

THE STEMONACEAE IN THE SOUTHEASTERN UNITED STATES¹

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STEMONACEAE Engler in Engler & Prantl, Nat. Pflanzenfam. II. 5: 8. 1887, nom. cons.

(STEMONA FAMILY)

Erect herbs [or subshrubs to scandent vines], usually glabrous [stems and petioles rarely hirsute], with creeping rhizomes [or tuberous roots], bearing raphides in some organs. Leaves distichous [decussate or whorled], simple, petiolate, [rarely sessile], without a sheathing base, exstipulate, often cordiform, with a midrib and [2–]several longitudinal nerves usually diverging near the base and interconnected by $\pm$ transverse veinlets, margins entire; stomata anomocytic. Inflorescences axillary, uniflorous or lax few-flowered cymose clusters [or several in crowded subumbellate clusters]; bracteoles inconspicuous, erect, linear-lanceolate. Flowers nearly actinomorphic [to strongly zygomorphic], perfect. Tepals 4, distinct [or basally connate], 1 pair enclosing the others in bud, green and sometimes reddish or purplish. Stamens 4, epitepalous; filaments short [usually basally connate]; anthers dehiscent introrsely by longitudinal slits; pollen grains monocolpate. Stigma sessile; ovary superior or nearly so, unilocular, bearing several anatropous, bitegmic, crassinucellar ovules on an apical [or basal] placenta. Capsule beaked, compressed, 2-valvate. Seeds with multicellular arillate appendages on and near the funicle; seed coat striate; endosperm fleshy to hard, initially nuclear (*Stemona*); megagametophyte of the Polygonum type (*Stemona*); embryo small, straight. (Fruit and seeds of *Stichoneuron* not known.) (Rox-

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burghiaceae Wallich, Pl. Asiat. Rar. **3**: 50. t. 282. 1832; including *Croomia* Nakai, Ic. Pl. Asiae Orient. **2**: 159. t. 60. 1937.) TYPE GENUS: *Stemona* Lour. (*Roxburghia* Banks in Roxb.)

Three genera with about 35 species, distributed throughout the monsoon region of eastern Asia, and with one disjunct species of *Croomia* Torrey & Gray in the southeastern United States. Two other species of *Croomia* occur in eastern Asia (Japan to eastern China). The two species of *Stichoneuron* Hooker grow in Bangladesh, India (Assam), and near the border between Malaysia and Thailand. The range of *Stemona* (ca. 30 species) extends from eastern India to eastern China (and Japan, where it was probably introduced), and southward through the Philippines and Indonesia to northern Australia.

The three genera are so distinct morphologically that botanists have frequently questioned the Stemonaceae as a natural assemblage. However, the genera have been separated taxonomically only once, when Nakai segregated *Croomia* and *Stichoneuron* as the family Croomiaceae. Any suggestion of division must take into account several noteworthy shared characteristics, including broad, petiolate leaves with longitudinal arcuate veins and without sheathing bases; partly amphivasal cauline vascular tissue in one or two rings; raphides; two pairs of sepaloid tepals bearing as many epitepalous stamens; and unilocular gynoecium with no style, often slightly sunken in the receptacle. Division of these genera into separate families is further complicated by a set of likenesses linking each of the genera to one of the other two.

Stemona is unique in having appendaged anthers, basal (vs. apical) placentation, large flowers, usually twining (vs. erect) habit, and highly organized, straight, transverse veinlets connecting the major foliar nerves. *Croomia* and *Stichoneuron* are further set off from *Stemona* by creeping rhizomes, minute pubescence or papillae on the filaments and inner faces of the tepals, and anthers borne obliquely with respect to the filaments.

Stichoneuron stands apart in its crowded, many-flowered inflorescences (vs. one or few flowers, usually on long, lax pedicels), major foliar nerves diverging from the midrib (vs. from the leaf base, but divergence from the midrib characterizes *Stemona japonica* Franchet & Sav., $2n = 14$), occasional pubescence of vegetative organs, and smooth (vs. papillose) leaf margins. Although seeds and fruits of *Stichoneuron* are unknown and its pollen and floral anatomy are scarcely known, each of these is a point of resemblance between *Croomia* and *Stemona*. In these two genera the seeds are striate and bear a tuft of arillate appendages, the flattened two-valved capsules have a short neck, the pollen is sometimes reticulate, and the vascularization of the ovary is similar.

Only in *Croomia* do the stems appear to lack vessel elements and have the vascular tissue in one ring (vs. in two), and only in this genus are there frequently free vein-endings in the leaf blade. *Stemona* and *Stichoneuron* are further distinguished by a tendency toward connation of the filaments and of the tepals; connation of the filaments occurs sporadically in *Croomia*.

Floral morphology has caused confusion, especially in *Stemona*, where two strange projections extend beyond the locules of each anther. One is vascularized and appears to be a prolongation of the connective; the other is a solid parenchymatous adaxial appendage inserted immediately distal to the locules. These unusual stamens have been interpreted as involving petals and nectaries. Comparison of early interpretations is available in Kunth, and Swamy provides a detailed recent view. Lachner-Sandoval observed that in some species the appendages block outcrossing, and that in *S. javanica* (Kunth) Engler pollen tubes grow from the anther to the stigma. Reports of perigyny pertain to all three genera, and authors are divided in opinion about the number of carpels comprising the gynoecium (see discussion under *Croomia*).

Taxonomic placement of the family has likewise generated diverse opinions (summarized in Burkill). Evidently because of the four-parted flower, vascular cylinder(s) in the stem, and some other superficial resemblances to dicotyledonous families, certain early authors placed each of the genera separately within that assemblage. Others saw an affinity with the aroids, but most have preferred placement in or near the Liliales and allies (especially the Asparagi of Jussieu or its components, which included *Dioscorea* L.). In recent treatments the Dioscoreaceae and its relatives have received the most attention as potential allies of the Stemonaceae. When Hutchinson separated the Dioscoreales from the Liliales he included the Stemonaceae in the former, and Burkill thought that the family originated from "proto-Liliales" in the vicinity of the Dioscoreaceae. Several authors have mentioned similarities to the Dioscoreales: for example, prolongation of the connective (*Stemona*); a distinct pith in the stem; a similar arrangement of metaxylem vessels in common and cauline bundles (*Stemona* and *Stichoneuron*); and tendencies toward an inferior position of the ovary, dwarfing, twining (*Stemona*), and rhizomes. Nevertheless, opinion is nearly unanimous that confidence in any placement must await accumulation of more information.

Uses in Asia are reported for all three genera. For example, *Croomia japonica* Miq. has been used as a treatment for rheumatism, and *Stichoneuron caudatum* Ridley as a tonic and (as suggested by a local name) as an abortifacient. Several species of *Stemona* are used in a number of ways throughout their ranges; at least three species are cultivated, especially *S. tuberosa* Lour., which is a source for candied roots and is eaten as a potherb. Extracts from underground organs of this and other species (known as *pai pu* in China and by the pharmaceutical name *Radix Stemone*) have antiseptic properties and are allegedly useful against rheumatism, various respiratory ailments, parasitic worms, skin diseases, lice, parasites on cattle, and termites. The genus has attracted the attention of chemists, resulting in an extensive literature. At least 16 alkaloids, which (according to Hegnauer) are usually distinguished by a lactone arrangement, have been isolated. Useful summaries of the chemical work are presented by both Edwards and Hegnauer.

Stemona tuberosa, a climbing vine with large, green and red, fetid flowers, is sometimes grown as a novelty in greenhouses.

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1. **Croomia** Torrey & Gray, Fl. N. Am. **1**: 663. 1840.

Erect, glabrous herbs to 35[–60] cm tall, with annual leafy shoots terminating persistent rhizomes, these bearing sheathing scale leaves sparsely along the horizontal portion and clustered at the upturned portion (the base of the leafy shoot). Scale leaves reddened when protruding above ground and with conspicuous longitudinal nerves not interconnected by transverse veinlets. Foliage leaves 3–6, distichous, clustered above a bare, ribbed, vertical internode, cordiform with an attenuate apex [or elliptic-ovate, cordate to rounded at base and acute to acuminate at apex], bearing 5–11 abaxially prominent longitudinal nerves, the two flanking the midrib extending to the apex, the others forming a marginal commissure, interconnected by $\pm$ transverse, anastomosing veinlets, often with free vein-endings, the leaf margins bearing bulbous papillae. Inflorescences long-pedunculate, nodding from leaf axils, (1 or) 2 or 3[–several]-flowered, with long, articulated pedicels, each subtended by a small, nearly linear, erect bracteole and with another near the middle, this in turn often subtending another pedicel. Flowers ca. 1 cm in diameter; tepals 4, green, often tinged with purple, free, nearly equal [or one much larger than the others], spreading, oblong-elliptic to ovate, often with recurved margins, papillose on the inner surface, with 3–5 nonanastomosing nerves. Stamens 4; filaments purple (in ours), ca. half the length of the tepals, broad and thickened, papillose; anthers orange, borne nearly perpendicular to the filaments, oval; pollen grains globose to ovoid, reticulate,



FIGURE 1. **Croomia**. a-m, *C. pauciflora*: a, flowering plant with rhizome, $\times \frac{1}{2}$; b, same, from above, $\times \frac{1}{2}$; c, flower bud just before opening, tepals somewhat re-

30–50 μm in the largest dimension. Ovary broadly conical, with 1 or 2 longitudinal groove(s) and a papillose stigmatic knob, bearing 2–6(–8) pendent ovules. Fruit flattened, broadly bottle shaped, the 2 valves opposite the inner tepals. Seeds globose-ovoid, dark colored, striate, bearing a tuft of multicellular appendages along and near the funicle. Embryo minute, clavate-capitate, broadened at the cotyledonary end. TYPE SPECIES: *C. pauciflora* (Nutt.) Torrey & Gray (*Cissampelos pauciflora* Nutt.). (Named for the lawyer and botanist Hardy Bryan Croom, 1797–1837, who collected in the Southeast and died with his family in a shipwreck off the coast of North Carolina.)

Probably three species: *Croomia pauciflora* in the southeastern United States; *C. japonica* Miq. (*C. kiusiana* Makino) of southern Japan, the Ryukyu Islands, and eastern China; and *C. heterosepala* (Baker) Okuyama (*C. japonica* Makino, *C. japonica* Miq. var. *heterosepala* Baker) of southern Japan. The Japanese species are known by the local names *hime-nabewari* and *nabewari* (*hime* = little; *nabe* = pot; *wari* = to break). They differ from the American species in their larger flowers, shorter petioles, more numerous nodes along the rhizome, and lesser tendency toward cordate leaf bases. These species, especially the populations in China, need further investigation.

Croomia pauciflora grows on various substrates (probably best on limestone) on rich, loamy, shaded slopes from the southern Appalachians of Alabama, southward (in similar habitats) into the Coastal Plain, across most of that state, and into Georgia and Florida along the Chattahoochee and Apalachicola rivers in ravines, on bluffs, and on islands. In Florida it grows in the shade of *Torreya taxifolia* Arnott and, according to Harper (1942), is associated with many herbs of Appalachian affinity.

Spreading by rhizomes, *Croomia pauciflora* forms abruptly bordered, probably clonal, colonies with sometimes hundreds of upright shoots. At the southern end of its range, flowering is during March and April; farther north, in May. It is reported to remain green through the summer. The section of rhizome corresponding to a leafy shoot bears five or six distichous scale leaves. The second scale leaf from the basal end subtends a bud from which a branch may arise. The third scale is perpendicular to the plane of distichy and subtends a bud that begins new rhizomatous growth the following year (see Tomlinson & Ayensu).

The species is rare and apparently vulnerable to disturbance, as well as slow to propagate and spread. It is thus listed as threatened at the national

volute, $\times 6$; d, open flower, stamens dehiscent, $\times 6$; e, flower, one tepal and stamen removed, ovary in vertical section, placentation apical, ovules anatropous, $\times 6$; f, undehiscent stamen, adaxial side, $\times 12$; g, young fruit, $\times 2$; h, same, in vertical section, arils developing from seeds, $\times 3$; i, immature seed nearly covered with strands of aril, $\times 6$; j, same, part of aril removed to show funiculus (note that some of aril is produced from funiculus), $\times 5$; k, opened fruit, $\times 2$; l, mature seed, aril removed, $\times 6$; m, same, in vertical section, seed coat and embryo unshaded, endosperm stippled, oriented as seed in "l," $\times 5$.

level (Ayensu & Filippis) and at the state level in Georgia and Alabama. In Florida, where feral pigs feed upon the rhizomes, it is designated as endangered (Ward).

Asa Gray assigned *Croomia* to the Berberidaceae but later perceived its relationship with *Stemona* and added it to the Stemonaceae (Roxburghiaceae).

As an anatomical curiosity, *Croomia* has been the subject of several studies. It differs from most monocots in that the vascular systems of the upright stem and rhizome are organized into discontinuous cylinders with pith and cortex on either side. Some of the vascular tissue is amphivasal, taking the form of discrete bundles in the upright stem and a dissected cylinder in the rhizome. Both *Stemona* and *Stichoneuron* have raphides in some organs and vessel elements in the stem. Whether or not these are present in *Croomia* is pertinent to the question of the circumscription of the family, but there are contradictions in the literature concerning both. I have seen scattered isodiametric and elongate crystals in the stem and petiole of *C. pauciflora* but have found vessel elements only in the root.

Tomlinson & Ayensu interpreted the ovary as being unicarpellate, with two vascular bundles corresponding to the dorsal and ventral bundles of a conduplicate carpel; they suggested that the similar ovary of *Stemona* may be of the same structure, although it has a basal placenta. Others have described the ovary of *Stemona* as bicarpellate. Swamy interpreted the two bundles as the dorsal bundles of a pair of carpels and considered the ventral bundles to be represented by the small traces that extend from the receptacle to the basal ovules. Most authors have described the flowers as tending toward perigyny, but Ayensu thought the ovary "without question" to be superior.

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