANE.

A genus of about 100-125 species widely distributed in tropical, subtropical, and temperate regions of the world. Eight to ten species occur in our area.

In the early literature the North American species were generally grouped in two or three subgeneric categories of undesignated rank, based on either leaf shape (flat or cylindrical) or the presence or absence of pubescence. Wilson (N. Am. Fl.) recognized 23 species, but no subgeneric groupings. In Poellnitz's provisional monograph of the genus (1934), 104 species were disposed in two subgenera, one with two sections and eight subsections. For lack of comparable material, Poellnitz could not key all of the species to their appropriate subsections, but each is described and discussed in detail. The American species have since been monographed by Legrand, who recognized six subgenera, of which three, containing about 62 species, occur in the Western Hemisphere. All



FIG. 1. *Portulaca*. a-h, *P. oleracea*: a, flowering and fruiting branch, $\times 1/2$; b, flower in semidiagrammatic vertical section to show perigynous floral organs and basal placentation, $\times 6$; c, nearly mature fruit inclosed above by accrescent sepals — note bracteole at base of ovary, $\times 3$; d, same, with perianth removed to show top of ovary with constricted apex and persistent style, $\times 5$; e, base of circumscissile fruit after dehiscence, with persistent funicles from basal placenta, $\times 5$; f, upper part of fruit after dehiscence, with mature accrescent sepals, included remains of gelatinous-deliquescent petals and stamens (not visible), and top of pericarp, $\times 5$; g, seed, $\times 25$; h, embryo, oriented as in seed, $\times 25$. i-m, *P. pilosa*: i, branches with terminal flower and fruit, $\times 1/3$; j, flower bud just before anthesis to show sepals connate at base, $\times 8$; k, flower with forward petals depressed to show stamens and style, $\times 4$; l, withered perianth (sepals and petals, stamens not visible) adhering to upper part of circumscissile pericarp, $\times 10$; m, base of fruit after dehiscence, showing four ascending basal placentae, one bearing a seed, $\times 10$.

of our species belong in subgenus *PORTULACA*. Several species of the southern United States (*P. coronata*, *P. neglecta*, *P. parvula*, *P. phaeosperma*, *P. retusa*) fall into synonymy through the expansion of species limits and ranges. Our species are discussed here under their older, more familiar names, followed by their disposition in Legrand's system.

Four flat-leaved species, with carinate to subcarinate sepals, and usually with yellow flowers, have been described in our area. *Portulaca oleracea* L. (pusley, pursley, purslane, pigweed), $2n = 18, 45, 52$, and 54 , is a common procumbent weed of waste places, fields, and cultivated areas, with almost world-wide distribution. Its flat, fleshy, obovate-cuneate to spatulate leaves; strongly keeled sepals; yellowish, apically notched petals; and black, granulate seeds are characteristic. Birds have been observed to eat the seeds and may have played a role in the widespread distribution, but its origins are lost in antiquity (see discussion in De Candolle). West of the Mississippi River in Arkansas, Kansas, and Missouri, the place of *P. oleracea* may be taken by *P. neglecta* Mack. & Bush, which differs in its upright ascending habit; larger size; larger, broader, and thinner leaves; more numerous stamens; muricate seeds; and different flowering time. Where the two occur together, *P. oleracea* flowers open at about 9:30 A.M., while those of *P. neglecta* open at about 7:40 A.M. Poellnitz suggested that *P. neglecta* may be only a variety of *P. oleracea*. The closely related *P. retusa* Engelm., ranging from Arkansas and Missouri to Arizona and Utah, is similar to *P. oleracea* in its procumbent habit, but differs from both of the above in its thinner, retuse leaves; more slender habit; smaller flowers; and echinate-tuberculate seeds. All three species were recognized by Poellnitz, but Legrand reduced *P. neglecta* and *P. retusa* to synonymy under *P. oleracea*.

The fourth flat-leaved species, *Portulaca coronata* Small (including *P. lanceolata* Engelm.,² not Haw.), inhabits granite outcrops and sandy soils in South Carolina (very rare), Georgia, and Mississippi. In the southwestern United States it ranges from the granitic region of western Texas to lower California. The species is especially marked by the flaring, corona-like rim surrounding the ovary just below the line of dehiscence, as well as by its subcarinate sepals, lanceolate leaves, yellow (to orange or red-tinged) petals with acute tips, and gray seeds. According to McVaugh it is often found growing with *P. Smallii* on the granitic flat-rocks of the Southeast, but in slightly more shaded conditions. In Legrand's system, *P. coronata* becomes a synonym of *P. umbraticola* HBK., which ranges to Cuba, Central America, and much of South America.

The six remaining species of the area have more or less cylindrical leaves, dorsally rounded sepals, and, for the most part, characteristic pubescence of the leaf axils and inflorescences. *Portulaca pilosa* L., $2n =$

² According to Fosberg, *P. coronata* Small is the only name available for *P. lanceolata* Engelm., since *P. lanceolata* Haw. (1803), antedating Engelmann's name by 47 years, was validly published for a species now referred to *Anacampseros*. In his original description of *P. coronata* (1896) Small compared it with *P. lanceolata* Engelm. Wilson (1932) considered *P. coronata* a synonym of *P. lanceolata*, but Poellnitz (1934) treated the two as different species with very different seeds.

16, has conspicuous stipules of tufted whitish hair in its leaf axils, and whitish to brownish hairs around the flowers. Its small, obovate, notched petals are usually purplish pink, with a small mucronate tip at the base of the notch. It is reported on sandhills and in dry, sandy soils of woods, roadsides, and cultivated grounds from the Carolinas to Florida, and westward to Texas, as well as in the West Indies, Mexico, and Central and South America.

Portulaca Smallii P. Wils., $2n = 16$, has only slightly tufted axils and pale brown hairs in the inflorescence surrounding inconspicuous flowers with deep lavender to pure white petals. The species is abundant in the shallow soils of surface depressions and particularly of the marginal ecotone of granite flat-rocks in North Carolina and in Georgia to DeKalb and Pike counties (but not in South Carolina or Alabama). This species is very closely related to, and possibly derived from, *P. pilosa*, the two being distinguished chiefly by the endemism of the former and the greater overall size and larger number of stamens in the latter (Cotter & Platt). *Portulaca suffrutescens* Engelm. is a linear-cylindric-leaved suffrutescent perennial with copper or yellow-brown (buff), notched petals, and black, rounded-tuberculate seeds. It ranges from Arkansas to Arizona and Mexico. *Portulaca grandiflora* Hook. (rose-moss, moss-rose), $2n = 18, 36$, a native of South America, has escaped cultivation and become widely naturalized in North America and Europe. Its flowers, 2–5 cm. in diameter, are larger than those of any of the native species and have 40 or more stamens. Flower color ranges from white to pink, red, orange, salmon, or yellow. Its cylindric leaves also have hair-tufted axils.

Portulaca parvula Gray, with ascending branches, copiously hairy nodes, nearly cylindrical leaves, yellow, orange, or copper petals (red, according to Wilson and Poellnitz), and stipitate capsules, occurs from western Missouri and Arkansas westward to Colorado, California, and southward into Mexico. This species was redefined by Johnston, who segregated the purple-flowered plants included in it by Gray as *P. mundula* I. M. Johnston (Mexico to Oklahoma, Kansas, and Missouri). Such plants have also been included under *P. pilosa* L., but Johnston considered that species attributable to specimens from Curaçao, and not conspecific with the plants of Mexico and the southwestern United States. Legrand, however, reduced *P. mundula* to varietal status under *P. pilosa* and the remainder of *P. parvula* to synonymy under *P. halimoides* L.

Portulaca phaeosperma Urb. has small yellow flowers surrounded by brownish to whitish hairs and nearly cylindrical leaves with inconspicuously tufted axils. It is found in sand-dunes, scrub, and shell-mounds of southern peninsular Florida and the Keys, southward throughout the West Indies to Yucatán and Curaçao. According to Legrand, *P. phaeosperma* is synonymous with *P. rubricaulis* HBK.

Chromosome counts indicate that basic numbers in *Portulaca* may be $x = 4, 5, 8$, and 9 . At least two chromosome series are present, with $2n = 8, 16$, and 48 in one, and $2n = 18, 36, 45, 54$, and 108 in the other. The Japanese 'Jewel' strain of *P. grandiflora* is reported to have

$2n = 10$, while *P. quadrifida* L. has $2n = 50$ (Bouharmont). These data indicate that chromosomal duplications or deletions, concurrent with polyploidy, have played an important part in the evolution of the genus. There are no records of natural interspecific hybridization, and attempted reciprocal crosses (involving *P. grandiflora* and *P. marginata* HBK. in one case, *P. grandiflora* and *P. grandiflora* 'Jewel' in the other) have failed. Bouharmont reports very irregular meiosis in an artificial hybrid between the African *P. centrali-africana* R. E. Fries, $2n = 108$, and *P. Kermesiana* N. E. Br., $2n = 108$. He also found chromosomes to be much larger in *P. foliosa* and *P. grandiflora* than in other species.

Ikeno's efforts to explain color variation in *Portulaca grandiflora* in terms of simple Mendelian principles was only partially successful. Blakeslee attributed various changes and reversions in habit and in petal coloration (sectorial and periclinal chimeras, stripes and spots) to spontaneous vegetative mutations. Other cytological peculiarities include the presence of polyploid cells ($2n = 36, 72$) in adventitious roots of *P. grandiflora* and *P. foliosa* (Bouharmont) and the formation of up to 12 secondary cells of varying size within the primary epidermal cells of *P. grandiflora* (Czeika). The presence of betacyanins has been confirmed in *P. grandiflora*, *P. oleracea*, and *P. pilosa* (Wohlpart & Mabry).

The opening and closing of flowers in response to light intensity and temperature have been studied by several workers. Iwanami *et al.* concluded that temperature controls flowering time in *Portulaca grandiflora*, while Cotter & Platt suggest that light is the controlling factor in *P. Smallii*. Lebrun found that three vegetative races of *P. quadrifida* from different sources show a divergence of behavior under the same conditions appreciably corresponding to the difference in local times of their places of origin. Similarly, offspring of an artificial hybrid between *P. centrali-africana* and *P. Kermesiana* were intermediate in their behavior to those of the two parents.

On the basis of floral vascular anatomy Sharma suggests that the pentamerous floral condition in *Portulaca* is derived from a basically bimerous plan, with a biseriate (rather than uniseriate) perianth, and a modified androecium consisting basically of two cycles. The ovary in *Portulaca* is generally considered to be semi-inferior to inferior, but Soetiarso & Ball have demonstrated that in *P. grandiflora* all the floral organs arise on the flanks of the floral apex as in a hypogynous flower, and that all except the carpels are then lifted on the lip of the floral cup. They conclude that perigyny is an ontogenetically late development in *P. grandiflora* and may be interpreted as a derived condition.

The anthers of *Portulaca tuberosa* and *P. grandiflora* have binucleate tapetal cells and binucleate pollen grains at anthesis, but *P. oleracea* has multinucleate tapetal cells and trinucleate grains. Seed coat morphology may be an important specific character, but is not necessarily consistent in all species. Kowal states that in both *P. oleracea* and *P. sativa* L. seeds occur with sculpturing of two forms and that a particular specimen may produce seeds of one or both types.

Several species of the genus are grown as garden ornamentals. *Por-*

tulaca oleracea is reported in Jamaican folk-lore to be of value in the treatment of cardiovascular diseases (possibly due to the presence of (—)-noradrenaline in relatively high amounts in the fresh plant tissues), as a diuretic, and as an antiscorbutic. It is also widely cultivated and used as a vegetable or salad-green, or as fodder for pigs. *Portulaca pilosa* is sometimes used as a diuretic, an emmenagogue, and as a stomach tonic. High oxalate or nitrate content in plants of *P. oleracea* and other species may prove toxic to livestock.

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Tribe CALANDRINIEAE Fenzl

Subtribe Calandrininae [Franz]

2. *Talinum* A. L. de Jussieu, Gen. Pl. 312. 1789, nom. cons. prop.

Annual or perennial, glabrous, succulent herbs, subshrubs [or shrubs], with simple or branched, short to elongate stems with fleshy, tuberous roots or rhizomes. Stems frequently terminating in wiry, short or long peduncles. Leaves alternate to subopposite or basally tufted, exstipulate, cylindrical or flattened, entire, fleshy. Inflorescence a terminal or axillary, wiry-peduncled cyme, or flowers sometimes solitary on short pedicels in the leaf axils. Sepals 2, deciduous or persistent. Petals 5, rarely more, free or connate at the base, often showy, purplish to red, pink, yellow, or white, ephemeral. Stamens 5–100, alternate with or opposite the petals or in fascicles opposite and basally affixed to the petals; filaments slender, sometimes colored. Style elongate, deeply 3-parted to subcapitately lobed or capitate, equaling or exceeding the stamens; ovary superior, unilocular (at least above); ovules numerous, amphitropous, placentation free central. Fruit a unilocular many-seeded, chartaceous capsule, dehiscing loculicidally from the apex to the base by 3 valves. Seeds compressed, round-reniform, dull gray or shiny brown to black, smooth, striate, or tuberculate, distinctly to indistinctly arillate. Embryo peripheral, incompletely annular; endosperm starchy. (*Talinum* Adans., 1763, nom. superfl.; *Heli-anthemoides* Medic., *Phemeranthus* Raf., *Litanum* Nieuwl.) LECTOTYPE SPECIES: *T. patens* A. L. Juss., nom. illegit. = *T. paniculatum* (Jacq.) Gaertn., typ. cons. prop.; see J. E. Dandy, Taxon **18**: 465. 1969. (Origin of name obscure, said to be derived from the aboriginal name of an African species.) — FAME FLOWER.

A genus of about 50 species distributed in the tropical, subtropical, and temperate regions of both hemispheres, but best developed in North America (30–35 species), and particularly in Mexico (Rose & Standley).

The genus was last monographed by Poellnitz (1934) who recognized 47 species but found no basis for maintaining the three sections established by De Candolle (§ *Phemeranthus* Raf., with cylindrical leaves; § *Talinastrum* DC., with flat leaves; and § *Talinellum* DC., since transferred to *Calandrinia* HBK.).

Eight species are now recognized in our area, six wholly or partially east of, and two mostly west of the Mississippi River. Two flat-leaved species frequent the lowlands, forming erect, suffrutescent plants ranging

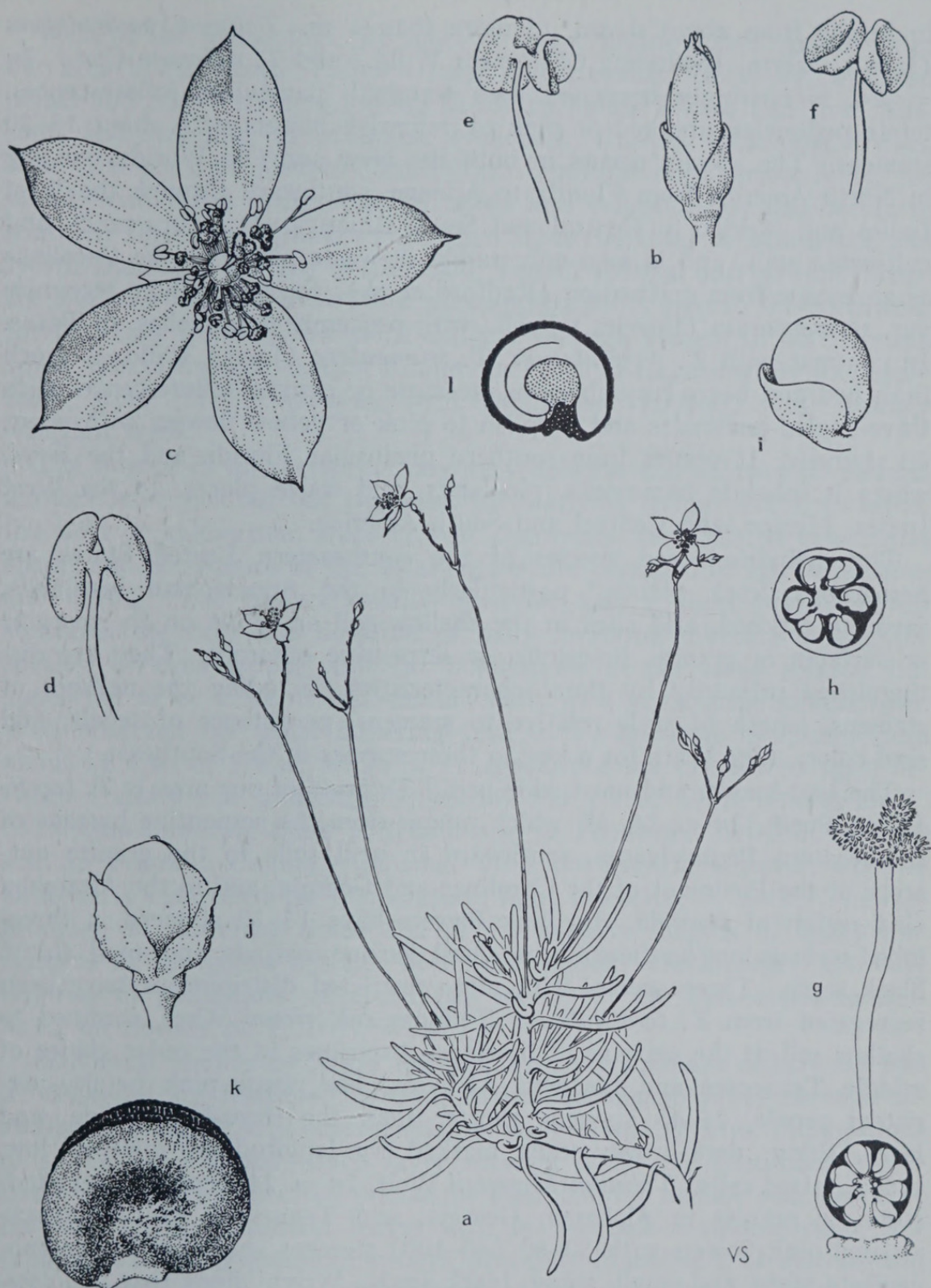


FIG. 2. *Talinum*. a-l, *T. calcaricum*: a. flowering plant, $\times 1/2$; b. flower bud, shortly before anthesis to show sepals, $\times 3$; c. flower, $\times 3$; d. stamen before anthesis, $\times 20$; e, f. two views of stamen after anthesis, $\times 20$; g. gynoecium with one side of ovary removed to show free-central placentation, $\times 10$; h. cross section of ovary showing placentation and remnants of septa, $\times 10$; i. lateral view of ovule at time of anthesis showing aril beginning to grow from funiculus, $\times 40$; j. fruit just before dehiscence, $\times 5$; k. seed with thin, tightly investing aril imperfectly developed (the two sides not meeting at midline of seed), $\times 25$; l. seed in section, the curved embryo surrounding endosperm (black stipples), diagrammatic, $\times 15$.

in height from about 6 dm. to more than 1 m. *Talinum paniculatum* (Jacq.) Gaertn. (including "*T. patens* Willd." and *T. reflexum* Cav.), $2n = 24$, is sparingly branched with terminal, paniculate inflorescences, terete peduncles, and red or pink to yellowish flowers with about 15–20 stamens. The species occurs in both the New and Old Worlds, ranging in North America from Florida to Arizona, southward through the West Indies and Mexico to Central and South America. It favors sandy and cultivated soils, and is seen only rarely in waste places in the Carolinas as an escape from cultivation (Radford *et al.*). Several authors recognize var. *sarmentosum* (Engelm.) Poell., with procumbent branches, in Texas. In contrast with *T. paniculatum*, *T. triangulare* (Jacq.) Willd. is much branched and bears corymbiform, racemose or cymose inflorescences with three-angled peduncles and purplish to pink or yellow flowers with about 30 stamens. It occurs from southern peninsular Florida and the Keys, where it inhabits hammocks, pinelands, and waste places, to the West Indies, Mexico, and Central and South America.

The cylindric-leaved species of the southeastern United States are herbaceous "rock plants," particularly in the Appalachian highlands, favoring exposed, arid sites in the shallow soil or debris on the margins or surfaces of granite, limestone, or serpentine outcrops. They are distinguished primarily by floral characteristics, including the number of stamens, length of style relative to stamens, persistence of sepals, and seed color. (See Ware for a key to these species in the Southeast.)

The best-known and most widespread *Talinum* of our area is *T. teretifolium* Pursh, $2n = 24, 48$, which ranges from the serpentine barrens of southeastern Pennsylvania, southward in acid soils to the granite outcrops of the Piedmont of the Carolinas and Georgia, and to the Altamaha Grit region of Georgia. Its pink flowers have 15–20 stamens, a three-lobed style as long as the stamens, small deciduous sepals, and small, shiny, black seeds. Three species with more restricted distributions have been segregated from *T. teretifolium*. *Talinum calcaricum* Ware, confined to shallow soil at the margins of limestone exposures in the cedar glades of middle Tennessee and northern Alabama, has purple-pink petals, persistent sepals, 25–45 stamens shorter than the three-lobed style, and large, shiny, dark-brown seeds marked by longitudinal rows of low, broad, raised cells. *Talinum Mengesii* Wolf, $2n = 24$, occurring on sandstone or granite in Alabama, Georgia, and Tennessee, has deciduous-sepaled pink flowers with 50–80 (40–100) stamens shorter than the subcapitate style, and small, shiny, black seeds. Wright finds that "*T. teretifolium* is replacing *T. Mengesii* on granite outcrops in central Georgia where their distribution ranges overlap, and where their niche requirement appears to be very similar." *Talinum appalachianum* Wolf, $2n = 24$, is confined to granite outcrops along the Coosa River in two counties of Alabama. Its flowers have five stamens which alternate with the petals, and there are sometimes one or two extra stamens opposite the petals. The three-lobed style is longer than the stamens, and the seeds at maturity are smooth and brown.

West of the Mississippi two more or less cylindric-leaved species enter our area in Arkansas. *Talinum calycinum* Engelm., $2n = 24$, with red petals and 30–45 stamens, occurs in southernmost Illinois and from Missouri and Arkansas to Montana, Nebraska, Kansas, Oklahoma, Texas, New Mexico, and Mexico (Poellnitz). *Talinum parviflorum* Nutt., $2n = 48$, with white to rose-colored petals and 4–8 stamens, also occurs in southern Illinois and ranges northward from Arkansas to Minnesota and North Dakota, westward to Colorado, Texas, Arizona, and possibly Mexico. *Talinum rugospermum* Holz. may approach our area to the northwest, for it occurs from northwestern Indiana through Illinois to northeastern Iowa, Wisconsin, and eastern Minnesota. It is distinguished by its deeply trifid style, 12–25 stamens with subglobose anthers, and strongly wrinkled seeds.

The flowers of all the species are very delicate and ephemeral. Several authors have pointed out the need for studying living plants, in either the field or cultivation, since critical characters, such as the color, size, shape, and persistence of the floral organs, are damaged or lost in pressing and drying. The flowers usually open for only a short period in full sunshine, the time and duration of daily flowering differing among the species, or even among different populations of the same species, but appearing to be more or less characteristic in a given geographical area. Wolf observed the usual flowering time in *T. Mengesii* to extend from about 11 A.M. to 5 P.M., while in *T. appalachianum* the flowers open between 3 and 4 P.M. and close between 5 and 6 P.M. Ware reports for *T. calcaricum* flowering times of 1 to 6 P.M. in Tennessee, but 3:30 to 6:00 P.M. in Franklin County, Alabama. It is not known, however, whether anthesis is controlled by temperature, light intensity, or both. The significance of flowering times and of the relative lengths of styles and stamens in the genus has not been investigated. Harshberger, the only reporter of pollinators, observed two species of the hymenopteran *Calliopsis* on flowers of *T. teretifolium*.

Ecological studies by Ware have shown that *Talinum calcaricum* and *T. Mengesii* are restricted to their narrow ecological niches through inability to compete with other species in more favorable sites. Adaptations of species of *Talinum* which favor survival under the conditions of extreme drought which often prevail in their habitat include succulence of leaf and stem, cylindrical leaves with low surface-to-volume ratio, few sunken stomata, pronounced cuticle, profusely branched root system, and the ability to flower even when a water deficit exists in the leaves (Gup-till, Harshberger, Ware).

Steiner found no record of interspecific hybridization in *Talinum*, and his attempts to cross *T. teretifolium* with *T. parviflorum* and *T. parviflorum* with *T. aurantiacum* Engelm., $2n = 48$, of the southwestern United States were unsuccessful. Both his chromosome counts (eight species) and those of others indicate a polyploid series with $2n = 24, 48$, and 72. He also reported polyploid cortical cells with $2n = 96$ in the root tips of *T. parviflorum*. Ware tried the crosses *T. calcaricum* ×

calycinum, *T. calcaricum* \times *Mengesii*, and *T. Mengesii* \times *calcaricum*, but the resulting low seed yields led him to conclude that partial genetic barriers exist between these morphologically similar taxa.

On the basis of seed morphology and anatomy, Kowal proposed that "*Talinum patens* Willd." and *T. reflexum* Cav., which have been treated as conspecific with *T. paniculatum* since early in this century, are distinct species. In our specimens the development of the aril varies considerably in different species. At maturity the seeds of *T. calcaricum*, *T. Mengesii*, and *T. teretifolium* are enclosed in a fragile, membranaceous, although tightly investing, aril, and all appear dull gray. Disintegration or removal of the aril reveals a shiny dark brown seed in *T. calcaricum*, and shiny black seeds in the other two species.

Guignard found the embryology of *T. paniculatum* to be the same as that of *Portulaca oleracea* and some species of *Calandrinia* (i.e., Polygonum-type embryo sac, solanad-type embryogeny). Anatomical details of the genus include the presence of unicellular epidermal papillae and drusiform calcium-oxalate crystals in the leaves. Incomplete septa have frequently been described in the unilocular ovary. The pollen of *T. teretifolium* is 12-forate (i.e., with \pm circular apertures distributed evenly over the surface of the grain), with three of the fora larger than the rest (Franz, Erdtman), while that of *T. triangulare* var. *crassifolium* Hort. are about 18-rugate (i.e., with elongate apertures distributed evenly over the surface), with a thin, psilate exine (Huang). Sharma describes the floral vascular anatomy of *T. paniculatum* and interprets the androecium as consisting of two alternate cycles of stamens. Saponins are reported in the leaves of *T. paniculatum*.

The genus is of little economic importance. *Talinum paniculatum* (Jewels of Opar) and *T. triangulare*, as well as several western American species are grown as border or rock-garden plants for their foliage, and red, white, or yellowish flowers. The roots of *T. aurantiacum* Engelm. are cooked and eaten by Indians of the southwestern United States, while the leaves of *T. portulacifolium* (Forsk.) Aschers., of Africa and of *T. triangulare* in the Americas, are sometimes cultivated as a leafy vegetable. *Talinum cuneifolium* (Vahl) Willd. is used in Tanganyika as an aphrodisiac.

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Subfamily MONTIOIDEAE Franz

3. *Claytonia* Linnaeus, Sp. Pl. 1: 204. 1753; Gen. Pl. ed. 5. 96. 1754.

Small perennial [or annual] unbranched herbs from deep-seated corms, [branched or unbranched tap-roots, rhizomes or stolons], producing 1 to many succulent, scapose flowering stems. Leaves basal, 1 to many in a rosette, petiolate [or sessile], \pm fleshy, glabrous, exstipulate, narrowly linear to lanceolate, oblanceolate, elliptic, spatulate, narrowly ovate, or oblong. Flowering stems bearing 2 opposite, sessile to petiolate leaves, \pm similar to the basal leaves, a small herbaceous bract at the base of the lowest pedicel, and one or more reduced bracts above. Inflorescence a loose, terminal, racemose scorpioid cyme bearing up to 19 showy pedicellate flowers, the pedicels often spreading or recurving in fruit. Sepals 2, free, ovate, rounded, obtuse or acute at apex, persistent. Petals 5 [or fewer] slightly united basally, broadly oblong to obovate, exceeding the sepals (or exceeded by the stamens and sepals in *C. virginica* f. *micropetala* Fern.), apex rounded to truncate or slightly emarginate, pink to white, with pink veining, rarely yellow; convolute in the bud, drying in place. Stamens 5, opposite the petals; filament adnate to the petal claw; anthers pink; pollen mostly 3-colpate. Gynoecium 3-carpellate; style 1, with 3-cleft stigma; ovary superior, often 3-angled, unilocular usually with 6 (3–6) ovules on a basal placenta. Fruit a membranaceous, ovoid capsule dehiscing by 3 valves, the valves often inrolling after dehiscence. Seeds shiny, brown to black, smooth to alveolate, orbicular to lenticular. Embryo with 1 or 2 cotyledons, peripheral, curved around the endosperm. LECTOTYPE SPECIES: *C. virginica* L.; see Britton & Brown, Illus. Fl. No. U.S. ed. 2. 2: 37. 1913. (Named for John Clayton, 1686(?)–1773, English doctor and botanist, resident of eastern Virginia from 1705, who contributed material to Gronovius for the *Flora Virginica*.) — SPRING BEAUTY.

A distinctly North American genus of about 32 species, when considered in the broad sense of Gray or Poellnitz, or of about 20 species when interpreted in the narrower sense of Greene, Robinson, Rydberg, Pax & Hoffman, Swanson, and Nilsson. Two complex species (*C. virginica* L. and *C. caroliniana* Michx.) of sect. CLAYTONIA occur in eastern North America. The remaining species, including *C. lanceolata* Pursh, *C. tuberosa* Pallas ex Willd., and *C. umbellata* S. Wats., closely related to ours, are distributed from the Rocky Mountains, westward to the Pacific Ocean, northward to Alaska, and westward to eastern Siberia and the Kamchatka Peninsula.

Both species of our area are cormose perennials inhabiting shady woodlands, grassy banks, wet meadows, and bog habitats or in association with bald granite exposures (in South Carolina, plants of this habitat are more robust than those of adjacent habitats). The two differ mainly in leaf shape and size. *Claytonia virginica* (spring beauty, rose elf, grass flower), with two varieties and two forms, has linear to linear-oblanceolate

leaf blades more than eight times longer than broad (Davis, Voss) and gradually narrowed to the petiole. It occurs from Nova Scotia and New Brunswick, westward across southern Quebec and Ontario to Minnesota, and southward to Texas and Georgia (Davis). The more northern *C. caroliniana* is generally smaller than *C. virginica*, with possibly darker flowers, and has spatulate leaves less than eight times longer than broad, with the blade narrowed abruptly to the petiole. It ranges from southwestern Newfoundland, westward through southern Quebec and Ontario and the northern parts of the border states to eastern Minnesota, southward through Nova Scotia to New England and along the Appalachians to western North Carolina and northern Georgia, and westward through Kentucky and Tennessee to northwestern Arkansas. Davis says that the two "seldom grow in the same immediate area, but when they do *C. virginica* blooms earlier." Voss, however, describes sites in central Michigan in which populations of the two species are thoroughly intermixed. Here their flowering periods overlap, but *C. caroliniana* reaches its peak of flowering slightly earlier than *C. virginica*. No obvious evidence of hybridization was seen, however. Uttal reports a hybrid swarm between the two species at a location in Virginia where highly disturbed conditions have broken down the ecological barriers usually separating them there.

Narrow-leaved and broad-leaved taxa are recognized within *Claytonia virginica* by Davis, Fernald, Gleason & Cronquist, and Lewis *et al.* This variation is apparently correlated with chromosome numbers. At least 45 different chromosomal races are known in *C. virginica*, with numbers ranging from $2n = 12$ to about 191. Rothwell, and Lewis *et al.*, have worked out the chromosomal evolution of *C. virginica* throughout its range. Lewis proposes that "*C. virginica* has evolved from an ancestral narrow-leaved race having $n = 6$ from which the widespread $n = 12 \pm$ and southern $n = 7$ races arose. From the latter was derived an $n = 14$ race also common in the south. These races and at least some of their higher polyploid derivatives make up the narrow-leaved var. *acutiflora* (= var. *Simsii* of Davis). From continuing autoaneuploidy at the diploid level evolved the $n = 8$ race where, we believe, particular chromosomal redundancies with certain genetic combinations or duplications lead to the expression of broad leaves. Such plants became widespread in the north as did the morphologically similar $n = 16 \pm$ race. These races and their derivatives, largely aneutetraploids, represent the more recently evolved broad-leaved var. *virginica*. We agree with Davis . . . that no other gross morphological features correlate with leaf width."

Similar lines of evolution in chromosome number, although less extensive, are also known in *Claytonia caroliniana* L., in which reported chromosome numbers range from $2n = 16$ to 38, and in the western *C. lanceolata*, $2n = 16$ to 72.

The generic and subgeneric classification of *Claytonia* is chaotic. Two to ten infrageneric categories, designated or incorrectly cited as subgenera and sections, have been recognized. The nomenclature is con-

fusingly intertwined with that of the closely related *Montia* L. and various segregate genera. The boundary between the two is indistinct, prompting numerous transfers of species and sections. The *Claytonia-Montia* complex has been interpreted in three divergent ways, all of which have found some support in recent literature.

Claytonia has been distinguished from *Montia* either on meristic grounds (e.g., by Linnaeus, Gray, Poellnitz) or on the basis of habit (e.g., by Greene, Swanson). In the former case *Claytonia* is said to have 5 more or less equal petals slightly connate basally, usually 5 stamens, and capsules with several seeds (up to 6), while *Montia* is distinguished by distinctly unequal basally connate petals, 3 stamens, and 2 or 3 ovules and seeds per capsule. In this "broad" sense Gray (1887) recognized twenty species of *Claytonia*, but only one of *Montia* (*M. fontana* L.).

Torrey & Gray (1838) recognized four sections in *Claytonia* (*Claytonia*, *Limnia* (Haw.) Torr. & Gray, *Alsinastrum* Torr. & Gray, *Naiocrene* Torr. & Gray). Much later (1887) Gray divided the species of the genus among two subgenera or sections (it is not clear which) and 7 subgroups based on habit ("section" *Euclaytonia* with subgroups *Cormosae*, *Caudicosae*, and *Rhizomatosae*; "section" *Limnia* (Haw.) Torr. & Gray, with subgroups *Limnia*, *Alsinastrum* Torr. & Gray, *Naiocrene* Torr. & Gray, and *Montiastrum* Gray).

In the subsequent literature these subgroups are referred to as sections, although Gray apparently did not designate them as such. More recently, Poellnitz placed 32 species of *Claytonia* in 10 sections and recognized only five species of *Montia*. This restricted view of *Montia* finds support in recent papers by Moore and by Walters who recognize only *M. fontana* L., with four subspecies, distinguished by characters of the seed coat, in Europe, North America, and Australia.

A second approach to the complex is to transfer certain sections of *Claytonia* to *Montia*. Swanson, in pointing out transitional floral types in both genera, notes that all Montioideae are basically pentamerous and draws generic and sectional lines primarily on plant habit (as did Greene and others before him), rather than on a meristic basis. In Swanson's narrower circumscription *Claytonia*, with about 20 species in four sections (*Caudicosae* (Gray) Poell., *Rhizomatosae* (Gray) Poell., *Claytonia*, and *Limnia* (Haw.) Torr. & Gray), becomes limited to those perennial and annual species forming an unbranched basal rosette from a tuber, taproot, or rhizome, and producing upright, axillary, scapose flowering branches bearing a single pair of opposite leaves subtending the generally simple inflorescence ("section" *Euclaytonia* and "section" *Limnia-Limnia* of Gray). The remaining species (subgroups *Naiocrene*, *Alsinastrum*, and *Montiastrum* of Gray) are transferred to *Montia*, which is then characterized by plants of varying habit which are branched above the base, with cauline leaves and axillary or terminal inflorescence. Swanson recognizes eight species of *Montia*, in four sections (*Montia*, *Limnalsine*

(Rydb.) Pax. & Hoffm., *Naiocrene* (Torr. & Gray) Pax & Hoffm., *Montiastrum* (Gray) Pax & Hoffm.), in North America.

The third approach to the complex is that of Rydberg (followed by Pax & Hoffmann) who also restricted *Claytonia*, recognizing only two subgenera (*Euclaytonia* and *Belia* (Steller) Rydb., treated as sections by Pax & Hoffmann). In contrast to previous workers, however, Rydberg established segregate genera for the sections or species excluded from *Claytonia* (*Crunocallis* Rydb., *Limnalsine* Rydb., *Limnia* L., *Montiastrum* (Gray) Rydb., and *Naiocrene* (Torr. & Gray) Rydb.). Such splitting has been supported and furthered by Nilsson, who segregated three new monotypic genera primarily on the basis of pollen morphology (*Maxia* Ö. Nils., *Mona* Ö. Nils., *Neopaxia* Ö. Nils.), raising the number of genera in the complex to ten.

Swanson considers the members of sect. CAUDICOSAE, with heavy tap-roots, to be primitive within the genus. The RHIZOMATOSAE and the cormose CLAYTONIA species are considered to be progressively more advanced, and the taprooted annuals of sect. LIMNIA are thought to be most advanced. Lewis and Suda find that trends in chromosomal morphology (decreasing size, increasing asymmetry, increase in satellite number) support Swanson's sequence. Their data suggest at least two lines of evolution in *Claytonia*, "from sect. *Caudicosae* through sect. *Rhizomatosae* to sect. *Claytonia*, and from a taxon similar to *C. sibirica* ($2n = 12, 24, 36, 48$; in sect. *Caudicosae*) to sect. *Limnia*."

Flower color in our species ranges from white to dark pink, with pink to rose veining. In *Claytonia virginica* a yellowish blotch often occurs above the claw of the petal. Orange-yellow-flowered variants are reported in *C. virginica* (f. *lutea* R. J. Davis) from Maryland and Pennsylvania, as well as in the western *C. lanceolata* from Idaho and Washington. Flowering occurs in the spring for two to three weeks, beginning in late March in Kentucky, with a new flower opening every day and lasting for 2-3 days. Anthesis is apparently controlled by temperature, with not more than two flowers open at the same time on an inflorescence (Wood). The plants are apparently outbreeding, adapted to insect pollination by Dipterans and Hymenopterans (Lovell), but self-pollination occurs if the flowers fail to open due to poor weather conditions. Flowers of *C. virginica* are proterandrous, being functionally staminate the first day, pistillate the second and third days. The life cycle of *Andrena erigeniae* (Hymenoptera), a common short-tongued bee pollinator that appears and disappears with the flowers of *C. virginica*, may be keyed to that of the plant species. Seed dispersal through forcible ejection has been observed in *C. alsinoides* Sims and *C. sibirica* L., with the seeds shooting out 1-1.5 meters.

Pollen of *Claytonia* (sensu Greene and Swanson) is mostly tricolpate, with some grains 6-rugate, as opposed to polyrugate or dodecacolpate in those former species of *Claytonia* which are now placed in *Montia* or the various segregate genera. Pollen-grain size in *C. virginica* has been found to be slightly larger in tetraploids than in diploids.

Anatomical and developmental aspects of the embryo sac, embryo, seed, and young sporophyte of *Claytonia virginica* are reported in detail by several workers. This species differs from other members of the genus in usually having only one developed cotyledon in the embryo. In the seedling, formation of the corm begins in the first year through abnormal development of pericyclic cells of the primary root. The corm soon becomes covered with a protective layer of cork.

The genus is of no particular economic significance. In parts of West Virginia *Claytonia caroliniana* is known as "tangle-gut." The leaves are eaten as "spring-greens" after being steeped in hot grease. Leaves of *C. perfoliata* Donn ex Willd. ($2n = 12, 24, 36$) are eaten like spinach. A tea was made for use as a diuretic from leaves of *C. sibirica* L. The starchy tubers or taproots of *C. virginica*, *C. caroliniana*, and *C. acutifolia* Pallas are edible.

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BASELLACEAE Moquin-Tandon, *Chenopod. Monogr. Enum.* x. 1840, nom. cons.

(MADEIRA-VINE FAMILY)

A small family of herbaceous, somewhat succulent, glabrous, (?dextrorsely) twining vines, lax herbs [or subshrubs?] producing annual shoots from perennial, fleshy rhizomes or tubers; leaves fleshy, alternate, exstipulate, sessile or petioled; inflorescence an axillary or terminal raceme, spike, or panicle of numerous small flowers, each subtended by a small bract; bracts of the pedicel 2, small, opposite, membranaceous or fleshy, caducous or persistent; flowers regular, bisexual [or unisexual]; sepals (involucral bracts?) 2, free or basally connate; petals (tepals?) 5, membranaceous or slightly fleshy, basally connate to form a shallow floral cup, aestivation quincuncial or imbricate; stamens 5, inserted on lip of floral cup or on bases of the petals; filaments [erect or] recurved in bud; anthers 4-locular, insertion of filament basal or versatile; gynoecium of 3 united carpels; ovary superior, unilocular; ovule 1, basal, campylotropous to anacampylotropous; styles 3, basally united, stigmas slender, \pm bifid [or capitate to clavate, or style 1 with capitate stigma entire to 3-lobed]; fruit a utricle [or berry], included in the perianth; seed 1, with copious endosperm; embryo annular [or spirally twisted]. TYPE GENUS: *Basella* L.

A family of four or five genera containing 15–20 species, most native to the New World tropics or the Andean regions of South America. *Basella*, including about five species and thought to have originated in the tropics of the Old World, has probably achieved its present pantropic distribution through cultivation. Of the New World genera, *Tournonia* Moq. and *Ullucus* Loz. are monotypic, *Anredera* Juss. (*sensu stricto*) is generally considered to be monotypic, and *Boussingaultia* HBK. consists of 10–15 species. *Anredera* and *Boussingaultia* were united by Baillon, and more recently by van Steenis, under *Anredera*. The family is represented in the southeastern United States only by a single species of *Anredera* (*A. leptostachys*), of the tribe Boussingaultieae Benth. & Hook.

The genera of Basellaceae fall into two natural groups: those with spirally twisted embryos and stamen filaments erect in the bud (*Basella*, *Tournonia*, *Ullucus*) and those with annular embryos and filaments out-

wardly reflexed in the bud (*Anredera*, *Boussingaultia*). These two groups have consistently been given systematic recognition as tribes, subtribes, or series, when included in the Chenopodiaceae (Endlicher, Bentham & Hooker, Baillon), or as subfamilies or tribes of the Basellaceae (Moquin-Tandon, Engler, Ulbrich, Eckardt). Franz treated the Baselleae as a tribe of subfam. Montioideae in the Portulacaceae and included the five genera of Basellaceae and the transitional genus *Portulacaria* Jacq.

Anatomically the Basellaceae differ from Chenopodiaceae in the absence of anomalous secondary growth and in the presence of bicollateral stelar bundles resulting from the tardy development of internal phloem. Bicollateral bundles, and similar features of floral ontogeny and morphology, are shared with some Montioideae (Portulacaceae).

Observations on *Basella rubra* L. and *Anredera vesicaria* (Lam.) Gaertn. f. indicate that the Basellaceae share with other Centrospermae possession of betacyanin pigments (here basellain-r, basellain-v) in place of anthocyanins. Saponins have been found in the seeds of this species, while calcium oxalate occurs in the form of druses and single crystals. Slime cells occur in parenchymatous tissues of the various taxa, and stomata of the rubiaceous type occur on both surfaces of the leaves.

As in the Portulacaceae, the perianth is interpreted as either biseriate, with two sepals and five petals, or uniseriate, with a single cycle of five sepals (or tepals) subtended by two large involucre bracts. The position of the five stamens in opposition to the five "sepals" suggests the loss of either the corolla or an intervening cycle of stamens, most probably the latter. According to Payer, and Eichler, the floral plan in *Basella rubra* is basically trimerous, the present pentamerous cycles each arising as successive whorls of three, one member of the outer perianth and androecial cycles aborting. Sharma considers the basal placentation of *B. rubra* to represent an extreme reduction from an originally axile placentation.

Embryological characteristics of the family include bitegmic ovules in which the inner integument forms the micropyle. Within a bulky nucellus the chalazal megaspore of a linear tetrad develops into Polygonum-type embryo sac. The endosperm is initially nuclear, later becoming cellular. Anthers of the family are tetrasporangiate and produce a glandular tapetum of multinucleate cells. Pollen grains are three celled when shed.

The pollen of the family is polymorphic. Grains are spheroidal in all genera except *Basella*, in which elaboration of the exine in the interapertural areas has produced a cubical shape. Aperture configuration varies from a basic pattern of six furrows arranged as on the sides of a cube (*Basella*, some species of *Boussingaultia*), through reduction in size and increase in number of apertures (as in "*Boussingaultia leptostachys*," *Ullucus tuberosus*), to many pores distributed evenly over the surface of the grain (*Anredera vesicaria*). Similar patterns occur in Portulacaceae and other families of Centrospermae.

Knuth states that pollination in *Basella rubra* is largely cleistogamous, with a few chasmogamous flowers pollinated by small, short-tongued in-

sects. Observations on the floral biology of American taxa are lacking. Structures resembling berry-like fruits found in an inflorescence of *Anredera leptostachys* from southern Texas were originally mistaken for fruits, but proved on dissection to be the much enlarged, fleshy petals enclosing an insect larva. The insect attack apparently stimulates this aberration of growth in the host flower.

Chromosome counts from species of three genera suggest that the base number of the family is 12, with $2n = 24, 48$, and 60 in *Basella*, 24 and 28 in *Boussingaultia*, and 24 or 36 in *Ullucus*.

The family is of economic importance in that several species are cultivated for their fleshy leaves, which are used as a substitute for spinach (*Basella rubra*), or for their fleshy, starchy rhizomes or tubers (*Ullucus*, *Anredera vesicaria*, species of *Boussingaultia*). The tubers of *Ullucus tuberosus* are an ancient and important food crop in Bolivia, Chile, Colombia, Peru. *Basella rubra* and some species of *Anredera* and *Boussingaultia* which are cultivated as ornamentals have become naturalized in many places. The reddish pigments of *Basella rubra* fruits are used in Asia as food coloring and may serve as a substitute dye for carmine.

The dextrorsely twining habit often cited in descriptions of the Basellaceae is open to question. Nevling notes that this characteristic is seldom constant among climbers, and Sloane's illustration of *Anredera vesicaria* shows leftward twining stems.

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1. *Anredera* A. L. de Jussieu, Gen. Pl. 84. 1789.³

Twining or scrambling, herbaceous vines with slender, much branched, somewhat fleshy, glabrous and sometimes reddish stems produced annually from fleshy rhizomes or tubers. Leaves alternate, exstipulate, petioled [or sessile], slightly fleshy, entire margined, blades suborbicular to elliptic, ovate [or cordate], with apex acute to acuminate [or obtuse], and base gradually or abruptly narrowed [to truncate or cordate]. Inflorescence axillary or terminal, a simple nodding raceme, racemose spike, or panicle, with numerous small, sessile or pedicellate flowers in axils of small bracts. Bracts of the pedicel 2, small, opposite, free or deciduous [or basally connate and persistent at level of pedicel articulation]. Flow-

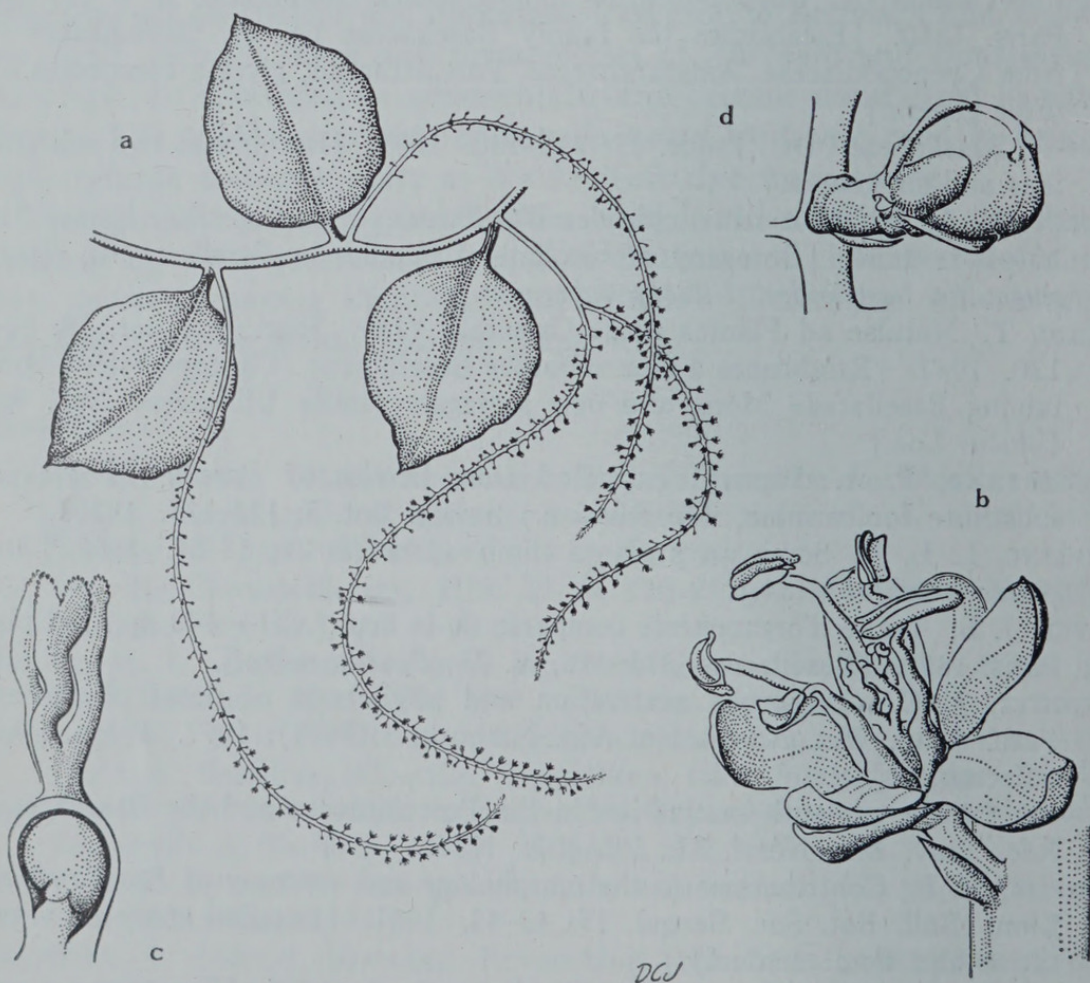


FIG. 3. *Anredera*. a-d, *A. leptostachys*: a, part of stem with inflorescences, $\times 1/2$; b, flower, $\times 12$; c, partial vertical section of gynoecium to show ovule, $\times 24$; d, teratological flower, the tepals accrescent from insect attack — note thickened pedicel, $\times 6$.

³ According to Rickett (1960), the investigation of a proposal to conserve the name *Anredera* Juss. (1789) over *Fallopia* Adans. (1763) has shown that "the actual type of *Anredera* (Sloane's specimen in BM) . . . is not *Polygonum scandens* L. as stated in the proposal. The genus is therefore not identical with *Fallopia*, the names are not even taxonomic synonyms. *Anredera* therefore stands without conservation, so far as *Fallopia* is concerned."

ers fragrant, perfect [or imperfect]. Sepals 2, \pm adnate to the floral cup, nearly flat to boat-shaped [keeled or narrowly to broadly winged along the back]; slightly shorter than [to slightly exceeding] the petals at anthesis. Petals 5, small, white or greenish [turning purple at maturity in some species] thin or somewhat fleshy, united basally to form a short floral tube, more or less spreading at maturity. Stamens 5, opposite and inserted on the petal bases. Filament filiform or subulate, recurved in the bud. Anthers oblong [to ovate], versatile, pollen rugate or polyforate. Ovary small, superior, ovoid [or slightly compressed] 1-locular. Styles 3, free, with bifid, papillose stigmas [or styles variously fused below, with capitate to clavate stigmas, or style 1, with capitate, 3-lobed stigma]. Ovule 1, basal, subsessile [or sessile]. Fruit a utricle with fleshy or parchment-like pericarp, enclosed by the perianth. Seed erect, lenticular, with crustaceous [or coriaceous] seed-coat. Embryo semiannular [to annular]. Cotyledons plano-convex [or subclavate]. TYPE SPECIES: *Anredera spicata* J. F. Gmel. = *Anredera vesicaria* (Lam.) Gaertn. f.; see Gmel. Linn. Syst. Nat. 2: 454. 1791, and P. Wilson, N. Am. Fl. 21: 337. 1932. (Derivation of generic name unknown.) — MADEIRA-VINE.

A New World genus of 10–15 species, inhabiting tropical regions from southern Florida and southernmost Texas, through Central America (about three species), to northern South America (about 13 species); represented in our area only by *Anredera leptostachys* (Moq.) Steenis in southern Florida, and in southern Texas by both *A. leptostachys* and *A. vesicaria* (Lam.) Gaertn. *Anredera leptostachys* is distinguished by its three bifid styles and wingless sepals, while *A. vesicaria*, better but erroneously known as *A. scandens* (L.) Moq., has broadly winged sepals and three undivided styles. Both species belong to sect. ANREDERA (see below) and may be most closely related to the South American *A. cordifolia* (Tenore) Steenis and *Boussingaultia floribunda* Moq.

The distribution of *Anredera leptostachys* in our area is not well defined, but it is known from Dade, Monroe, and Collier counties, Florida. The best known location appears to be Key West, where the species has been collected in hammocks and where it is said to occur in vacant lots and fence rows.

In his original circumscription of the Basellaceae Moquin-Tandon (1840) recognized two genera in his subfamily Anredereae Endl.: *Anredera* Juss., characterized by winged sepals ("perigone") and *Boussingaultia* HBK. with wingless sepals. He later (1849) segregated a third genus, *Tandonia* Moq., to accommodate those species of *Boussingaultia* distinguished primarily by ovaries bearing a single style with capitate stigma. Bentham and Hooker, however, reunited the two genera, and *Tandonia* has since been accorded only sectional rank.

Volkens divided *Boussingaultia* into two sections: TANDONIA (Moq.) Volk., containing the single-styled species, and EUBOUSSINGAULTIEAE Volk., containing the three-styled species. In the latter section Volkens included the type of the genus, *B. baselloides* HBK. Hauman, how-

ever, in the only recent revision of *Boussingaultia*, pointed out that the original description of *B. baselloides* mentions a single style, with a capitate, three-lobed stigma, and that the flower erroneously figured by Volkens for the type species is one of *B. leptostachys* Moq., with three bifid styles. The type species thus belongs to Volkens's section TANDONIA. Hauman replaced the name EUBOUSSINGAULTIEAE with sect. MOQUINELLA Haum. He further clarified some areas of confusion in identification and nomenclature, and provided a "provisional" enumeration of specimens and a key to thirteen species but did not give detailed descriptions for them. Ulbrich accepted Hauman's treatment of the genus.

Baillon, and more recently van Steenis, reduced *Boussingaultia* to synonymy under the older *Anredera*. Van Steenis states that winged sepals occur in some species of *Boussingaultia* and that the difference between the two genera is only a matter of degree in the development of the wings. In his expanded genus *Anredera* van Steenis recognizes two sections (*Tandonia* (Moq.) Volk. and *Anredera*) based on the bracts ("lower bracteoles") of the pedicel rather than on the styler characteristics formerly used. Section TANDONIA, with bracts basally connate and persistent on the pedicel, is not changed in composition. Section ANREDERA, with bracts free and caducous, is formed by the addition of *Anredera vesicaria* (as *A. scandens*) to the former sect. MOQUINELLA Haum. of *Boussingaultia*. The systematics of the genus is currently in a state of flux, since van Steenis transferred only a few species of *Boussingaultia* to *Anredera*. The remaining species must be cited under *Boussingaultia* until formally transferred. Soukup attempted to transfer several South American species, but his combinations are invalid for lack of proper basionym citation. The genus is badly in need of critical study and revision.

A tendency toward imperfect or functionally imperfect flowers may exist within the genus. Van Steenis concluded that the flowers of the type specimens of *Boussingaultia baselloides* HBK. "appear . . . female with small barren anthers." He also states that fruits of *Anredera cordifolia* have never been found and that *A. scandens* (= *A. vesicaria*) does not produce seed in Malaysia. Furthermore, Hauman describes sexually dimorphic flowers of *Boussingaultia ramosa* (Moq.) Hemsley, and Heimerl describes a collection of "*B. gracilis*" from southern Brazil in which "all flowers are female." The presence and extent of dioecism among the species of *Anredera* should be investigated.

Beille described the floral vascular anatomy of "*Boussingaultia baselloides*" (cultivated). He found five vascular bundles in the pedicellar stele, each bundle supplying a single trace to a "sepal" and its opposing stamen, and three of the bundles each supplying a single trace to one of the three carpels. There are no vestigial vascular traces in the intervals between the "sepals," from which he concluded that the abortion of the "corolla" is complete.

Chromosome counts for the genus indicate that both diploid and tetraploid species exist: $n = 12$ for *Anredera cordifolia*, and $n = 24$ in *Boussingaultia diffusa* (Moq.) Volk.

Anredera leptostachys, *A. cordifolia*, and *A. vesicaria* are widely grown as ornamental vines for their foliage and fragrant flowers. They can be propagated vegetatively from their fleshy rhizomes or tubers, or in *A. cordifolia* from small tubercles which form in the leaf axils. Webb reports that plants of "*Boussingaultia baselloides*," naturalized in New South Wales, Australia, are suspected of causing death of cows (symptoms of irritant poisoning). Hot-water extracts of these plants proved fatal to experimental rabbits.

A tangle of misidentification has developed around plants of *Boussingaultia* collected in South America and those cultivated and naturalized in various areas. Many of these have been identified as *B. baselloides* HBK., but they are specimens of *Anredera cordifolia* (including *B. gracilis* Miers, *B. gracilis* f. *pseudo-baselloides* Haum., and *B. baselloides* sensu Hook. Bot. Mag. pl. 3620). Hauman states that very few of the many specimens labeled *B. baselloides* which he examined were correctly identified and that most were attributable to *B. gracilis*. The latter was introduced into horticulture during the 18th century and has become widespread. For this reason references in the literature to *B. baselloides* HBK., such as those of Webb, are especially subject to question.

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