

THE GENERA OF VIOLACEAE IN THE SOUTHEASTERN
UNITED STATES ¹

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VIOLACEAE Batsch, Tab. Affin. Reg. Veg. 57. 1802, 'Violariae.'

(VIOLET FAMILY)

Herbs [to shrubs (sometimes scandent) or trees] with alternate [rarely opposite], simple, usually stipulate leaves. Flowers [regular or] irregular, bisexual [rarely unisexual or polygamous], 5-merous (except gynoecium), solitary to few in the leaf axils [or in racemose or cymose inflorescences]. Sepals distinct [rarely connate at base], imbricate [or open] in bud, usually persistent. Petals distinct, hypogynous, usually imbricated, unequal [or equal], the lowermost larger than the others and often spurred, saccate, or gibbous at base. Stamens 5, alternipetalous, hypogynous, the lowermost two [or all the stamens] often with a gland-, [scale-], or spur-like nectary on the back (abaxial side) [the glands sometimes connate into a "staminal sheath"]; filaments distinct [or connate]; anthers 2-locular at anthesis, introrse, longitudinally [very rarely transversely] dehiscent, connivent or connate into a sheath around the ovary, the broad connective usually produced beyond the anthers into a membranaceous appendage. Gynoecium 3 [rarely 2, 4, or 5]-carpellate, syncarpous; stigma simple [rarely 3-5-lobed]; style simple, terminal, sometimes flexuous in the lower part, [filiform to] columnar or clavate, with variously shaped apex ("stylar head"); ovary superior, 1-locular, with 1-many anatropous ovules on each of 3 parietal placentae. Fruit a loculicidal, 3-valved cap-

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The results of the study of Violaceae are somewhat more voluminous than had been anticipated. In order to provide a better understanding of the taxonomic-biological complexity of *Viola* an outline of the subsections has been considered an exceptional necessity. The key for the sections is based chiefly on the shape of the stylar head, a character which at least in some cases is liable to subjective perception and evaluation. The literature on *Viola* is very extensive and the references included are more numerous than usual.

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sule [or a berry, very rarely nutlike]. Seeds with endosperm, often carunculate. TYPE GENUS: *Viola* L.

A family of 18 [primarily tropical] genera with about 800 species distributed all over the world. Only *Viola*, *Melicytus*, and *Hymenanthera* occur chiefly or exclusively in the temperate zone, the first being of wide distribution, the two latter centered in New Zealand. Of the remaining genera nine are tropical American, two tropical African, one South Pacific (New Caledonia, Fiji, New Guinea), one Hawaiian, and two exclusively (*Rinorea*, with ca. 260 species) or primarily (*Hybanthus*, with ca. 80 species) pantropical. The family appears to be a very natural one, especially the subfamily *Violoideae* Melch. (including 17 genera), which is subdivided into the tribes *Rinoreae*, with regular or slightly irregular flowers (e.g., *Rinorea*, *Gleospermum*, *Rinoreocarpus*), and *Violeae*, with markedly irregular flowers (e.g., *Hybanthus* and *Viola*).

All the genera appear to be entomogamous, but pollination data have been reported only for *Viola*. Cleistogamy is known only in *Viola* and *Hybanthus*, which have also been investigated in regard to embryology. The cytogenetics of *Viola* have been studied extensively; however, there are available only a few chromosome counts for five additional genera, i.e., *Rinorea*, $2n = 24$ (1 sp.), *Decorsella*, $2n = 20$ (monotypic), *Hybanthus*, $2n = 24$ (1 sp.), *Melicytus*, $2n = 32, 64, 96$ (4 spp., 3 vars.), and *Hymenanthera*, $2n = 32, 64$ (6 spp.). Taking into consideration these and the chromosome numbers in *Viola* (*q.v.*) one may assume that the polyploidy may be of wide distribution in the family and probably played an important role in the origin of species. *Anchietea* (South America) and *Decorsella* (Africa) are notable for capsules dehiscing when very young (almost immediately after the pollination of the ovary) so that the seeds mature uncovered.

The family is closely related to Flacourtiaceae and through the latter with Turneraceae, Malesherbiaceae, and Passifloraceae. A relationship with Cistaceae seems probable.

The economic significance of the family is mainly based on the ornamental value of numerous species of *Viola*.

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KEY TO THE GENERA OF VIOLACEAE

Sepals not auricled at base; lowermost petal gibbous at base; anthers connate, the abaxial glands of the two lowermost stamens connate. . . 1. *Hybanthus*.
 Sepals auricled at base; lowermost petal spurred at base; anthers connivent, the abaxial spurs of the two lowermost stamens distinct. 2. *Viola*.

1. *Hybanthus* Jacquin, Enum. Pl. Carib. 2. 1760, nom. cons.²

Herbs [to shrubs] with alternate [opposite] leaves. Flowers small [or medium-sized], greenish white [white or blue to violet], pediceled, solitary to few in leaf axils [or in racemose, rarely cymose, inflorescences]. Sepals distinct, imbricate in bud, nearly equal. Petals distinct, imbricate, slightly [or considerably] unequal, the lowermost always largest and gibbous or saccate at base. Stamens with filaments distinct [or connate], each of the 2 [rarely 4] lowermost bearing a nectar gland [or spur] on back (abaxial side), the glands connate into one 2-lobed [or entire] nectary [or distinct]; anthers connate [or connivent] into a sheath inclosing the ovary, each connective prolonged beyond the anther into a membranaceous appendage. Gynoecium 3-carpellate; stigma small, simple; style usually club-shaped, the apex hooked [or slightly curved], with stigmatic opening directed forward [abaxially]; ovary 1-locular; ovules 2-integumented with a thick nucellus, 3 [to numerous] on each placenta. Capsule 9[-many]-seeded; seeds relatively large, globose [or ovoid], carunculate, with copious endosperm and large, straight, axile embryo with flat cotyledons. (Including *Cubelium* Raf., *Ionidium* Vent., *Solea* Spreng.) TYPE SPECIES: *H. havanensis* Jacq. (Name from Greek, *hybos*, hump-backed, and *anthos*, flower, referring to the gibbous flowers.)

A largely pantropical genus of about 80 species centered in tropical South America but extending into the Temperate Zones in Uruguay, Argentina, and Chile, in southern Australia, and in North America. The northernmost species is *Hybanthus concolor* (T. F. Forst.) Spreng. (*Cubelium* Raf., *Ionidium* Benth. & Hook. f. ex S. Wats., *Solea* Ging. ex DC.), green violet, a perennial herb with alternate leaves and small greenish-white flowers solitary in two's or three's in the leaf axils, which ranges from Georgia to Mississippi, Arkansas, and Kansas, northward to Wisconsin (?), Michigan, southern Ontario, New York, and Connecticut. Two other species, *H. verticillatus* (Ort.) Baill. (*H. linearis* (Torrey) Shinnery) and *H. attenuatus* (Humb. & Bonpl.) G. K. Schulze reach their

² Conservation unnecessary; see Rickett & Stafleu, Taxon 8: 314. 1959.

northern limits westward beyond our range in Kansas and Colorado and in southern Arizona, respectively.

The occurrence of small, cleistogamous flowers with petals reduced or wanting and with two or five glandless stamens has been recorded in *H. concolor* and in the South American *H. communis* (St. Hil.) Taub. and *H. Ipecacuanha* (L.) Baill. Only *H. parviflorus* (L. f.) Baill., $2n = 24$, has been investigated cytologically. The rhizome and roots of *H. Ipecacuanha* have sometimes been used as a substitute for true ipecac (*Cephaelis Ipecacuanha* (Brot.) A. Rich., and *C. acuminata* Karst., Rubiaceae), an emetic. Roots of several other species are used locally in South America and Asia as emetics and against diarrhea. Although the genus includes spiny shrubs to rosette plants, the delimitation of subgeneric categories awaits a much-needed taxonomic revision. *Hybanthus* is presumably most closely related to *Viola* (Melchior).

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2. *Viola* Linnaeus, Sp. Pl. 2: 933. 1753; Gen. Pl. ed. 5. 402. 1754.

Herbs [rarely shrubs or subshrubs], often acaulescent, with alternate, petioled [or sessile] leaves. Flowers usually on 1-flowered, solitary peduncles borne in the axils of cauline leaves or (in acaulescent species) directly from the rhizome and stolons; cleistogenes often following the normal, chasmogamous flowers. Sepals subequal, auricled at base. Petals unequal, the lowermost the largest and spurred at base. Stamens with short, distinct filaments, the 2 lowermost bearing spurlike [or wartlike] nectaries projected into the spur of the lowest petal; anthers usually connivent into a sheath inclosing the ovary, each connective produced at apex into a conspicuous, membranaceous appendage; pollen 3(4-6)-colpate, spheroidal to ellipsoidal, smooth, medium-sized to large. Stigma

simple, terminating a stylar beak or situated on the abaxial side, rarely on the summit, of the beakless stylar head; style \pm columnar, curved \pm forward (rarely upward) at apex, terminating in a beak (rostrum), or enlarged upward into a \pm capitate, sometimes margined and helmet-like [or variously appendaged], abaxially beaked or beakless stylar head; ovules 3—many on each placenta, 2-integumented, with a thick nucellus. Seeds globular to obovoid, usually smooth, often carunculate; endosperm copious; embryo straight, axile, with rather thick, plano-convex cotyledons. LECTOTYPE SPECIES: *V. odorata* L.; see Britton & Brown, Illus. Fl. North. U. S. ed. 2. 2: 546. 1913. (Name classical Latin, *Viola*, the digammated form of Greek, *iolon*, a diminutive of *ion*, a violet, or some other flower.)

A genus of about 400 species, of world-wide distribution, centered in the North Temperate Zone, restricted to mountains in the tropics. A few species occur in the Arctic Zone in the Old World and in the Subarctic Zone of North America; the southernmost limits are South Africa, New Zealand (3 spp., 2 endemic), and Tierra del Fuego. Although the Andes of South America abound with endemic species exhibiting a great diversity of floral patterns, only a small number are known from the tropical mountains of the Eastern Hemisphere. The Hawaiian Islands are notable for eight endemic, mostly frutescent (single-stemmed) species (often with racemose inflorescences) which represent a special section, *NOSPINIUM* W. Becker (e.g., *V. tracheliifolia* Ging., *V. robusta* Hilleb., $2n =$ ca. 76, *V. mauensis* Mann, $2n =$ 82, ca. 85, ca. 86). Nearly 80 species in four of fourteen sections recognized by Becker (1925) are represented in North America.

The tentative classification followed below is essentially that of Clausen (1929 and especially 1951) and is based mainly on floral characters (especially the type of stylar head), chromosome numbers, and, to a lesser degree, crossing relationships. The sections given in the key are divided into subsections within which the species are connected by fertile to partially sterile hybrids and between which connections are usually through sterile hybrids. Intersectional hybrids are difficult to produce, and only two instances of vigorous but completely sterile intersectional hybrids are known. No intersectional hybrids involving sect. *MELANIUM* have been produced. Chromosome numbers have been reported for about 160 species.

KEY TO THE SECTIONS OF VIOLA IN THE SOUTHEASTERN UNITED STATES

- A. Upper portion of style variously shaped, beaked or beakless, without a lip-like appendage ("lip") at base of the stigmatic opening; rhizomatous perennials, usually with bractlike stipules.
- B. Style enlarged upward, capitate, beakless, the stigma within a minute opening on the lower (abaxial) side of the stylar head; flowers usually yellow, or white with bases of petals and/or spur yellow; usually caulescent. Sect. *CHAMAEMELANIUM*.

- B. Style various, beaked at apex, very rarely beakless; flowers blue to violet, creamy, or white (without any yellow).
- C. Style clavate, depressed-capitate and often margined, beaked on the lower side of the stylar head (or in *V. pedata* obliquely concave at summit, beakless); acaulescent. Sect. *PLAGIOSTIGMA*.
- C. Style \pm columnar, apex beaked and \pm bent or curved forward, rarely almost straight pointing forward and upward; acaulescent or caulescent. Sect. *VIOLA*.
- A. Upper portion of style capitate-globular, beakless, bearing on the lower side a wide stigmatic opening with a "lip" at its base; flowers bluish white, creamy, or lavender (or yellow and/or blue to dark violet); usually caulescent annuals or biennials with large, leaflike, pinnately dissected, \pm lyrate, stipules. Sect. *MELANIUM*.

Section *CHAMAEMELANIUM* Ging. (sensu Clausen), including North American and Eurasian species forming a polyploid series on a base of six ($2n = 12, 24, 36, 48 (60), 72$), is considered to be the most primitive of the genus (Clausen, 1929). Six subsections occur in North America, three in our area. Subsection *Nudicaules* W. Becker comprises yellow-flowered caulescent violets with one to few basal leaves and stems leafy only toward the summit. The four eastern North American species, *V. pubescens* Ait. ($2n = 12$), *V. eriocarpa* Schwein. (*V. pensylvanica* Michx., fide Fernald) ($2n = 12$), *V. hastata* Michx., and *V. tripartita* Ell., occur in our area. Putative natural hybrids intermediate in morphology and ecology between the first two species have been recorded (Russell, 1960), and the lines between the two are often blurred. Subsection *Canadenses* W. Becker (*Erectae*, *Canadenses* W. Becker) includes North American white-flowered caulescent violets ("Canada violets") represented in our area by *V. canadensis* L. ($2n = 24$), lacking stolons and ranging from Alabama to Tennessee and North Carolina and west- and northward far beyond our area, and the stoloniferous *V. rugulosa* Greene, which reaches its southern limit in northwestern North Carolina and eastern Tennessee. Experimental hybrids between the two are vigorous and fertile, and both intergrade in areas of overlap, suggesting their treatment as parts of a single species (Russell, 1960). Cleistogamous flowers are not produced in this subsection. Subsection *Orbiculares* Pollard sensu stricto (subsect. *Rotundifoliae* Clausen, ined. 1929, not Borbas, 1892) includes only *V. rotundifolia* Michx., $2n = 12$, a yellow-flowered stemless violet, which extends southward along the Appalachians to Georgia and Tennessee. The species is relatively invariable, and there are no indications of hybridization or introgression with other species. This subsection seems to form a transition to sect. *PLAGIOSTIGMA* (Clausen, 1929). No natural hybrids between subsections have been found, and experimental crosses have either failed or produced dormant seeds or weak seedlings.

Section *PLAGIOSTIGMA* Godr. (sensu Clausen, 1951) (§ *Nomimium* Ging., in part; § *Nomimium* subsect. *Plagiostigma* auct.) comprises Eurasian and North American white- to violet-flowered acaulescent species forming a polyploid series based on twelve ($2n = 24, 48, 72, 96$), with

some exceptions ($2n = 44, 54, 56$). Subsection *Primulifoliae* Gershoy (§ *Nomimium*, *Stolonosae* Kupff. sensu W. Becker, in part; § *Plagiostigma* subsect. *Stolonosae* Clausen, 1951; *Stolonosae*, *Primulifoliae* Gershoy) includes usually stoloniferous white violets with slender, cordlike rhizomes, cleistogamous flowers with erect peduncles, and ellipsoid green capsules. *Viola lanceolata* subsp. *lanceolata* and *vittata* (Greene) Russell (*V. vittata* Greene), both $2n = 24$; *V. Macloskeyi* F. E. Lloyd subsp. *pallens* (Banks) M. S. Baker (*V. pallens* (Banks) Brainerd), $2n = 24$; and *V. primulifolia* L. subsp. *primulifolia* and *villosa* (Eaton) Russell (including *V. rugosa* Small), both $2n = 24$, represent the group in our area. These species seem to intercross freely, and putative natural hybrids of all of them have been recorded. Experimental hybrids between *V. Macloskeyi* subsp. *pallens* and *V. lanceolata*, as well as *V. primulifolia*, have been reported to be fertile.

Subsection *Blandae* Pollard, in part (*Stolonosae* ser. *Blandae* Gershoy, *Incognitae* Clausen), is composed of the closely related *Viola incognita* Brainerd and *V. blanda* Willd., which differ from the preceding white-flowered species in the prostrate peduncles of cleistogamous flowers, the ovoid, purplish or reddish capsules, and the chromosome number ($2n = 44$). Primarily northeastern, both reach their southern limits in our area. Where the two are in contact "there is morphological intergradation, due to relatively unrestricted intercrossing" (Russell, 1955).

Subsection *Boreali-Americanae* W. Becker, the acaulescent "blue" violets, includes exclusively North American species with fleshy, thickened rhizomes without stolons, blue-to-violet flowers (white in albinic forms), and a common chromosome number ($2n = 54$). About ten of the twenty-five species recorded from our area are primarily or exclusively southeastern. Others (as *Viola papilionacea* Pursh [including *V. Priceana* Pollard], *V. palmata* L., *V. cucullata* Ait., *V. sagittata* Ait., and *V. fimbriatula* Sm.) are of wide distribution in eastern North America. The species intercross freely, and numerous natural and experimental hybrids, the latter vigorous and usually fertile, are known. Introgression seems to be frequent. At least some of the species probably should be reduced to subspecific rank. This subsection is one of the most difficult groups taxonomically, both because of general morphological similarities and because "frequent hybridization tends to obliterate not only the morphological differences, but also the more sharply marked ecological preferences" (Russell, 1960). Experimental hybrids between subsects. *Primulifoliae* and *Boreali-Americanae*, $2n = 39, 51$, are sterile.

Subsection *Pedatae* Pollard differs from the preceding primarily in the clavate beakless style, obliquely concave at the summit and bearing the stigma within a small protuberance near the center of the cavity, as well as in chromosome number ($2n = 56$). The single species, *Viola pedata* L., widely distributed in eastern North America, is considered to be most closely related to *V. Brittoniana* Pollard (*Boreali-Americanae*). The absence of cleistogamous flowers has been regarded as characteristic, but these have been recorded by Hills (1946) in plants cultivated in England.

No natural hybrids are known, and experimental attempts have failed. However, Russell and Bowen concluded (on the basis of vegetative features alone!) that a form with unusual leaf variation in North Carolina was probably the result of hybridization and subsequent introgression between *V. pedata* and *V. primulifolia* subsp. *villosa* (subsect. *Primulifoliae*).

Section VIOLA (§ *Nomimium* Ging., in part; § *Rostellatae* Boiss. sensu Clausen, 1951) includes North American, Eurasian, and North African species of a polyploid series based on ten ($2n = 20, 40, (60), 80$). Subsection *Uncinatae* Kupff. comprises acaulescent, often stoloniferous violets with the style curved in a hook at the tip and the seeds not forcibly scattered from the capsule. *Viola odorata*, sweet or English violet, $2n = 20$, has been introduced and has become locally established in various parts of the United States. The North American-Eurasian subsect. *Rosulantes* Borb. includes caulescent blue violets with tufted stems and rosulate basal leaves, rather slender styles beaked and bent at the apex, and seeds forcibly ejected from the capsules. The Eurasian species are diploid or tetraploid, but the North American, with the exception of the western *Viola Howellii* ($2n = \text{ca. } 80$), are diploid. *Viola conspersa* Reichenb., *V. rostrata* Pursh, and *V. striata* Ait., all $2n = 20$ and linked by partially fertile hybrids, reach their southern limits in our area, while *V. Walteri* House, $2n = 20$, is primarily southeastern. *Viola adunca* Sm., of more northern distribution, apparently also belongs to this group.

Section MELANIUM Ging. includes about 50 almost exclusively Eurasian and North African species exhibiting a variety of chromosome numbers in a modified six- or ten-series. Only subsect. *Tricolores* W. Becker sensu Clausen (1929) (*Calcaratae*, *Tricolores* W. Becker) including species with chromosome numbers based on $x = 6$ ($2n = 14, 16, 24, 26, 34, 36, 48$) is represented in North America. *Viola Rafinesquii* Greene (*V. Kitaibeliana* R. & S. var. *Rafinesquii* (Greene) Fern.), $2n = 34$, a small annual (or biennial) with bluish-white, creamy, or rarely lavender flowers, occurs from Georgia to Texas and northward beyond our limits. Being distinct from the related European species morphologically and from *V. Kitaibeliana*, $2n = 14, 16, 24, 36, 48$, especially in the chromosome number, it is also supposedly the only species of sect. MELANIUM which produces cleistogamous flowers (Gershoy, 1934). The nativity of this species in North America has been neither proved nor disproved. *Viola arvensis* Murr., $2n = 34$, introduced from Europe, has been recorded as naturalized in North Carolina and northward to Newfoundland, Michigan, and Alberta. *Viola tricolor* L., $2n = 26$, from Eurasia and North Africa, and especially its garden forms of hybrid origin (pansies, "violas," etc.), are commonly cultivated. The *Tricolores* as a group are notable for the occurrence of polyploidy and polysomaty.

The violets, in general, seem to show a preference for acid soil, the degree of acidity varying with each species, although growth of plants "is not correlated with the soil acidity alone, but is influenced by a combination of this factor with moisture, texture, and fertility" (McCullough, 1941). Vegetative reproduction by rooting stolons (e.g., in

Primulifoliae and *Blandae*) or by the detachment of rooting lateral, superficial branches of the rhizome (e.g., in *Boreali-Americanae*), more rarely by adventitious buds on roots (in *Pedatae*), permits the survival of sterile hybrids. Mycorrhiza have been found in *Viola palustris* L. and *V. biflora* L.

Although apparently often self-fertile, the chasmogamous flowers are adapted to cross-fertilization, self-pollination being prevented by the position of the stigma in regard to the anthers, and/or by configuration of the stigma, or by proterandry (*V. lanceolata*, *V. Macloskeyi*). Thysanoptera (especially Thripidae) and various Diptera, Hymenoptera, and Lepidoptera have been recorded as pollinators, the short-tongued species pollinating the short-spurred flowers, the long-tongued the long-spurred violets. These insects usually are in a reverse position (the head down) when sucking the nectar. Details of pollination differ somewhat in different sections. *Viola arvensis* is self-fertilized, and self-pollination occurs early, in the flower buds.

In the great majority of the species of sects. CHAMAEMELANIUM, VIOLA, and PLAGIOSTIGMA, the chasmogamous flowers are followed by reduced, mostly apetalous, closed, highly fertile, cleistogamous flowers with 2-5, \pm reduced, spurless stamens and flexuous and much curved styles, so that the stigma is brought into contact with the anthers. The pollen grains germinate within the anthers, and the pollen tubes penetrate the anther walls into the stigma. The presence of dimorphic pollen grains in both chasmogamous and cleistogamous flowers in *V. odorata* var. *praecox* Gregory is noteworthy; only one kind of these pollen grains is germinable in the chasmogamous, and only the other in the cleistogamous, flowers (Madge, 1929). Semicleistogamous flowers forming a transition between chasmo- and cleistogamous flowers are often observed. In many hybrids the sterility involves only the chasmogamous flowers, seeds being produced by the cleistogamous flowers. Apomixis, although presumed by some earlier taxonomists, has not been proved in *Viola*. Myrmecochory has been reported in several species.

Many species are valued ornamentals. Roots of *Viola tricolor* and *V. odorata* contain a saponin and an alkaloid, *violin*, and are official (expectorants) in some countries. A medicinal preparation, *traviolin*, is obtained from the leafy stems of *V. tricolor* in the U.S.S.R. *Viola odorata* is extensively cultivated in Europe for use in perfume manufacturing.

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