JOURNAL

OF THE

ARNOLD ARBORETUM

VOL. 46 APRIL 1965 NUMBER 2

THE GENERA OF POLYGONACEAE IN THE SOUTHEASTERN UNITED STATES [1]

SHIRLEY A. GRAHAM AND C. E. WOOD, JR.

POLYGONACEAE A. L. de Jussieu, Gen. Pl. 82. 1789, "Polygoneae," nom. cons.

(BUCKWHEAT FAMILY)

Annual or perennial herbs, shrubs, trees, or vines, often with conspicuously swollen nodes, the nodes completely or partly surrounded by a membranaceous or scarious sheath, the ocrea, or this reduced to a row of hairs or completely wanting in a few genera. Leaves entire [rarely pinnatifid or palmately cleft], alternate or whorled [or opposite], petiolate to sessile, membranaceous to fleshy or leathery, occasionally articulated at the base with the stem. Inflorescences diverse, the flowers seldom solitary, mostly clustered into few-flowered fascicles, each fascicle subtended by a bract and each flower by a persistent sheath (ocreola) and occasionally also by 2 scarious bractlets; rarely fascicles subtended by and partly included in an involucre, the flowers subtended at the base only by numerous bractlets. Flowers regular, with a variable number of parts, mostly 3- or 5-merous, bisexual or unisexual, the base (receptacle?) narrowed into a short or long stipe which articulates with the pedicel. Tepals (2–)5 or 6, in 2

[1] Prepared for a generic flora of the southeastern United States, a joint project of the Gray Herbarium and the Arnold Arboretum made possible through the support of George R. Cooley and the National Science Foundation and under the direction of Reed C. Rollins and Carroll E. Wood, Jr. The scheme follows that outlined at the beginning of the series (Jour. Arnold Arb. **39**: 296–346. 1958). The area covered in this, as in former treatments, is bounded by and includes North Carolina, Tennessee, Arkansas, and Louisiana. Material included in the descriptions in brackets applies to species outside this area, and references marked by an asterisk have not been seen by the authors.

Drs. Richard A. Howard and Ben W. Smith have reviewed the treatments of *Coccoloba* and of *Rumex* subg. *Acetosa*, respectively; their suggestions and corrections are gratefully acknowledged. Dr. Howard has generously allowed us to report two chromosome counts made by him; and Dr. R. B. Channell collected excellent flowering and fruiting material which has been indispensable in the study of *Brunnichia*. The illustrations were prepared by Arnold D. Clapman.

whorls, imbricate or quincuncial in bud, often petaloid, ± united, forming a short to long floral tube, persistent and sometimes enlarging in fruit. Stamens (3–)5–8 (9), inserted perigynously in 2 whorls, variously arranged but generally paired, occasionally alternating with nectariferous teeth and/or united into an annulus surrounding the ovary; filaments filiform, generally of two lengths, those opposite the internal whorl of tepals longest; anthers 2-locular, longitudinally dehiscent, versatile or basifixed; pollen of diverse types. Gynoecium (2–)3-carpellate, syncarpous; stigmata punctate, capitate, fimbriate, or flabelliform; styles 1–3, included to exserted; ovary 1, superior, lenticular or pyramidal, 1-locular, rarely incompletely 3-locular at base, sessile or slightly stalked; ovule 1, basal, on a short and thick or long and thin funiculus, orthotropous, the inner integument longer than the outer at anthesis and forming the micropyle. Fruit a lenticular or pyramidal (3-angled) achene, scarcely to entirely inclosed by the membranaceous tepals or the leathery or fleshy, accrescent floral tube. Embryo developing in the micropylar end of the seed, straight or curved, lying in one of the angles of the seed or along the middle of one side, outside of and curved around the abundant mealy or horny, sometimes ruminate endosperm or centered in it; perisperm wanting; radicle superior; cotyledons of diverse shapes. Embryo sac development normal (Polygonum type). TYPE GENUS: *Polygonum* L.

Predominantly of the North Temperate Zone, consisting of about 30 genera and 700 species; represented in the southeastern United States by seven genera. The family is a very natural and easily recognized one, but infrafamilial categories are much debated. At least five major classifications, none of which is entirely satisfactory, have been proposed (cf. Meissner, Bentham & Hooker, Dammer, Gross, and Jaretzky). The classification of Gross, which seems to be most in accord with the commonly accepted relationships of the genera, is followed here, although the subfamilial sequence is not considered by the writers to be an expression of the order of evolution within the family.

Two genera, *Fagopyrum* Mill. and *Emex* Campd., included in Small's *Manual of the Southeastern Flora*, are not known to be naturalized in the Southeast. *Fagopyrum esculentum* Moench (*F. sagittatum* Gilib., *Polygonum Fagopyrum* L.), buckwheat, $2n = 16$, grown extensively as a grain in Russia, is cultivated to a limited extent in the United States. Although escaping to roadsides and other disturbed areas, it probably does not persist for more than a season, at least in our area. The genus is included, however, in the key to genera because of its occurrence as a waif. The Mediterranean *Emex spinosa* (L.) Campd. is a waif evidently rarely introduced as seed in ballast but apparently not persistent in the Southeast.

Various authors have related the Polygonaceae to several families, including the Chenopodiaceae, Phytolaccaceae, Basellaceae, and Caryophyllaceae, mainly on the basis of the unilocular ovary and single basal ovule.

The family is now generally regarded as derived from and advanced over the Caryophyllaceae.

Floral anatomy of the Polygonaceae has been studied intensively. The most recent workers, Laubengayer and Vautier, agree that the basic floral plan is three-merous, with whorled parts, as in *Eriogonum* and *Rumex*, and that the five-merous condition, found, for example, in *Polygonum*, is derived. In five-merous flowers one tepal is bivalent, as shown by its position partly in and partly out of the two whorls of tepals and by its two vascular traces. (In some cases, the second trace may be reduced or missing, but the tepal generally remains intermediate in position between the two whorls.)

According to Laubengayer, the unilocular, uniovulate ovary was derived from a multiovulate gynoecium with free-central placentation by suppression of the lower portion of the ovary and by adnation of the lower part of the placenta to the lower ovary wall. The "funiculus" is, then, the remaining portion of the free-central placenta. Joshi, however, believes the ovule is borne on a true funiculus, with only the basal end of the stalk perhaps representing a vestige of a free-central placenta. (See Laubengayer and Vautier for summaries of the views of other authors on various aspects of the floral anatomy.)

The characteristic ocrea of the Polygonaceae has been interpreted variously as an outgrowth of the sheathing base of the petiole, as the product of the fusion of either a row of adjacent stipules or two lateral stipules, or as an expanded axillary stipule.

The pollen morphology is extremely diverse. The basic type from which others are thought to have been elaborated is ellipsoid, heavy- and smooth-walled, and has three long furrows, each with a central germ pore. It is found in such entomophilous genera as *Eriogonum*, *Fagopyrum*, and *Antigonon*, and in some insect-pollinated species of *Polygonum*. Evolution of the pollen grain is thought to have proceeded from this in two directions: in insect-pollinated species (such as *Polygonum Persicaria*), toward further elaboration of exine sculpture with concomitant reduction of furrows and increase in number of pores, and in wind-pollinated species toward reduction in number of pores and the thickness of exine, and loss of furrows.

The family is of minor economic importance, including a few food plants (e.g., *Fagopyrum*, *Rheum Rhaponticum* L.), some tropical timber trees, a number of ornamentals, and some noxious weeds. *Fagopyrum* was formerly the major commercial source of a flavonol, rutin, which strengthens capillary blood-vessel walls, preventing hemorrhage in victims of high blood pressure (cf. Couch, Humphreys).

REFERENCES:

BAILLON, H. Polygonacées. Hist. Pl. **11**: 367–400. 1892.

BENTHAM, G., & J. D. HOOKER. Polygonaceae. Gen. Pl. **3**: 88–105. 1883.

BUCHINGER, M. Nota sobre la subdivisión de la familia de las Poligonáceas. Bol. Soc. Argent. Bot. **7**: 42, 43. 1957.

COUCH, J. F. Rutin for the capillaries. Yearb. U. S. Dep. Agr. **1943/47:** 711–715. 1947. [Obtained from *Fagopyrum*.]

DAMMER, U. Polygonaceae. Nat. Pflanzenfam. III. **1a:** 1–36. 1892.

DUKE, J. A. Polygonaceae. *In*: R. E. WOODSON, JR., & R. W. SCHERY, Flora of Panama. Ann. Missouri Bot. Gard. **47:** 323–359. 1960. [Including general information on *Rumex*, *Polygonum*, *Coccoloba*, *Antigonon*; treatment of *Coccoloba* by R. A. HOWARD.]

EDMAN, G. Zur Entwicklungsgeschichte der Gattung *Oxyria* Hill, nebst zytologischen, embryologischen und systematischen Bemerkungen über einige andere Polygonaceen. Acta Hort. Berg. **9:** 165–291. 1929. [Includes much of general interest about the family; large bibliography.]

EMBERGER, L. La structure de la fleur des Polygonacées. Compt. Rend. Acad. Sci. Paris **208:** 370–372. 1939. [See also Rev. Gén. Bot. **51:** 581–638. 1940.]

GEITLER, L. Zur Morphologie der Blüthen von *Polygonum*. Österr. Bot. Zeitschr. **78:** 229–241. 1929.

GROSS, H. Beiträge zur Kenntnis der Polygonaceen. Bot. Jahrb. **49:** 234–339. 1913. [Morphology, anatomy, taxonomy.]

HUMPHREYS, F. R. The occurrence and industrial production of rutin in south-eastern Australia. Econ. Bot. **18:** 195–253. 1964. [From leaves of *Eucalyptus macrorrhyncha*; includes review of use of *Fagopyrum* and flowers of *Sophora japonica* as major sources; large bibliography.]

JARETZKY, R. Beiträge zur Systematik der Polygonaceae unter Berücksichtigung des Oxymethylanthrachinon-Vorkommens. Repert. Sp. Nov. **22:** 49–83. *pl. 22*. 1925.

———. Histologische und karyologische Studien an Polygonaceen. Jahrb. Wiss. Bot. **69:** 357–490. 1928.

JOSHI, A. C. The nature of the ovular stalk in Polygonaceae and some related families. Ann. Bot. II. **2:** 957–959. 1938.

KNUTH, P. Handbook of flower pollination. vol. 3. (Transl. J. R. A. DAVIS.) iv + 644 pp. Oxford. 1909. [*Rumex*, 337–340; *Polygonum*, 341–349.]

LAUBENGAYER, R. A. Studies in the anatomy and morphology of the polygonaceous flower. Am. Jour. Bot. **24:** 329–343. 1937. [Includes all genera of our area except *Antigonon*.]

MAHONY, K. L. Morphological and cytological studies on *Fagopyrum esculentum*. Am. Jour. Bot. **22:** 460–473. *pls. 1, 2*. 1935; II. Embryogeny. *Ibid.* **23:** 129–133. 1936.

MEISSNER, C. F. Monographiae generis Polygoni prodromus. iv + 169 pp. *7 pls*. Genève. 1826.

———. Polygonaceae [except Eriogoneae]. DC. Prodr. **14:** 1–186. 1856.

MITRA, G. C. The origin, development and morphology of the ochrea in *Polygonum orientale* L. Jour. Indian Bot. Soc. **24:** 191–199. 1945.

PERDRIGEAT, C. A. Anatomie comparée des Polygonées et ses rapports avec la morphologie et la classification. Actes Soc. Linn. Bordeaux **55:** 1–91. *pls. 1–3*. 1900.

RECHINGER, K. H., fil. Polygonaceae. *In*: G. HEGI, Illus. Fl. Mittel-Europa. ed. 2. **3:** 352–436. 1958. [*Rumex*, *Oxyria*, *Rheum*, *Polygonum*, *Fagopyrum*.]

RIDLEY, H. N. The dispersal of plants throughout the world. xx + 744 pp. *22 pls*. Kent, England. 1930. [See index for scattered references on dispersal of *Rumex*, *Polygonum*, and *Brunnichia*.]

ROBERTY, G., & S. VAUTIER. Les genres de Polygonacées. Boissiera **10:** 7–128.

1964. [An unsatisfactory treatment based on gross morphology and the unique evolutionary ideas of Roberty; much "splitting" of categories between family and species, much "lumping" at the specific level (e.g., *Rumex* [ca. 100 spp.] reduced to 10 spp. and *Eriogonum* [ca. 150 spp.] reduced to 8 spp., with 72 names, mostly of well-marked species of the western U. S., equated with the distinctive *E. tomentosum* of the southeastern U. S.); not all names included; inadequate material studied; useful bibliography.]

SINNOTT, E. W., & I. W. BAILEY. Investigations on the phylogeny of angiosperms. 3. Nodal anatomy and the morphology of stipules. Am. Jour. Bot. **1**: 441–453. 1914.

SIRRINE, E. Structure of the seed coats of Polygonaceae. Proc. Iowa Acad. Sci. **2**: 128–135. *pls. 7–9*. 1895.

SOUÈGES, R. Recherches sur l'embryogénie des Polygonacées. Bull. Soc. Bot. France **66**: 168–199. 1919. [*Polygonum Persicaria.*] *Ibid.* 75–85. [*Rheum.*]

TUTIN, T. G., ed. Polygonaceae. *In*: T. G. TUTIN, V. H. HEYWOOD, *et al.*, eds., Fl. Europaea **1**: 75–89. 1964. [*Koenigia, Polygonum, Bilderdykia, Reynoutria, Fagopyrum, Oxyria, Rheum, Rumex, Emex, Muehlenbeckia, Calligonum, Atraphaxis*; treatments of various genera prepared by T. G. TUTIN, D. A. WEBB, K. H. RECHINGER, and WEBB & A. O. CHATER.]

VAUTIER, S. La vascularisation florale chez les Polygonacées. Candollea **12**: 219–343. 1949. [Including all genera of our area.]

WEBB, D. A., & A. O. CHATER. Polygonaceae. *In*: V. H. HEYWOOD, ed., Flora Europaea. Notulae systematicae ad Floram Europaeam spectantes No. 2. Repert. Sp. Nov. **68**: 187–189. 1963. [Includes discussion of generic limits in Polygonaceae, especially *Polygonum, sensu lato.*]

WILLIAMS, B. C. The occurrence of intercellular canals in root tips of plants in the Polygonaceae and the Labiatae. (Abstr.) Am. Jour. Bot. **37**: 668. 1950.

WODEHOUSE, R. P. Pollen grains in the identification and classification of plants. VI. Polygonaceae. Am. Jour. Bot. **18**: 749–764. *pl. 51*. 1931. [Includes descriptions of pollen of *Eriogonum, Rumex, Polygonum, Antigonon.*]

WOODCOCK, E. F. Observations on the development and germination of the seed in certain Polygonaceae. Am. Jour. Bot. **1**: 454–476. *pls. 45–48*. 1914. [Includes *Rumex, Fagopyrum, Polygonum, Polygonella.*]

KEY TO THE GENERA OF POLYGONACEAE

General characteristics: *leaves mostly alternate and entire; nodes usually swollen and surrounded by a membranaceous sheath; flowers regular, the tepals forming a floral tube with the base narrowed into a stipe and articulated with the pedicel; ovary 1, superior, 1-locular, with a single basal orthotropous ovule; fruit a lenticular or 3-angled achene.*

A. Plants herbaceous or suffrutescent, occasionally (in *Polygonum*) twining climbing vines without tendrils.

B. Flowers subtended by and partly inclosed in an involucre; ocreae wanting; stamens 9. . . . . 1. *Eriogonum.*

B. Flowers not involucrate, subtended by membranaceous ocreolae; ocreae present; stamens (3–)5–8 (9).

C. Tepals 6, the outer spreading or reflexed and remaining small in fruit, the inner erect, enlarging in fruit and often with conspicuous, raised venation or callosities. ..... 2. *Rumex.*

C. Tepals (2–)4 or 5 (6), all erect (the outer sometimes reflexed in fruit in *Polygonella*), without raised venation or callosities.

D. Tepals remaining small in fruit; achene pyramidal, exserted; embryo embedded in the endosperm; cotyledons convolute; flowers in small panicles, the upper appearing corymbiform. ..... [*Fagopyrum.*]

D. Tepals enlarging in fruit; achene lenticular or pyramidal, generally inclosed by the tepals; embryo in one angle of the achene outside the endosperm; cotyledons accumbent or incumbent, not convolute; flowers in panicles or spikelike racemes.

E. Branches nodal, not adnate to the internode; flowers 2 to several at a node in fascicles, the ocreolae imbricate, small and inconspicuous, scarcely unilaterally flared. ..... 3. *Polygonum.*

E. Branches appearing internodal due to adnation to the internode above the node of origin; flowers solitary at the nodes, in the axils of conspicuous, imbricated, unilaterally flared ocreolae. ..... 4. *Polygonella.*

A. Plants shrubs, small trees, or tendril-bearing vines.

F. Plants shrubs or small trees; leaves thick, leathery, reniform to orbicular; ocreae present; fruit an achene surrounded by a fleshy floral tube. ..... 5. *Coccoloba.*

F. Plants tendril-bearing vines; leaves membranaceous, ovate to deltoid; ocreae wanting or much reduced; fruit a 3–6-angled achene inclosed by membranaceous to leathery tepals.

G. Tepals rose-red, membranaceous; stipe remaining narrow in fruit; stigmata reniform-capitate. ..... 6. *Antigonon.*

G. Tepals yellow-green, leathery; stipe expanding in fruit to form a broad unilateral wing; stigmata irregularly flabelliform. ..... 7. *Brunnichia.*

Subfam. ERIOGONOIDEAE Meissn.

Tribe ERIOGONEAE [Dumort.]

1. **Eriogonum** Michaux, Fl. Bor.-Am. 1: 246. *pl. 24.* 1803.

Herbaceous, suffrutescent, or occasionally shrubby, bi- or triennials or perennials [or annuals] with large taproots, inhabiting open, dry, sandy or rocky regions; densely woolly [rarely glabrous]; branching di- or trichotomously; nodes lacking ocreae. Leaves basal in rosettes and cauline [or basal only], petiolate to sessile, the blade often decurrent on the petiole, the lower (abaxial) surface densely silver or brown tomentose. Basal leaves diverse in shape and size, in ours narrowly to broadly elliptic to oblanceolate; cauline leaves alternate, whorled [or opposite], narrowly to broadly elliptic, becoming bracts toward the top of the plant. Bracts foliaceous [or stipuliform], connate at base of involucre. Inflorescences

diverse, basically cymose; floriferous branches axillary and/or terminal; flowers subtended by and partly included within a turbinate [to cylindrical], 3–5(–8)-lobed involucre, the involucres solitary on the peduncle [or clustered]. Flowers 3-merous, the base narrowed into a long stipe [or this nearly wanting], bisexual, subtended at the base by numerous linear or lanceolate, scarious, setiferous to villous bractlets; flowers many [rarely 1] in an involucre, exserted at anthesis. Tepals 6, petaloid, white to yellow [or red], ovate to linear, erect or nearly so at anthesis, enlarging and remaining erect in fruit or the outer whorl becoming oriented at right angles to the pedicel and the inner remaining erect, covering the fruit. Stamens 9, two opposite each outer tepal and one opposite each inner tepal, persistent; filaments pilose at base, exserted [or included]; anthers versatile; pollen ellipsoid, tricolpate with long, tapering furrows, the exine thick, coarsely granular with 3 meridional strips between the furrows. Gynoecium 3-carpellate; stigmata 3, capitate; styles 3, filiform, long and exserted [or short and included]; ovary 3-angled, glabrous or villous. Fruit a 3-angled (or -winged?) ovate- or oblong-pyramidal, beaked achene. Embryo straight [or curved], centered [or excentric] in mealy endosperm; cotyledons thick, orbicular; radicle shorter [or longer] than cotyledons. TYPE SPECIES: *E. tomentosum* Michx. (Name from Greek, *erion,* wool, and *gonu*, knee, in reference to the tomentose pubescence and the geniculate nodes of some species.) — UMBRELLA-PLANT.

A North American genus of about 150 species in four subgenera and 14 sections, best developed in the western United States and well known for the taxonomic difficulties it presents. The four species occurring in the Southeast belong to subg. ERIOGONUM (subg. *Eueriogonum* S. Wats.),[2] comprised of perennials with turbinate involucres without angles or nerves and two to five or more foliaceous bracts, and sect. ERIOGONUM (§ *Eriantha* Benth.), having flowers with a stipelike base, achenes not winged, and embryo straight, centered in the endosperm.

Most widespread in the Southeast is *Eriogonum tomentosum* Michx., occurring from South Carolina to Florida along the sand hills of the inner part of the Coastal Plain. It is easily recognized by the dense, brown tomentum on the undersurface of the leaves and by the whorled cauline leaves. The three other southeastern species, *E. longifolium* Nutt., *E. Harperi* Goodman, and *E. floridanum* Small, have white pubescence and alternate cauline leaves. They and the eastern Texas *E. vespinum* Shinners

[2] It is not clear whether the names proposed by Watson (1877) were meant to be subgenera or sections. He refers to them as sections and indicates to which section the earlier names of Bentham (1856) and Torrey & Gray (1870) belong. The rank of Bentham's and Torrey & Gray's names also is unclear, being indicated only by the sectional sign (§), which was commonly used by the latter authors to indicate subgenera (see footnote 4 in Brizicky, Jour. Arnold Arb. **44**: 62. 1963). In a later work, Watson (1879) arranged the names in such a way as to suggest that his were of subgeneric and Torrey & Gray's of sectional rank. Bentham & Hooker considered Watson's names sections and Torrey & Gray's names series. Following recent authors (Coville & Morton, Munz & Keck, and Anderson), Watson's names are treated here as subgenera and Bentham's and Torrey & Gray's as sections.

are morphologically so similar that maintenance of four species is highly questionable, and a re-evaluation of their taxonomy is recommended. *Eriogonum longifolium* occurs in Texas, Oklahoma, Kansas, southern Missouri, and Arkansas, while *E. Harperi* is described as endemic to Colbert and Franklin counties in northwestern Alabama. Specimens examined from the area of Hot Springs, Arkansas, are difficult to place in either. *Eriogonum floridanum,* endemic to central peninsular Florida, differs from the preceding two species in having generally larger flowers, 6–10 mm. long *vs.* 4–8 mm. long, with very long pedicels (exceeding 1 cm.) in pedunculate, rather than nearly sessile, involucres. *Eriogonum vespinum* is distinguished from *E. longifolium* only in being less densely pubescent and having slightly longer peduncles and floral stipes.

Chromosome numbers, mostly undocumented, of several species of the western United States have been reported ($2n$ = 18, 22, 24, 32, 34, 40, and 80), the most common number being $2n = 40$. At least two western species, *Eriogonum fasciculatum* Benth. and *E. nudum* Dougl., include polyploid races of $2n = 40$ and 80. The basic gametic number is thought to be $x = 10$, with hybridization and aneuploid increases and decreases accounting for the wide range of numbers. Natural hybrids of several species are known or suspected, but production of artificial hybrids is hampered by the difficulty of emasculating the small flowers, each of which produces but a single seed.

The genus is considered to be closely related to the endemic American *Chorizanthe* R. Br. and *Oxytheca* Nutt., the only other members of the family with involucrate, nine-staminate flowers.

REFERENCES:

Under family references see LAUBENGAYER, VAUTIER, and WODEHOUSE.

ANDERSON, F. W. "Indicative" Eriogonums. Bot. Gaz. **12:** 250–252. 1887. [*E. ovalifolium* in Montana not indicative of silver in the soil.]

ANDERSON, J. M. A revision of *Eriogonum* section *Pedunculata*. Diss. Abstr. **20:** 2509. 1960.*

BENTHAM, G. Eriogoneae. DC. Prodr. **14:** 5–28. 1856.

COVILLE, F. V., & C. V. MORTON. *Eriogonum intrafractum*, a new species and new subgenus from Death Valley, California. Jour. Wash. Acad. Sci. **26:** 303–306. 1936. [Subg. *Clastomyelon.*]

GANDOGER, M. Le genre *Eriogonum* (Polygonaceae). Bull. Soc. Bot. Belg. **42:** 183–200. 1905. [Includes descriptions of 23 new spp. and many new vars., all from the U. S.]

GOODMAN, G. J. A new *Eriogonum* from the Southeast. Bull. Torrey Bot. Club **74:** 329–331. 1947. [*E. Harperi.*]

MUNZ, P. A., & D. D. KECK. A California flora. 1681 pp. Berkeley, Calif. 1959. [*Eriogonum*, 332–354.]

SHINNERS, L. H. *Eriogonum vespinum* (Polygonaceae), a new species from eastern Texas. Field Lab. **22:** 68, 69. 1954.

STEYERMARK, J. A. Rare Missouri plants. V. Umbrella plant (*Eriogonum longifolium*). Missouri Bot. Gard. Bull. **44:** 106, 107. 1956.

STOKES, S. G. The genus *Eriogonum*, a preliminary study based on geographic distribution. 132 pp. San Francisco. 1936.

——— & G. L. STEBBINS. Chromosome numbers in the genus *Eriogonum*. Leafl. West. Bot. **7**: 228–233. 1955.

TORREY, J., & A. GRAY. A revision of the Eriogoneae. Proc. Am. Acad. Sci. **8**: 145–200. 1870. [*Eriogonum*, 146–190.]

WATSON, S. Descriptions of new species of plants, with revisions of certain genera. Proc. Am. Acad. Sci. **12**: 246–278. 1877. [*Eriogonum*, 254–269.]

———. Contributions to American botany. II. Descriptions of some new species of North American plants. *Ibid.* **14**: 288–303. 1879. [*Eriogonum*, 295, 296.]

Subfam. POLYGONOIDEAE [Meissn.]

Tribe RUMICEAE Dumort.

2. **Rumex** Linnaeus, Sp. Pl. 1: 333. 1753; Gen. Pl. ed. 5. 156. 1754.

Herbaceous annuals or perennials of open, generally disturbed habitats. Plants glabrous, with long taproots; ocreae scarious, cylindrical, the margins often becoming shredded with age. Leaves basal and cauline, entire, sometimes with crisped or undulate margins, membranaceous to subcoriaceous, long-petiolate, lanceolate [linear] to ovate, the base acute to obtuse or hastate, the apex acute; cauline leaves alternate, the upper ones reduced. Inflorescence composed of [a single terminal or] several axillary panicles, the flowers mostly 3 to several in an axillary fascicle at each node. Flowers 3-merous, green or reddish, bisexual or unisexual, the plants monoecious, polygamomonoecious, or dioecious; when monoecious the ♂ flowers borne above (distal to) the ♀ ones. Tepals 6, slightly united at base, forming a short floral tube which is narrowed into a long stipe shorter than to exceeding the pedicel; 3 outer tepals linear, reflexed and remaining small in fruit; 3 inner tepals ("valves") broadly ovate, erect and accrescent, inclosing the fruit, in some species developing raised reticulations and/or thickened callosities ("grains" or tubercles) on 1 or all 3 tepals, or with a prominent midvein on the outer (abaxial) side of each, the margins entire or variously toothed. Stamens 6, in pairs opposite the outer whorl of tepals; filaments short; anthers basifixed; pollen spheroidal, 18–32 μ in diameter, 3–6-colporate, the furrows long and narrow, variously arranged depending on the number present, the exine finely to coarsely reticulate. Gynoecium 3-carpellate; stigmata 3, fimbriate; styles 3; ovary 3-angled. Fruit a 3-angled, pyramidal achene. Seed coat smooth, shining. Embryo nearly straight, lying along the middle of one side of the achene; cotyledons linear to lanceolate, generally parallel or rarely perpendicular to wall of achene. (Including *Acetosa* Mill., *Acetosella* (Meissn.) Fourr.) LECTOTYPE SPECIES: *R. Patientia* L.; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. 1: 653. 1913. (Name adopted by Linnaeus from ancient Latin.) — DOCK, SORREL.

A genus of over 100 species, world-wide in distribution, although poorly represented in tropical regions. About 50 species and hybrids are reported from North America, 11 of these introductions from Europe.

Thirteen to fifteen species in three of the four subgenera occur in the southeastern United States. Several species are widely distributed as noxious weeds of cultivated ground and roadsides.

Subgenus RUMEX (*subg. Lapathum* Pers.) is comprised of annuals and perennials, with leaf bases round to cuneate, never sagittate or hastate, flowers bisexual and inner tepals with or without callosities. The chromosomes are the smallest in the genus, $x = 10$, and $2n$ ranges from 20 to 200. Polyploidy and inter- and intraspecific hybridization have been reported in both sections of the subgenus.

In sect. RUMEX (§ *Simplices* Rech. f.), the single stem is unbranched with a terminal inflorescence. The six species of this section which occur in the southeastern United States are of European origin and are highly polymorphic, mostly with several subspecies. *Rumex crispus* L., $2n = 60$; *R. pulcher* L., $2n = 20$; and *R. obtusifolius* L., $2n = 40$ and 60, are widespread in the United States. Growing along roadsides and in waste places throughout our area, they are occasionally sympatric (e.g., in New Orleans, Louisiana; Tallahassee, Florida; and Granger and Hawkins counties, Tennessee). Putative natural hybrids of *R. crispus* × *R. obtusifolius* have been reported from Louisiana and of *R. crispus* × *R. pulcher* from Virginia. *Rumex crispus* in Great Britain is composed of several races, all evidently interfertile (Rechinger, 1961). Although widely distributed in the northern and western states, *R. conglomeratus* Murr., $2n = 20$, appears in our area only in the more easterly parts of North Carolina. Also common elsewhere in the United States but of limited distribution in the Southeast are *R. Patientia* L., $2n = 60$, known from scattered localities in Tennessee and North Carolina, and *R. maritimus* L. var. *fueginus* Dusén (confused by Small with *R. persicarioides* L.), $2n = 40$, reported from Little Rock, Arkansas. According to Rechinger (1937), *R. sanguineus*, $2n = 20$, is probably not present in the Southeast but has been confused by American taxonomists with *R. conglomeratus*.

Section AXILLARES Rech. f., characterized by plants with leafy axillary branches and secondary inflorescences, has its center of development in North America. Extra-American species are believed by Rechinger, on the basis of their isolated systematic position, to be relics of ancient lines of evolution. Seven species of this section have been collected in the Southeast, but *R. mexicanus* Meissn. and *R. cuneifolius* Campd., native to Mexico and South America, respectively, are known from limited material which suggests they are not established introductions. *Rumex verticillatus* L., $2n = 48$, 60, *R. floridanus* Meissn., and *R. fascicularis* Small, restricted to the Atlantic and Gulf coastal plains, are distinguished from one another on the basis of slight morphological differences which scarcely support specific rank. Also occurring on the Coastal Plain in Louisiana is *R. chrysocarpus* Moris (*R. Berlandieri* Meissn., *R. Langloisii* Small). *Rumex altissimus* Wood, $2n = 20$, widely distributed in the eastern and central United States, is known from most of the Southeastern States, generally occurring inland from the Coastal Plain. Several experi-

mental crosses made among species in the section (see Sarkar) show a high degree of pairing and good seed-set in the F_1 generation of the diploids, but completely sterile triploid and tetraploid hybrids.

Subgenus ACETOSA (Mill.) Reichenb., morphologically and cytologically the most variable subgenus, includes about 40 species in six sections, with a predominantly Old World distribution (most abundant in northern and eastern Africa, southern Europe, and the Middle East). The plants are shrubs or perennial or annual herbs and are hermaphroditic or dioecious, commonly with hastate or sagittate leaves, and inner tepals much longer than the achene and mostly without callosities. Chromosome numbers vary from $2n = 8$ to 40. The dioecious annual, *Rumex hastatulus* Baldw. ex Ell., $2n = 8$ ♀, 9 ♂, or $2n = 10$ ♀, 10 ♂, is the only member of sect. ACETOSA subsect. AMERICANAE Löve & Sarkar; its nearest relatives are the western American *R. paucifolius* Nutt. ex S. Wats. (§ *Paucifoliae* Löve & Sarkar) and the Old World *R. Acetosa* L. and *R. thyrsiflorus* Fingerh. (§ *Acetosa*), both with $2n = 14$ ♀, 15 ♂ and adventive in northeastern America. *Rumex hastatulus* is widespread in sandy soils of the Coastal Plain from North Carolina to northern Florida, west to Texas and Oklahoma, and occurs in the adjacent Piedmont on disturbed, well-drained sites.

Sex determination in *Rumex hastatulus, R. Acetosa*, and *R. paucifolius*, $2n = 14$ and 28, has been studied by several workers. An X/A balance mechanism of sex determination similar to that originally discovered in *Drosophila* occurs in *R. Acetosa*, with sex expression determined by the ratio of autosomes to X chromosomes, the Y chromosomes having no effect. Sex expression in *R. paucifolius* appears, on the other hand, to follow the more primitive X/Y scheme, discovered in *Silene* (*Melandrium*) and described later in *R. Acetosella*, in which strong male factors are located in the Y chromosome and the effects of the autosomes are secondary to the influence of XX *versus* XY.

Two karyologically distinct races differing in sex-chromosome morphology and chromosome number occur in *Rumex hastatulus*. The differences in karyotype have involved loss of one autosomal pair and the appearance of multiple Y chromosomes, changes which Smith has postulated to be the result of two successive translocations. Populations from North Carolina to Florida and Mississippi have a modified X/A mechanism ($2n = 6 + XX$ ♀ and $6 + XY_1Y_2$ ♂). Although sex is determined primarily by the ratio of X chromosomes to autosomes, the Y chromosomes are not entirely neutral but contain a region which enhances the expression of maleness. Populations from Louisiana and Texas to Oklahoma and Arkansas have ten chromosomes in both sexes ($2n = 8 + XX$ ♀ and $8 + XY$ ♂). The genetics of sex determination in this western race have not yet been analyzed.

Staminate plants of *Rumex hastatulus* are "heterogametic," producing male- and female-determining pollen in equal numbers; carpellate plants are "homogametic." In North Carolina, carpellate plants (57%) are more abundant than staminate (43%). Smith has suggested that the disparity in sex ratio in *R. hastatulus* may be attributable to a differential

selection favoring either the female-determining pollen or the female-determined embryos prior to the seedling stage, a phenomenon which has been demonstrated in *R. Acetosa* and in other dioecious plant species. Apogamy occurs in a few species of the subgenus but accounts for only an estimated 1–2% of seed-set.

Subgenus ACETOSELLA (Meissn.) Rech. f. consists of a polyploid series of perennial dioecious herbs with hastate or sagittate leaf bases and callus-free tepals which generally do not exceed the achene. One to four species are recognized, depending mainly on the emphasis placed on chromosome number. Löve (1944b), maintaining that "polyploidy alone seems to catapult a species into being," has recognized four species: *Rumex angiocarpus* Murb., $2n = 14$; *R. tenuifolius* (Wallr.) Á. Löve, $2n = 28$; *R. Acetosella* L., *sensu stricto*, $2n = 42$; and the arctic *R. graminifolius* Rudolph ex Lamb., $2n = 56$. The morphological distinctions between these are few, mostly quantitative, and tend to disappear when populations are studied over the entire range. Hexaploids ($2n = 42$) with the character of *R. angiocarpus* (tepals adnate to the fruit) have recently been found in populations from Europe, Canada, and Australia (Johnson & Briggs, p. 166). This complex, including Eurasian weeds of nearly cosmopolitan distribution, is represented in our area by diploid and hexaploid plants. Sex chromosomes are present, and the sex-determining mechanism is thought to be of the X/Y type. *Rumex Acetosella* is generally considered an indicator of acid, worn-out soils, but Artist, finding that the species grows on soils of pH 4.5–8.5, believes its distribution is probably dependent on a combination of several ecological factors, rather than on pH alone.

Pollination in *Rumex* is almost exclusively anemophilous, although insects occasionally are attracted by the red fruiting inflorescences. The fimbriate stigmata are well adapted to receiving air-borne pollen. *Rumex crispus* and *R. obtusifolius* are distinctly proterandrous; several other species are reportedly self-pollinated. Experimental crosses between subgenera have been unsuccessful.

Floral structure in *Rumex* is believed to have been derived by reduction from the basic three-merous type possessed by the closely related *Rheum*. Internal vascular bundles and internal phloem have been described from several species of *Rumex*, including *R. crispus*, *R. Patientia*, and *R. conglomeratus*. The perennial species without internal bundles are considered the oldest members of the genus.

The genus is of little economic importance. The leaves of some species are eaten as salad greens, the oxalic acid content imparting a slightly sour taste. Roots of *Rumex hymenosepalus* Torr., canaigre, contain up to 30% tannin and have been suggested as a commercial source of tannin. Some weedy species, such as *R. crispus*, are pests in cultivated areas, but can be controlled by cutting away the taproot to three inches below the soil surface, since regenerative capacity has been found lacking in the rest of the taproot (Healy).

REFERENCES:

Under family references see DUKE, KNUTH, LAUBENGAYER, RECHINGER, RIDLEY, SOUÈGES, TUTIN, VAUTIER, WODEHOUSE, and WOODCOCK.

AHLES, H. E., C. R. BELL, & A. E. RADFORD. Species new to the flora of North or South Carolina. Rhodora **60:** 10–32. 1958. [*R. Patientia*, 13, 14.]

ALLEN, C. E. The genotypic basis of sex-expression in angiosperms. Bot. Rev. **6:** 227–300. 1940.

ANONYMOUS. Canaigre. Bull. Misc. Inf. Kew **1890:** 63–69. 1890. *Ibid.* **1894:** 167, 168. 1894. [*R. hymenosepalus.*]

ARTIST, R. C. The value of *Rumex Acetosella* as an acid indicator. Butler Univ. Bot. Stud. **2:** 81–91. 1932.

CHANCELLOR, A. P. Studies on the ecology of some species of the genus *Rumex*. Brit. Weed Control Conf. Proc. **3:** 197–203. 1956.*

DUDGEON, W. Morphology of *Rumex crispus*. Bot. Gaz. **66:** 393–420. *pls. 17–19.* 1918. [Floral morphology.]

FINK, B. Contribution to the life-history of *Rumex*. Minn. Bot. Stud. **2:** 137–153. *pls. 9–12.* 1899.

FREEMAN, O. M. Notes on the flora of Polk County, North Carolina. Castanea **20:** 37–57. 1955. [*R. hastatulus*, *R. pulcher*, 45.]

GILBERT, N. W., & D. S. BLACK. Canaigre: a potential domestic source of tannin. U. S. Dep. Agr. Prod. Res. Rep. **28.** 32 pp. 1959.*

HARPER, J. L., & A. P. CHANCELLOR. The comparative biology of closely related species living in the same area. IV. *Rumex*: interference between individuals in populations of one and two species. Jour. Ecol. **47:** 679–695. 1959. [*R. obtusifolius*, *R. crispus*, *R. conglomeratus*, *R. sanguineus*, *R. Hydrolapathum.*]

HEALY, A. J. Control of docks. New Zealand Jour. Sci. Tech. A. **34:** 473–475. 1953.

JACQUETY, Y. Étude de la couche protectrice sur les souches de deux *Rumex*. Compt. Rend. Acad. Sci. Paris **243:** 1437–1439. 1956. [*R. crispus*, *R. obtusifolius.*]

———. Description et histogenèse d'une souche primaire de *Rumex obtusifolius* DC., dans sa phase en rosette. *Ibid.* **245:** 2528–2531. 1957.

———. Morphologie de l'inflorescence de *Rumex obtusifolius* D. C. *Ibid.* **247:** 1481–1484. 1958.

JENSEN, H. W. Meiosis in *Rumex*. I. Polyploidy and the origin of new species. Cytologia **7:** 1–22. *pl. 1.* 1936; II. The origin and behavior of the so-called sex chromosomes in *Rumex*. *Ibid.* 23, 24. *pls. 2, 3.* [Incorrectly rejects the existence of sex-chromosomes.]

JOHNSON, L. A. S., & B. G. BRIGGS. Taxonomic and cytological notes on *Acetosa* and *Acetosella* in Australia. Contr. New S. Wales Natl. Herb. **3:** 165–169. 1962.

JOSHI, A. C. The anatomy of *Rumex* with special reference to the morphology of the internal bundles and the origin of the internal phloem in the Polygonaceae. Am. Jour. Bot. **23:** 362–369. 1936.

KITANI, Y. A new root-tip stain technique on *Rumex Acetosa*. (Abstr.) (In Japanese.) Jap. Jour. Genet. **31:** 302. 1956.*

KRAUSE, E. H. L. *Lapathon* und *Patience*. Untersuchungen über die Geschichte von *Rumex Patientia*. Beih. Bot. Centralbl. **24**(2): 6–52. 1908. [*R. Patientia* in early literature; its uses.]

LÖVE, Á. Physiological differences within a natural polyploid series. Hereditas **28:** 504–506. 1942. [*Rumex* subg. *Acetosella.*]

———. The dioecious forms of *Rumex* subgenus *Acetosa* in Scandinavia. Bot. Not. **1944:** 237–254. 1944a. [Establishes 4 sects. in subg. *Acetosa.*]

———. Cytogenetic studies on *Rumex*, subg. *Acetosella.* Hereditas **30:** 1–136. 1944b. [Bibliography of 189 references covering topics of polyploidy and sex chromosomes in plants; distribution maps of subg. *Acetosella.*]

———. Agamospermy in *Acetosa. Ibid.* **35:** 390–393. 1949.

———. Sex determination in *Rumex.* Proc. Genet. Soc. Canada **2:** 31–36. 1957.*

——— & N. SARKAR. Cytotaxonomy and sex determination of *Rumex pauci-folius.* Canad. Jour. Bot. **34:** 261–268. 1956.

MCVAUGH, R. The vegetation of the granitic flat-rocks of the southeastern United States. Ecol. Monogr. **13:** 119–166. 1943. [*R. hastatulus*, 140; distribution map, 154.]

MAHESHWARI, P. Origin and development of internal bundles in the stem of *Rumex crispus.* Jour. Indian Bot. Soc. **8:** 89–117. *pls. 1, 2.* 1929.

——— & B. SINGH. On the internal bundles in the stem of *Rumex Patientia* L. Proc. Indian Acad. Sci. **45:** 153–157. 1942.*

MAREK, S. Morphological and anatomical features of the fruits of genera *Polygonum* L., *Rumex* L. and keys for their determination. (In Polish; English summary.) Monogr. Bot. **2:** 77–161. *pls. 1–13.* 1954.

NELSON, J. C. The gender of *Rumex.* Am. Bot. **25:** 55, 56. 1919.

NOLTE, M. Rhizomerfall mit vegetativer Vermehrung bei *Rumex.* Bot. Jahrb. **76:** 224–250. 1954.

NORDSTEDT, O. Apogami hos *Rumex.* Bot. Not. **1907:** 238. 1907.

RECHINGER, K. H., fil. Vorarbeiten zu einer Monographie der Gattung *Rumex.* [I.] Beih. Bot. Centralbl. **49**(2): 1–132. *pls. 1–3.* 1932; II. Die Arten der Subsektion *Patientiae.* Repert. Sp. Nov. **31:** 225–283. *pls. 135, 136.* 1933; III. Die süd- und zentralamerikanischen Arten der Gattung *Rumex.* Ark. Bot. **26A**(No. 3): 1–58. *pls. 1–6.* 1934; IV. Die australischen und neuseeländischen Arten der Gattung *Rumex.* Österr. Bot. Zeitschr. **84:** 31–52. 1935; V. The North American species of *Rumex.* Publ. Field Mus. Bot. **17:** 1–151. 1937; VI. Versuch einer natürlichen Gliederung des Formenkreises von *Rumex bucephalophorus* L. Bot. Not. **1939:** 485–504. 1939; VII. Rumices Asiatici. Candollea **12:** 9–152. 1949; VIII. Monograph of the genus *Rumex* in Africa. Bot. Not. Suppl. **3**(3): 1–114. 1954.

———. Lines of evolution and geographical distribution in *Rumex* subgen. *Lapathum.* Watsonia **1:** 19–23. 1949.

———. Notes on *Rumex Acetosa* L. in the British Isles. *Ibid.* **5:** 64–66. *pls. 4, 5.* 1961. [Includes observations on *R. crispus.*]

SARKAR, N. M. Cytotaxonomic studies on *Rumex* section *Axillares.* Canad. Jour. Bot. **36:** 947–996. 1958.

SAYRE, J. D. Physiology of stomata of *Rumex Patientia.* Science **57:** 205, 206. 1923.

SMITH, B. W. Sex chromosomes and natural polyploidy in dioecious *Rumex.* Jour. Hered. **46:** 226–232. 1955.

———. The mechanism of sex determination in *Rumex hastatulus.* Genetics **48:** 1265–1288. 1963.

———. The evolving karyotype of *Rumex hastatulus.* Evolution **18:** 93–104. 1964.

Trelease, W. A revision of the American species of *Rumex* occurring north of Mexico. Missouri Bot. Gard. Rep. 3: 74–98. *pls. 13–33.* 1892.

Weill, J., & M. Bournérias. × *Polygonorumex Guineti* J. Weill (*Rumex obtusifolius* L. × *Polygonum Hydropiper* L.). Bull. Soc. Bot. France **93**: 321–326. 1946.

Tribe Polygoneae [Persicarieae Dumort.]

3. **Polygonum** Linnaeus, Sp. Pl. 1: 359. 1753; Gen. Pl. ed. 5. 170. 1754.

Annual or perennial herbs, shrubs, or twining vines of diverse, commonly moist habitats, often occurring as tenacious weeds in disturbed areas. Plants glabrous or pubescent; stems erect or prostrate, simple or branched, unarmed or with short recurved spines, the nodes often conspicuously swollen; ocreae completely or partly surrounding the nodes, cylindrical, membranaceous or scarious, often becoming hyaline with age, the distal margin entire, shredded, or bearing 1 to many short awns. Leaves basal and/or cauline, membranaceous [to ± fleshy], entire [rarely lyrate-pinnatifid or palmately cleft], alternate, sessile or petiolate, mostly linear to ovate, occasionally cordate, hastate, or sagittate, in some articulated with the stem. Inflorescence composed of axillary fascicles of 1 to several spirally arranged, pedicellate flowers; fascicles solitary in the axils of leaves or arranged into 1 or more terminal or axillary racemes (termed "spikes"), less commonly the racemes of fascicles paniculate [rarely the lower half of the inflorescence bulbil-bearing]. Flowers regular, green or white to pink or red, commonly 5-merous, bisexual or functionally unisexual, the stipe generally short, occasionally long; pedicel articulated with the flower, subtended by a scarious ocreola. Tepals (2–)4 or 5 (6), ± distinct, petaloid, erect, accrescent, completely or partly inclosing the achene, the outer ones smooth or keeled, rarely developing into broad wings in fruit. Stamens (3–)5–8 (9), the number and arrangement variable within each species, generally included, alternating with short, oblong, flattened nectariferous teeth, or the teeth lacking; anthers versatile; pollen of diverse types, some characterizing sections of the genus. Gynoecium (2–)3-carpellate; stigmata 2 or 3, punctate, capitate, or fimbriate; style 1 and deeply cleft or 2 or 3, included to exserted, straight and deciduous, or hooked at the apex, indurated and persistent; ovary lenticular or 3-angled. Fruit a lenticular or 3-angled pyramidal achene, both types occasionally occurring on the same plant. Seed coat smooth and shiny or rough and dull, light to dark brown. Embryo in one of the angles of the achene, outside of and curved around the abundant mealy or horny endosperm; cotyledons linear to lanceolate, accumbent or incumbent. (Including *Antenoron* Raf., *Bilderdykia* Dumort., *Bistorta* Mill., *Duravia* (S. Wats.) Greene, *Persicaria* Mill., *Pleuropteropyrum* Gross, *Pleuropterus* Turcz., *Reynoutria* Houtt., *Tiniaria* (Meissn.) Webb & Moq., and *Tracaulon* Raf.) Lectotype species: *P. aviculare* L.; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. 1: 659.

1913. (Name from ancient Greek, *polygonon,* an herb, from *poly,* many, and *gonu,* knee, the swollen nodes producing the appearance of jointed stems.) — KNOTWEED, SMARTWEED.

A highly variable and taxonomically difficult genus of about 150 species, nearly world wide in distribution and composed of several natural species-groups, the taxonomic ranks of which are much in dispute. In recent years data from cytology, palynology, floral anatomy, and chemistry have been used in an attempt to determine the relationships of the taxa and to devise a more natural classification. Unfortunately, emphasis often has been placed on one technique, without regard for existing information from other studies, thus leading to conflicting classifications. There is a need for correlation and careful weighing of all data in future studies of *Polygonum, sensu lato.*

The system followed here is, in general, modified from those of Steward, Steyermark, and Gleason. The infrageneric divisions, being based almost solely on variable vegetative characters, are considered sections of the genus. Thus defined, *Polygonum* is divided into eight sections, five of which occur in our area. Section TOVARA, distinguished from the rest of *Polygonum* mainly by its persistent, indurated, hooked styles, is considered by some taxonomists to be worthy of generic rank. However, to establish a genus in this family on the basis of a single character, even a floral one, is out of keeping with the magnitude of differences upon which the other genera of Polygonaceae are based. Section TINIARIA is considered to include sect. PLEUROPTERUS, since morphological distinctions between the two, though present in the species of our area, are lacking in several Asiatic species (e.g., *P. baldschuanicum* Regel, a woody vine with capitate stigmata but a much-branched paniculate inflorescence). Identical pollen morphology (see Hedberg), as well as chemical similarities (Jaretzky), support this union. *Fagopyrum* Mill., which differs from *Polygonum* in having nonaccrescent tepals, the embryo embedded in the endosperm, cotyledons rolled around the radicle, and more or less corymbiform inflorescences, is maintained as a distinct genus.

The pollen of *Polygonum* is of interest because of its unusual diversity; sectional limits within the genus are marked in several cases by distinct pollen types. Of additional interest is Doida's discovery that the number of pollen grains formed in each locule (microsporangium) is generally consistent for the species, a highly unusual phenomenon in the Angiospermae. In *P. Persicaria,* for example, the archesporial cell acts directly as the pollen mother-cell, dividing to form four microspores in each locule. Rarely it divides to form two pollen mother-cells, resulting in eight pollen grains. In *P. lapathifolium* and *P. sagittatum* there are eight pollen grains in each locule, and in *P. aviculare, P. Convolvulus,* and *P. orientale,* thirty-two. Other species have several pollen mother-cells, and the number of pollen grains may be 64, 128, or 256. Species with porate pollen have fewer grains per locule than those with colporate pollen. The number of pollen grains does not characterize sections.

Numerous chromosome counts have been made, but, unfortunately, many are unreliable due to questionable identifications and lack of voucher specimens. On the basis of all reported counts there seems to be no correlation between chromosome numbers and recognized sectional limits, wide ranges being found in each section.

Section POLYGONUM (§ *Polygonum* DC., § *Avicularia* Meissn., *Polygonum* L., *sensu stricto*; including *Duravia* (S. Wats.) Greene) is comprised of generally prostrate, much-branched annuals, with small leaves usually less than 2 cm. long and articulated at the base with the stem and flowers in axillary clusters. The pollen is spheroid-prolate, 3- or 4-colporate with furrows ½–⅘ the length of the polar axis, elliptic pores, and a smooth or granulate exine. Chromosome numbers of $2n = 20$, 22, 24, 40, 60, and 66 have been reported. Several widely distributed species of the section are present in our area, including the polymorphic *P. aviculare* L. (*P. neglectum* Bess., *P. buxiforme* Small), $2n = 20$, 22, 40, 60; the coastal American endemic *P. glaucum* Nutt., $2n = 20$, 40; *P. erectum* L., $2n = 40$; and *P. tenue* Michx., $2n = 20$. Equally widespread in the United States, but of more restricted occurrence in the Southeast (mainly in Louisiana, Arkansas, and Tennessee), are *P. ramosissimum* Michx., $2n = 20$; *P. prolificum* (Small) Robins., $2n = 60$; and *P. camporum* Meissn. The Asiatic *P. argyrocoleon* Steud. ex Kuntze has been collected as a waif on the outer banks of North Carolina.

The species of sect. POLYGONUM reportedly are inbreeding, the flowers being self-pollinated and perhaps also cleistogamous. In recent work on *P. aviculare* and related species, Styles has suggested that both hybridization and apomixis are rare, the extreme variability in morphology resulting from the influence of seasonal changes and of environmental factors in general.

Section PERSICARIA (Mill.) DC.[3] (*Persicaria* Mill.) includes plants of low, wet habitats and waste ground, with flowers in axillary or terminal spikes or racemes. The leaves are mainly elliptic to lanceolate and cauline, the tepals are neither keeled nor winged, and the branched stems are glabrous or pubescent, without recurved prickles. The pollen is spheroid, polyporate, with scattered circular pores and a reticulate exine. Reported chromosome numbers include $2n = 20$, 22, 24, 40, 44, 60, and 66. The section is the largest of the genus, with about 100 species. Of the 14 species in the Southeast, at least five are introductions from Europe or Asia: *Polygonum lapathifolium* L. (*Persicaria lapathifolia* (L.) S. F. Gray), $2n = 22$; *P. Persicaria* L. (*Pers. Persicaria* (L.) Small), $2n = 40$, 44; *P. Hydropiper* L. (*Pers. Hydropiper* (L.) Opiz), $2n = 20$, 22; *P. caespitosum* var. *longisetum* (De Bruyn) Steward; and *P. orientale* L. (*Pers. orientalis* (L.) Spach), $2n = 22$, 24. The last two occur only in the northern part of our area, while the other three are widespread. Species

[3] *Persicaria* was used by authors before De Candolle as an infrageneric category (e.g., see Linnaeus, Sp. Pl. 1: 360. 1753) but without clear indication of rank. De Candolle (Lamarck & De Candolle, Fl. Franç. ed. 3. 3: 365. 1805) appears to have been the first to apply the name without question to a section of *Polygonum*.

indigenous in our area are the variable, often aquatic *P. coccineum* Muhl. (*Pers. Muhlenbergii* (S. Wats.) Small); *P. densiflorum* Meissn. (*Pers. portoricensis* (Bert.) Small) and *P. hirsutum* Walt. (*Pers. hirsuta* (Walt.) Small), of the Atlantic coastal plain; and three highly variable species, *P. pensylvanicum* L. (*Pers. pensylvanica* (L.) Small), *P. hydropiperoides* Michx. (*Pers. opelousana* (Riddell) Small, *Pers. setaceum* (Baldwin) Small), and *P. punctatum* Ell. (*Pers. punctata* (Ell.) Small, *P. robustius* (Small) Fern.). *Polygonum bicorne* Raf. (*Pers. longistyla* (Small) Small) extends from the west into Louisiana, Arkansas, and Mississippi. *Polygonum mississippiense* Stanford (*Pers. mississippiensis* (Stanford) Small) has been described from Mississippi and *Persicaria paludicola* Small, 1933 (not *Pers. paludicola* (Makino) Nakai, 1926), from the Everglades, Florida. The northeastern *Polygonum Careyi* (*Pers. Careyi* (Olney) Greene), although included in Small's *Manual*, does not appear to extend southward into our area.

A number of species in sect. PERSICARIA have both terrestrial and aquatic forms (sometimes remarkably unlike) which can be changed from one to the other by merely changing the habitat. Such amphibious species are often sterile, spreading by means of rhizomes. Cleistogamy is reported in the section, and a tendency in the flowers toward separation of the sexes is apparent in some species, e.g., *P. hydropiperoides*. Several putative hybrids have been recorded between species of sect. PERSICARIA, especially in Europe (for a list of hybrids see G. Hegi, Illus. Fl. Mittel-Europa, ed. 2. 3: 396–400. 1958), but almost no controlled experimental studies have been made. Careful biometrical, ecological, and cytological studies are needed for a better understanding of the species limits in this, as in the other sections of *Polygonum*.

Section ECHINOCAULON Meissn. (*Tracaulon* Raf.) is closely related to and at times has been combined with sect. PERSICARIA, from which it differs mainly in the sagittate or hastate leaves, reflexed prickles on the angles of the stem, and reclining, creeping, or climbing habit. The pollen is indistinguishable from that of sect. PERSICARIA. Chromosome numbers of $2n = 20$, 22, 24, 40, 44, 60, and 66 have been reported for the section. Two species, *P. sagittatum* L. (*Tracaulon sagittatum* (L.) Small), with sagittate leaves, and *P. arifolium* (*T. arifolium* (L.) Raf.), with hastate leaves, occur in tidal marshes and other wet places in our area. The Brazilian *P. Meisnerianum* Cham. & Schlecht. var. *Beyrichianum* Meissn., easily recognized by its cordate, narrowly lanceolate leaves and dichotomously branched inflorescence with glandular hairs, was collected, probably as a waif, along the Tchefuncta (Chefuncte) River, St. Tammany Parish, Louisiana, in the late 1800's.

Section TOVARA (Adans.) Benth. & Hook.[4] (*Antenoron* Raf.[5]), com-

[4] Torrey (Fl. State N. Y. 2: 151. 1843), apparently, was the first to use *Tovara* as an infrageneric category of *Polygonum*, but without clear indication of rank. The first certain use of *Tovara* as a section of *Polygonum* appears to be that of Bentham & Hooker (Gen. Pl. 3: 98. 1880).

[5] If sect. TOVARA is recognized at the generic level, the name *Tovara* Adans. (Fam.

prised of one to three species disjunctly distributed in eastern America and eastern Asia, is distinguished by an elongate spikelike inflorescence, a 4-parted floral tube, and a persistent style, 2-parted to the base with recurved, hooked tips, which in fruit becomes very rigid and bent obliquely downward. According to Hedberg, the pollen is spheroid and 12-porate, with oblong pores arranged as though along the 12 edges of a cube; the exine is finely reticulate.

The eastern American *Polygonum virginianum* L. var. *virginianum* (*Antenoron virginianum* (L.) Roberty & Vautier, *Tovara virginiana* (L.) Raf.) is widely distributed in shady bottom lands and thickets, from Quebec to northern Florida, west to eastern Texas and Minnesota, with disjunct populations in central Mexico (Hidalgo and Puebla). A glabrous variety, *P. virginianum* var. *glaberrimum* (Fern.) Steyerm., was described from our southeastern coastal states. The eastern Asiatic members of this section have been considered as either two distinct species (*P. filiforme* Thunb. and *P. apoënse* Elmer) or three varieties of *P. virginianum*, depending on the emphasis placed on density of pubescence, shape and size of leaves, shape of base of leaves, and color of tepals. *Polygonum virginianum* var. *filiforme* (Thunb.) Nakai, distributed from southern Korea and Japan to southwestern China, has a reported chromosome number of $2n = 44$.

The dispersal mechanism of fruits in this group is unique in the family. During maturation of the fruit a separation layer forms across the pedicel, leaving only the vascular cylinder intact. When the fruits are mature, disturbance of the plant causes the vascular cylinder to break and the fruits to be catapulted forcibly as much as three or four meters. The origin of the catapulting force has not been satisfactorily explained in modern physiological terms (cf. Reed & Smoot). In addition to being thrown from the parent plant, the fruits, with their persistent hooked styles, may catch in the coats of animals, becoming dispersed over even greater areas.

Section TINIARIA Meissn. (including *Reynoutria* Houtt., 1777; *Bilderdykia* Dumort., 1827; *Tiniaria* (Meissn.) Webb & Moq., 1846; and *Pleuropterus* Turcz., 1848) is comprised of annual or perennial trailing or erect plants with axillary or terminal spikes or panicles. The tepals are keeled or winged, the stigmata capitate or fimbriate, and the pollen similar to that of sect. POLYGONUM, but with furrows generally more than $\frac{4}{5}$ the length of the polar axis and a smooth to finely reticulate exine. Chromosome numbers of $2n = 20$, 22, 40, 44, and ca. 88 have been reported for the section.

Three species occur in our area. *Polygonum Convolvulus* L. (*Bilderdy-*

Pl. 2: 276. 1763) cannot be used, since it has been rejected in favor of a later homonym, *Tovaria* Ruiz & Pav. (Prodr. 49. 1794; see Int. Code Bot. Nomencl. 263. 1961), of the Tovariaceae or Cruciferae. The later name is an orthographic variant of the earlier, both having been designated in honor of a 16th century Spanish physician, Simón a Tovar. *Tovara* is replaced by the next oldest legitimate generic name, *Antenoron* Raf. (Florula Ludov. 28. 1817; type species: *A. racemosum* Raf. = *A. virginianum* (L.) Roberty & Vautier).

kia Convolvulus (L.) Dumort.), $2n = 20$ and 40; *P. scandens* L. var. *scandens* (*B. scandens* (L.) Greene); and *P. scandens* var. *cristatum* (Engelm. & Gray) Gleason (*B. cristata* (Engelm. & Gray) Greene and *B. dumetorum* sensu Small), $2n = 20$, are widespread in the Southeast and beyond. *Polygonum cilinode* Michx. (*B. cilinodis* (Michx.) Greene), of the northeastern United States, reaches its southern limit in Tennessee and North Carolina. In addition, the Japanese *P. cuspidatum* Sieb. & Zucc. (*Pleuropterus Zuccarinii* Small, *Reynoutria japonica* Houtt.), $2n =$ 44 and ca. 88, and *P. sachalinense* F. Schmidt ex Maxim. (*Reynoutria sachalinensis* (Maxim.) Nakai), flowering bamboo, are often cultivated for their vigorous erect growth and showy panicles of flowers. Both species persist after cultivation and are very difficult to eradicate due to an extensive, spreading rhizome system. In the Northeast, escapes are becoming obnoxious weeds. Both species have been collected in Tennessee and North Carolina and may be expected elsewhere in our area in the future, if not controlled.

Extrafloral nectaries are found in several species of sect. TINIARIA (e.g., *P. Convolvulus* and *P. sachalinense*). They consist of a circular to oval depression at the base of the petiole on the abaxial side containing multicellular, short-stalked, glandular trichomes. Fully developed before the leaf unfolds, the nectaries are thought to function as hydathodes, providing a release for excess turgidity developed during formation of the leaf.

REFERENCES:

Under family references see DUKE, GEITLER, JARETZKY (1925), KNUTH, LAUBENGAYER, MITRA, RECHINGER, RIDLEY, SHARMA, SOUÈGES (1919), TUTIN, VAUTIER, WEBB, WODEHOUSE, and WOODCOCK. Under *Rumex* see MAREK and WEILL & BOURNÉRIAS.

AHLES, H. E., C. R. BELL, & A. E. RADFORD. Species new to the flora of North or South Carolina. Rhodora **60**: 10–32. 1958. [*P. hirsutum*, 13.]

——— & A. E. RADFORD. Species new to the flora of North Carolina. Jour. Elisha Mitchell Sci. Soc. **75**: 140–147. 1959. [*P. sachalinense*, 141.]

BRENCKLE, J. F. Notes on *Polygonum* (*Avicularia*). [I.] Photoperiodism and taxonomy. Bull. Torrey Bot. Club **68**: 491–495. 1941; Notes on the *Avicularia*. II. Phytologia **2**: 169–171. 1946; Notes on *Polygonum*. III. *Ibid.* 402–406. 1948; [IV.] On some Asiatic Polygonums. *Ibid.* **3**: 300–303. 1950; Notes on *Polygonum*. V. *Ibid.* 361–366.

BURK, C. J. Distribution records and range extensions from the North Carolina outer banks. Castanea **26**: 138, 139. 1961. [*P. sawatchense*, 139, redetermined by H. E. Ahles as *P. argyrocoleon*.]

COULTER, S. Cleistogamy in the genus *Polygonum*. Bot. Gaz. **17**: 91, 92. 1892.

DOIDA, Y. On the pollen grain formation in genus *Polygonum*. (In Japanese; English summary.) Bot. Mag. Tokyo **70**: 31–37. 1957.

———. Cytological studies in *Polygonum* and related genera. I. *Ibid.* **73**: 337–340. 1960.

———. Consideration on the intrageneric differentiation in *Polygonum*. 1–2. (In Japanese; English summary.) Jour. Jap. Bot. **37**: 3–12, 81–88. 1962.

FASSETT, N. C. The variations of *Polygonum punctatum*. Brittonia **6**: 369–393. 1949.

FERNALD, M. L. The variations of *Polygonum pensylvanicum*. Rhodora **19**: 70–73. 1917.

FLANAGIN, V. L. A report on starch storage in septate fibers of *Polygonum coccineum* var. *pratincola*. Trans. Kans. Acad. Sci. **64**: 304–310. 1961.

FUCHS, C. Sur le développement des structures de l'appareil souterrain du *Polygonum cuspidatum* Sieb. et Zucc. Bull. Soc. Bot. France **104**: 141–147. 1957.

HEDBERG, O. Pollen morphology in the genus *Polygonum* L. s. lat. and its taxonomical significance. Sv. Bot. Tidskr. **40**: 371–404. 1946.

HENDRICKS, H. V. Torsion studies in twining plants. Bot. Gaz. **68**: 425–440. 1919; II. *Ibid.* **75**: 282–297. 1923. [*P. Convolvulus*.]

HOLM, T. *Polygonum*: sectio *Tovara*. Bot. Gaz. **84**: 1–26. *pls. 1, 2*. 1927.

JUSTICE, O. L. Viability and dormancy in seeds of *Polygonum amphibium* L., *P. coccineum* Muhl., and *P. hydropiperoides* Michx. Am. Jour. Bot. **31**: 369–377. 1944.

KEARNEY, T. H., JR. Cleistogamy in *Polygonum acre*. Bot. Gaz. **16**: 314. 1891. [= *P. punctatum*.]

LI, H. L. The genus *Tovara* (Polygonaceae). Rhodora **54**: 19–25. 1952.

LÖVE, Á., & D. LÖVE. Chromosomes and taxonomy of eastern North American *Polygonum*. Canad. Jour. Bot. **34**: 501–521. 1956.

MARTIN, A. C. Identifying *Polygonum* seeds. Jour. Wildlife Manag. **18**: 514–520. 1954.

MEEHAN, T. *Polygonum virginianum*. Meehan's Monthly **7**: 181, 182. *pl. 10*. 1897.

REED, H. S., & I. SMOOT. The mechanism of seed-dispersal in *Polygonum virginianum*. Bull. Torrey Bot. Club **33**: 377–386. 1906.

SALISBURY, E. J. The extra-floral nectaries of the genus *Polygonum*. Ann. Bot. **23**: 229–242. *pl. 16*. 1909.

SCHOLZ, H. Bestimmungsschlüssel für die Sammelart *Polygonum aviculare* L. Verh. Bot. Ver. Brandenb. **98-100**: 180–182. 1960.

SCHOTSMAN, H. D. The anatomy of the glands of some *Polygonum* varieties and hybrids. (In Dutch; English summary.) Nederl. Kruidk. Arch. **57**: 262–276. 1950. [Includes *P. Persicaria*, *P. lapathifolium*, *P. Hydropiper*.]

SHARP, A. J. *Tovara* in Mexico. Rhodora **54**: 305, 306. 1952. [*P. virginianum*.]

SHINNERS, L. H. *Polygonum bicorne* Raf. instead of *P. longistylum* Small. Rhodora **59**: 265–267. 1957.

SIMMONDS, N. W. *Polygonum* L. em. Gaertn. *In*: Biological flora of the British Isles. Jour. Ecol. **33**: 117–143. 1945. [Description of sects. occurring in British Isles; list of fungi and insects associated with the genus; detailed treatment of life history and ecology of *P. Persicaria*, *P. petecticale*, and *P. lapathifolium*.]

SMALL, J. K. A monograph of the North American species of the genus *Polygonum*. Mem. Dep. Bot. Columbia Coll. **1**: 1–183. *pls. 1–84*. 1895.

SOUÈGES, R. Embryogénie des Polygonacées. Développement de l'embryon chez le *Polygonum Persicaria* L. Compt. Rend. Acad. Sci. Paris **168**: 791–793. 1919; Le développement de l'embryon chez le *Polygonum aviculare* L. *Ibid.* **178**: 409–412. 1924.

SPERRY, J. J. The anatomy of the inflorescence of *Polygonum viviparum* L. (Abstr.) Trans. Tex. Acad. Sci. **26**: 55, 56. 1943.

STANFORD, E. E. The inflorescence and flower-form in *Polygonum*, subgenus *Persicaria*. Rhodora **27**: 41–47. 1925.

———. Possibilities of hybridism as a cause of variation in *Polygonum*. *Ibid.* 81–89.

———. The amphibious group of *Polygonum*, subgenus *Persicaria*. *Ibid.* 109–112, 125–130, 146–152, 156–166.

———. *Polygonum pensylvanicum* and related species. *Ibid.* 173–184.

———. *Polygonum hydropiperoides* and *P. opelousanum*. *Ibid.* **28**: 11–17, 22–29. 1926.

———. *Polygonum Hydropiper* in Europe and North America. *Ibid.* **29**: 77–87. 1927.

STEWARD, A. N. The Polygoneae of eastern Asia. Contr. Gray Herb. **88**: 1–129. *pls. 1–4.* 1930.

———. The case for *Polygonum cuspidatum* Sieb. & Zucc. Rhodora **32**: 223–225. 1930.

STYLES, B. T. The taxonomy of *Polygonum aviculare* and its allies in Britain. Watsonia **5**: 177–214. 1962.

SUGANO, N., & K. HAYASHI. Anthocyanin of the seedlings of a *Polygonum*. Studies on anthocyanins. XXXII. Bot. Mag. Tokyo **73**: 231–233. 1960. [*P. Hydropiper*.]

WITTS, K. J. The germination of *Polygonum* species in the field and in the glasshouse. Jour. Ecol. **48**: 215–217. 1960. [*P. Persicaria, P. aviculare, P. Convolvulus*.]

4. **Polygonella** Michaux, Fl. Bor.-Am. **2**: 240. 1803.

Heather-like, subherbaceous annuals or suffrutescent perennials, mainly of sand hills, scrublands, and waste places. Branches many, erect, adnate to the parent stem for approximately half the length of the internode. Leaves alternate, narrowly linear to spathulate, caducous or persistent, sessile, articulated with and appearing to arise from the free upper edge of the membranaceous, cylindrical ocrea. Inflorescence racemose, terminal on primary and lateral branches, the flowers solitary in the axils of imbricated ocreolae and slightly to well exserted from them; ocreolae unilaterally flared to an acute or acuminate apex, the margin entire or bearing several short to long, bristle-like hairs. Flowers bisexual or functionally unisexual (the plants dioecious, gynodioecious, or gynomonoecious); pedicel broader and longer than the stipe and subtended by 2 lanceolate, keeled, scarious bractlets, or bractlets wanting. Tepals 5, slightly fused, forming a short floral tube, erect (the outer tepals occasionally tardily reflexed), in 2 whorls of 2 outer and 3 inner ones, or (in subg. *Thysanella*) 2 outer, 2 inner, and 1 transitional one, white to red, accrescent, the margins entire to fimbriate. Stamens 8, in 2 whorls; filaments mostly included, alike (subg. *Thysanella*) or the inner whorl of 3 dilated near the base forming 2 lateral nectariferous teeth (subg. *Polygonella*); anthers versatile; pollen prolate, 12–40μ long, tricolporate, the pores equatorially arranged, the furrows longitudinally elongated, the exine reticulate. Gynoecium 3-carpellate; stigmata 3, punctate; styles 3, filiform, free to the base; ovary 3-angled, slightly stalked. Fruit a shiny yellow to brown or gray pyramidal achene. Embryo straight, in one of the angles of the seed; cotyledons oblong, thick and fleshy; radicle equalling or exceeding

cotyledons. (Including *Delopyrum* Small, *Dentoceras* Small, and *Thysanella* A. Gray.) TYPE SPECIES: *P. parvifolia* Michx. = *P. polygama* (Vent.) Engelm. & Gray. (Name a diminutive of *Polygonum*.) — JOINTWEED.

Indigenous to the eastern United States, with two subgenera and nine species, all but *Polygonella Parksii* Cory (endemic to Atacosa and Wilson counties, Texas) occurring in the Southeast.

Subgenus THYSANELLA (A. Gray) Horton[6] (*Thysanella* A. Gray, *Polygonella* § *Thysanella* (Gray) Roberty & Vautier) has inner tepals fimbriate, filaments alike, and pedicels subtended by bractlets within the ocreolae. It consists of *Polygonella fimbriata* (Ell.) Horton var. *fimbriata* (*T. fimbriata* (Ell.) A. Gray), of Florida, Georgia, and Alabama, and var. *robusta* (Small) Horton (*T. robusta* Small), $2n = 32$, endemic to Florida.

Subgenus POLYGONELLA (§ *Delopyrum* (Small) Roberty & Vautier, § *Dentoceras* (Small) Roberty & Vautier), with inner tepals entire, the inner whorl of filaments dilated near the base, and pedicels not subtended by bracteoles within the ocreolae, composes the remainder of the genus. The species are distinguished by such characters as habit, type of margin on the ocreolae, number of ocreolae in a raceme, shape and size of leaves, and color and position of tepals during flowering and fruiting.

The procumbent, mat-forming *Polygonella myriophylla* (Small) Horton (*Dentoceras myriophylla* Small) is endemic to the southern part of the Florida lake region. *Polygonella ciliata* Meissn. var. *ciliata* and var. *basiramia* (Small) Horton (*Delopyrum ciliatum* (Meissn.) Small and *D. basiramia* Small), both $2n = 22$, are also restricted to Florida. *Polygonella macrophylla* Small, $2n = 28$, occurs on the Gulf Coast of Alabama and northern Florida. More widespread are *P. gracilis* (Nutt.) Meissn. (*Delopyrum gracile* (Nutt.) Small, *Delopyrum filiforme* Small), $2n = 22, 24$; *P. polygama* (Vent.) Engelm. & Gray (*P. brachystachya* Meissn., *P. Croomii* Chapm.), $2n = 28$; and *P. americana* (Fisch. & Mey.) Small. The first two are species of the Coastal Plain; the latter is generally piedmontane, occurring sporadically from South Carolina to central New Mexico. *Polygonella articulata* (L.) Meissn. (*Delopyrum articulatum* (L.) Small), $2n = 32$, is the only species of the genus in the northeastern United States, reaching its southern limit in northeastern North Carolina. It is regarded as the most primitive species of *Polygonella* by Horton, who also believes that the modern species of the genus evolved in Florida from an ancestral stock forced southward by Pleistocene glaciations.

Internodal branching characteristic of *Polygonella* is lacking in the rest of the family. The wood anatomy is characterized by a lack of parenchyma in annuals and by axile xylem parenchyma in perennials. Starch is stored in the xylem in an unusual cell type which resembles a

[6] The taxonomic treatment follows the recent revision of *Polygonella* by J. H. Horton. We have also relied on this paper for much of the general information concerning the genus.

fiber in shape and pitting, but is nucleate and living at maturity. The floral anatomy is, by reduction, the simplest in the family (Vautier). Each tepal has a single trace which connects with the main vascular supply; the other floral parts are supplied by single free traces which end in the floral tube. No anatomical evidence of a double trace to the fused inner and outer tepal can be seen in this genus. Reported chromosome numbers form an aneuploid series ($2n = 22, 24, 28, 32$).

REFERENCES:

Under family references see LAUBENGAYER, VAUTIER, and WOODCOCK.

HORTON, J. H. A taxonomic revision of *Polygonella* (Polygonaceae). Brittonia **15:** 117–203. 1963. [Includes distribution maps of each sp.]

SMALL, J. K. The relation between the genera *Thysanella* and *Polygonella* as shown by a hitherto unobserved character. Bull. Torrey Bot. Club **24:** 47, 48. 1897. [Internodal branching in *Thysanella* and *Polygonella*.]

Subfam. COCCOLOBOIDEAE Dammer

Tribe COCCOLOBEAE [Dumort.]

5. **Coccoloba** P. Browne ex Linnaeus, Syst. Nat. ed. 10. 997, 1007, 1367. 1759, nom. cons.

Dioecious shrubs or trees [vines] of warm sandy coasts and hammocks; nodes often swollen or geniculate. Leaves evergreen [or deciduous], thick and leathery [or membranaceous], alternate, variable in size and shape, ours reniform to orbicular or oblong to elliptic with apex obtuse and base cordate to acute, the surfaces minutely punctate [or the upper surface pitted and lower with superficial or sunken glands]; petioles short, attached to the stem near the base of [or well above] the partly deciduous tubular ocrea. Inflorescence a many- to few-flowered raceme [spike or panicle], less than to exceeding the leaves, terminal on primary and lateral branches. Flowers regular, greenish or yellowish white, unisexual or functionally so, campanulate, with a short floral tube, the stipe mostly equal to or shorter than the pedicel, the young buds completely covered by the ocreola which ruptures as they mature; pedicels [less than to] exceeding the length of the ocreola. Staminate flowers in 2–5-flowered, bracteate fascicles at the nodes, each flower subtended and surrounded by the persistent ocreola which incloses the adjacent flower and its ocreola, additional ocreolae of aborted flowers occasionally also present, the filaments long, exserted, the styles short, included. Carpellate flowers solitary at the nodes, subtended by a bract and surrounded by an ocreola, the filaments short, the anthers sterile, the styles long, exserted. Tepals 5, greenish white. Stamens (7) 8; filaments broadest at base and united into an annulus surrounding the ovary, without nectariferous teeth; anthers versatile; pollen prolate, ca. $50 \times 40\mu$, tricolporate, the furrows extending nearly to the apices of the grain, the pores slightly elongated equatorially, the exine finely reticulate, tectate-perforate. Gynoecium 3-carpellate; styles 3, the dilated apices stigmatic; ovary 1-locular, some-

times incompletely 3-locular at base; ovule on a long funiculus. Fruit an achene with 3 major ridges, surrounded by the fleshy floral tube, the tube persistent, accrescent, rose-purple to nearly black when mature, the lobes covering the apex of the achene [or the lobes alone accrescent, surrounding the achene]; seed filling the upper part of achene, the lower part with spongy tissue. Embryo straight, the radicle short, the cotyledons orbicular; endosperm ruminate. (*Coccolobis* P. Browne, Civ. Nat. Hist. Jamaica 209. 1756, invalidly published; *Guaiabara* Mill. Gard. Dict. Abr. ed. 4. 1754, nom. rejic.) LECTOTYPE SPECIES: *C. Uvifera* (L.) L. (*Polygonum Uvifera* L.), typ. cons. (Name from Greek, *coccos*, berry, and *lobos*, lobed, in reference to the fleshy, lobed floral tube surrounding the fruit.)

An indigenous tropical and subtropical American genus of about 170 species and one of the few tropical genera in the family. The greatest number of species (about 85) occurs in South America (about 44 in Brazil); two reach their northern limit in peninsular Florida. The sea grape, *Coccoloba Uvifera*, $2n = 132$,[7] a characteristic shrub or small tree of warm, sandy shores from Florida to northern Argentina, is immediately recognizable by its large orbicular to reniform leaves and the dense clusters of sweet-acid, rose-purple fruits (nearly black when fully mature). The pigeon plum, *C. diversifolia* Jacq. (*C. laurifolia* Jacq., *C. floridana* Meissn.), $2n = 22$, a tree to about 20 m. tall, with generally smaller, oblong to elliptic leaves and nearly black fruits, inhabits hammocks and scrublands in Florida, the Bahamas, the Greater Antilles, and Antigua. Both range along the east coast of Florida north approximately to Merritt Island; on the west coast *C. Uvifera* occurs at least as far north as Manatee County, but *C. diversifolia* is restricted to the southern counties. Hybrids of the two are known from Everglades National Park, Florida, and Prov. Pinar del Río, Cuba. *Coccoloba Uvifera* also hybridizes with several other species elsewhere in its range.

The taxonomy of the genus presents numerous difficulties. Many species have at least two names, one based on a staminate, the other on a carpellate plant, the unisexual condition having been discovered only recently (cf. Howard, 1949). Morphologically, the flowers vary little among species, while vegetative characters which, for lack of floral differences, must be used in classification, are extremely variable. In collecting *Cocco-*

[7] Previously unreported chromosome counts by Prof. R. A. Howard, Arnold Arboretum: *Coccoloba Uvifera* ♂, $2n = 132$ (meiotic count), *R. A. & E. S. Howard 10211*, Miami Beach, Dade County, Florida, 18 May 1948 (NY); *C. diversifolia*, $2n = 22$, seedling grown in Cambridge, Mass., from fruits of *R. A. & E. S. Howard 8976*, Arroyo del Oro, Prov. San Juan, Dominican Republic, 15 Sept. 1946 (GH).

An earlier count of $2n =$ ca. 80 for *Coccoloba Uvifera* (Edman, Acta Horti Berg. **9**: 270. 1929) is open to question, for it is possible that this was obtained from either hybrid or apomictic material of *C. Uvifera*. Since the name *C. diversifolia* has been applied incorrectly to several different species, Jaretzky's count of $2n =$ ca. 200 (Jahrb. Wiss. Bot. **69**: 441. 1928) may have been obtained from another species. Apparently both reports are undocumented by herbarium specimens.

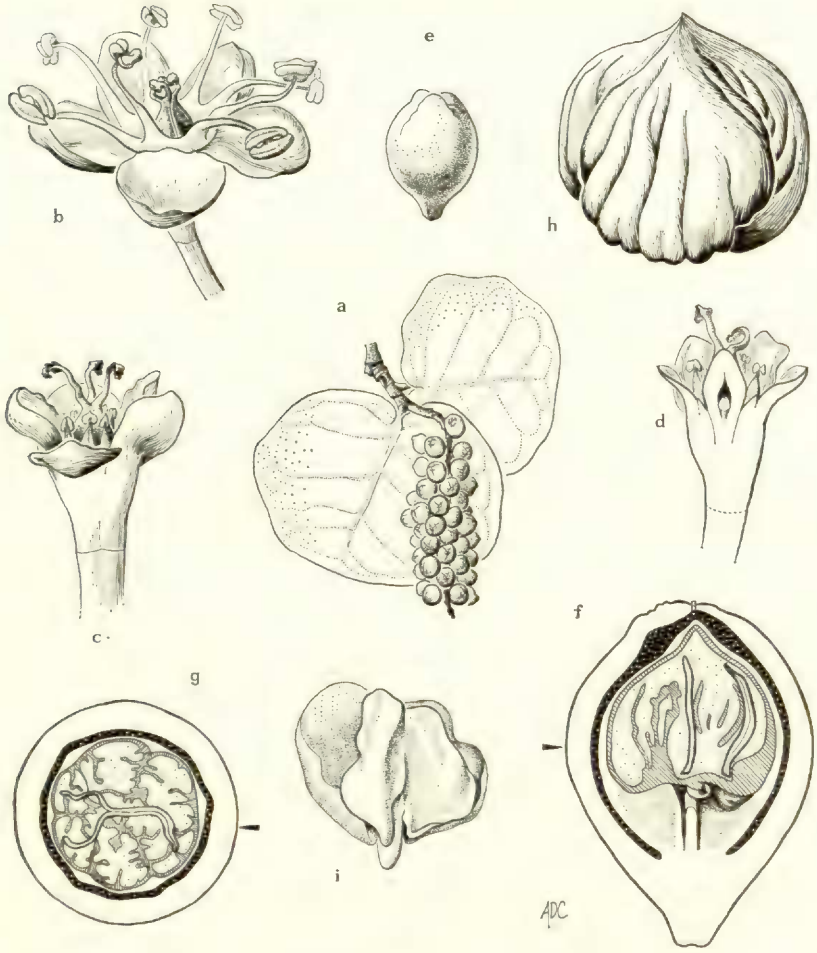

FIG. 1. **Coccoloba.** a–i. *C. Uvifera*: a, fruiting branchlet, × ¼; b, staminate flower, × 6; c, carpellate flower with staminodia, × 6; d, carpellate flower in semidiagrammatic vertical section to show floral tube and basal orthotropous ovule, × 6; e, nearly mature fruit completely inclosed by accrescent perianth, × 1; f, fruit in semidiagrammatic vertical section at level marked beside "g," showing accrescent perianth (unshaded), stony wall of achene (black with white stipples) with persistent style arm, spongy tissue below seed (fine shading) transitional to denser tissue (unshaded) surrounding seed, seed on stout funiculus, seed coat (hatched) penetrating endosperm (coarsely stippled) — note seed cut off-center, cotyledons appearing in section, two to right, one to left (cf. "g"), × 3; g, fruit in diagrammatic cross section at approximate level marked beside "f," the embryo cut through cotyledons, the perianth, achene wall, spongy tissue, seed coat, and endosperm as in "f," × 3; h, seed, × 4; i, embryo, inverted from position in seed, × 4. In "b–d" note articulation of stipe with pedicel.

loba care should be taken to represent the diversity of growth habit and leaf variability within the population. Adventitious shoots, which tend to have longer internodes and larger leaves than the normal stems, should also be included. Since the fruit of many species changes in shape as it matures, comparisons of size and shape can be made only with fully mature fruits.

A successful ornamental, *Coccoloba Uvifera* is planted along seasides in warmer regions of the world for its hardiness and attractive fruiting racemes and evergreen foliage. It has been reported in cultivation since 1690 and has become naturalized in several places in southeastern Asia and on some Pacific islands. Two variegated leaf forms are propagated. It is successful also as a pot plant, requiring little care except pruning. Jelly is sometimes made from the fruit. *Coccoloba diversifolia*, with bronze-colored juvenile leaves, is planted as a street tree in southernmost Florida. Both species are considered good honey plants, and birds feed on the fleshy fruits. Little work has been done on the biology of the genus, although hybridization apparently is frequent, and apomixis is suspected. Fossil leaves of *Coccoloba* are known from the Paleocene or Eocene of Alaska and also have been reported from Alabama, Mississippi, Texas, Arkansas, Louisiana, Tennessee, Kentucky, and Wyoming.

REFERENCES:

Under family references see DUKE, LAUBENGAYER, and VAUTIER.

HOLLICK, A. The Tertiary floras of Alaska. U. S. Geol. Surv. Prof. Pap. **182**: 1–185. *pls. 1–122*. 1936. [*Coccoloba*, 112, 113, *pls. 121, 122*.]

HOOKER, W. J. *Coccoloba Uvifera*. Bot. Mag. **59**: *pl. 3130*. 1832.

HOWARD, R. A. The genus *Coccoloba* in Cuba. Jour. Arnold Arb. **30**: 388–424. 1949. [*C. Uvifera*, 409; *C. diversifolia*, 423]; Studies in the genus *Coccoloba*. II. The identification of *Coccoloba Swartzii* Meisner and *Coccoloba barbadensis* Jacquin and their relatives. *Ibid.* **37**: 317–339. 1956; III. The Jamaican species. *Ibid.* **38**: 81–106. 1957; IV. The species from Puerto Rico and the Virgin Islands and from the Bahama Islands. *Ibid.* **38**: 211–242. 1957; V. The genus in Haiti and the Dominican Republic. *Ibid.* **39**: 1–48. 1958; VI. The species from the Lesser Antilles, Trinidad and Tobago. *Ibid.* **40**: 68–93. 1959; VII. A synopsis and key to the species in Mexico and Central America. *Ibid.* 176–203, 205–220; IX. A critique of the South American species. *Ibid.* **41**: 213–229, 231–258. 1960; X. New species and a summary of distribution in South America. *Ibid.* **42**: 87–95. 1961; XI. Notes on the species in Asia. *Ibid.* 107–109.

———. A history of the genus *Coccoloba* in cultivation. Baileya **6**: 204–212. 1958.

LAMOTTE, R. S. Catalogue of the Cenozoic plants of North America through 1950. Geol. Soc. Am. Mem. **51**. 381 pp. 1952. [*Coccoloba*, 128.]

LINDAU, G. Monographia generis Coccolobae. Bot. Jahrb. **13**: 106–229. *pl. 5*. 1890.

———. Zur Entwicklungsgeschichte einiger Samen. Ber. Deutsch. Bot. Ges. **9**: 274–279. *pl. 17*. 1891. [*C. populifolia*, 276–279, *pl. 17, figs. 7–13*.]

———. Nachträge und Berichtigungen zu meiner Monographia Generis Coccolobae. Bot. Jahrb. **14**(Beibl. 31): 14–16. 1891.

SARGENT, C. S. *Coccolobis*. Silva N. Am. **6**: 113–120. *pls. 298–300*. 1894.
YINGLING, H. C. Some aspects of the anatomy of *Coccolobis Uvifera* (L.) Jacq. Ohio State Univ. Abstr. Doctors' Diss. **40**: 343–352. 1943.

6. **Antigonon** Endlicher, Gen. Pl. 310. 1837.

Herbaceous to woody, perennial vines; stems lightly to densely pubescent, often with geniculate nodes; lateral branches leafy or modified as tendrils; ocreae short, with a nearly entire margin, membranaceous and falling away on old stems or reduced to a fine line; axillary buds 2, one forming a lateral branch, the other an inflorescence, one or both sometimes suppressed. Leaves deltoid to cordate or hastate, the blades in ours not decurrent on the petiole. Inflorescence of terminal and axillary racemes bearing lateral tendrils, especially on their distal portions, and terminating in a forked tendril; flowers borne at the nodes, 3–5 in a fascicle, the fascicles subtended by an acuminate bract and each flower subtended by a membranaceous, persistent ocreola. Flowers bisexual, pedicellate, the pedicel persistent, the stipe and pedicel nearly equal in length. Tepals 5, forming a short floral tube, bright rose-red [purplish red or greenish white to yellow], persistent, inconspicuous in flower, accrescent, enlarging 3 or 4 times, inclosing the fruit, and often becoming very showy, the outer tepals cordate to ovate, the inner oblong. Stamens 8 (7–9), the filaments bearing scattered glandular-capitate hairs and alternating with small triangular, nectariferous teeth, the filaments and teeth united half their length to form a broad cuplike annulus around the ovary, the base of the annulus fleshy; anthers versatile; pollen subprolate, ca. 50 × 40μ, tricolporate, the furrows extending nearly to the apices and with the membranes lightly flecked with scattered granules, the pores elongated equatorially, the exine thick, finely reticulate. Gynoecium 3-carpellate; stigmata 3, reniform-capitate; styles 3, filiform, generally included; ovary 3-angled, slightly stalked, surrounded by the fleshy base of the annulus; ovule on a long, thin funiculus. Fruit a 3-angled achene. Seed with mealy, ruminate endosperm; embryo slightly excentric. (*Corculum* Stuntz, U. S. Dep. Agr. Bur. Pl. Indus. Bull. **282**: 86. 1913.) LECTOTYPE SPECIES: *A. leptopus* Hook. & Arn.; see Hooker & Arnott, Bot. Capt. Beechey's Voy. 308. *pl. 69*. 1840, and Britton & Wilson *in* Sci. Surv. Porto Rico Virgin Is. **5**: 265. 1924. (Name from Greek, probably from *anti*, similar to, and *gonu*, knee, alluding to the geniculate nodes; cf. *Polygonum*.) — CORAL-VINE, MOUNTAIN-ROSE.

A Central American genus of two or three species: *Antigonon guatimalense* Meissn. (*A. macrocarpum* Britt. & Small); *A. flavescens* S. Wats., perhaps only a greenish-white color form of *A. leptopus*; and the well-known *A. leptopus* (*Corculum leptopus* (Hook. & Arn.) Stuntz), Confederate vine, $2n = 40$, ca. 44, 48, a widely cultivated ornamental vine with cordate to hastate leaves and showy racemes of accrescent rose-colored flowers. *Antigonon leptopus* is planted throughout the warmer parts of

the Southeast and apparently has become naturalized in several scattered localities in Florida. Its natural range is described as Baja California and Chihuahua, south to Oaxaca, Mexico. In Florida the plant blooms continuously from early spring to late fall and may reach a height of 10 m., climbing by means of tendrils. Abundant viable seeds and edible tubers are produced, from which new plants sprout in the spring. The genus is insect pollinated, as the brightly colored tepals and copious nectar indicate. A white-flowered form (= *A. flavescens?*) is occasionally cultivated.

REFERENCES:

Under family references see DUKE, VAUTIER, and WODEHOUSE.

BAILEY, L. H. *Antigonon.* Standard Cyclopedia of Horticulture. ed. 2. **1**: 304. 1928.

HOOKER, J. D. *Antigonon leptopus.* Bot. Mag. **96**: *pl. 5816.* 1870.

ORDETX, G. S. Coral vine, a perennial honey source. Glean. Bee Cult. **82**: 656, 657. 1954.*

RAO, V. S. A contribution to the morphology of *Antigonon leptopus* Hook. & Arn. Jour. Indian Bot. Soc. **15**: 105–114. 1936. [Mega- and microsporogenesis.]

STANDLEY, P. C. *Antigonon. In*: Trees and shrubs of Mexico. Contr. U. S. Natl. Herb. **23**: 247, 248. 1922.

7. **Brunnichia** Banks ex Gaertner, Fruct. Sem. Pl. 1: 213. *pl. 45, fig. 2.* 1788.

Perennial, woody, high-climbing, tendril-bearing vines of riverbanks and low damp ground, mostly growing in trees or thickets. Stems ridged [or nearly terete], glabrous or slightly pubescent; lateral branches short, ending in tendrils; axillary buds 2, one forming a lateral branch, the other suppressed or forming an inflorescence; ocreae short and entire, glabrous or pubescent, continuous with the base of the petiole or reduced to a row of hairs flanking each side of the base of the petiole. Leaves alternate, petiolate, ovate to oblong, the apex acute to acuminate, the base rounded to truncate. Inflorescence of densely flowered terminal and axillary panicles or racemes; flowers borne at the nodes, 3–5 in a fascicle, each fascicle subtended by a bract and each flower by a persistent, hyaline, lanceolate-subulate ocreola. Flowers bisexual, the stipe much longer than the short pedicel, the floral tube and stipe 3-ridged, with one ridge [or two] expanding in fruit to form a flattened, leathery wing. Tepals 5, whitish- or yellowish-green, oblong to elliptic, leathery, slightly united at base, forming a short floral tube, reflexed at anthesis, connivent in fruit, both tepals and pedicel accrescent. Stamens 8 (7–10); filaments exserted, persistent; anthers versatile; pollen subprolate, ca. 45 × 35μ, tricolporate, the furrows extending nearly to the apices of the grain, the pores slightly elongated equatorially, the exine thick, reticulate, tectate-perforate. Gynoecium 3-carpellate; stigmata 3, obscurely bilobed and irregularly flabelliform; styles 3, exserted, persistent; ovary 3-ridged; ovule basal in the spongy tissue of the locule, the funiculus long and

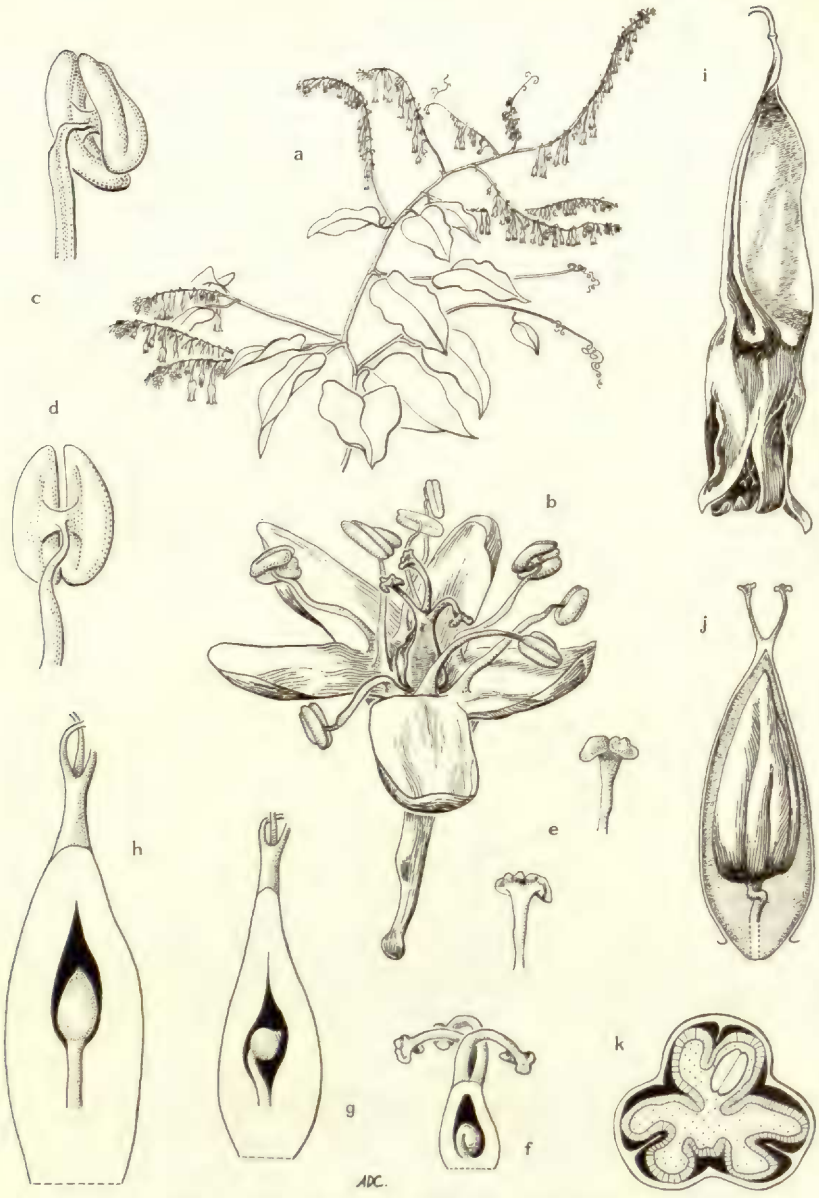

FIG. 2. **Brunnichia.** a–k, *B. cirrhosa*: a, flowering and fruiting branch, × ¼; b, flower disarticulated from pedicel, × 8; c, d, stamens, the anther-halves bent forward in "d" to show connective, × 16; e, two views of stigma, × 16; f–h, ovary in semidiagrammatic vertical section to show successive changes in orientation of ovule, beginning at anthesis — note incompletely developed outer integument of ovule, × 8; i, mature accrescent calyx with wing, the achene not visible, × 2; j, achene in semidiagrammatic vertical section to show seed sur-

thin, at anthesis anatropously bent so that the micropyle is directed downward, later straightening, the micropyle then directed upward (cf. FIG. 2).[8] Fruit a 3–6-angled achene inclosed in the persistent, accrescent floral tube; seed filling upper part of achene, spongy tissue the lower part. Embryo embedded in endosperm along one angle of achene; cotyledons oblong; endosperm mealy, ruminate. TYPE SPECIES: *B. cirrhosa* Gaertn. (Named for the Danish naturalist M. T. Brunnich, 1737–1827.) — EARDROPS, BUCKWHEAT VINE.

A genus of one American and two African species. The American *Brunnichia cirrhosa*, $2n = 48$, is found generally on rich bottom-land soils and along riverbanks of the south-central United States, from southern Illinois and Missouri, south to Texas and Louisiana, and is of sporadic occurrence eastward along the Coastal Plain to Florida and South Carolina. *Brunnichia erecta* Asch., ranging from Liberia to the Congo, and *B. africana* Welw., of Angola, have been segregated as *Afrobrunnichia* Hutch. & Dalz., primarily on the basis of the two- rather than one-winged pedicels.

The genus is most closely related to *Muehlenbeckia* Meissn. and is of no economic importance.

REFERENCES:

Under family references see LAUBENGAYER, RIDLEY, and VAUTIER.

DAMMER, U. Zur Kenntnis der afrikanischen *Brunnichia*-Arten. Bot. Jahrb. **26**: 347–357. 1899. [See also J. HUTCHINSON & J. M. DALZIEL, Bull. Misc. Inf. Kew **1928**: 28. 1928, and Fl. W. Trop. Afr. ed. 2. 1: 139. 1954.]

LEWIS, W. H., H. L. STRIPLING, & R. B. ROSS. Chromosome numbers for some angiosperms of the southern United States and Mexico. Rhodora **64**: 147–161. 1962. [*B. cirrhosa*, 150.]

SMALL, J. K. Morphological notes on the genus *Brunnichia*. Bull. Torrey Bot. Club **21**: 131, 132. 1894. [*B. cirrhosa*.]

[8] In a family characterized by orthotropous ovules, *Brunnichia cirrhosa* is remarkable in that the long, slender funiculus of the ovule is bent over at the apex, the micropyle thus facing the base of the locule. As Laubengayer (1937, p. 337) comments, however, it is essentially "still an orthotropous ovule, even though it does face in the opposite direction." As the ovary and ovule continue to develop after anthesis, the growth of the funiculus brings the ovule to an erect position, with the micropyle directed upward, as in other members of the family. The enlarging seed fills the upper part of the locule, while a spongy (flotation?) tissue occupies the remainder of the cavity. At maturity the seed has become so large that the funiculus is pushed downward, developing a crook or "kink" just beneath the seed. (Cf. FIG. 2, f–h, j.) Vautier (1949, p. 275) found a similar orientation of the ovule in *B. africana*, but thought that the ovule was at first orthotropous, later taking an anatropous position "which it does not seem, however, to keep up to the end of its development" (translation supplied). In *B. cirrhosa* the funiculus is anatropously bent long before anthesis, even in the very smallest buds which could be dissected.

---

rounded by spongy tissue (stippled) filling fruit, × 4; k, diagrammatic cross section of fruit and seed cut through cotyledons of embryo (upper right), the endosperm stippled, the seed coat hatched, the space between seed and achene wall black — note three remnants of spongy tissue giving appearance of partial partitions, × 8.