
JOURNAL
OF THE
ARNOLD ARBORETUM

VOL. 51

JULY 1970

NUMBER 3

THE GENERA OF ACANTHACEAE IN THE
SOUTHEASTERN UNITED STATES¹

ROBERT W. LONG

ACANTHACEAE A. L. de Jussieu, Gen. Pl. 102. 1789, "Acanthi," nom. cons.

(ACANTHUS FAMILY)

Herbs [shrubs] or vines [rarely small trees]. Leaves simple, opposite exstipulate; pubescence of stems and leaves of simple hairs; cystoliths of various forms often present in parenchyma or epidermis. Inflorescences basically cymose (dichasial), often condensed in leaf-axils, modified into racemes or panicles, or flowers sometimes solitary. Flowers perfect, nearly actinomorphic to zygomorphic; bracts and bracteoles usually present and often colored, sometimes large and enclosing the flower. Calyx segments 5, occasionally 4, not infrequently fused, persistent. Corolla sympetalous, the limb 5-lobed or bilabiate, rarely 1-lipped, lobes convolute or imbricate in bud. Nectariferous disk nearly always present, below ovary.

¹Prepared for a generic flora of the southeastern United States, a project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation (Grant GB-6459X, principal investigator Carroll E. Wood, Jr.). The treatment in this paper, which is the 52nd published in the series, follows the format established in the first paper (Jour. Arnold Arb. 39: 296-346. 1958). The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with additional information in brackets. References which have not been seen and verified are marked by an asterisk.

The manuscript for this paper was prepared while I held a Mercer Research Fellowship at the Arnold Arboretum in the latter half of 1968. I want to express my thanks for the facilities extended to me during my stay in Cambridge and to the several people who have aided substantially with this treatment of the Acanthaceae. Dr. Carroll Wood has spent a great deal of time in editing and checking the manuscript, in making numerous additions and suggestions, in preparing the dissections for and supervising the illustrations, and in preparing the legends for them. The illustrations are the work of the late Dorothy H. Marsh (FIGURE 5, i-n) and of Diane C. Johnson and Virginia Savage, whose initials will be found on the appropriate ones. Mrs. Mary C. Dillon carefully checked most of the references and the abbreviations of books and journals, and Mrs. Nancy Dunkly verified most of the remainder and prepared the typescript. My appreciation is extended to them all.

Stamens 4 (5), didynamous, or 2 (staminodia often present in 2-stamened flowers, 1, 2, or seldom 3), epipetalous; anthers 1- or 2-loculate, longitudinally dehiscent, the connective of various widths; pollen very variable, of many kinds, mostly tricolporate. Gynoecium of 2 united carpels; stigmas simple or 2-cleft or -lobed, the posterior lobe often aborted or wanting; style filiform, simple; ovary 2-loculate, superior, placentation axile (parietal in Nelsonioideae), ovules 2-10 in each locule, anatropous, amphitropous, or campylotropous, 1-integumented, tenuinucellate. Fruit typically a 2-valved loculicidal capsule [drupaceous in Mendoncioideae]. Seeds 4(2)-20, usually flat, without endosperm [endosperm present in Nelsonioideae] borne on hooklike projections, the modified funiculi of the ovules, termed retinacula or jaculators, these papilliform or apparently lacking in a few genera; seeds usually dispersed through sudden opening of fruit; seed coat smooth or roughened, often mucilaginous when moistened; embryo straight or bent; cotyledons broad and flat. Embryo-sac development normal, monosporic (Polygonum type), embryogeny generally conforming to Onagrad type (Nelsonioideae) or Solanad type (Ruellioideae). Chromosome numbers $x = 7-18, 20, 21$. (Including Thunbergiaceae Bremek., Mendonciaceae Bremek.) TYPE GENUS: *Acanthus* L.

A pantropical family of about 250 genera and 2600 species with four main centers of distribution: Indo-Malaya, Africa, Brazil, and Central America. About 12 genera, including the two largest, *Justicia* (about 300 species) and *Ruellia* (about 225 species), are pantropical. Of the remaining genera about 40 per cent are confined to the Western Hemisphere. Approximately 120 genera are monotypic and restricted in range. Relatively few taxa are found in the United States; only three genera occur in the Northeastern States, seven additional ones are indigenous to the Southeastern States, and a few more are represented by species in the southwestern United States.

The family has long been noted for its taxonomic difficulty. Some authorities (e.g., Lindau, Grant, Melchior) consider the Acanthaceae to be a natural family, presumably monophyletic in origin, while others (e.g., Van Tieghem, Bremekamp) have viewed the original composition of the group as being artificial, presumably polyphyletic. For the great majority of genera the family may be recognized by the presence of the peculiar structure of the funiculus that becomes hook-shaped in the mature fruit, and is termed the retinaculum or jaculator. This structure, however, is not typical of three of the subfamilies that contain a few genera of uncertain relationship.

The family also is characterized by the presence of cystoliths in the leaves and stems of most (but not all) genera and by the explosive dehiscence of the mature capsule. Cystoliths are visible as slight protuberances or, more commonly, as streaks in the epidermis. Bracts and bracteoles are generally present and are often showy. Classification within the family is based primarily on minor characters of the androecium, particularly the anthers, and on pollen sculpture. Such bases for classification

often make difficult the accurate identification of genera and species. A wide variety of life forms is found, including many hygrophiles, xeromorphic species with spiny or acicular leaves, lianas, and even mangrove plants. Arborescent forms are rare, and most species are shrubs or herbs with opposite, usually decussate, entire, exstipulate leaves. In the tropics the Acanthaceae, particularly the "Strobilanthes" group of the Old World, are conspicuous, showy elements of the local vegetation. Santapau, for example, listed 42 genera found in the immediate vicinity of Bombay, India.

Various genera have been the subject of anatomical and morphological investigations. Detailed accounts and references have been given by Solereder, who also made special reference to the occurrence and morphology of cystoliths. These appear in the form of silicified bodies with or without a cellulose skeleton. Linsbauer earlier had shown that their nature and distribution are valuable in the recognition of genera, especially in the Ruellieae and Odontonemateae. Slightly lignified cystoliths occur in the pith of certain species of *Ruellia*, and pigmented cystoliths are reported for *Ruellia*, *Sanchezia*, and *Strobilanthes*. In addition to cystoliths, calcium oxalate crystals may be secreted in the form of prisms, needles, or other shapes.

Solereder reported that petiolar anatomy exhibited either a single arc-shaped vascular strand, or a concentric group of separate bundles with the ends of the crescent very much incurved in some species, or a circle of more or less separate bundles (e.g., *Thunbergia*), or, rarely, a cylindrical vascular strand (e.g., *Crossandra*). The epidermis is occasionally papillose (e.g., *Ruellia*). Stomata are present on both leaf surfaces in some species but are confined to the lower surface in others, and they are nearly always caryophyllaceous, although in at least *Lepidagathis* they are rubiaceous. A wide assortment of both glandular and nonglandular hairs is reported for various genera.

The family is characterized anatomically by the presence of anomalous secondary thickening that occurs in a number of genera. This usually appears as inconspicuous groups of intraxylary and interxylary phloem and as bundles of bodies (described as acicular fibers) that resemble large raphides. The vessels typically are very small (less than 50μ) or extremely small (less than 25μ). Wood is semi-ring-porous, and the vessel elements have fine, spiral thickenings, simple perforations, and scanty parenchyma. The vascular system of *Justicia americana* has been found to consist of seven distinct steles, one central and six arranged around the circumference. The meristeles and the central medullary bundle anastomose at the node. The axis of the inflorescence in most genera is monostelic, but in some respects the stem anatomy resembles certain Campanulaceae because of the presence of a medullary bundle. The roots generally contain less well-developed xylem. Unusually long root hairs, intraxylary phloem, and pitted lignified pith are also recorded for certain genera.

The anatomy of several Ruellieae, including *Blechum*, *Dyschoriste*,

Hemigraphis, *Hygrophila*, and *Ruellia*, has been described in detail by Tchouproff, who also attempted, rather unsuccessfully, to show relationships graphically by means of anatomical comparisons. Danert analyzed leaf, bud, and floral arrangements in selected genera, including *Blechnum*, *Justicia*, *Ruellia*, and *Thunbergia*. He concluded that Acanthaceae exhibit "plagiotropic" growth owing to the presence of a "Sprossendodermis," a character he attributed to phylogenetically older stocks. Vesque suggested an anatomical characterization of the family, but only in connection with the leaf anatomy. He also gave a classification of cystoliths.

The Acanthaceae have long been notorious for their very great variation in pollen morphology, useful in taxonomic diagnosis. Probably no other family has such a wide range of pollen morphological features as the Acanthaceae. Early detailed studies of acanthaceous pollen were made by Bischoff, Fritzsche, and Von Mohl, but the taxonomic value of pollen characters in the classification of the family was first pointed out by Radlkofer. It was on the basis of his work that Lindau elaborated the use of pollen morphology as the chief basis for his classification of the family in Engler & Prantl's *Die Natürlichen Pflanzenfamilien*. Hallier, who reported both three-porous and sparsiporous grains in *Pseuderanthemum*, was among the first to question seriously whether pollen is any more valid than floral morphology as a tool for determining relationships. Later students of the family have continued to emphasize the use of pollen, however.

Raj, after an exhaustive survey of pollen types in 260 species of 103 genera, concluded there are considerable grounds for doubting the convincing use of pollen as a basis for classification, although he apparently is in general agreement with Bremekamp's use of pollen in his revisionary studies. The Thunbergioideae have the largest pollen, varying from 60 to 100 μ , anomatreme, spheroidal, eight-colpate; Nelsonioideae show much less variation and typically have three-colpate, prolate pollen; the Acanthoideae sensu Lindau have a very wide range of pollen types, including two-porate bilateral, pantoporate, polyporate, and the most common form, three-colporate, found in most of the tribes. Although many tribes form homogeneous groups, others, such as the Ruellieae and Odontonemateae, have various kinds of pollen sculpturing.

Recent studies of pollen and its use as a taxonomic tool in the family have not been altogether reassuring. Bhaduri concluded that the pollen of Nelsonioideae closely resembles that of *Andrographis* (Ruellioideae), although Raj strongly disagreed. Sharma & Vishnumittre found four widely different pollen types in *Eranthemum* and *Pseuderanthemum*. Bremekamp's rearrangement of tribes and genera is based primarily on his interpretation of pollen relationships. This has led him to recognize a number of segregate genera, especially in the Ruelliinae, based on minor pollen differences. It has yet to be established whether or not these "splinter" taxa are worthy of recognition.

The Acanthaceae also have a great range of chromosome numbers. Twenty different haploid numbers have been determined, with $n = 7, 9,$

10, 13-22, 25, 26, 28, 30, 31, 34, 40, and 66. Basic numbers of (5) 6, 7, 8, 9, 10, and 11 are known, most species generally falling into one of three series, $x = 7, 8, \text{ or } 9$, with $x = 7$ represented by the greatest number of genera. The lowest haploid number ($n = 7$) is found in *Thunbergia*; the chromosomes of *Elytraria* are among the smallest in the family, about 1μ in length chiefly with median centromeres. Pizzolongo & D'Arienzo examined *Acanthus* cytologically and reported the genus as dibasic, with $x = 7$ or 8 ; *A. spinosus* is a sterile polyploid with $2n = 112$, but the closely related octoploid *A. mollis*, $2n = 56$, and decaploid *A. montanus*, $2n = 80$, are fertile. Grant, who studied the family cytologically, largely to investigate generic relationships, concluded that polyploidy, especially aneuploidy, has undoubtedly occurred and that the wide range of numbers represents an ascending and descending aneuploid series. Aneuploidy is probably responsible for the large number of genera and species. Grant found that all but three of the 18 genera, where more than one species was examined, had euploids, aneuploids, or both types of polyploids present. Narayanan used cytological studies to demonstrate the close relationships of some genera and intrageneric groups. Grant also based some of his speculations regarding relationships within the Justicieae on chromosome numbers.

The considerable embryological literature in Acanthaceae has been reviewed by Schnarf, Mauritzon, and, most recently, by Maheshwari & Negi. Detailed references are also given by Davis. The linear tetrad develops into a Polygonum-type embryo sac; the embryogeny follows either the Onagrad (*Elytraria*) or Solanad type. Mauritzon pointed out that the endosperm shows a mode of development peculiar to the Tubiflorae; this is a cellular type of endosperm that results from free nuclear divisions followed by wall formation in the central chamber. The first two divisions result in a row of three cells which form the endosperm proper, while the micropylar and chalazal cells develop into haustorial organs. The chalazal haustorium is lacking in *Thunbergia*. Bhaduri concluded that *Acanthus* and *Crossandra* ought to be considered the basic type for the family because they lack the free nuclear stage. The advanced type would then be represented by *Ruellia* and *Adhatoda* (*Justicia*) where free nuclear divisions occur. Supernumeraries and persistent antipodals are found rarely in the family, although Hartman reported them in *Aphelandra*.

Embryological data have been adduced by Johri & Singh as evidence that the Nelsonioideae properly belong in the Acanthaceae, and not in the Scrophulariaceae, as proposed by Bremekamp, who discounted the importance of comparative embryological similarities in Acanthaceae. The family continues to provide considerable interest for the plant embryologist, however. A recent investigation by Sahi presented the details of the distinctive embryo sac and embryogeny of *Andrographis* that throw some light on the taxonomic relationships of this genus.

Unfortunately, the floral biology of the family is not as well understood as the embryology. Characteristically, the flowers are proterogynous, nectar-yielding, and brightly colored and are often arranged in large in-

florescences. Usually, insects hit the downward directed tips of the pollen sacs and are dusted with pollen on the back. The insect transfers the pollen to projecting stigmas of another flower. Premature dispersal of pollen is apparently prevented by the hairs that frequently surround the anthers. Highly specialized pollinating systems involving extrafloral nectaries have been reported in *Thunbergia*. Ornithophily (hummingbirds) and possibly myrmecophily may be factors in the pollinating systems of red-flowered rain-forest species of *Aphelandra*.

Uphof reported cleistogamy in six genera of Acanthaceae. Tharp & Barkley found that all paniculate taxa of *Ruellia* in Texas are cleistogamous, and Long & Uttal discovered that all species of *Ruellia* of the eastern United States are cleistogamous during part of the reproductive cycle. The general occurrence and importance of cleistogamy in Acanthaceae have yet to be evaluated, but they deserve further attention. Monocarpy apparently is common in the Old World genus *Strobilanthes*; after a number of years of vegetative growth, the plants flower, then die off. Santapau has observed, however, that renewed vegetative growth may occur after flowering in *S. callosus* Nees if there has been an abundance of rain.

Seeds are dispersed for short distances by the explosive dehiscence of the ripe capsule. Bremekamp attributed this mechanism to the progressive loss of water from the maturing fruit. Many genera have seeds covered with hairs or scales that become erect with moistening; possibly this is an adaptation that helps to anchor the seed in a suitable substratum.

Breeding studies and hybridization experiments are few in number. Meeuse & DeWet have reported natural and artificial intergeneric hybrids between the South African *Ruttya*, $2n = 36$, and *Ruspolia*, $2n = 42$. They suggested that the vigorous but completely sterile hybrid ($2n = 39$) may have horticultural value and that other intergeneric hybrids may occur. Lindau did not place these two genera in the same tribe. Long has made numerous intrasectional and a few intersectional hybrids in *Ruellia*. Investigations reported thus far suggest that large scale cross-breeding work in Acanthaceae would be of considerable value both taxonomically and horticulturally. Perhaps the difficulty of obtaining materials of this largely tropical group accounts for the dearth of genetic experiments in the family.

Little is known about the phytochemistry of the family, perhaps because no important poisonous, medicinal, or useful species are known. Pharmacological investigations of drugs from certain genera have been made, and diuretic and antiasthmatic effects have been credited to members of the family. Chemical constituents include polyphenols, essential oils, non-volatile isoprenoid compounds, heterosides, and alkaloids. Arndt, Eggers, & Jordaan have determined by spectrographic analysis the structure of five new alkaloids obtained from the South African genus *Anisotes* and some flavenoid studies have recently been reported by Nair. Obviously, much remains to be learned concerning the chemotaxonomy of genera in the family.

The Acanthaceae have had a long, tortuous history, taxonomically, since they were first recognized as "Acanthi" by B. de Jussieu in 1759. The

name was adopted by A. L. de Jussieu, who placed eight genera in the group. A general discussion of the family and its affinities was given by Lindley, who included a list of genera supplied by Nees and references to the early literature. Nees's account in De Candolle's *Prodromus* was the first comprehensive treatment of the family, and it established limits for many genera that have been followed up to the present. Endlicher, following Nees, divided the "order" Acanthaceae into three tribes, Thunbergieae, Nelsonieae, and Echmatacanthi, the last further divided into seven subtribes. On the basis of floral morphology Bentham & Hooker recognized 120 genera in five tribes: Thunbergieae, Nelsonieae, Ruellieae, Acantheae, and Justicieae, with the Ruellieae further divided into five subtribes, the Justicieae into six.

Radlkofer demonstrated the value of pollen characters in the classification of Acanthaceae and, as mentioned above, Lindau greatly expanded the critical use of pollen characters in his treatment of the family. Lindau distinguished four subfamilies, Nelsonioideae, Mendoncioideae, Thunbergioideae and Acanthoideae. Van Tieghem proposed that the "Thunbergiacées" be a separate family to consist of three tribes, "Thunbergiées," "Mendonciées," and "Nelsoniées." He proposed dividing the remaining Acanthaceae into two subfamilies, the "Acanthoïdées" (without cystoliths), and the "Justicioïdées" (with cystoliths). Wettstein was in general agreement with this change because he concluded there was close affinity between Lindau's first three subfamilies. However, instead of regarding them as a distinct family, he placed them all in Thunbergioideae, thereby reducing Lindau's subfamilies to tribes. Interestingly, this was the original position taken by Nees, whose Anechmatacantheae (without retinacula) and Echmatacantheae (with retinacula) correspond to Wettstein's Thunbergioideae and Acanthoideae.

More recently, Bremekamp has made a revision of the family based largely, but not entirely, on detailed pollen characters. He divided the Acanthoideae sensu Nees into Acanthoideae and Ruellioideae, while abandoning Lindau's familiar "Contortae" and "Imbricatae." Lindau's 16 tribes were reduced to seven, largely through transfers and expansion of tribal circumscriptions. Bremekamp changed his mind about an earlier reduction of Nelsonioideae to a mere subtribe of Acantheae and removed them from the family, recommending they be placed in the vicinity of the Rhinanthae (Scrophulariaceae). He raised Lindau's Mendoncioideae and Thunbergioideae to family status and made numerous changes in generic limits, especially in Old World tropical taxa. On the basis of his palynological studies, Raj concurred with Bremekamp's revisions, but Grant said there is no "cytological criterion" to suggest that the subfamilies are sufficiently different to be considered separate families. Grant maintained that the evidence from chromosome studies suggested that a classification based on pollen morphology may be somewhat artificial.

Wernham suggested that the Thunbergieae are closely related to the Convolvulaceae, but that they ought to be classified with Acanthaceae because of their "primitive" retinacula. Melchior maintained the same

general classification of the family as Lindau, while admitting that the subfamilies are indeed strongly marked. Leonard also followed Lindau's circumscriptions in his treatment of tropical American groups.

Changes in and additions to the general classification of Acanthaceae continue to the present, with the general tendency of one school (represented by Bremekamp and Raj) to emphasize minor differences in pollen morphology, anther, and other floral characters in recognizing numerous segregate taxa; and the other school (represented by Melchior and Leonard) to follow the broad generic interpretations of Lindau. Melchior stated the situation accurately when he said, "Auch die natürliche Gliederung der Acanthaceae . . . ist noch in Fluss."

The phylogenetic relationships of Acanthaceae are also controversial. Baillon thought the family was related to both the Scrophulariaceae and the Labiatae on the basis of stamen morphology and to the Bignoniaceae on the basis of calyx and fruit characters. He thought Acanthaceae were also related to Boraginaceae and to Convolvulaceae through their nearly actinomorphic flowers. Bessey considered Acanthaceae as descended from Scrophulariaceae or groups ancestral to them. Engler and Diels placed the family between Globulariaceae and Myoporaceae in the vicinity of the large and complex Gesneriaceae. Hegnauer, on the basis of phytochemical evidence, suggested that there is close relationship with the Verbenaceae-Labiatae complex, but he may also have been influenced by Wettstein, who had placed Acanthaceae in the Tubiflorae between Bignoniaceae and Verbenaceae. Apparently, students generally agree that Thunbergioideae is the most primitive subfamily on the basis of anatomical, embryological, cytological, and palynological grounds.

Melchior considered the family to be an old, highly developed and very natural group distinguished by the "sling mechanism," pollen morphology, and the presence of cystoliths and thought that certain parallel developments have occurred in the closely related Scrophulariaceae. Bremekamp stated a diametrically opposing view that Acanthaceae sensu Lindau cannot be regarded as a natural entity. He attempted to resolve this problem by excluding what he considers are extraneous elements, as the Thunbergiaceae, the Mendonciaceae, and the Nelsonieae. Bremekamp's "natural" Acanthaceae is closely similar, then, to Lindau's subfamily Acanthoideae. Raj concluded from his pollen studies, particularly of the sporoderm, that Acanthaceae sensu Bremekamp is an assemblage of primitive and advanced tribes. He concluded that the Strobilantheae, Barlerieae, and Andrographideae are primitive, while Justicieae, Aphelandreae, and Acantheae are the most advanced.

As in most angiospermous groups, there is a sketchy fossil record. Velenovsky & Viniklar believe Acanthaceae date back to Cretaceous times because of their identification of fossils as *Strobilanthes*. Raj, from photographs by Kuyl, Muller, & Waterbolk, identified fossil pollen taken from Miocene deposits as resembling that of *Ruellia* and *Sanchezia*. Because there are so few tree-forms in the family and most taxa are tropical, it is unlikely that fossil woods will be discovered. Investigations of fossil pollen

appear to be the most promising avenue for historical documentation of Acanthaceae.

The family is of little economic importance. A few plants have been reported to have medicinal properties, but none is included in modern works on materia medica. Bremekamp pointed out that the leaves of two new species of the Indonesian genus *Filetia* contain inulin, a carbohydrate not previously found in the family. Burkart listed a number of species, notably *Justicia campestris* Griseb., that can be used for emergency forage. Metcalfe & Chalk reported that blue dyes have been obtained from *Strobilanthes* species and yellow dyes from *Justicia* species, but they apparently have no economic value. The family is best known horticulturally for its many unusual and interesting ornamental plants that occur in the tropics.

Because of their tropical nature, it is not surprising that the Acanthaceae of the southeastern United States reach their best development in Florida. Some genera only reach southern Florida, and others, such as *Justicia* and *Ruellia*, are best represented in the United States within the state boundaries. Other genera represented in Florida, such as *Barleria* and *Hemigraphis*, are apparently not well established outside of cultivation, and still others are found only in gardens. *Andrographis* has been reported as occurring on chrome ore piles in Virginia but probably is not established in our flora. These three genera are included in the key unnumbered and in brackets.

Cultivated members of the Acanthaceae in the southeastern United States, particularly in Florida, include *Acanthus montanus* T. Anders. (leaves spiny); *Aphelandra tetragona* (Vahl) Nees (scarlet corollas, hooded upper lobes); *Crossandra infundibuliformis* (L.) Nees (bright scarlet-orange corollas); *Eranthemum pulchellum* Andr. (*E. nervosum* (Vahl) R. Br. ex Roem. & Schult.) (blue curved corollas); *Fittonia Verschaffeltii* E. Coem. (creeping herb; leaves white or red veined); *Graptophyllum pictum* Griff. (shrubs, leaves variously marked, corollas purplish or red, two lipped); various species of *Jacobinia* that resemble *Justicia* (brightly colored two-lipped corollas, inflorescences various); *Odontonema strictum* Kuntze (corollas bright red, flowers in close racemes); *Pachystachys coccinea* (Aubl.) Nees (*Jacobinia coccinea* (Aubl.) Hiern) (shrub with dense heads of scarlet flowers); *Peristrophe speciosa* (Roxb.) Nees (herb, flowers violet, subtended by two large bracts); *Pseuderanthemum atropurpureum* (Bull ex De Vos) Radlk. (leaves purplish or yellow blotched); *Sanchezia nobilis* Hook. f. (corollas yellow, with yellow revolute rims); and *Strobilanthes Dyeriana* Mast. (*Perilepta Dyeriana* (Mast.) Bremek.) (distinctive rose-purplish foliage).

REFERENCES:

- ANDERSON, T. An enumeration of the species of Acanthaceae from the continent of Africa and the adjacent islands. Jour. Linn. Soc. Bot. 7: 13-54. 1864a.

- . On the identification of the Acanthaceae of the Linnean Herbarium, in the possession of the Linnean Society of London. *Ibid.* 111–118. 1864b.
- . An enumeration of the Indian species of Acanthaceae. *Ibid.* 9: 425, 426. 1867.
- ARNDT, R. R., S. H. EGGERS, & A. JORDAAN. The alkaloids of *Anisotes sessiliflorus* C. B. Cl. (Acanthaceae) — 5 new 4-quinazolone alkaloids. *Tetrahedron* 23: 3521, 3532. 1967. [Structure by spectrographic analysis.]
- ASTUDILLO, R. V. A study of the vegetative characters of the different species of the family Acanthaceae in Mount Makiling and their taxonomic importance. *Philip. Jour. Forestry* 19: 15–40. 1963.*
- BAILLON, H. Monographie des Acanthacées. *Hist. Pl.* 10: 403–466. 1891. [Divides family into six series.]
- BECKNER, J. *Hemigraphis reptans* (Acanthaceae), a new Florida weed. *Sida* 3: 118, 119. 1967.
- BENOIST, R. Recherches sur la structure et la classification des Acanthacées de la tribu des Barlériées. *Thèses Fac. Sci. Univ. Paris* 1465 (Sér. A:706): 5–105. 1912. [Includes references to earlier literature.]
- . Contribution à la flore des Acanthacées de l'Afrique française. *Not. Syst. Paris* 2: 284–288. 1912; 289, 290. 1913. [Notes and comments on 6 genera; includes key to *Thunbergia* spp.]
- . Acanthacées de Madagascar. *Bull. Mus. Hist. Nat. Paris* 31: 386–388. 1925. [Includes key to *Mendoncia* and new spp. in genus.]
- BENTHAM, G., & J. D. HOOKER. Acanthaceae. *Gen. Pl.* 2: 1060–1122. 1886. [Treatment prepared by Bentham.]
- BHADURI, S. A contribution to the morphology of pollen grains of Acanthaceae and its bearing on taxonomy. *Calcutta Univ. Jour. Dep. Sci. II.* 1: 25–38. 1944. [*Acanthus*, *Crossandra*, *Adhatoda*, and *Ruellia*.]
- BREMEKAMP, C. E. B. On the opening mechanism of the acanthaceous fruit. *S. Afr. Jour. Sci.* 23: 488–491. 1926. (Cf. *Bot. Centralbl.* 159: 218. 1930.) [Role of water-loss in sudden opening of fruit.]
- . Notes on the Acanthaceae of Surinam. *Rec. Trav. Bot. Néerl.* 35: 130–171. 1938. [Includes key to genera and spp. based on pollen characters.]
- . Materials for a monograph of the Strobilantheae (Acanthaceae). *Verh. Nederl. Akad. Wet. Afd. Natuurk. 2.* 41(1): 1–306. pls. 1–6. 1944. [Rejects Strobilantheae as artificial, refers emended Strobilantheae to broadened Ruellieae.]
- . Notes on the Acanthaceae of Java. *Ibid.* 45(2): 1–78. 1948. [Discussions of generic problems in *Justicia*, *Thunbergia*, *Hygrophila*, *Asystasia*, *Dicliptera*.]
- . The delimitation of the Acanthaceae. *Proc. Nederl. Akad. Wet. C.* 56: 533–546. 1953.
- . The Acantheae of the Malesian Area. I. General considerations. *Ibid.* 58: 162–171. 1955a.
- . Notes on some acanthaceous genera and species of controversial position. *Acta Bot. Neerl.* 4: 644–655. 1955b. [Emphasizes use of pollen morphology in classification of genera and higher categories.]
- . A revision of the Malaysian Nelsonieae (Scrophulariaceae). *Reinwardtia* 3: 157–261. 1955c. [*Staurogyne* Wall., *Nelsonia* R. Br., and *Elytraria* Vahl; *Ophiorrhizophyllum* Kurz and *Gynocraterium* Bremek. also belong to Nelsonieae.]

- . New Bornean Acanthaceae. *Blumea* 10: 151–175. 1960. [New genus and new tribe, *Borneacanthus*, Borneacanthaceae.]
- . Remarks on the position of some Australian Acanthaceae. *Acta Bot. Neerl.* 11: 195–200. 1962. [Realignments in Ruelliinae and Justiciinae.]
- . On the systematic position of the Australian Nelsonias and Thunbergias and of the *Ruellia* species which by Domin were referred to *Aporuella* Clarke. *Proc. Nederl. Akad. Wet. C.* 67: 301–306. 1964. [Includes *Brunoniella*, nov. gen.]
- . Studies in the flora of Thailand. 32. Scrophulariaceae, Nelsonieae; Thunbergiaceae; Acanthaceae. (Second list.) *Dansk. Bot. Ark.* 23: 195–224. 1965a. [Includes descriptions of new genera and spp.]
- . Delimitation and subdivision of the Acanthaceae. *Bull. Bot. Surv. India* 7: 21–30. 1965b.
- & N. E. NANNENGA-BREMEKAMP. A preliminary survey of the Ruelliinae (Acanthaceae) of the Malay Archipelago and New Guinea. *Verh. Nederl. Akad. Wet. 2.* 45(1): 1–39. 1948.
- BURKART, A. Acantáceas indígenas como forrajeras de emergencia. *Darwiniana* 6: 192–202. 1 pl. 1943.
- BURKILL, I. H., & C. B. CLARKE. Acanthaceae. *In*: W. T. THISELTON-DYER, ed., *Fl. Trop. Afr.* 5: 1–192. 1899; 193–262. 1900.
- CAROTHIE, H. Anatomía de la madera de dos géneros de las Acantáceas. *Revista Forest. Venez.* 4: 7–15. 1961. [Vessel elements larger in *Bravaisia* than in *Trichanthera*.]
- CLARKE, C. B. Acanthaceae. *In*: J. D. HOOKER, ed., *Fl. Brit. India* 4: 387–512. 1884; 513–558. 1885.
- DANERT, S. Über die Symmetrieverhältnisse der Acanthaceen. *Flora* 140: 307–325. 1953.
- DAVIS, G. L. Systematic embryology of the angiosperms. viii + 528 pp. New York. 1966. [Acanthaceae, 31, 32; extensive bibliographic references.]
- DE, A. Cytological investigations in the family Acanthaceae. *Sci. Cult.* 32: 198, 199. 1966.
- . Cytological, anatomical and palynological studies as an aid in tracing affinity and phylogeny in the family Acanthaceae. I. Cytological studies. *Trans. Bose Research Inst.* 29: 139–175. 1966; II. Floral anatomy. *Ibid.* 30: 27–43. 1967; III. General anatomy. *Ibid.* 51–65; IV. Palynology and final conclusion. *Ibid.* 31: 17–29. 1968.
- DE BARY, A. Comparative anatomy of the vegetative organs of the phanerogams and ferns. (Transl. and annot. F. O. BOWER & D. H. SCOTT.) xvi + 659 pp. Oxford. 1884. [Acanthaceae, 137–143.]
- DETHAN, G. Des Acanthacées médicinales. Thèse. École Supér. Pharm. Paris. vii + 186 pp. 1896. [Anatomical and pharmacological information.]
- ELLIS, J. L. Chromosome numbers in some members of the Acanthaceae. *Sci. Cult.* 28: 191, 192. 1962. [*Barleria*, *Crossandra*, *Ecbolium*, *Justicia*, *Petalidium*, *Strobilanthes*.]
- ENDLICHER, S. Acanthaceae. *Gen. Pl.* 696–708. 1839.
- ERDTMAN, G. Pollen morphology and plant taxonomy. Angiosperms. xii + 539 pp. frontisp. Stockholm; Waltham, Mass. 1952. [Acanthaceae, 30–32.]
- , B. BERGLAND, & J. PRAGLOWSKI. An introduction to a Scandinavian pollen flora. *Grana Palynol.* 2: 1–92. 1961. [Revised pollen terminology.]
- GIGANTE, R. Embriologia dell'*Acanthus mollis* L. *Nuovo Giorn. Bot. Ital.* II. 36: 5–33. pls. 1–10. 1929.

- GOOD, R. D'O. *Anomacanthus*, a new genus of Acanthaceae. Jour. Bot. London **61**: 161-164. 1923. [Vine related to *Mendoncia* with unusually large fruit up to 10 cm. in diam.]
- GRANT, W. F. Cytogenetic and cytotaxonomic studies in *Eupatorium*, *Celosia*, and Acanthaceae. Ph.D. diss. Univ. Virginia, Charlottesville. 1953.
- . A cytogenetic study in the Acanthaceae. Brittonia **8**: 121-149. 1955.
- GRAY, A. Acanthaceae. Synop. Fl. N. Am. **2**: 321-331. 1878.
- HALLIER, H. Indonesische Acanthaceen. Nova Acta Acad. Leop.-Carol. **70**: 195-240. pls. 9-16. 1897.
- . Über *Pseuderanthemum metallicum* sp. n. und das System der Acanthaceen. Ann. Jard. Bot. Buitenzorg **15**: 26-36. pl. 9. 1898. [Raises questions regarding value of pollen characters in determining phylogenetic relationships.]
- HARTMANN, A. Zur Entwicklungsgeschichte und Biologie der Acanthaceen. Flora **116**: 216-258. 1923. [Includes *Ruellia*, *Hemigraphis*, *Thunbergia*, *Blechum*, *Barleria*, *Beloperone*.]
- HEGNAUER, R. Chemotaxonomie der Pflanzen. Band 3. Dicotyledoneae Acanthaceae-Cyrillaceae. 743 pp. Basel & Stuttgart. 1964. [Acanthaceae, 41-49.]
- HESS, R. W. Identification of New World timbers. Trop. Woods **86**: 14-25. 1946. [Acanthaceae, 15-20; includes key to genera based on microscopic anatomy; *Bravaisia* and *Trichanthera* attain tree size.]
- HOBEIN, M. Über den systematischen Wert der Cystolithen bei den Acanthaceen. Bot. Jahrb. **5**: 422-440. 1884.
- HUARD, D. Origine de quelques anomalies observées chez des pollens d'Acanthacées. Pollen Spores **7**: 19-26. 1965. [Meiotic abnormalities produce aborted pollen in *Jacobinia*, *Crossandra*.]
- JOSEPH, J. Chromosome numbers and abnormalities observed in a few members of Acanthaceae. Curr. Sci. Bangalore **33**: 56, 57. 1964. [*Nelsonia*, *Justicia*, *Ecbohium*, *Cardanthera*.]
- KAUR, J. Chromosome numbers in Acanthaceae. II. Sci. Cult. **31**: 531, 532. 1965; III. *Ibid.* **32**: 142, 143. 1966.
- KNUTH, P. Handbook of flower pollination. Vol. 3. (Transl. J. R. A. DAVIS.) iv + 644 pp. Oxford. 1909. [Acanthaceae, 237-240. In German ed. cf. **3**(2): 149-157. 1905.]
- KUYL, O., J. MULLER, & H. WATERBOLK. The application of palynology to oil geology with reference to western Venezuela. Geol. Mijnbouw **3**: 49-76. 1955.
- LAKELA, O., & F. C. CRAIGHEAD. Annotated checklist of the vascular plants of Collier, Dade, and Monroe counties, Florida. 95 pp. Fairchild Trop. Gard. & Univ. Miami Press, Coral Gables. 1965. [Acanthaceae, 82, 83.]
- & R. W. LONG. Plants of the Tampa Bay area. 109 pp. Univ. South Florida Bookstore, Tampa. 1970. [Acanthaceae, 83, 84.]
- LEONARD, E. C. Botany of the Maya area. Miscellaneous Papers. X. The Acanthaceae of the Yucatan Peninsula. Carnegie Inst. Publ. **461**: 191-238. 1936.
- . The Acanthaceae of Colombia. Contr. U.S. Natl. Herb. **31**: 1-117. 1951; 119-322. 1953; 323-781. 1958.
- . A new genus of Acanthaceae from Mexico. Wrightia **2**: 1-3. 1959a. [*Lundellia*, related to *Aphelandra*.]
- . Five new species and one new variety of Acanthaceae recently col-

- lected in Venezuela. *Bol. Soc. Venez. Ci. Nat.* **21**: 7-15. 1959b. [New spp. in *Justicia*, *Ruellia*.]
- & L. B. SMITH. *Sanchezia* and related American Acanthaceae. *Rhodor* **66**: 313-343. 1964. [Includes new spp.]
- LIEBAU, O. Beiträge zur Anatomie und Morphologie der Mangrove-Pflanzen, insbesondere ihres Wurzelsystems. *Beitr. Biol. Pflanzen* **12**: 182-213. 1913. [*Acanthus ilicifolius*, a mangrove plant.]
- LILLO, M. Catalogo de las Acantáceas Argentinas. *Lilloa* **1**: 21-66. 1937.
- LINDAU, G. Beiträge zur Systematik der Acanthaceen. *Bot. Jahrb.* **18**: 36-64. *pls.* 1, 2. 1894.
- . Acanthaceae. *Nat. Pflanzenfam.* IV. **3b**: 274-354. 1895.
- LINDLEY, J. Acanthaceae. *Nat. Syst. Bot.* ed. 2. 284, 285. 1836. [Early references to family, together with revised classification.]
- LINSBAUER, K. Über die kalkfreien Cystolithen der Acanthaceae. *Ber. Deutsch. Bot. Ges.* **39**: 41-49. 1921. [Details of development of cystoliths.]
- LUBBOCK, J. A contribution to our knowledge of seedlings. Vol. 2. viii + 608 pp. London; 646 pp. New York. 1892. [Acanthaceae, 348-365.]
- MAHESHWARI, P., & V. NEGI. The embryology of *Dipteracanthus patulus* (Jacq.) Nees. *Phytomorphology* **5**: 456-472. 1955. [Includes review of embryological research in family.]
- MAITI, P. C. Andrographolide: the active principle of Kalmegh. *Bull. Bot. Surv. India* **6**: 63-65. 1964. [Kalmegh is *Andrographis paniculata*, prescribed for liver ailments; includes bibliography.]
- MARTIN, A. C. The comparative internal morphology of seeds. *Am. Midl. Nat.* **36**: 513-660. 1946. [Acanthaceae, 627, 628, 629, 646.]
- MAURITZON, J. Die Endosperm und Embryoentwicklung einiger Acanthaceen. *Lunds Univ. Årsskr.* II. Sect. 2. **30**(5): 1-41. 1934.
- MEEUSE, A. D. J., & J. M. J. DE WET. \times *Ruttyruspolia*, a natural intergeneric hybrid in Acanthaceae. *Bothalia* **7**: 439-441. 1961.
- MELCHIOR, H. Acanthaceae. *Engler's Syllabus der Pflanzenfamilien.* ed. 12. **2**: 456-460. 1964.
- METCALFE, C. R., & L. CHALK. Acanthaceae. *Anat. Dicot.* **2**: 1014-1023. 1950.
- MEYER, P. G. Beitrag zur Kenntnis der Acanthaceen Südwestafrikas. *Mitt. Bot. Staatssam. München* **2**: 300-306, 368-385. 1957.
- . Die Acanthaceae und Euphorbiaceae Südwestafrikas. Inaugural-Diss. Naturw. Fak. Ludwig-Maximilians Univ. München. 1961. [Includes keys to spp.]
- MOHAN RAM, H. Y. Endosperm and embryo development in some Acanthaceae. *Proc. 43rd Indian Sci. Congr.* **1956**(3): 235. 1956. [*Peristrophe*, *Adhatoda*, and *Barleria*.]
- . Embryological characters in the classification of the Acanthaceae. *Proc. IX Int. Bot. Congr.* **2**: 267. 1959.
- . Endosperm in *Eranthemum nervosum*. *Curr. Sci. Bangalore* **28**: 169, 170. 1959.*
- . The development of the seed in *Andrographis serpyllifolia*. *Am. Jour. Bot.* **47**: 215-219. 1960. [Endosperm cellular from beginning.]
- & P. MASAND. Endosperm and seed development in *Andrographis echioides* Nees. *Curr. Sci. Bangalore* **31**: 7, 8. 1962.*
- & ———. Embryology of *Nelsonia campestris* R. Br. *Phytomorphology* **13**: 82-91. 1963.
- & M. WADHI. Endosperm in Acanthaceae. *Ibid.* **14**: 388-413. 1964. [Systematic review of studies in various genera; includes bibliography.]

- NAIR, A. G. R. Luteolin as a characteristic flavone of Acanthaceae. *Curr. Sci. Bangalore* 34: 79, 80. 1965.*
- NARAYANAN, C. R. Somatic chromosomes in the Acanthaceae. *Jour. Madras Univ. B.* 21: 220-231. 1951a.*
- . Nucleolar conditions in meiosis of *Barleria Prionitis*. *Ibid.* 232-235. 1951b.
- . Note on chromosome fragmentation in meiosis of *Barleria Prionitis*. *Ibid.* 236, 237. 1951c.*
- . Studies in the Acanthaceae; microsporogenesis in *Justicia Betonica*, *Barleria Prionitis* and *Ruellia tuberosa*. *Ibid.* 26: 189-207. 1956.
- NATARAJAN, A. T. Studies in the morphology of pollen-Tubiflorae. *Phyton Buenos Aires* 8: 21-42. 1957. [Survey of morphology of pollen of 81 spp., 58 genera, in 10 families, including *Thunbergia*, *Ruellia*, *Asystasia*, *Hygrophila*, *Andrographis*, *Justicia*, and *Barleria*.]
- NEES VON ESENBECK, C. G. Acanthaceae Indiae Orientalis. *In*: N. WALLICH, *Pl. Asiat. Rar.* 3: 70-117. 1832.
- . Characters of new species of Indian Acanthaceae. *Comp. Bot. Mag.* 2: 310, 311. 1837.
- . Acanthaceae. *DC. Prodr.* 11: 46-519. 1847.
- . Acanthaceae. *In*: K. F. P. VON MARTIUS, *Fl. Brasil.* 9: 6-163. pls. 1-31. 1847.
- PAL, M. Chromosome numbers in some Indian angiosperms I. *Proc. Indian Acad. Sci. B.* 60: 347-351. 1964. [*Aphelandra*, *Barleria*, *Dianthera*, *Justicia*.]
- PAX, F. See L. RADLKOFER.
- PHATAK, W. G., & K. B. AMBEGAOKAR. Embryological studies in Acanthaceae — the female gametophyte. *Jour. Univ. Baroda* 4: 87-97. 1955.* [Female gametophyte of *Elytraria acaulis*, *Barleria Prionitis*, and *Acanthus ilicifolius*. Cf. *Proc. Indian Sci. Congr. Assoc.* 43(3, abstr.): 227. 1955.]
- & ———. Embryological studies in Acanthaceae — endosperm and embryo development in *Barleria Prionitis* L. *Jour. Univ. Baroda* 5: 73-87. 1956.*
- & ———. Embryological studies in the Acanthaceae V. Development of embryo sac and endosperm in *Blepharis maderaspatensis* (L.) Roth. *Proc. Indian Acad. Sci. B.* 57: 88-95. 1963.
- PIZZOLONGO, P., & M. D'ARIENZO. Contributo alla cariologia del genere *Acanthus*. *Ann. Fac. Sci. Agr. Portici Univ. Stud. Napoli III.* 30: 175-183. 1965.
- RABIGER, F. H. Untersuchungen an einigen Acanthaceae und Urticaceae zur Funktion der Cystolithen. *Planta* 40: 121-144. 1951. [Includes discussion of possible role of cystoliths in photosynthesis.]
- RADFORD, A. E., H. E. AHLES, & C. R. BELL. Manual of the vascular flora of the Carolinas. lxi + 1183 pp. Univ. of North Carolina Press, Chapel Hill. 1968. [Acanthaceae, 971-974.]
- RADLKOFER, L. Ueber den systematischen Werth der Pollenbeschaffenheit bei den Acanthaceen. *Sitz-ber. Math.-Phys. Akad. Wiss. München II.* 13: 256-314. 1883. [First called attention to value of pollen characters in systematics of family. See F. PAX, *Bot. Jahrb.* 5(Lit-ber.): 19, 20. 1884, for a critical review.]
- RAJ, B. Pollen morphological studies in the Acanthaceae. *Grana Palynol.* 3: 3-108. 1961.

- RAO, V. S. The floral anatomy of some Bicarpellatae. I. Acanthaceae. Jour. Univ. Bombay II. 21(5,B): 7-34. 1953.
- RECORD, S. J. Classification of various anatomical features of dicotyledonous woods. Trop. Woods 47: 12-27. 1936. [Includes references to Acanthaceae.]
- REED, C. F. *Andrographis*, a genus of Acanthaceae new to eastern United States. Castanea 26: 128. 1961. [*A. echinoides* Nees on chrome ore piles near Newport News, Va.]
- RICKETT, H. W. Wild Flowers of the United States. Vol. 2. The southeastern States. Part 2, pp. 323-688. pls. 117-241. New York. 1968. [Acanthaceae, 444-449, pls. 164, 165. Species of *Ruellia*, *Dyschoriste*, *Stenandrium*, *Dicliptera*, and *Justicia* illustrated in color.]
- RUSSOW, E. Mittheilungen über secretführende Intercellulargänge und Cystolithen der Acanthaceen, so wie über eine merkwürdige bisher nicht beobachtete Erscheinung in einzelnen Weichhaftzellen mehrerer Arten der genannten Familie. Sitzber. Naturf-ges. Univ. Dorpat 5: 308-316. 1880.
- SAHI, B. G. Embryo sac endosperm in *Andrographis paniculata* Nees (Acanthaceae). Curr. Sci. Bangalore 35: 368, 369. 1966. [Distinctive embryo sac and mature embryo.]
- SANTAPAU, H. The Acanthaceae of Bombay. Univ. Bombay Bot. Mem. 2: 1-104. 1951. [Keys to genera together with descriptions.]
- . Notes on the Acanthaceae of Bombay. Jour. Bombay Nat. Hist. Soc. 51: 349-368. 1954. [Corrections and appendix to 1951 paper.]
- . The flowering of *Strobilanthes*. *Ibid.* 56: 677. 1959. [Absence of typical monocarpy in *S. callosus* Nees.]
- SAYEEDUD-DIN, M. Some common Indian herbs with notes on their anatomical characters. III. *Andrographis echinoides* Nees. Jour. Bombay Nat. Hist. Soc. 41: 548-550. 1940. [General anatomy.]
- SCHAFFNIT, E. Beiträge zur Anatomie der Acanthaceen-Samen. Beih. Bot. Centralbl. 19(1): 453-521. 1906. [Detailed anatomical study of the 4 types of seeds described for family.]
- SCHNARF, K. Vergleichende Embryologie der Angiospermen. vi + 354 pp. Berlin. 1931. [Contains review of embryology of Acanthaceae, especially early literature.]
- SCHREMMER, F. *Acanthus mollis*, eine europäische Holzbienenblume. Österr. Bot. Zeitschr. 107: 84-105. 1960. [Includes pollination by *Xylocopa*.]
- SCOTT, F. M. Cystoliths and plasmodesmata in *Beloperone*, *Ficus*, and *Boehmeria*. Bot. Gaz. 107: 372-378. 1946.
- SELL, Y. Les complexes inflorescentiels de quelques Acanthacées. Étude particulière des phénomènes de condensation, de racémisation, d'homogénéisation et de troncation. Ann. Sci. Nat. Bot. XII. 10: 225-300. 1969.
- SHARMA, B. D., & VISHNU-MITRE. Contribution to the pollen morphology of the genera *Eranthemum* L. and *Pseuderanthemum* Radlkof. (Acanthaceae). Proc. Natl. Inst. Sci. India B. 29: 520-526. 1963. [Four pollen types occur in 15 spp. of 2 genera.]
- SOLEREDER, H. Systematische Anatomie der Dicotyledonen. xvi + 984 pp. Stuttgart. 1899. [Acanthaceae, 692-705.]
- SREEMADHAVAN, C. P. *Bremekampia* (Acanthaceae): a new generic name. Bull. Bot. Surv. India 6: 323, 324. 1964. [New name for *Haplanthus*.]
- STEENIS, C. G. G. J. VAN. Gregarious flowering of *Strobilanthes* (Acanthaceae) in Malaysia. Ann. Bot. Gard. Calcutta 150 Anniv. Vol.: 91-97. 1942.
- TAKIZAWA, Y. Die Struktur der Pachytanchromosomen einiger Acanthaceen,

- sowie eine Reihe neu bestimmter Chromosomenzahlen. *Cytologia* 22: 118–126. 1957. [Identification of heterochromatic regions in meiotic chromosomes in *Thunbergia*, *Strobilanthes*, *Hemigraphis*, *Ruellia*, *Aphelandra*, *Peristrophe*, *Hypoestes*, *Thyrsacanthus*, *Fittonia*, *Justicia*, *Beloperone*.]
- TCHOUPROFF, O. Quelques notes sur l'anatomie systématique des Acanthacées. *Bull. Herb. Boiss.* 3: 550–560. 1895.
- TIEGHEM, P. VAN. Structure du pistil et de l'ovule du fruit et de la graine des Acanthacées. *Ann. Sci. Nat. Bot.* IX. 7: 1–24. 1908. [Thunbergiaceae proposed; not validly published.]
- UPHOF, J. C. Cleistogamic flowers. *Bot. Rev.* 4: 21–49. 1938. [Cleistogamy occurs in 6 genera of Acanthaceae.]
- VELENOVSKY, J., & L. VINIKLAR. New contributions to the Cretaceous flora of Bohemia, 3. (Abstr.) *Biol. Abstr.* 5: 234, Abstr. 2413. 1931.
- VESQUE, J. Sur quelques formations cellulosiennes locales. 1. Éléments nouveaux dans le liber des Acanthacées. *Ann. Sci. Nat. Bot.* VI. 11: 181–185. *pl.* 9. 1881.
- . Caractères des principales familles Gamopétales, tirés de l'anatomie de la feuille. *Ibid.* VII. 1: 183–360. *pls.* 9–15. 1885. [Acanthaceae, 326–335; some anatomical characterizations of family, includes classification of cystoliths.]
- WERNHAM, H. F. Floral evolution with particular reference to the sympetalous dicotyledons. *New Phytol.* 11: 145–166. 1912.
- WETTSTEIN, R. VON. *Handbuch der systematischen Botanik*. ed. 4. x + 1152 pp. Leipzig, Wien. 1933–1935. [Acanthaceae, 909–911.]
- WILLIS, J. C. *A dictionary of the flowering plants and ferns*. ed. 7. (Revised by H. K. AIRY SHAW.) xxii + 1214 pp. + Key to the families of flowering plants (liii pp.). Cambridge, England. 1966. [Includes Mendonciaceae Bremek., Thunbergiaceae Bremek.]

KEY TO THE GENERA OF ACANTHACEAE IN THE SOUTHEASTERN UNITED STATES

- A. Retinacula papilliform or absent; herbs [shrubs] or vines without cystoliths; anthers 2-loculate; fruit a beaked or cuspidate capsule; seeds 4 to many.
- B. Vines; ovules 2 in each locule; calyx [annular or] toothed; stamens 4[or 2], basal lobes of anther spurred or blunt; capsule beaked; pollen spheroidal, spirotreme (subfam. Thunbergioideae). 1. *Thunbergia*.
- B. Erect herbs; ovules numerous in each locule; calyx more or less equally 5-parted; stamens 2, basal lobes of anther blunt; capsule beaked or cuspidate; pollen 3-colpate, syncolpate, prolate (subfam. Nelsonioideae). 2. *Elytraria*.
- A. Retinacula hooklike, subulate, truncate or more or less fimbriate at tip; herbs with or without cystoliths; anthers 1- or 2-loculate; fruit not beaked; seeds 2 to many.
- C. Shoots not articulated; cystoliths absent; stamens 4, anthers 1-loculate; pollen colpate (subfam. Acanthoideae). 3. *Stenandrium*.
- C. Shoots articulated; cystoliths present; stamens 2 or 4, if 4 then at least 2 provided with 2-loculate anthers; pollen colpate or porate (subfam. Ruellioideae).
- D. Aestivation of corolla contorted; stamens usually 4; corolla actinomorphic, subactinomorphic or zygomorphic.
- E. Calyx actinomorphic or nearly so; stamens didynamous; inflorescence various.

- F. Corolla limb actinomorphic or nearly so; capsule stipitate.
 - G. Inflorescence spiciform; bracts large, closely imbricate; corollas not projecting beyond the bracts. . . 4. *Blechum*.
 - G. Inflorescence axillary, or axillary and terminal, cymose, racemose, or paniculate, rarely in heads; bracts usually small, rarely imbricate; corollas projecting well beyond the bracts.
 - H. Calyx lobes lanceolate or linear; anther sacs blunt; corolla limb actinomorphic or subactinomorphic. 5. *Ruellia*.
 - H. Calyx lobes bristle-like; anther sacs awned or pointed at the base; corolla limb subactinomorphic. 6. *Dyschoriste*.
- F. Corolla zygomorphic, bilabiate; capsule cylindrical, not stipitate.
 - I. Inflorescence racemose; stamens united in a short tube; 2 fascicles or rows of hairs present on posterior of the corolla. [*Hemigraphis*].
 - I. Inflorescence axillary, clustered, or flowers apparently solitary; stamens didynamous; corolla without hairs. 7. *Hygrophila*.
- E. Calyx zygomorphic, the segments very dissimilar, posterior one usually largest, anterior pair more or less united; stamens not didynamous; inflorescence a dense terminal spike. . . [*Barleria*].
- D. Aestivation of corolla cochlear; stamens 2 or 4; corolla zygomorphic, usually strongly bilabiate.
 - J. Ovules six or more in each locule; capsule not stipitate. [*Andrographis*].
 - J. Ovules two in each locule; capsule more or less distinctly stipitate.
 - K. Stamens 4. 8. *Asystasia*.
 - K. Stamens 2.
 - L. Stems 6-angled; calyx subtended by two partially united bracts; placenta separating from the mature capsule valves. 9. *Dicliptera*.
 - L. Stems subterete or slightly quadrangular; bracts distinct; placenta remaining attached to the valves of the capsule. 10. *Justicia*.

Subfam. THUNBERGIOIDEAE Lindau

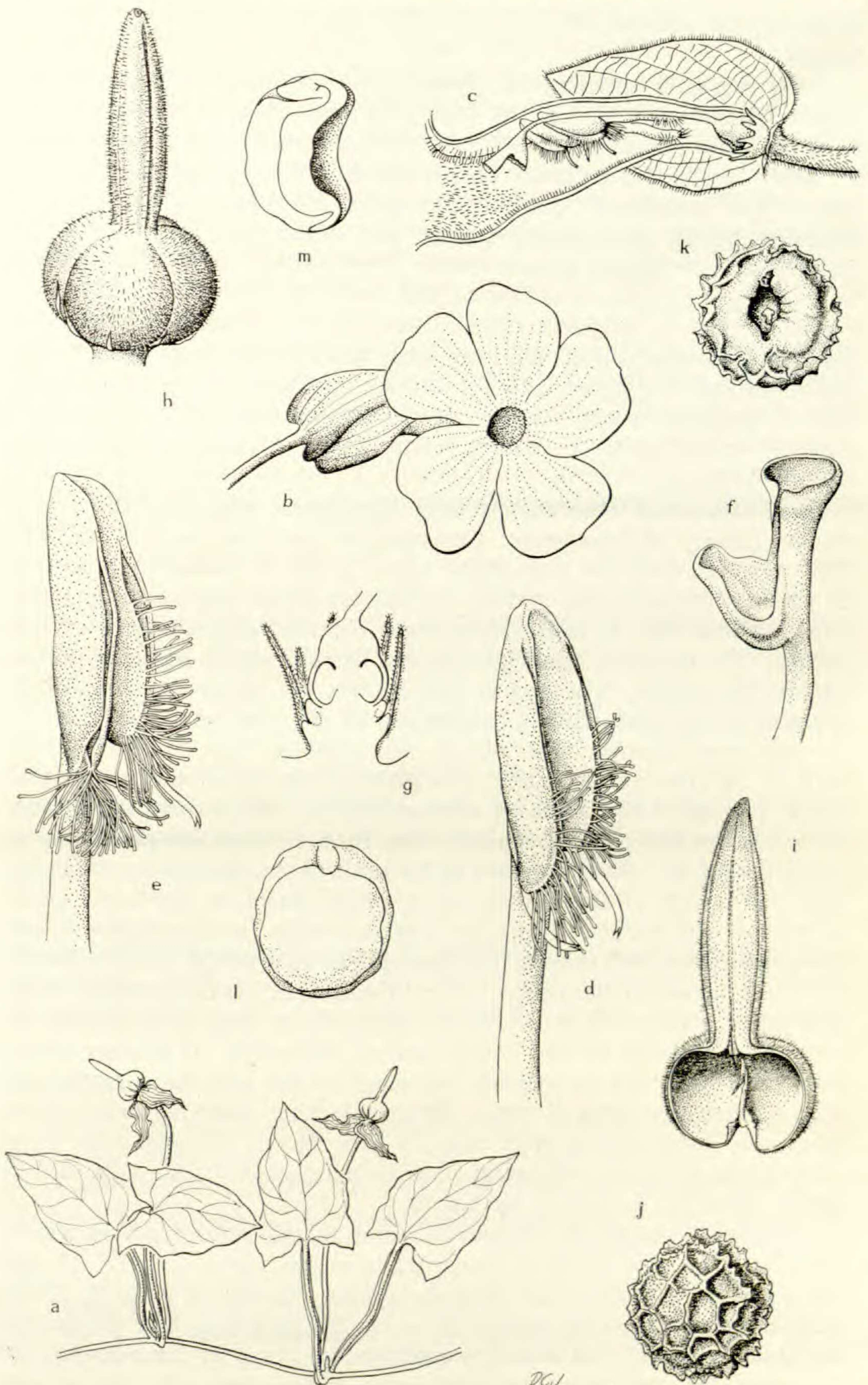
1. *Thunbergia* Retzius, Physiogr. Sällsk. Handl. 1(3): 163. 1776, nom. cons.

Climbing, often twining herbaceous [or woody] vines [or shrubs] with articulated stems. Leaves prevailingly sagittate, hastate, or cordate at the base. Flowers large, pedunculate, solitary in the axils [or in racemes, rarely cymose]; subtending bracts 2, spathaceous, large. Calyx persistent [variously reduced or shortly cupuliform, truncate] or 5-16-lobed. Corolla subactinomorphic to slightly zygomorphic, large, funnelform or salverform, tube slender, short, curved or straight, enlarged into a spreading 5-lobed

limb. Stamens didynamous, attached near the base of the tube; anthers with an apiculate connective, appendaged at base; pollen large, mostly 85–100 μ in diameter, spirotreme, spheroidal. Disc present, fleshy. Stigma infundibular or peculiarly 2-lobed (see FIG. 1f); ovary fleshy, ovules 2 in each locule, funiculus pulvinate. Capsule rounded, coriaceous, abruptly flat-beaked, subtended by persistent bracts, loculicidally dehiscent; seeds 2 in each valve. Seeds semiglobose, with a conspicuous excavation on the inner side; retinacula none. (Not *Thunbergia* Montin, Vet. Akad. Handl. Stockholm 34: 288. *pl.* 11. 1773, nom. rejic. = *Gardenia* Ellis [Rubiaceae].) TYPE SPECIES: *T. capensis* Retz. (Named for Carl Pehr Thunberg, 1743–1822, Swedish student and successor to Linnaeus, who traveled in Japan and South Africa and wrote floras of these regions, later professor of botany at Uppsala.) — CLOCK-VINE.

About 200 species of the Old World tropics, with 12 or more occurring in the American tropics and subtropics in cultivation or more or less naturalized, two of these in peninsular Florida. *Thunbergia alata* Bojer ex Sims, $2n = 18$, a slender, herbaceous vine with winged petioles and pale yellow to orange corollas, usually with a dark-purple “eye,” is locally abundant along roadsides in moist thickets and near abandoned homesites southward from Brevard and Sarasota counties, Florida. It is a native of East Africa but is now thoroughly naturalized in many tropical areas. None of the Florida specimens has the rusty-villous pubescence found on younger stems and leaves of many specimens from the West Indies. Bremekamp (1948) formally described several new varieties in *T. alata* in Java based on degrees of pubescence of stems and leaves, but they hardly appear worthy of taxonomic recognition. The Indo-Malayan *T. fragrans* Roxb. (*T. volubilis* Pers.), also a smooth, herbaceous vine with usually hastate leaves but with white corollas, has been collected in hammocks along the Indian River, Brevard County, Florida. A number of varieties, again based on pubescence and on leaf shape, have been recognized in this species by both Nees and Clarke. *Thunbergia grandiflora* Roxb., $2n = 28, 56$, an herbaceous or somewhat woody twining vine with large, bright-blue to white, more or less campanulate corollas, a native of India, is cultivated in southern Florida and may persist after cultivation, but apparently has not become established as an escape. All three species belong to sect. THUNBERGIA (§ *Euthunbergia* Benth.

FIG. 1. *Thunbergia*. a–m, *T. alata*: a, portion of vine with nearly mature fruits, $\times \frac{1}{2}$; b, flower, $\times 1\frac{1}{2}$; c, same in partial section, corolla lobes not shown, one bract removed, calyx and disc intact, to show relative positions of stamens and gynoecium, $\times 3$; d, outer stamen, $\times 12$; e, inner stamen, $\times 12$; f, stigma, $\times 12$; g, ovary, disc, and calyx in section cut to show placentation of two of four ovules, $\times 8$; h, mature fruit before dehiscence, $\times 3$; i, inner surface of valve of capsule after dehiscence, $\times 3$; j, seed, abaxial surface, $\times 6$; k, same, adaxial surface, $\times 6$; l, embryo, abaxial surface — note radicle and position of cotyledons, $\times 6$; m, same, in vertical section, adaxial surface to right — note radicle, plumule, and folding of cotyledons, $\times 6$.



& Hook.) on account of their two-lobed stigmas and solitary axillary flowers.

The remarkable anatomy of *Thunbergia* has occasioned studies by Chodat, Roulet, and Mullenders. Interxylary phloem is produced directly from the inner surface of an otherwise normal cambium in *T. mysorensis* T. Anders. (sect. HEXACENTRIS (Nees) Benth. & Hook.) and in *T. grandiflora*. This "centrifugal" phloem is produced independently of the other secondary tissue. Also, xylem bridges that differentiate in a tangential fashion occur in normal phloem tissue. The presence of medullary xylem in a number of species is similar to that found in *Mendoncia*.

Roulet also investigated certain intrageneric relationships from an anatomical comparison of the stem and the morphology of pollen. He concluded that *T. fragrans* and *T. alata* are not closely related, but rather that *T. fragrans* is more closely allied with the African *T. hastata*, *T. capensis*, and *T. hirta*; *T. alata* is related to *T. reticulata* and *T. annua*, of East Africa.

Some interesting observations have been made regarding the reproductive biology of *Thunbergia*. Cammerloher (see also Faegri & Van der Pijl) reported that the extra-floral nectaries of *T. grandiflora* function as part of the pollination system. Certain carpenter bees, such as *Xylocopa aestuans* and *X. latipes*, have been observed as pollinators of this species. The bee must crawl into the corolla tube and in so doing pushes against the stigma. The stigma and anthers are in an expanded outer chamber of the tube, while a constriction in the tube separates this from a small inner chamber that incloses the ovary and nectary. The thick wall of the tube at the constriction prevents tearing of the corolla and blocks passage of the insect. A narrow channel runs down to the nectary alongside the style, and the insect must extend its tongue along this to reach the nectar. Hairs attached to the anthers are touched by the insect and this results in the anthers being pulled down on its back, which is dusted with pollen. *Xylocopa* bees are often nectar "thieves" and from the outside will chew a hole through the base of the corolla thereby obtaining access to the nectar. This "illegitimate" circumvention of the pollinating mechanism is prevented, however, by ants attracted to the extrafloral nectaries on the bracts, pedicel, and calyx. If another insect, such as a *Xylocopa*, is similarly attracted by the extrafloral nectar, the ants aggressively chase it away. Flowers lacking these nectaries almost invariably have corollas with holes in their bases. Various other floral adaptations to insect pollination have been reported for *T. alata* and *T. erecta* (Benth.) T. Anders. by Knuth.

Cytological studies in *Thunbergia* point to the widespread occurrence of polyploidy. Mangenot & Mangenot have reported $2n = 32, 48,$ and 64 for three species, which suggests a base number of $x = 8$. Other numbers reported for the genus ($2n = 18, 28$) may have resulted through aneuploidy. Additional counts would be important in *Thunbergia*, but the available evidence already suggests that variation in chromosome number has been important in speciation within the genus.

The classification of plants related to *Thunbergia* has been a matter of long-standing controversy. Nees (1847) maintained *Thunbergia*, *Meyenia* Nees, and *Hexacentris* Nees as separate genera. Anderson, however, did not, and later Bentham & Hooker treated the three as sections of an inclusive *Thunbergia*. Radlkofer suggested on the basis of pollen and anatomical characters restoration of *Meyenia* to generic rank. He was followed by Lindau (1893), who treated *Thunbergia*, *Meyenia*, and *Pseudocalyx* as constituting subfam. Thunbergioideae, while placing the tropical American *Mendoncia* in a separate subfamily, Mendoncioideae, on the basis of its drupaceous fruit, absence of retinacula, and pollen morphology. (Lindau's is the most recent review of *Thunbergia* in its entirety. In it he established four sections based on the morphology of the stigma and the inflorescence.) Roulet (1894), after a detailed anatomical study, concluded that the three genera could not be maintained separately. Van Tieghem, however, disagreed and, stressing pollen, anther dehiscence, and petiolar anatomy, restored *Hexacentris* to generic rank and concurred with Radlkofer and Lindau in maintaining *Meyenia* as distinct from *Thunbergia*.

Bremekamp initially accepted the inclusion of *Thunbergia* in the Acanthaceae but later (1953) decided to follow Van Tieghem (1908; see under Family References), who had proposed the establishment of a separate family, Thunbergiacées, on the basis of the rostrate capsule and distinctive excavation on the ventral side of the seeds. Bremekamp thought *Thunbergia* to be more closely related to Mendoncioideae, Bignoniaceae, and Pedaliaceae than to Acanthaceae. Both Lindau and Bremekamp attached great taxonomic significance to pollen types in their classification of *Thunbergia*, and Raj concurred with Bremekamp that Thunbergioideae ought to be raised to family status on the basis of pollen characters. He also recommended that *Meyenia* be excluded from the family and transferred to the Pedaliaceae, again on the basis of pollen characters. It appears obvious that the uncertainty of the relationships of *Thunbergia* cannot be removed by conventional taxonomic approaches. Additional information derived from cytogenetical and chemotaxonomic techniques is very desirable for this genus.

REFERENCES:

- Under family references see ANDERSON (1864a), BAILLON (p. 423), BENTHAM & HOOKER, BREMEKAMP (1938, 1948, 1965), CLARKE, HARTMANN, KNUTH (p. 239), LINDAU (1895), NEES (1847), RAJ, SOLEREDER, and VAN TIEGHEM.
- BENOIST, R. Contribution à la connaissance des Acanthacées africaines et malgaches. Not. Syst. Paris 11: 137-151. 1944. [*Thunbergia*, 144-149.]
- BOR, N. L., & M. B. RAIZADA. Some beautiful Indian climbers and shrubs VIII. *Thunbergia*. Jour. Bombay Nat. Hist. Soc. 42: 685-697. 1941. [Includes key to 9 cultivated species.]
- BREMEKAMP, C. E. B. The *Thunbergia* species of the Malesian area. Verh. Nederl. Akad. Wet. Afd. Natuurk. 2. 50(4): 1-90. 1955.
- BURKILL, I. H. *Thunbergia*. Bull. Natl. Bot. Gard. Lucknow 22: 1-9. 1958.

- CAMMERLOHER, H. Zur Kenntnis von Bau und Funktion extra-floraler Nektarien. Biol. General. 5: 281–302. 1929. [Floral biology of *T. grandiflora*.]
- CHODAT, R. Sur l'origine des tubes criblés dans le bois. Bibliot. Univers. Arch. Sci. Phys. Nat. Genève III. 27: 229–239. *pl.* 1. 1892.
- CURTIS, S., & W. J. HOOKER. *Thunbergia alata*: (*albiflora*). Bot. Mag. 62: *pl.* 3512. 1836.
- FAEGRI, K., & L. VAN DER PIJL. The principles of pollination ecology. ix + 248 pp. Pergamon Press, Toronto, London, etc. 1966. [*T. grandiflora*, 162–164, with drawings.]
- HERKELOTS, G. A. C. *Thunbergia*. Occas. Notes Hong Kong Hort. Soc. 1: 14–21. 1931. [Notes on cultivated spp., including *T. alata*, *T. fragrans*.]
- LINDAU, G. Übersicht über die bisher bekannten Arten der Gattung *Thunbergia* L. f. Bot. Jahrb. 17(Beibl. 41): 31–43. 1893.
- MANGENOT, S., & G. MANGENOT. Enquête sur les nombres chromosomique dans une collection des espèces tropicales. Revue Cytol. Biol. Vég. 25: 411–447. 1962. [*T. erecta*, $2n = 64$; *T. laevis*, $n = 24$; *T. togoensis*, $2n = 32$.]
- MULLENDERS, W. L'origine du phloème interxylemien dans les genres *Thunbergia* et *Stylidium*. Cellule 51: 1–48. 1947. [Includes *T. fragrans* and *T. grandiflora*.]
- NAIR, A. G. R., S. NAGARAJAN, & S. S. SUBRAMANIAN. Chemical composition of nectar in *Thunbergia grandiflora*. Curr. Sci. Bangalore 33(13): 401. 1964.*
- PIJL, L. VAN DER. Houtbij bloemen bij *Costus*, *Bauhinia*, *Centrosema* en *Thunbergia*. Trop. Nat. 30: 5–14. 1941.* [Pollination of *T. grandiflora*.]
- RADLKOFER, L. Ein Beitrag zur afrikanischen Flora. Abh. Naturw. Ver. Bremen 8: 369–442. 1884. [Includes discussion of systematics of *Thunbergia* based on anatomy and pollen morphology.]
- ROULET, C. Résumé d'un travail d'anatomie comparée systematique du genre *Thunbergia*. Bull. Herb. Boiss. 1: 370–386. 1893.
- . Recherches sur l'anatomie comparée du genre *Thunbergia* Lin. fil. *Ibid.* 2: 259–326, 342–383. 1894.
- SHIBATA, K. Estudios citologicos de plantas colombianas silvestres y cultivados. Jour. Agr. Sci. Tokyo Agr. Coll. 8: 49–62. 1962. [Chromosome numbers in *Thunbergia*.]
- SIMS, J. *Thunbergia fragrans*. Bot. Mag. 44: *pl.* 1881. 1817; *Thunbergia grandiflora*. *Ibid.* 50: *pl.* 2366. 1822; *Thunbergia alata*. *Ibid.* 51: *pl.* 2591. 1825.
- TIEGHEM, P. VAN. Restauration du genre Hexacentre dans la famille nouvelle des Thunbergiacées. Ann. Sci. Nat. Bot. IX. 7: 111–116. 1908.

Subfam. NELSONIOIDEAE Lindau

2. *Elytraria* Michaux, Fl. Bor.-Am. 1: 8. 1803, nom. cons.

Acaulescent [or caulescent] rigid herbs with basal rosettes. Leaves alternate or sometimes subopposite, basal [or crowded at the ends of branches]. Flowers borne in dense, scapose, terminal spikes, peduncles and inflorescence bearing imbricate, coriaceous bracts; bracteoles subtending calyx somewhat shorter than the calyx. Calyx 4-parted, scarious, segments narrow, dentate or entire at the apex. Corolla blue or white, tube cylindrical, limb slightly bilabiate, lower lip 3-lobed. Stamens 2, barely

exserted, anthers sometimes awn-tipped at the base, 2-loculate, locules equal, parallel; staminodia usually absent; pollen 3-colpate, syncolpate, prolate, about $30 \times 40 \mu$ in diameter, shed at the 2-celled stage. Ovary 2-loculate, placentation parietal, ovules 6–10 in each locule, amphitropous, funicular obturator and retinaculum absent. Capsule narrow, acute at apex, contracted at base, thick-walled, with explosive dehiscence. Seeds more or less flattened; embryo spatulate, slightly bent; endosperm present, ruminant. Embryo sac with persistent antipodal cells, often becoming binucleate; endosperm cellular, conforming to the Pedicularis type; embryogeny conforming to Lythrum-variation of Onagrad type. (*Tubiflora* J. F. Gmel., nom. rejic.) TYPE SPECIES: *E. virgata* Michx., nom. illeg. = *E. caroliniensis* (J. F. Gmel.) Pers. (Name derived from Greek *elytron*, sheath, referring to the coriaceous bracts that cover the scapes and subtend the flowers.)

A small genus of perhaps 15 species in the tropics and subtropics of both Old and New worlds. The American species were treated by Leonard, who recognized twelve species in the Western Hemisphere. In our flora the genus is represented by *Elytraria caroliniensis* (J. F. Gmel.) Pers. var. *caroliniensis* (*E. virgata* Michx., *Tubiflora caroliniensis* [Walt.] J. F. Gmel.), which occurs on the Coastal Plain from southern South Carolina to southern peninsular Florida (Lee County), where it is locally abundant in bottomlands, wet pine barrens, and in calcareous gravel. It is a well-marked species with large, basal leaves in a rosette, and a stout, virgate scape with one or more spikes. In southern Florida (Collier and Dade counties) a narrow-leaved form, *E. caroliniensis* var. *angustifolia* (Fern.) Blake (*Tubiflora angustifolia* (Fern.) Small) is sometimes frequent locally, also in wet or rocky soil. Beyond our range, *E. bromoides* Oerst., a somewhat dwarf form that may prove to be a geographic subspecies of the *E. caroliniensis* complex, occurs in Texas.

The taxonomic position of *Elytraria* and that of the Nelsonioideae have been controversial since St. Hilaire first included the genus in the Acanthaceae (1805). Sprengel, for one, did not accept this decision and transferred the genus to the Scrophulariaceae (1817), a course also followed by Link (1821). Lindley (1847) placed *Elytraria* in his segregate family Nelsoniaceae. Lindau established the subfamily Nelsonioideae because, on the basis of the general habit of the plants, the presence of papilliform retinacula in a number of genera, and the presence of explosively dehiscent capsules, he believed the genera properly belong in the Acanthaceae. The Nelsonioideae, including five genera, three of them monotypic, is the largest of his first three subfamilies. After a detailed study of various groups of genera, Bremekamp (1953, 1965) proposed that the Nelsonioideae be transferred to the Scrophulariaceae "in the vicinity of the Rhinanthae." Earlier, however, Bhaduri had expressed the view that possibly the Nelsonioideae did not even deserve subfamily rank, since the pollen resembles that of *Acanthus* and *Crossandra*, of the Acanthoideae, and is not otherwise distinctive.

Johri & Singh challenged Bremekamp's views and after a detailed study of microsporogenesis, megagametogenesis, embryogeny, and endosperm formation concluded that *Elytraria* is in general conformity with other members of the Acanthaceae. The only feature of special interest is the formation of peripheral endosperm cells that form prominent ridges owing to unequal growth. This imparts an uneven or ruminant appearance to the structure, a feature uncommon in Acanthaceae. In an elaborate defense, Bremekamp (1965) emphasized the alternate leaves, parietal placentation, scapose habit, and type of endosperm in Nelsonioideae, all characters that tend to associate the group with Scrophulariaceae, particularly tribe Rhinanthae. He concluded that Johri & Singh did not prove that the Nelsonioideae belong with the Acanthaceae, although he not only ignored the embryological data, but also the pollen characters and the hemiparasitism of Rhinanthae, a characteristic unknown in Nelsonioideae. Morton has reported $2n = 38$ for three African species of *Elytraria*, suggesting a base number similar to that for other Acanthaceae. Martin described what he termed a "spatulate," slightly bent embryo in *Elytraria*, although the Acanthaceae generally produce non-spatulate, strongly bent embryos. Certainly the total evidence is equivocal, and one must conclude that the position of *Elytraria* and other Nelsonieae is uncertain at the present time. Probably no special advantages would accrue from a transfer to the Scrophulariaceae since other problems would then arise. Additional cytological information, as well as genetic and chemotaxonomic evidence, ought to shed light on the systematic position of the group.

REFERENCES:

- Under family references see BAILLON (p. 425), BHADURI, BREMEKAMP (1938, 1942, 1953, 1965), LEONARD (1951), LINDAU (1895), MARTIN, and RAJ.
- JOHRI, B. M., & H. SINGH. The morphology, embryology, and systematic position of *Elytraria acaulis* (L. f.) Lindau. Bot. Not. 112: 227-251. 1959.
- LEONARD, E. C. The American species of *Elytraria*. Jour. Wash. Acad. Sci. 24: 443-447. 1934. [Six spp.; taxonomic synopsis only, with keys.]
- . New species of *Elytraria* from the West Indies and Peru. *Ibid.* 28: 308-313. 1938. [*E. prolifera*, *E. crenata*, *E. planifolia*, *E. Klugii*, spp. nov. Genus limited to Cuba and Hispaniola in W. Indies.]
- . Two new tropical American species of Acanthaceae. Proc. Biol. Soc. Wash. 52: 17, 18. 1939. [*E. macrophylla*, from San Luis Potosí, Mexico, and a *Mendoncia* from Venezuela.]
- MORTON, J. K. The West African species of *Elytraria* (Acanthaceae), a taxonomic and cytological study. Revista Biol. Lisbon 1: 49-58. 1956.
- SMALL, J. K. *Tubiflora acuminata*. Addisonia 18: 55, 56. pl. 604. 1934. [*E. bromoides* Oerst.]
- WARD, D. B. The genus *Anonymos* and its nomenclatural survivors. Rhodora 64: 87-92. 1962. [*E. caroliniensis* (J. F. Gmel.) Pers.]
- WILBUR, R. L. The identity of Walter's species of *Anonymos*. Jour. Elisha Mitchell Sci. Soc. 78: 125-132. 1962. [*E. caroliniensis* (J. F. Gmel.) Pers.]

Subfam. ACANTHOIDEAE Lindau emend. Bremek.

Tribe APHELANDREAE Nees emend. Bremek.

Subtribe Aphelandrinae Bremek.

3. *Stenandrium* Nees in Lindley, Nat. Syst. Bot. ed. 2. 444. 1836, nom. cons.

Perennial acaulescent [caulescent or suffrutescent] herbs. Leaves entire, often radical. Flowers borne in scapose spikes [or subsessile or sessile, peduncles axillary, leafless], simple [or branched]; bracts herbaceous, imbricate, lanceolate to ovate, entire [sometimes dentate]; bracteoles

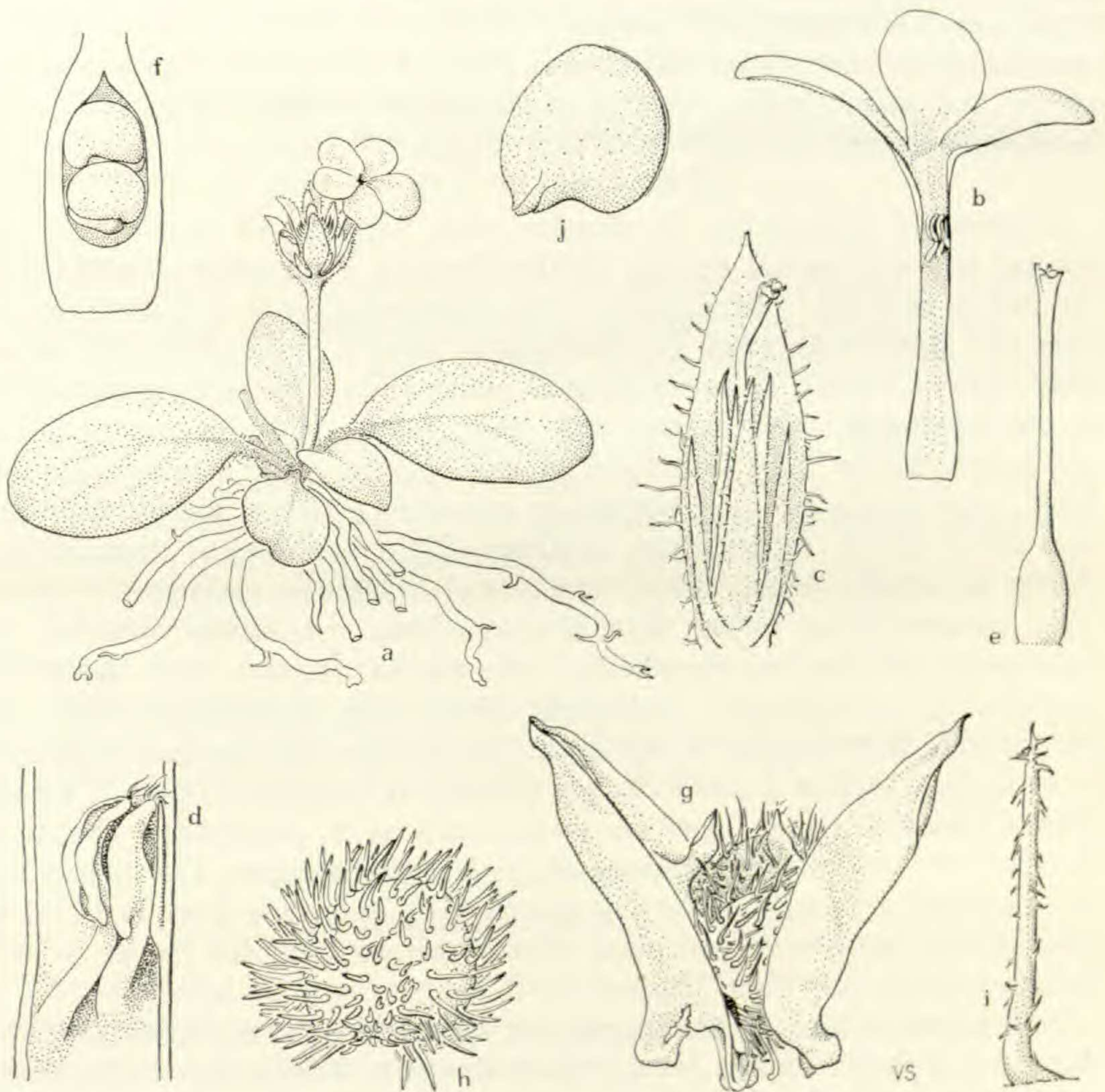


FIG. 2. *Stenandrium*. a-j, *S. dulce* var. *floridanum*: a, flowering plant, $\times 1$; b, corolla in vertical section to show position of stamens and staminodium, $\times 3$; c, flower with bract and two bracteoles, corolla removed, $\times 4$; d, portion of corolla tube in vertical section showing two of four stamens and staminodium, $\times 15$; e, gynoecium, $\times 6$; f, ovary in vertical section to show septum and two ovules, $\times 15$; g, open capsule with two of four seeds retained — note retinacula above, $\times 15$; h, seed with echinate seed coat, after moistening, $\times 5$; i, single spine-like hygroscopic hair from seed coat, after moistening, $\times 25$; j, embryo, moistened, oriented as in seed (h), $\times 5$.

subtending calyx short, setaceous. Calyx lobes 5, subequal, narrow, acute, striate-nerved. Corolla infundibuliform, pinkish, purple [or white], tube cylindrical, slender, somewhat oblique and slightly enlarged at the throat, limb [4- or] 5-lobed, spreading, lobes rounded, subequal, retuse or obovate, imbricate. Stamens didynamous, adnate in the throat of the tube, included; filaments very short; anthers 1-loculate, linear, connivent or almost cohering in pairs, mucous at base; pollen variable, spheroidal, with indistinct apertures [or 3-colpate, prolate, reticulate or anomotreme, pantoporate]. Disc inconspicuous, truncate. Style filiform, stigma subclavate, obconical, simple or obscurely 2-lobed; ovules 2 in each locule. Capsule subfusiform, oblong to subterete; seeds 4, or sometimes fewer by abortion, orbicular, plano-compressed, minutely muricate, echinate [to hispid], each subtended by a long retinaculum. (*Gerardia* L., nom. rejic.) LECTOTYPE SPECIES: *S. mandioccanum* Nees. (Name from Greek *stenos*, narrow, and *andros*, male, referring to the narrow anthers characteristic of the Aphelandreae.)

A genus of remarkable distribution with perhaps 30 species, all in tropical and subtropical regions of the Western Hemisphere, except for one that is endemic to Madagascar. Our representative is *S. dulce* (Cav.) Nees var. *floridanum* Gray (*S. floridanum* (Gray) Small, *Gerardia floridana* (Gray) Small), an inconspicuous, uncommon, low herb of seasonally wet pinelands, moist sandy soil, and grassy roadsides of southern peninsular Florida, from Citrus and Osceola counties south into the Florida Keys. Our plants are very similar in appearance to the highly variable var. *dulce*, which ranges from southern Chile to Mexico; they differ chiefly in usually having upper bracts and bracteoles glabrous or sparingly hirsute-ciliate, rather than hirsute. They are highly variable in pubescence and in leaf morphology, the blades varying from narrowly spatulate to suborbicular. Individual plants may be from 4–6 cm. to 15 cm. tall. Superficially, *S. dulce* var. *floridanum* also appears to be related to the Mexican *S. subcordatum* Standl., of Yucatan, and to *S. mexicanum* Leonard. Other Mexican plants, such as *S. fasciculare* (Benth.) Wasshausen may also be elements of the *S. dulce* complex. Our plants do not, however, appear to be closely related to *S. barbatum* Torr. & Gray, a very hirsute, many-stemmed plant with numerous, crowded leaves, which occurs in Texas and New Mexico.

The relationships of the genus are apparently with other tropical American Aphelandrinae. Nees (1847) thought *Stenandrium* to be nearest *Crossandra*. He divided the 16 species into two informal groups, "Acaulia vel subacaulia . . ." and "Caulescentes . . ." Strangely, Bentham & Hooker placed the genus in the tribe Justiceae, subtribe Asystasiinae, among genera to which it bears no relation. Lindau followed Nees in placing *Stenandrium* in Aphelandreae; his classification suggested intergeneric relationships with the monotypic Central American *Strobilacanthus* Griseb. and with the large tropical American genus *Aphelandra* R. Br. Lindau recognized two unequal sections, sect. STENANDRIUM

(§ *Schizostenandrium* Lindau) and sect. SPHAEROSTENANDRIUM Lindau, based entirely on differences in pollen morphology. Our species would be placed in the latter. The present subgeneric disposition of species must be considered unsatisfactory, since one species, the Brazilian *S. trinerve* Nees, has one variety in one section, another variety in the other! Bremekamp initially placed the genus in Acantheae (1948) but later returned it to the Aphelandreae (1965).

Stenandrium is one of several genera of Acanthaceae that exhibit a wide range of pollen types. Raj found that the pollen of *S. barbatum* was 3-colpate, goniotreme, prolate; that of *S. trinerve* anomotreme, spheroidal; that of *S. Pohlii* Nees (Brazil) 6-7-porate, spheroidal; and that of *S. droseroides* Nees 3-colpate, prolate, with finely reticulate sculpturing. Pollen-grain size, however, was fairly uniform. With this much variation in pollen morphology it appears that pollen characters are not a sound basis for future monographic revision.

Chromosome counts are highly desirable, since not a single species of *Stenandrium* has been reported on cytologically.

REFERENCES:

- Under family references see BAILLON (p. 461), BREMEKAMP (1948, 1953, 1965), GRAY, HALLIER (1898), LINDAU (1895), LEONARD (1953), LINDLEY (1836), NEES (1847), and RAJ.
- LEONARD, E. C. Acanthaceae Americanae novae vel criticae. *Wrightia* 2: 75-82. 1960. [Includes description and figure of *S. Carolinae* Leonard & Proctor and formal publication of *S. bracteosum* (Britt. & Millsp.) Britton ex Leonard, comb. nov., a close relative of the new sp.]
- . A new *Stenandrium* from the State of Durango, Mexico. *Ibid.* 83-85. [S. *pelorium* Leonard, an unusually large sp.]
- STANDLEY, P. C. Three new plants from Yucatan. *Jour. Arnold Arb.* 11: 47, 48. 1930. [Includes *S. subcordatum* Standl.]
- THIERET, J. W. Proposal for the conservation of the generic name *Stenandrium* Nees versus *Gerardia* L. (Acanthaceae). *Taxon* 5: 58. 1956.

Subfam. RUELLIOIDEAE Bremek.

Tribe RUELLIEAE Nees emend. Bremek.

The Ruellieae as redefined by Bremekamp (1944) and Bremekamp & Nannenga-Bremekamp (1948) is a large tribe composed of several subtribes, none of which is precisely delimited. They all, however, are characterized by usually contorted aestivation of the corolla lobes, by spheroidal or ellipsoidal, 3- or more-porate pollen grains, and by reticulate, spinulose, or banded pollen surfaces. Lindau's tribes Hygrophileae, Petalidieae, Strobilantheae, and Barlerieae, are retained as subtribes with considerable emendation by Bremekamp; they are distinguished largely on the basis of differences in pollen morphology. The descriptive anatomy of several genera of Ruellieae showing comparative relationships was reported by Tchouproff.

Subtribe *Blechinae* Bremek.4. *Blechum* P. Browne, Civ. Nat. Hist. Jamaica 261. 1756.

Perennial herbs. Leaves petiolate, entire, repand, dentate or crenate. Flowers small, sessile or on very short pedicels in the axils of bracts; inflorescence a more or less dense, terminal [or axillary] spike or spiciform raceme; bracts imbricate, ciliate, broad, suborbicular [or elongate]. Calyx deeply 5-parted, segments linear-subulate, nearly equal [or unequal, almost bilabiate]. Corolla infundibuliform, white or purplish; tube elongate, slender; limb short, nearly equally 5-lobed, contorted in aestivation, barely or not extending beyond the subtending bracts of the flower. Stamens didynamous, included, adnate about the middle of the tube; anthers 2-loculate, muticous, locules parallel; pollen 3-colporate, syncolporate, spheroidal, about 47μ in diameter. Style filiform; stigma subulate, obscurely lobed, the posterior lobe minute; ovules few to 6 in each locule. Capsule broadly oblong [ovoid or orbicular], with a short, narrow base. Seeds suborbicular, plano-compressed, surface with mucilaginous hairs when moistened; supporting retinacula acute; septum breaking away in the mature capsule. TYPE SPECIES: *Ruellia Blechum* L. = *Blechum Brownei* Juss. (Apparently a Greek name for wild pennyroyal, *Mentha Pulegium* L.)

Blechum is a small genus of ten or possibly fewer species of herbs indigenous to the American tropics; one species has been introduced into the Old World tropics as a weed and is now rather common in warm climates of the world. In general, the genus is recognized by its dense, sometimes 4-sided spike, very reduced flowers, and the mature capsules in which the septum breaks away from the capsule wall. Our single representative is *B. Brownei* (*B. pyramidatum* (Lam.) Urban; cf. Bremekamp, 1938, p. 149), $2n = 34$, which occurs as an occasional naturalized weed in extreme southern Florida, usually in damp soil and in the margins of mangrove areas (*Lakela* 26876, GH, USF). The species can be easily recognized by its dense, conspicuously bracteate, 4-sided spikes and small flowers. It is widely distributed throughout the American tropical regions in open cultivated or waste places, in both dry and moist soil, from eastern and southern Mexico through Central America and the West Indies to northern South America. It has been introduced as a weed in the Old World tropics.

The intergeneric relationships of *Blechum* are uncertain. Nees (1847) placed the genus in his subtribe Dicliptereae, believing it to be allied to *Dicliptera* and *Rungia* on the basis of the detachable septa in mature capsules of all three genera. Nees's reference to the occurrence of *Blechum* in Madagascar and the East Indies is unclear, since he does not record any of the eight species described as having been found there. Bentham & Hooker placed the genus in the subtribe Petalidiinae, while recognizing that its three to many ovules per locule made it dissimilar to other genera

in the group. Lindau classified *Blechum* in his tribe Petalidieae together with four other genera, but Bremekamp & Nannenga-Bremekamp (1948) removed it to a subtribe of its own because of its racemose inflorescence and peculiar pollen. It should also be pointed out that they stated that the separation of Petalidiinae, Blechinae, and Ruelliinae is based only on differences in the morphology of pollen. Melchior has gone a step farther and recognized the tribe Blecheae (including only *Blechum*) and has placed it near the Barlerieae.

Grant reported that *Blechum Brownei* has 34 somatic chromosomes, as does *Ruellia*, and said that karyology and chromosome number indicated affinity of the two genera and provided little evidence for their separation. Satellite chromosomes were observed in both genera, with the satellites attached by a slender thread to the short arm of a chromosome with a subterminal centromere. He suggested that *Blechum* may have been derived by hybridization of plants with basic chromosome numbers of $x = 8$ and $x = 9$. Leonard (1951) also emphasized the similarity of *Blechum* and *Ruellia*, pointing out that the only conclusive difference between the two is the breaking away of the septum from the mature capsule in *Blechum*, while it remains intact in *Ruellia*. The type species of *Blechum* was first thought to be a *Ruellia* because of its close morphological similarity to that genus.

Oersted recognized in *Blechum* two subgenera based on morphology of the calyx and bracts, BLECHUM (subg. *Eublechum* Oerst.) and CHILOBLECHUM, which were treated as sections by Lindau (1895) with the species about equally divided between the two. In his treatment of Acanthaceae of the West Indies Lindau (1900) recognized three species of *Blechum*, with the others restricted to Central America and Mexico, but both sections are represented over the range of the genus.

REFERENCES:

- Under family references see BAILLON (p. 433), BENTHAM & HOOKER, BREMEKAMP & NANNENGA-BREMEKAMP (1948), GRANT, LEONARD (1951), LINDAU (1895), MELCHIOR, NEES (1847), and RAJ.
- JUSSIEU, A. L. DE. Mémoire sur le *Dicliptera* et le *Blechum*, genres nouveaux de plantes, composés de plusieurs espèces auparavant réunies au *Justicia*. Ann. Mus. Hist. Nat. Paris 9: 251-271. 1807.
- LINDAU, G. Acanthaceae. In: I. URBAN, Symb. Antill. 2: 170-250. 1900. [*Blechum*, 185-188.]
- OERSTED, A. S. Mexico og Centralamerikas acanthaceer. Vidensk. Medd. Naturl. For. Kjøbenhavn 6: 113-181. 1854. [Subg. *Chiloblechum*.]

Subtribe Ruelliinae Bremek.

5. *Ruellia* Linnaeus, Sp. Pl. 2: 634. 1753; Gen. Pl. ed. 5. 238. 1754.

Perennial caulescent herbs [or shrubs], usually pubescent. Leaves sessile or petioled, mainly entire, undulate [rarely dentate]. Flowers large

and showy (usually), or small and cleistogamous, solitary, or more often clustered in the leaf axils, or borne in terminal or axillary cymes or cymose panicles; bracteoles sessile or subsessile, narrow, small [or sometimes oblong to lanceolate, herbaceous, imbricate, and conspicuous]. Calyx deeply 5-parted or cleft, the segments linear or narrow, acute, subequal [or posterior lobe larger, or 2-lipped]. Corolla infundibuliform, purple, lavender, white [red, rose, or yellow], sometimes saccate; tube short to long (sometimes quite long), narrow below, straight or oblique; limb of 5 obtuse, spreading lobes, nearly regular [or 2 posterior lobes connate at the base forming a lip], aestivation convolute; cleistogamous flowers with corolla small, tubular, closed. Stamens 4, rarely 5, didynamous, adnate below the throat, included [or exerted]; anthers parallel, 2-loculate, oblong-sagittate, muticous; filaments dilated at the base, anterior filaments larger; pollen 3-porate, spheroidal, from 47 to 99 μ in diameter. Disc inconspicuous [or frequently conspicuous]. Style slender, usually slightly recurved at apex; stigma simple, subulate or 2-lobed, the lobes equal or posterior lobe short or obsolete; ovules 2–10 in each locule, anatropous. Capsules linear-oblong, narrow, or clavate, somewhat flattened, base very short or contracted into a solid, elongate stipe. Seeds 4–20, plano-compressed, suborbicular, with a mucilaginous coat that exhibits, after moistening, tapered, short hairs with walls marked internally by rings or spirals; retinacula elongate, acicular, hooked. $2n = 34$. (Including *Aphragmia* Nees in Lindl., *Arrhostoxylum* Nees in Mart., *Cryphiacanthus* Nees, *Dipteracanthus* Nees.) LECTOTYPE SPECIES: *Ruellia tuberosa* L.; see Britton & Brown, *Illus. Fl. No. U.S. ed. 2. 3: 241. 1913.* (Named in honor of Jean de la Ruelle, 1474–1537, a French physician and herbalist.)

The second largest genus of Acanthaceae with about 250 species distributed throughout the tropics and subtropics; relatively few species in the temperate regions of North America; six indigenous species and three introductions in the southeastern United States. The genus has an interesting quadricentric distribution that corresponds in general to that for the family, with centers of variation in Brazil, Indo-Malaya, Central America, and Africa. The circumscription of *Ruellia* adopted here is essentially that of Lindau (1895). The genus has long been recognized as taxonomically very difficult, and Lindau freely admitted that his intrageneric classification was tentative.

Our most important species is the polymorphic *Ruellia caroliniensis* (J. F. Gmel.) Steud. subsp. *caroliniensis*, *sensu stricto* (*R. hybrida* Pursh, *R. parviflora* *sensu* Small), which occurs throughout the Southeastern States in a wide variety of habitats, such as bottomlands, sandy woods, limestone soils, old fields, disturbed sites, scrub vegetation, etc. Fernald described six varieties, in addition to the typical one, and five forms, primarily on the basis of slight differences in leaf shape and on pubescence patterns. These appear to be of doubtful taxonomic value, since they describe minor variations induced by environmental modification or by small genetic differences. In southern peninsular Florida occurs an en-

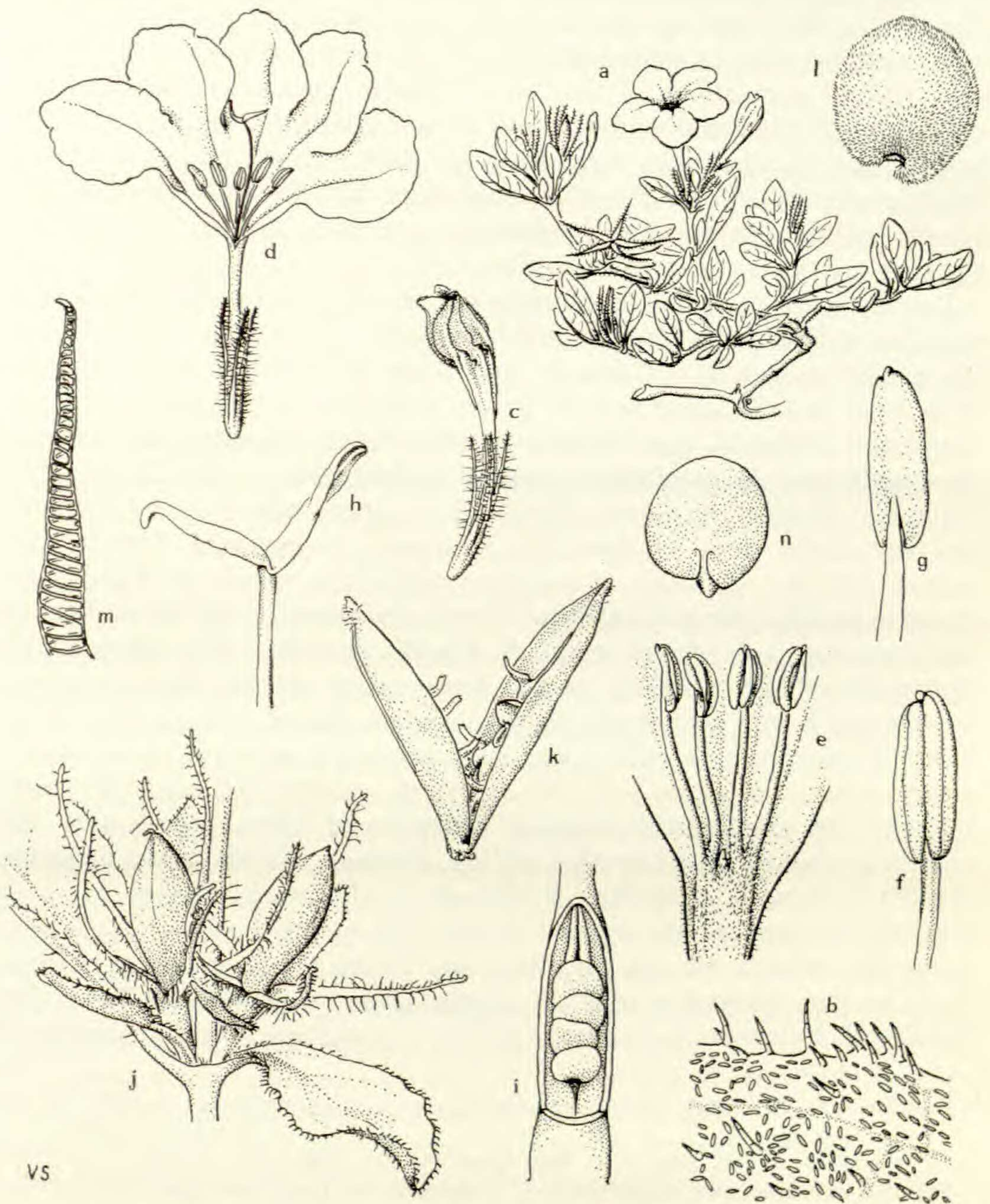


FIG. 3. *Ruellia*. a-j, *R. caroliniensis* var. *heteromorpha*: a, flowering and fruiting branch, $\times \frac{1}{2}$; b, portion of leaf, showing trichomes and cystoliths, $\times 12$; c, flower bud, $\times 1$; d, flower with five stamens, corolla partly laid open, $\times 1$; e, androecium of flower with four stamens and staminodium, $\times 3$; f, g, two views of anther, $\times 8$; h, stigmata, $\times 8$; i, ovary in partial section to show placentae and ovules of one locule, $\times 12$; j, node with two nearly mature fruits, $\times 2$. k-n, *R. humilis*: k, open capsule showing retinacula, one aborted seed remaining in right-hand valve, $\times 3$; l, seed with covering of hygroscopic hairs, after moistening, $\times 6$; m, small hair (about half as long as most) from seed coat, showing internal spiral and annular thickenings, $\times 200$; n, embryo from moistened seed, $\times 6$.

demic variety, *R. caroliniensis* subsp. *caroliniensis* var. *succulenta* (Small) R. W. Long² (*R. succulenta* Small), a distinctive ecotype generally restricted to the Everglades region. *Ruellia caroliniensis* subsp. *ciliosa* (Pursh) R. W. Long³ is found in dry pinelands and scrub vegetation from South Carolina to central Florida, thence west to southeastern Louisiana. Hybrid populations of the two subspecies are frequent in northern and central Florida in disturbed sites. A second endemic variety, *R. caroliniensis* subsp. *ciliosa* var. *heteromorpha* (Fern.) R. W. Long,⁴ occurs in sandy pinelands and in disturbed sites from Volusia and Lee counties, Florida, south into the Keys. Hybrid populations of the two endemic varieties are not uncommon in southern Florida.

Fernald also described a number of new but doubtfully important varieties in *R. humilis* Nutt., a highly variable species that is found only in the western part of our area, in open fields, dry prairies, and rocky soil from Iowa and Kansas south to Texas, extending into western Virginia, Tennessee, Alabama, and western Florida. Some introgression between *R. humilis* and *R. caroliniensis* occurs in their area of overlapping distribution. *Ruellia noctiflora* (Nees) Gray is endemic to wet pinelands and savannahs from southwestern Louisiana to northern Florida and eastern Georgia; it is one of our most distinctive species because of its elongate corolla tube and capsule. Genetic evidence (Long, unpublished) indicates that it is related to the *R. humilis* complex. The Ozarkian *R. pedunculata* Torr. ex Gray subsp. *pedunculata* extends from southern Illinois south into western Louisiana, eastern Texas, and eastern Oklahoma in calcareous or rocky soils. A disjunct subspecies, *R. pedunculata* subsp. *pinetorum* (Fern.) R. W. Long,⁵ a smaller and smoother form but with the characteristic elongate peduncles of subsp. *pedunculata*, occurs in low pinelands of South Carolina, northern Florida, and Louisiana. *Ruellia strepens* L. (including *R. strepens* f. *cleistantha* (Gray) McCoy) reaches its greatest development in the Mississippi basin and adjacent areas and extends into the Carolinas and Virginia, principally in bottomlands and on calcareous soils. A related taxon, *R. Purshiana* Fern. (including *R. Purshiana* f. *clausroflora* Fern.), is endemic to the mountainous

✓² *Ruellia caroliniensis* subsp. *caroliniensis* var. *succulenta* (Small) R. W. Long, stat. nov.

R. succulenta Small, Bull. N.Y. Bot. Gard. 3: 437. 1905.

✓³ *Ruellia caroliniensis* subsp. *ciliosa* (Pursh) R. W. Long, stat. nov.

R. ciliosa Pursh, Fl. Am. Sept. 2: 420. 1814.

Dipteracanthus ciliosus (Pursh) Nees, Linnaea 16: 204. 1842.

R. humilis sensu Small, Fl. Southeast. U.S. 1084. 1903, and Man. Southeast. Fl., 1933, non Nutt.

✓⁴ *Ruellia caroliniensis* subsp. *ciliosa* (Pursh) R. W. Long var. *heteromorpha* (Fern.) R. W. Long, stat. nov.

R. heteromorpha Fernald, Rhodora 47: 32. 1945.

R. hybrida sensu Small, Fl. Southeast. U.S. 1084. 1903, non Pursh, Fl. Am. Sept. 2: 420. 1814.

✓⁵ *Ruellia pedunculata* Torr. ex Gray subsp. *pinetorum* (Fern.) R. W. Long, stat. nov.

Ruellia pinetorum Fernald, Rhodora 47: 24. 1945.

region and Piedmont plateau from western Maryland south to Alabama, in woods and on calcareous or acid soils. The morphology of the plant suggests that it may be of hybrid origin involving *R. strepens* and *R. caroliniensis*, although Uttal reported that the two species grow in adjacent areas and apparently do not hybridize. All these species represent sect. *DIPTERACANTHUS* (Nees) Lindau.

A second group of species in our flora has been introduced into Florida from tropical America. The Mexican and Antillean *R. Brittoniana* Leonard emend. Fern. (*R. malacosperma* sensu Small, non Greenman), of sect. *PHYSIRUELLIA* Lindau, has escaped from cultivation and is naturalized in waste areas and around former homesites in southern Florida, possibly in Louisiana, and also in Texas. A single collection of *R. malacosperma* Greenm., of sect. *RUELLIA*, from Key West, Florida, indicates that this plant is locally escaped. Apparently *R. Lorenziana* Griseb., an Argentinian species of sect. *RUELLIA* related to *R. tuberosa* L., is a new addition to our flora that is locally naturalized near Homestead, Florida. Although Britton & Millspaugh in their *Bahama Flora* state that *R. tuberosa* occurs in the southern United States, no specimens of this common tropical weed have been seen from our area.

Ruellia is the only acanthaceous genus for which there is some information about interspecific relations as determined by hybridization tests. Probably one of the first interspecific hybrids was made by Müller, who successfully crossed two Brazilian species, *R. formosa* and *R. silvaccola*. Morphologically intermediate hybrids were produced by almost 50 per cent of the seeds formed from crossing experiments. Bowden reported a sterile hybrid, *R. ciliosa* (= *R. humilis* Nutt.?) \times *R. tuberosa*. Long successfully crossed *R. caroliniensis* with *R. humilis* and suggested that natural hybridization may be a factor causing the observed intergradation of these species in their area of overlapping distribution. From a study of breeding systems in populations of southern Florida, he concluded that the four taxonomic species involved are ecological races of a single polytypic species, *R. caroliniensis*. An investigation of interspecific hybrids resulted in the production of 22 different F_1 hybrids involving 12 North American taxa. Intersectional crosses, such as *R. brittoniana* \times *R. occidentalis*, produced partially or completely sterile but sometimes vigorous hybrids. Abnormal meiosis in these hybrids may account for the high sterility.

The breeding systems in both the eastern species and the Texan "paniculate" species centered on *R. nudiflora* involve showy, chasmogamous flowers and small, tubular, cleistogamous flowers. Chasmogamous flowers favor outcrossing both structurally and by regular proterogyny. Generally, cleistogamous flowers are produced more abundantly towards the end of the growing season in the eastern species (at the beginning, in the paniculate species) producing numerous fruits with good seeds. The total evidence suggests that local populations are predominantly autogamous, particularly in the northern portion of our range, but that outbreeding occurs frequently in populations from Florida.

Long concluded that no revision of the genus ought to be attempted

until a thorough investigation of the reproductive biology of *Ruellia* species has been completed. Genetic barriers to interspecific crossing are lacking between many species, although these same species have been placed in different genera by various authors (especially Bremekamp). If it can be assumed that crossability is correlated with evolutionary relationship, the broad generic interpretation of Lindau may be a more accurate reflection of the natural limits of *Ruellia* than the numerous segregate genera advocated by Bremekamp.

Embryo sac development and microsporogenesis have been studied by Mauritzon, Maheshwari & Negi, Narayanan, Mohan Ram, and Wall & Long. No walls form after the first reduction-division during pollen formation in *Dipteracanthus patulus*; quadripartition occurs by furrowing with tetrads decussate or isobilateral. The single-layered nucellus is completely absorbed by the time the four-nucleate stage of the embryo sac has been reached. Development of the embryo sac is of the *Polygonum* type, with the tip of the sac extending into the micropyle. Both synergids and antipodals are ephemeral, but pollen tubes persist, and remnants can be recognized even in mature seeds. The endosperm is of the cellular type and is composed of a two-nucleate micropylar haustorium, a four-nucleate chalazal haustorium, and a central chamber that later separates into a cellular upper portion and a free-nuclear lower portion. A notable feature is the occasional formation of twin embryos. Additional embryos may arise by the proliferation of some of the suspensor cells.

In an investigation to determine whether there are embryological differences between *Ruellia tuberosa* and *Dipteracanthus patulus*, Mohan Ram concluded that, in general, both show the same type of embryology, although twin embryos were not found in *R. tuberosa*. The only notable difference was the presence of a cellular basal apparatus, a structure apparently absent in *D. patulus*. Chromosome numbers may be different for the two genera, however. Kaur and De both report $2n = 44$ for *D. prostratus*; the somatic number for *R. tuberosa* is $2n = 34$. In any event, the investigations thus far in the genus clearly demonstrate the usefulness of experimental approaches to the definition of both genera and species. Hybridization tests may yet prove to be a more satisfactory means of defining natural groups than pollen characters or floral morphology within Ruelliinae.

The genus has little economic importance. A number of tropical species are popular cultivars, mostly in greenhouses. *Ruellia Devosiana* Morr. and *R. Makoyana* Hort. both have purplish leaves, usually with attractive white venation; the former has white corollas marked with purple or lilac, the latter bright reddish corollas. The bright-blue-flowered *R. squarrosa* Hort. is grown in southern Florida as a ground cover and rock garden plant.

Members of the subtribe Ruelliinae have pollen with three equatorial pores, or rarely four to seven evenly distributed pores, or "sparsiporous," alveolate, echinulate or granulate exines. In his key to the genera of Ruelliinae of the Malay Archipelago and New Guinea, Bremekamp included eight genera, four of which were included as synonyms by Lindau

in his treatment of *Ruellia*, and two of which are new. The recognition of segregates from *Ruellia* is based largely on inflorescence patterns, corolla morphology, and pollen sculpturing. For instance, *Ruellia* is said to differ from *Arrhostoxylum* in having pollen with smaller, shallower, more regular alveolae.

Ruellia was emended by Bremekamp and restricted to the four species centering on *R. tuberosa*, as treated by Leonard, but also including *R. malacosperma* Greenm., a circumscription coinciding with the original delimitation of *Cryphiacanthus* Nees. In contrast, Lindau (1895) used a broad, inclusive definition of *Ruellia*, including 19 segregate genera. He recognized nine sections (four monotypic) based on morphology of the capsule and the flower. His sect. RUELLIA is entirely American and corresponds with *Ruellia* L. emend. Bremek. His sect. DIPTERACANTHUS (Nees) Lindau corresponds in part to *Dipteracanthus* Nees emend. Bremek., although Bremekamp restricted the genus to paleotropical species with sparsiporous pollen and subringent corollas. It is not clear from Bremekamp's key in what genus our species would fall, although he stated that the closest allies of *Ruellia* L. emend. Bremek. are *Aphragmia* (based on *Ruellia inundata* HBK.) and *Arrhostoxylum* (based on *A. glabrum* Nees), both restricted to tropical and subtropical America. Most of our species possibly would fall into *Aphragmia*, resembling *Ruellia* in pollen, inflorescence, and seed characters, but differing in the clavate capsules with fewer seeds per capsule. Bremekamp also suggested that perhaps our species ought to be transferred to a new genus based on *R. strepens* L.

REFERENCES:

- Under family references see BAILLON (p. 426), BENTHAM & HOOKER, BREMEKAMP (1965), BREMEKAMP & NANNENGA-BREMEKAMP, DE, GRANT, KAUR (1966), LEONARD (1951; 1959), LINDAU (1895), MAURITZON, METCALFE & CHALK, NEES (1847), RAJ, SANTAPAU, SOLEREDER, and TCHOUPROFF.
- DIERS, L. Der Anteil an Polyploidien in den Vegetationsgürteln der Westkordillere Perus. *Zeitschr. Bot.* **49**: 437-488. 1961. [*R. floribunda* Hook., ca. $2n = 34$.]
- EVERETT, T. H. *Ruellia amoena*. *Addisonia* **22**: 55, 56. 1946.
- FERNALD, M. L. *Ruellia* in the eastern United States. *Rhodora* **47**: 1-38; 47-63; 69-90. 1945.
- FOERSTE, A. F. Notes on structures adapted to cross-fertilization. *Bot. Gaz.* **13**: 151-156. 1888. [Includes observations on a sp. of *Ruellia*.]
- HOLM, T. The root-structure of *Spigelia marilandica* L., *Phlox ovata* L. and *Ruellia ciliosa* Pursh. *Am. Jour. Pharm.* **78**: 553-559. 1906.
- . *Ruellia* and *Dianthera*: an anatomical study. *Bot. Gaz.* **43**: 308-329. pls. 11, 12. 1907. [General description of vegetative structures.]
- LECONTE, J. E. Observations on the North American species of the genus *Ruellia*. *Ann. Lyc. Nat. Hist. N. Y.* **1**: 140-142. 1824. [Habitat notes on *R. ciliosa* and *R. strepens*.]
- LEONARD, E. C. *Ruellia tuberosa* and a few of its close relatives. *Jour. Wash. Acad. Sci.* **17**: 509-520. 1927.
- LONG, R. W. Convergent patterns of variation in *Ruellia caroliniensis* and *R. humilis* (Acanthaceae). *Bull. Torrey Bot. Club* **88**: 387-396. 1961.

- . Biosystematic investigations in South Florida populations of *Ruellia* (Acanthaceae). *Am. Jour. Bot.* **51**: 842–852. 1964.
- . Artificial interspecific hybridization in *Ruellia* (Acanthaceae). *Ibid.* **53**: 917–927. 1966a.
- . The artificial hybridization of the tropical species *Ruellia Brittoniana* × *R. occidentalis* and its taxonomic significance. *Bull. Torrey Bot. Club* **93**: 181–187. 1966b.
- . Observations regarding the occurrence and relationships of *Ruellia Lorentziana* (Acanthaceae) in southern Florida. *Rhodora* **68**: 432–434. 1966c.
- . Origin of the “dwarf *Ruellia humilis*” (Acanthaceae) populations of central Florida. *Bull. Torrey Bot. Club* **95**: 16–27. 1968. [Apparently *R. caroliniensis* × *R. ciliosa* introgressants.]
- & L. J. UTTAL. Some observations on flowering in *Ruellia* (Acanthaceae). *Rhodora* **64**: 200–206. 1962. [Predominance of cleistogamous reproduction in natural populations.]
- McCoy, S. A cleistogamous *Ruellia*. *Am. Bot.* **43**: 22–24. 1937. [*R. strepens* var. *cleistantha* Gray, an autumnal form of the sp.]
- MAHESHWARI, P., & V. NEGL. The embryology of *Dipteracanthus patulus* (Jacq.) Nees. *Phytomorphology* **5**: 456–472. 1955. [Includes extensive bibliography.]
- MOHAN RAM, H. Y. Postfertilization studies in the ovule of *Ruellia tuberosa* Linn. *Lloydia* **23**: 21–27. 1960.
- MÜLLER, F. VON. Mischlinge von *Ruellia formosa* und *silvaccola*. *Abh. Naturw. Ver. Bremen* **12**: 379–387. 1892.
- PRAIN, D. *Ruellia Devosiana*. *Bot. Mag.* **137**: pl. 8406. 1911.
- STANDLEY, P. C. Two additions to the flora of Louisiana. *Torreyia* **14**: 21–24. 1914. [*R. spectabilis* = *R. Brittoniana* Leonard.]
- THARP, B. C., & F. A. BARKLEY. The genus *Ruellia* in Texas. *Am. Midl. Nat.* **42**: 1–86. 1949.
- UTTAL, L. J. Observations on *Ruellia Purshiana* (Acanthaceae) in Virginia. *Castanea* **30**: 228–230. 1965.
- . A plant-insect relationship in *Ruellia* L. (Acanthaceae) coincidental to autogamous populations. *Virginia Jour. Sci.* **17**: 46–48. 1966. [Destruction of seeds from early chasmogamous flowers by larvae of a noctuid moth, *Cobubatha*, favoring seed production by later cleistogamous flowers.]
- . Seed differentiation in east North American *Ruellia*. *Castanea* **33**: 254, 255. 1968.
- WALL, W. E., & R. W. LONG. Megasporogenesis and embryo sac development in *Ruellia caroliniensis* (Acanthaceae). *Bull. Torrey Bot. Club.* **92**: 372–377. 1965.
- WARD, D. B. The genus *Anonymos* and its nomenclatural survivors. *Rhodora* **64**: 87–92. 1962. [*R. caroliniensis* (J. F. Gmel.) Steud., 90.]
- WILBUR, R. L. The identity of Walter's species of *Anonymos*. *Jour. Elisha Mitchell Sci. Soc.* **78**: 125–132. 1962. [*R. caroliniensis* (J. F. Gmel.) Steud.]

Subtribe **Petalidiinae** Lindau emend. Bremek.

6. **Dyschoriste** C. G. D. Nees in Wallich, *Pl. Asiat. Rar.* **3**: 75, 81. 1832.

Perennial caulescent herbs [sometimes suffrutescent at base] with

glabrous or (more often) pubescent, erect, ascending [or prostrate] stems. Leaves sessile, subsessile [or petioled], usually entire [frequently fascicled]. Flowers in axillary clusters or cymes, sometimes solitary [rarely racemose], purplish, blue, or less commonly white, subtended by linear to oblong foliaceous bracts and bracteoles. Calyx deeply 5-cleft, lobes usually linear or subulate-setaceous, ciliate. Corolla-tube incurved or straight, cylindrical, often slightly ampliate at base, limb oblique, spreading, nearly regular to distinctly bilabiate. Stamens didynamous, a short and a long filament connate below and adnate to corolla tube, pubescent; anthers 2-loculate, more or less distinctly mucronate or aristate at base, locules equal, oblong, parallel to slightly divergent; pollen 3-colporate, prolate or occasionally subprolate, $40-50 \times 47 \times 28 \mu$. Stigma linear, anterior lobe somewhat flattened, oblique, posterior lobe rudimentary or absent; style filiform; ovary 2-locular, glabrous, ovules 2 or occasionally 1 in each locule. Capsule included in the persistent calyx, oblong-linear, 2-4-seeded, glabrous, separating with difficulty at maturity into 2 valves with 1 or 2 seeds within each valve held in position by the retinacula; capsule base contracted into a solid stipe; septum adnate. Seeds flat, orbicular or suborbicular, mucilaginous when wetted, hairs with faint rings or spiral thickenings within. (Including *Calophanes* D. Don, *Apassalus* Kobuski.) LECTOTYPE SPECIES: *D. depressa* (Wall.) Nees; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. 3: 240. 1913. (Name from Greek *dys*, difficult, and *choristos*, separable, in reference to the tenaciously coherent valves of the capsule.)

About 100 species widely distributed in the tropics and subtropics, with a few taxa extending into the warm-temperate regions of the world. About 40 supposed species are American, but it is probable that a monographic revision will reduce this number substantially.

Two species and two varieties occur in our area. *Dyschoriste humistrata* (Michx.) Kuntze (*Apassalus humistratus* (Michx.) Kobuski) is locally abundant in rich, sandy loam, limestone materials, and low river terraces from north-central Georgia to central peninsular Florida. *D. oblongifolia* (Michx.) Kuntze var. *oblongifolia*, $2n = 30$, is found on the Coastal Plain from South Carolina to Sarasota and Brevard counties, Florida, westward to Louisiana, in disturbed areas, sandy soil, pine barrens, and sandhills. It is quite variable both in leaf size and in pubescence of the stems and sepals. An endemic variety, *D. oblongifolia* var. *angusta* (Gray) R. W. Long,⁶ is locally abundant in extreme southern Florida and the Florida Keys in moist pinelands, disturbed sites, especially burned-over areas, rocky roadsides, limestone rocks, and similar places.

Nees (1832) established the genus by the transfer of species of earlier authors from *Ruellia* and *Justicia*. The key characters used were ". . . antherae bilocellatae, locellis parallelis aequalibus basi mucronatis. Capsula . . . prope a basi tetrasperma. . . . Dissepimentum adnatum." Only

⁶ *Dyschoriste oblongifolia* var. *angusta* (A. Gray) R. W. Long, comb. nov.

Calophanes angusta Gray, Synop. Fl. N. Am. 2: 324. 1878.

Dyschoriste angusta (Gray) Small, Fl. Miami 168. 1913; Fl. Florida Keys 135. 1913.

a year later David Don described his genus *Calophanes*, based on *Ruellia oblongifolia* Michx., apparently collected in Georgia. Both genera were used in later botanical literature, *Dyschoriste* representing Old World and *Calophanes*, New World taxa. Nees accepted this arrangement, but Bentham & Hooker, and later Clarke, placed *Dyschoriste* in the synonymy of *Calophanes*. Kuntze revived the earlier name; he was followed by Lindau, who placed the genus in his tribe Strobilantheae.

The complex problems in the typification of *Dyschoriste* have been discussed by Kobuski, who monographed the American species. His choice

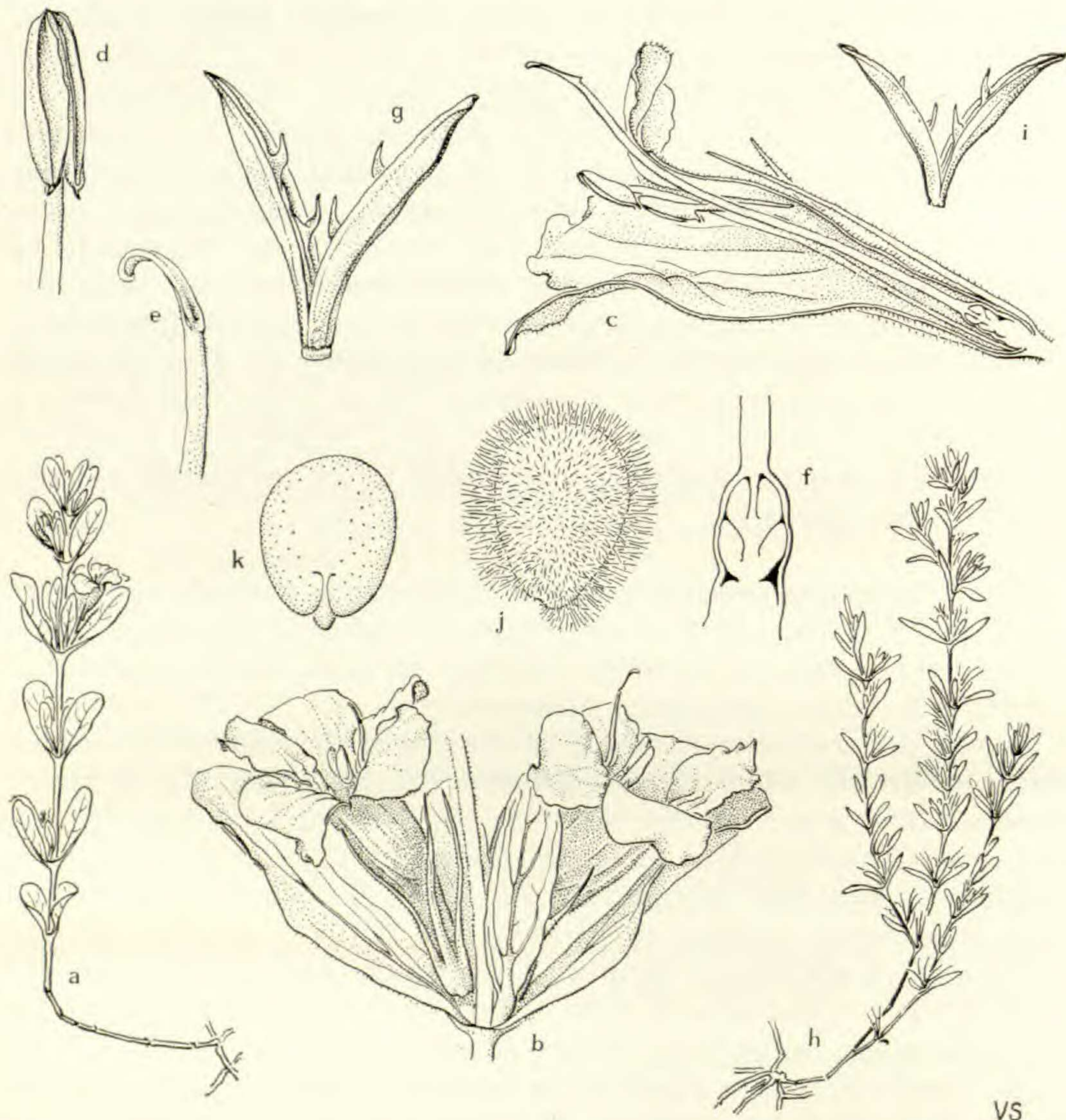


FIG. 4. *Dyschoriste*. a-g, *D. oblongifolia* var. *oblongifolia*: a, flowering stem, $\times \frac{1}{2}$; b, node with two flowers, one bractlet removed from pedicel of flower at left, $\times 2$; c, flower in longitudinal section, $\times 3$; d, anther after shedding of pollen, $\times 8$; e, stigma, $\times 10$; f, ovary in vertical section to show placentation, diagrammatic, $\times 10$; g, empty capsule with calyx removed—note retinacula, $\times 3$. h-k, *D. oblongifolia* var. *angusta*: h, branch with fruit, $\times 1$; i, empty capsule, $\times 3$; j, seed with hygroscopic hairs, after moistening, $\times 12$; k, embryo from moistened seed, $\times 12$.

of *Ruellia erecta* Burm. as the type is based on Kuntze's transfer of *Ruellia erecta* to *Dyschoriste* thereby making it the oldest known epithet in the genus. The choice presumes the accuracy of the identity and synonymy of the several taxa, including *D. depressa* Nees, that Clarke referred to *Calophanes Nagchana* Nees. *Ruellia erecta* is typified by a reference of Burmann to a plate and description by Van Rheedee. Unfortunately, the plant illustrated and described has alternate, lance-ovate leaves, annual roots, and an apparently one-lipped corolla. The calyx is described as four-parted, with two segments larger than the others. It is apparently not acanthaceous, but its true identity is uncertain. For the present the lectotype chosen by Britton & Brown seems to be the best available until the Old World plants can be examined.

Bremekamp (1955) transferred *Dyschoriste* from Strobilantheae to his Petalidiinae, a subtribe characterized by axillary cymes that rarely combine in a terminal panicle, by a subactinomorphic corolla never provided with a row of hairs functional in retaining the style, and, most importantly, by pollen grains that are prolate and banded, with three of the bands in the equatorial plane, dilated, and containing a pore. Most of the genera of the subtribe are tropical African in distribution, but *Dyschoriste* is pantropical. Kobuski decided not to place the American species in subgenera or sections because of the relative uniformity of morphological characters in the genus. Instead, he identified three distinct geographical areas where the species appear to be related: the southeastern United States (2 taxa); Texas and southern Arizona to the Isthmus of Tehuantepec (21 taxa); and South America (17 taxa).

Kobuski segregated his West Indian genus *Apassalus* from *Dyschoriste* on the basis of the much smaller leaves, smaller flowers, fruit characters, and muticous anther appendages. He considered it intermediate between the hypothetical ancestors of *Apassalus* and *Dyschoriste* proper in his interpretation. *Apassalus* was described as having only two seeds per capsule, but only one species (of three) has two seeds. The absence of anther appendages appears to be the only consistent character for the genus, and this hardly warrants recognition of a new genus in the Acanthaceae.

The phylogeny and relationships of *Dyschoriste* are obscure. The large number of closely allied species was considered by Kobuski probably to have evolved from common ancestral stock. He proposed that the taxa of the southeastern United States possibly are off-shoots of the widespread and morphologically generalized complex of *D. decumbens* (Gray) Kuntze, of Texas, Arizona, and Mexico, that developed parallel to the Mexican *D. Greenmanii* Kob. and *D. jaliscensis* Kob. Another morphological relationship is with the largely Texan *D. linearis* (Torr. & Gray) Kuntze. On the other hand, Kobuski thought that our southeastern taxa possibly are most closely related to his "*Apassalus* group" in the West Indies and have migrated into the United States from that direction. This theory assumes evolution of plants with large leaves, large flowers, anthers with appendages, and four-seeded capsules from plants with small flowers, muticous

anthers, and two-seeded capsules, a proposition that is difficult to accept. The absence of *Dyschoriste* in the Mississippi Valley does not rule out the possibility that the range of the genus prior to the Oligocene extended continuously across the southern United States. Possibly the distribution was then split into two parts by the encroachment of inland seas during later epochs of the Cenozoic. Such an interpretation would explain, at least in part, the relationship of our species with those of Texas and Mexico.

REFERENCES:

- Under family references see BAILLON (p. 428), BENTHAM & HOOKER, BREMEKAMP (1955b, 1965), GRANT, LINDAU (1895), NEES (1832, 1847), and RAJ.
- ALEXANDER, E. J. *Dyschoriste humistrata*. *Addisonia* 18: 25. *pl.* 589. 1933.
- BREMEKAMP, C. E. B. List of the Acanthaceae collected in Celebes by Dr. W. Kaudern and Dr. G. Kjellberg. *Sv. Bot. Tidskr.* 42: 372–403. 1948. [Includes *D. celebica* Bremek., sp. nov., and notes on pollen differences in *Dyschoriste* and *Hygrophila*.]
- KOBUSKI, C. E. A new genus of the Acanthaceae. *Ann. Missouri Bot. Gard.* 15: 1–8. 1928. [*Apassalus* Kob., gen. nov.]
- . A monograph of the American species of the genus *Dyschoriste*. *Ibid.* 9–90. [Includes 12 new species.]
- ROBERTSON, C. Florida flowers and insects. *Trans. Acad. Sci. St. Louis* 25: 277–324. 1927. [*D. oblongifolia* (as *Calophanes*), 285, 286; visited by long- and short-tongued bees, Diptera, and butterflies.]
- STERNON, F. Étude d'une plante médicinale mexicaine: *Dyschoriste* (*Calophanes*) *linearis* Gray. *Bull. Soc. Bot. Belg.* 65: 14–21. 1932. [Anatomical study demonstrating relationship with *Ruellieae*.]

Subtribe *Hygrophilinae* (Nees) Bremek.

7. *Hygrophila* R. Brown, *Prodr. Fl. Nov. Holland.* 479. 1810.

Perennial [or annual] erect, ascending [or diffuse] caulescent herbs; stems glabrous, sparsely pilose [or villous], unarmed [or with axillary spines]. Leaves entire, lanceolate to obovate. Flowers borne in axillary fascicles [or terminal heads, rarely solitary]; bracts linear [elliptic or lanceolate], ciliate; bracteoles lanceolate [or oblong], shorter than the calyx. Calyx tubular, segments 5 [4], equal to subequal, more or less fused to above the middle. Corolla tube cylindrical, ventricose at the apex, slightly ampliate; limb bilabiate, posterior lobe erect, concave, 2-cleft or 2-toothed, anterior segment 3-lobed, white [or pale purple]. Stamens didynamous [or 2 fertile stamens and 2 staminodia], not exserted, adnate to the tube above the middle; filaments glabrous, each pair connate at the base by a membrane, barely dilated; anthers oblong, mucous or submucronulate, 2-loculate, anther sacs parallel, divergent-sagittate. Pollen grains 3(4)-colporate, prolate spheroidal to subprolate spheroidal, varying in size from $35 \times 33 \mu$ to $70 \times 66 \mu$. Disc inconspicuous. Style long, pubescent; stigma subulate, incurved, posterior lobe abortive; ovules usually 6–8 in each locule [or rarely 2, up to 18]. Capsule narrow, oblong,

nonstipitate, the partition adnate. Seeds 12–18 [rarely 4, up to 36], orbicular-compressed; retinacula short, obtuse, acute. TYPE SPECIES: *Ruellia ringens* L. = *H. salicifolia* (Vahl) Nees (*H. angustifolia* R. Br.); cf. T. Anderson, Jour. Linn. Soc. Bot. 7: 113. 1864. (Name from Greek *hygros*, wet, and *philos*, loving, a reference to the usual habitat of the plants.)

A pantropical genus of about 80 species primarily of the Old World tropics but with a number of species in tropical America. Nees's treatment (1847) is the only account of the entire genus. He informally divided the 24 species into two groups based on the morphology of the inflorescence. Bentham and Hooker interpreted the genus broadly, reduced a number of Nees's segregate genera to synonymy, and did not recognize any subgeneric categories. Clarke divided *Hygrophila* into two subgenera, HYGROPHILA (§ *Euhygrophila* Clarke) and ASTERACANTHA (Nees) Clarke, based on the presence or absence of spines, on calyx morphology, and on the number of seeds per capsule. He stated that *Hygrophila* may have 40–100 minute seeds per capsule (surely a mistake!) but cited no species with more than 32. Lindau (1895) recognized five sections, but *Asteracantha* Nees was treated as a separate genus. Our single representative belongs to the largest and taxonomically most difficult section, HYGROPHILA (§ *Euhygrophila* Clarke emend. Lindau), which is distributed from tropical Asia to tropical America.

Hygrophila lacustris (Schlecht.) Nees, $2n = 32$, occurs from southwestern Georgia and western Florida to eastern Texas, with its greatest development apparently in the lower Mississippi River valley and delta region. It is also found in the West Indies. The plant is a weak-stemmed perennial herb with narrow, sessile leaves and sessile axillary clusters of small white flowers. *Hygrophila lacustris* appears to be related to the widespread tropical *H. conferta* Nees, of Mexico and Central America. Nees observed that *H. lacustris* differs from *H. conferta* only in having sessile, attenuate leaves and somewhat smaller corollas. Other relationships, also in tropical America, may include *H. portoricensis* Nees and *H. brasiliensis* (Spreng.) Lindau. *Hygrophila polysperma* (Roxb.) T. Anders., a native of the East Indies, has been reported by Reams as quickly establishing itself in lakes at Richmond, Virginia, when introduced, but it is doubtfully naturalized.

Although *Hygrophila* is pantropical, its relationships are apparently with Old World genera, particularly with the African *Brillantaisia* Beauv. and the largely East Indian *Synnema* Benth. Lindau suggested intergeneric relationships also with the African genera *Eremomastax* Lindau and *Mellera* S. Moore, but Bremekamp believed these genera properly belong in the subtribe Petalidiinae. The Hygrophilinae resemble the Petalidiinae in inflorescence characters, but differ in the bilabiate corolla and distinctive pollen sculpturing. Typically, *Hygrophila* produces pollen with three, rarely four, germ pores that have four grooves between two of the pores.

Reams, in an examination of environmentally induced variations in the

morphology and ontogeny of two types of hydathodes (water stomata and water-secretory trichomes), found that submerged leaves have water-stomata but nonfunctional, recessed trichome-hydathodes, while aërial or emersed leaves produce functional, bulbous trichome-hydathodes and water-stomata. Hydathodes are replaced by simple hairs on the bracts. The differentiation of the three kinds of trichomes begins immediately after the second cell-division of the primordium. Other evidences of the essentially aquatic nature of this genus were noted by Solereder who described the typical lacunar, hydrophytic cortex and the peculiar appearance of the interlocking parenchyma cells around the air chambers.

REFERENCES:

- Under family references see BAILLON (p. 430), BENTHAM & HOOKER, BREMEKAMP (1938, 1948, 1955b, 1965), CLARKE, LINDAU (1895), NEES (1847), RAJ, and SOLEREDER; under *Dyschoriste* see Bremekamp.
- BERTHOLDT, W. Siamese temple plant (*Hygrophila* sp.). *Aquarium Jour.* **29**: 386, 387. 1958.
- KUNDU, B. C. The morphology of the spines of *Hygrophila spinosa* T. Anders. *Jour. Bombay Nat. Hist. Soc.* **43**: 678-680. 1943. [Spines are modified branches.]
- LANGAWANKAR, J. D., N. L. PHALNIKAR, & B. V. BHIDE. Chemical investigation of *Hygrophylia* [sic] *spinosa* (N. O. Acanthaceae). *Jour. Univ. Bombay II.* **13(5A)**: 15-17. 1945.*
- MIÈGE, J. Quatrième liste de nombres chromosomiques d'espèces d'Afrique occidentale. *Revue Cytol. Biol. Vég.* **24**: 149-164. 1962. [*H. senegalensis* (Nees) T. Anders. and *H. spinosa* T. Anders., $2n = 32$.]
- RANGASWAMY, K. Cytomorphological studies in *Asteracantha longifolia* Nees (*Hygrophila spinosa* A. And.). *Proc. Indian Acad. Sci. B.* **14**: 149-165. 1941.
- REAMS, W. M., JR. The occurrence and ontogeny of hydathodes in *Hygrophila polysperma* T. Anders. *New Phytol.* **52**: 8-13. 1953.
- THORNE, R. F. Vascular plants previously unreported from Georgia. *Castanea* **16**: 29-48. 1951. [Includes *H. lacustris*.]
- STODOLA, J. *Encyclopedia of water plants.* 368 pp. T.F.H. Publications, Jersey City, N.J. 1967. [*H. polysperma*, *H. salicifolia*, 269, 271, 272, 275.]

Tribe JUSTICIEAE Nees emend. Bremek.

Subtribe Odontonematinae Lindau emend. Bremek.

8. *Asystasia* Blume, *Bijdr. Fl. Nederl. Indië* 796. 1825 [1826].

Perennial herbs [or shrubs], [erect,] procumbent or clambering, pubescent [or glabrous]. Leaves [narrowly lanceolate or] ovate, entire or somewhat dentate. Inflorescences terminal simple or branched racemes [or spikes], often unilateral; flowers opposite or alternate, solitary or glomerate in axils or bracts; bracts linear to narrowly deltoid, bracteoles minute. Calyx lobes 5, linear-setaceous [or lanceolate], subequal. Corolla purplish, blue, yellow, or white, infundibuliform, the limb 5-lobed, the tube straight or incurved, long, narrow or ventricose, the throat ampliate

or campanulate; aestivation imbricate. Stamens didynamous, or occasionally the posterior pair reduced to filiform staminodia, included; anthers 2-loculate, muticous at base or mucronate, locules parallel, equal, approximate, or unequal; pollen 3-porate (pleurotreme), prolate. Disc cupulate or annular. Style subulate; stigma obtuse or minutely 2-parted (or subcapitate); ovary with 2 ovules per locule. Capsule stipitate, pubescent [or glabrous], elliptic, the base contracted and solid, adnate; seeds 2-4 or fewer by abortion. Seeds ovate or compressed orbicular, irregularly angular, rugose or tuberculate, glabrous, retinacula elongate, subulate. TYPE SPECIES: *A. intrusa* (Forssk.) Blume. (Name possibly from Greek *asystatos*, not holding together, in reference to the wide-spreading valves of the dehisced capsules.)

A genus of possibly 40 species (although about 70 have been described) native to the Old World tropics, chiefly in the East Indies, India, and Africa, and now thoroughly naturalized in the New World tropics.

Asytasia is represented in our flora by *A. gangetica* (L.) T. Anders. (*A. coromandeliana* Nees), $2n = 50, 52$, a native of India. The plant is apparently a rather recent introduction into southern Florida where it has become naturalized as a lawn weed and has been found growing along the margins of pinelands (*Lakela 28452*, GH, USF). Our specimens appear to be identical or closely similar to those from the West Indies and other areas of tropical America where the species is used as a ground cover and has escaped from cultivation. The corolla color varies from pale bluish lavender to yellow or white with purplish darker lines on the limb.

The genus is in critical need of monographic revision. Nees described 15 species in his treatment of *Asytasia* for DeCandolle's *Prodromus*, and he included 7 varieties in the most variable species, *A. gangetica*. Bentham & Hooker enlarged the genus to include two groups of shrubs, *Dicentranthera* T. Anders., from the African tropics, and *Mackaya* Harv., from South Africa. Lindau (1895) placed *Asytasia* in its own tribe, Asystasiaceae, on the basis of its distinctive pollen and reduced number of seeds per capsule, but Bremekamp, in his realignment of the Justicieae (1965), transferred the genus to his emended Odontonematinae.

REFERENCES:

Under family references see BAILLON (p. 459), BENTHAM & HOOKER, BREMEKAMP (1948, 1965), KAUR, LEONARD (1953), LINDAU (1895), NEES (1847), and RAJ.

AKAMINE, E. K. Germination of *Asytasia gangetica* L. seed with special reference to effect of age on the temperature requirement for germination. *Pl. Physiol.* **22**: 603-607. 1947.

DE, A. Cytological investigations in the family Acanthaceae. *Sci. Cult.* **32**: 198, 199. 1966. [*A. gangetica*, $n = 25$, $2n = 50$.]

HOOKE, W. J. *Asytasia coromandeliana*. *Bot. Mag.* **72**: pl. 4248. 1846.

MANGENOT, S., & G. MANGENOT. Nombres chromosomiques nouveaux chez diverse dicotylédones et monocotylédones d'Afrique occidentale. *Bull. Jard.*

Bot. Bruxelles 27: 639-654. 1957. [$2n = 26$, a new number for *A. coromandeliana* (= *A. gangetica*) and the Acanthaceae; see also KAUR.]

NARAYANAN, C. R. Nuclear behavior and chromosomal aberrations in mitosis of *Acanthus ilicifolius* and *Asystasia coromandeliana*. Indian Jour. Genet. Pl. Breed. 11: 205-210. 1951.

Subtribe *Justiciinae* Bremek.

9. *Dicliptera* Jussieu, Ann. Mus. Hist. Nat. Paris 9: 267. 1807, nom. cons.

Perennial herbs [or shrubs], erect, ascending, or diffuse, pilose, hirtellous [or variously pubescent], with branching, often lax stems more or less hexagonal in cross-section. Leaves petioled, blades lanceolate to ovate, entire (or undulate). Flowers sessile, solitary or clustered in contracted cymes, these forming erect, secund, often lax spikes or panicles; bracts 2, frequently small, subulate; bracteoles 2 or 4, opposite in pairs and forming an involucl, the outer subequal, appressed, lanceolate or ovate. Calyx deeply 5-parted, the lobes linear-setaceous, equal or subequal, hyaline. Corolla red, violet, blue, pink, or white; tube narrow, resupinate, slightly ampliate; limb nearly regular or more often bilabiate, the upper lip entire, emarginate, or 2-toothed, flat or concave, the lower lip spreading, slightly 3-lobed; aestivation imbricate. Stamens 2, exerted but shorter than the upper lip, staminodia absent; anthers 2-loculate, anther sacs often unequal, muticous or the longer ones sometimes spurred; pollen 3-colporate, prolate or rarely perprolate, mostly $60 \times 25 \mu$ in diameter. Disc cupular, oblique-truncate, or sinuate-dentate. Style filiform; stigma entire or minutely 2-toothed; ovary with 2 ovules per locule. Capsule ovoid to suborbicular, subsessile, contracted into a short, solid stipe; placentae separating elastically from the walls and rupturing on dehiscence. Seeds 4 [or 2] or fewer by abortion, lenticular, with smooth, muricate, or squamose surface; retinacula uncinata, broadened at the base, acute tipped. (Including *Diapedium* Konig, nom. rejic., *Yeatsia* Small, *Gatesia* Gray.) TYPE SPECIES: *D. chinensis* (L.) Juss., typ. cons. (Name from Greek *diklis*, folding two ways, a double or folding door (*i.e.*, having two valves), and *pteron*, wing, in reference to the two recurved, apparently winged valves of the dehisced capsule.)

A large, taxonomically complex genus of possibly 150 species (although according to Leonard nearly 300 have been described) in the tropics, subtropics, and warm-temperate regions of the world, best developed in the East Indies, South Africa, and tropical South America. Three species in three sections occur in our area.

Section *DICLIPTERA* (§ *Platystegiae* Nees) is characterized by orbicular, ovate or elongate-ovate bracteoles, the bases not cuneate. *Dicliptera viridiflora* (Nees) R. W. Long,⁷ an endemic species of southwestern

⁷ *Dicliptera viridiflora* (Nees) R. W. Long, comb. nov.

Rhytiglossa viridiflora Nees in DC. Prodr. 11: 346. 1847.

Georgia and adjacent Florida in rich, wooded bottomlands of the Flint and Apalachicola rivers, where it may be locally abundant, has white, pale blue, or pink, nearly regular corollas in compacted spikes with conspicuous, ovate, acuminate bracts. The species appears to be morphologically close to the West Indian *D. martinicensis* Juss.

Section SPHENOSTEGIAE Nees, the largest subgeneric group, is characterized by floral bracts more or less cuneate at the base and is represented with us by *D. brachiata* (Pursh) Spreng. var. *brachiata* (*Diapedium brachiatum* (Pursh) Kuntze, *Diapedium attenuatum* (Gray) Heller), $2n = \text{ca. } 80$. Recognizable by its green, rather broad, wedge-shaped bracts, usually large, ovate-lanceolate to elliptic, long-petioled leaves, and strongly bilabiate, pink or reddish corollas, this erect herb is widely distributed on the Coastal Plain from Virginia to Texas, inland to Arkansas, Missouri, and Kansas in river bottoms, hammocks, and low ground. It is variable in morphology of leaf, bract, and pubescence; differences in the latter caused Fernald to describe two minor varieties from Texas.

Section DACTYLOSTEGIAE Nees is a small group of tropical American species characterized by the presence of two floral bracts larger than others in the involucl. Our representative is *D. assurgens* (L.) Juss. (*Diapedium assurgens* (L.) Kuntze), $2n = 80$, a West Indian weedy species characterized by stiffly erect stems, and conspicuous bright red or scarlet bilabiate corollas in narrow, terminal or axillary lax paniced spikes. Two varieties, both occurring in peninsular Florida, have been distinguished. Varietas *Vahlia* (Nees) Gomez (*D. Vahlia* Nees), with spatulate-mucronate outer involucl bracts, occurring from Lake County, south into the Florida Keys, is often common along roadsides, on shell mounds, in coral soil, and in hammocks. Less frequently, var. *assurgens*, characterized by subulate-attenuate bracts, can be found in extreme southern Florida, from Sanibel Island, Lee County, to the Florida Keys.

There is some evidence that polyploidy has been an important cause of variation in *Dicliptera*. Grant pointed out that both *D. assurgens* and *D. brachiata* are tetraploids in comparison with the Central American *D. resupinata*, which Sigiura reported as having a gametic chromosome number of 20. Because of their morphological similarities, it is possible that *D. brachiata* may have been derived either as an autopolyploid or allopolyploid derivative of *D. resupinata*. Kaur has reported the chromosome number of *D. elegans* as $2n = 20$ and that of *D. Leonotis* as $2n = 48$. Additional chromosome counts for *Dicliptera* species are very desirable.

In the only treatment for the entire genus, Nees (1847) established five sections (based on the morphology of the floral bracts), which were accepted, in general, by Lindau (1895). Initially, Bremekamp (1943) accepted Lindau's placement of *Dicliptera* in the tribe Odontonemateae,

Dicliptera Halei Riddell, New Orleans Med. Surg. Jour. 8: 756. 1852.

Gatesia laete-virens Gray, Proc. Am. Acad. Arts Sci. 13: 365. 1878.

Justicia laetevirens Buckley, Am. Jour. Sci. 45: 176. 1843, not *J. laetevirens* Vahl.

Yeatsia laete-virens (Buckl.) Small, Bull. Torrey Bot. Club 23: 405-410. 1896.

subtribe Diclipterinae but later transferred the genus to his emended Justiceae. Intergeneric relationships appear to be closest with the Old World tropical genera *Hypoestes* Soland. ex R. Br. and *Peristrophe* Nees, and possibly with *Rungia* Nees (although Bremekamp suggested that pollen and capsule characters indicate that *Rungia* ought to be in a different subtribe from *Dicliptera*). Pollen sculpturing apparently is not as useful a taxonomic tool in the Justiceae as in some other tribes of Acanthaceae. Eight different pollen types have been reported from a single anther of *D. javanica* (cf. Davis)!

Dicliptera needs a critical taxonomic review because the proposed intergeneric relationships and intrageneric alignments appear to be highly artificial, if not simply arbitrary. The present construction of subgeneric categories based on minor differences in the morphology of floral bracteoles does not seem to reflect any natural relationships of species groups within the genus. This emphasis on small differences has carried over into the description of species. Leonard included 29 species, 26 of them new, in his account of *Dicliptera* in Colombia. Morphological criteria for the separation of many of these new species are minimal, and it is probable that future study will prove them unworthy of taxonomic recognition.

REFERENCES:

- Under family references see BAILLON (p. 461), BREMEKAMP (1948, 1965), DAVIS, GRANT, LEONARD (1958), LINDAU (1895), NEES (1847), and RAJ.
- BREMEKAMP, C. E. B. L'identité du *Jacobinia suberecta* Andr. et la délimitation des Diclipterinae Lindau. *Boissiera* 7: 182-201. 1943.
- EVERS, R. A. Illinois flora: notes on *Limnoscadium*, *Dicliptera*, and *Iresine*. *Rhodora* 64: 282, 283. 1962. [Second locality for *D. brachiata* in s. Illinois.]
- FERNALD, M. L. Two varieties of *Dicliptera brachiata*. *Rhodora* 43: 287, 288. 1941. [Var. *glandulosa* (Scheele) Fern., Tex. to Vera Cruz, Mex., and var. *Ruthii* Fern., Tex.]
- GOMEZ, D. M. Catalogo de las periantias cubanas, espontaneas y cultivados. *Anal. Hist. Nat.* 23: 267-302. 1894. [*D. assurgens* var. *Vahlia*.]
- KAUR, J. Chromosome numbers in Acanthaceae I. *Curr. Sci. Bangalore* 34: 295. [*D. elegans* Dalz., $2n = 20$; *D. Leonotis* Dalz. ex Clarke, $2n = 48$.]
- SIGIURA, T. Studies in the chromosome numbers of higher plants III. *Cytologia* 10: 205-212. 1939. [Includes chromosome numbers for *Dicliptera*.]

10. *Justicia* Linnaeus, Sp. Pl. 1: 15. 1753; Gen. Pl. ed. 5. 10. 1754.

Perennial herbs [rarely shrubs] with erect or ascending, smooth or variously pubescent stems. Leaves petiolate, linear, lanceolate, or more often ovate to oblong, entire. Flowers small or moderately large, fascicled, or in lax terminal or axillary cymes, spikes or panicles [or solitary]; bracts various, often small, linear or subulate, distant, or sometimes both bracts and bracteoles conspicuous, large, imbricate. Calyx deeply 5 [or sometimes 4]-parted, cleft nearly to the base, segments subulate or linear, acute, nearly equal. Corolla white, red, pink, purple, sometimes with purple or white markings in the throat; tube short [rarely long], straight

or incurved, rather narrow, slightly ampliate above; limb bilabiate the upper lip erect or concave, incurved, spreading, frequently 2-dentate, external in bud, lower lip 3-lobed. Stamens 2, staminodia none, usually slightly exerted but not exceeding the corolla lips, adnate to the throat of the corolla; anther 2-loculate, anther sacs separated, more or less superposed, one or both sacs apiculate or produced into a spur or tail, lobes parallel or obliquely affixed, connective broad or narrow; pollen grains 2-porate, bilateral, ca. $66 \times 47 \times 40 \mu$, 3-colporate (pleurotreme), subprolate, ca. $28 \times 22 \mu$. Disc cupulate or cyathiform, entire or sinuately 2- or 3- or 5-lobed. Stigma entire, capitate, or minutely 2-dentate; style filiform; ovules 2 in each locule. Capsule ovate, oblong, clavate [or orbicular], contracted at the base into a short, solid stalk. Seeds 4 [or 2] or fewer by abortion, plano-compressed, suborbicular, smooth, foveolate-rugose, tuberculate or muricate; retinacula arcuate, acute, truncate below. (Including *Dianthera* L., *Beloperone* Nees, *Rhytiglossa* Nees, *Drejerella* Lindau.) LECTOTYPE SPECIES: *J. hyssopifolia* L.; see Hitchcock & Green, Int. Bot. Congr. Cambridge 1930. Nomencl. Propos. Brit. Bot. 116. 1929. (Named in honor of James Justice, a Scottish botanist and horticulturist of the 18th century, author of *The British Gardener's Calendar*, 1754.) — WATER-WILLOW.

The largest genus in the family with about 300 species distributed throughout the tropics and subtropics of both hemispheres and extending into the temperate region of North America.

The most widespread *Justicia* of our area is *J. americana* (L.) Vahl (*Dianthera americana* L.; including *J. mortuifluminis* Fern.), $2n = 26$, the common water-willow of margins of ponds, lakes, rivers, and occasionally swamps throughout most of the eastern United States and probably even into Mexico. *Justicia ovata* (Walt.) Lindau var. *ovata* (*J. humilis* Michx.) occurs on the Coastal Plain in swampy woods, shallow water, and bottomlands from southern Virginia to northern Florida; var. *lanceolata* (Chapm.) R. W. Long,⁸ $2n = 14, 14 + 1$, is found in wet soil and bottomlands from central Florida and Tennessee, west to Louisiana and Texas; var. *angusta* (Chapm.) R. W. Long,⁹ a narrower-leaved, smaller-flowered plant occurs as an endemic in central Florida, also in marshy places. Two other well-marked, endemic species also occur in Florida: *J. crassifolia* (Chapm.) Small is found in wet pinelands and glades in Gulf County at the mouth of the Apalachicola River, and *J. Cooleyi* Leonard & Monachino has been found in hammocks on limestones in Her-

⁸ *Justicia ovata* (Walt.) Lindau var. *lanceolata* (Chapm.) R. W. Long, comb. nov.

Dianthera ovata var. *lanceolata* Chapman, Fl. So. U.S. 304. 1860.

J. lanceolata (Chapm.) Small, Man. Southeast. Fl. 1231. 1933.

J. humilis Michx. var. *lanceolata* (Chapm.) Gleason, Phytologia 4: 24. 1952.

⁹ *Justicia ovata* (Walt.) Lindau var. *angusta* (Chapm.) R. W. Long, comb. nov.

Dianthera ovata var. *angusta* Chapman, Fl. So. U.S. 304. 1860.

J. angusta (Chapm.) Small, Man. Southeast. Fl. 1231. 1933.

nando County. A Mexican species, *J. Brandegeana* Wasshausen & Smith¹⁰ (*Beloperone guttata* T. S. Brandeg., *Drejerella guttata* (T. S. Brandeg.) Bremek.), has escaped and apparently become naturalized in peninsular Florida, especially in waste places, citrus groves, and around former habitations. This is the common "shrimp plant" that is grown widely for its attractive spikes of reddish-brown or greenish-yellow, ovate bracts and white flowers.

Our species need careful revision, for it is apparent that some of the forms intergrade and may, therefore, be conspecific. Experimental hybridizations should be especially useful in determining interspecific relationships, particularly in the *J. ovata* complex. It appears that our species are not closely related to tropical American taxa, although possibly *J. americana* may be allied to certain Mexican and Central American groups. *Justicia ovata* and *J. crassifolia* are possibly related to West Indian and Central American taxa, such as *J. secunda* Vahl and *J. filibracteolata* Lindau. Monachino and Leonard thought that *J. Cooleyi* is related to *J. Pringlei* Robins., of Mexico, and to *J. galapagana* Lindau, of the Galapagos Islands.

The taxonomic history is so complex that only a general review, and that only with special reference to taxa of our area, is possible here. Nees described the North American species under his *Rhytiglossa*, a confused assemblage of dissimilar elements supposedly from South Africa and America. He placed the genus in his tribe Aphelandreae, but later Bentham & Hooker transferred the group to their Justiceae and included it under *Dianthera*. For the most part, Bentham & Hooker followed Anderson in his general circumscription of *Justicia*, although he also included *Adhatoda* Medic. Bentham & Hooker recognized 11 sections in *Justicia*, but *Beloperone* and *Dianthera* were considered to be separate genera. It is not altogether clear from their descriptions where our species would be placed, but presumably they would be under *Dianthera*.

Lindau (1895) divided *Justicia* into three subgenera, JUSTICIA (subg. *Eujusticia* Lindau), GENDARUSSA (Nees) Lindau, and DIANTHERA (L.) Lindau based on morphology of the inflorescence and anther sac and to some extent on pollen sculpturing. Subgen. JUSTICIA, the largest division, was further divided into seven sections, three of which contained American taxa. Our species all belong to subgen. DIANTHERA which supposedly is characterized by blunt or short-stalked anther sacs.

Bremekamp (1948) was of the opinion that the generic circumscriptions of Anderson, Bentham, and Lindau were too vague and that their definitions of *Justicia* could not be held together any longer. He recommended that *Justicia* be confined to *J. hyssoipifolia* L., of the Old World, and

¹⁰ *Justicia Brandegeana* Wasshausen & L. B. Smith, Fl. Illus. Catarinense 1(Acan): 102. 1969.

Beloperone guttata T. S. Brandege, Univ. Calif. Publ. Bot. 4: 278. 1912; non *Justicia guttata* Wall. Pl. Asiat. Rar. 1: 24. pl. 28. 1830.

Calliaspidia guttata (T. S. Brandeg.) Bremek. Verh. Nederl. Akad. Wet. Afd. Natuurk. 2. 45(2): 54. 1948.

Drejerella guttata (T. S. Brandeg.) Bremek. Philip. Jour. Sci. 80: 14. 1952.

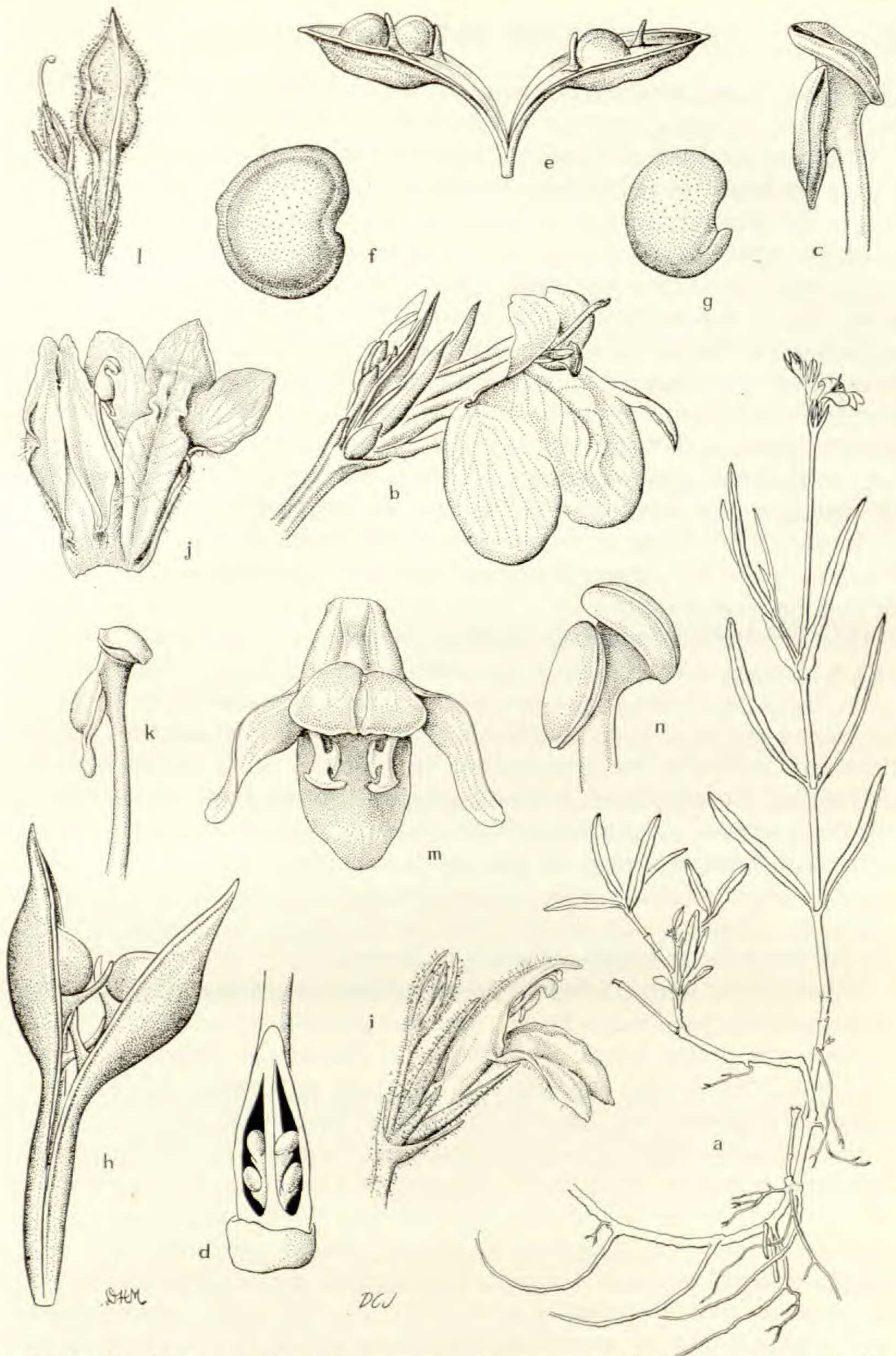


FIG. 5. *Justicia*. a-g, *J. ovata* var. *angusta*: a, small plant with flower, $\times \frac{1}{2}$; b, flower and flower buds, $\times 3$; c, anther, $\times 10$; d, disc and ovary with one side removed to show four ovules, $\times 12$; e, drying fruit, one seed removed — note retinacula, $\times 3$; f, moistened seed, $\times 6$; g, embryo from same, $\times 6$. h, *J. crassifolia*: opening fruit with two seeds, four retinacula, $\times 3$. i-l, *J. Cooleyi*: i, flower and bud, lateral view, $\times 4$; j, corolla with one stamen, opened out, $\times 4$; k, anther, from below, $\times 10$; l, partially mature fruit and flower from which corolla has fallen, $\times 2$. m, n, *J. americana*: m, corolla with stamens, from above, $\times 3$; n, anther from below, $\times 10$.

Dianthera (based on *D. americana* L.) be restricted to the New World. There is no evidence from pollen morphology to suggest that *Dianthera* ought to be retained as a genus, although Grant thought there is some cytological basis for recognizing the genus. The slight morphological difference for their separation is based on the position of the anther sacs, which are stalked obliquely at the tip of a branched connective in *Dianthera*, while in *Justicia* one anther sac is borne horizontally or obliquely at the tip of the connective and one is borne perpendicularly, or nearly so, below it. In both instances the anther sacs are blunt, not pointed at the base, a character Lindau considered of sufficient weight to place all species of *Justicia* of the United States in his subgen. DIANTHERA. Leonard (1958) united both *Dianthera* and *Beloperone* under *Justicia* after pointing out that continuous variation in anther characters made it impractical to maintain the separate genera. Bremekamp transferred *Beloperone guttata* to still another segregate genus, *Drejerella*. Until additional evidence is available, a broad interpretation of the genus appears to be more in keeping with the facts.

Inter- and intrageneric relationships in *Justicia* have been the subject of a wide variety of investigations. Mohan Ram & Sehgal studied pollen-grain formation, embryo-sac development, and embryogeny in *J. simplex* D. Don, a native of tropical Africa and Asia. They reported that chalazal haustoria generally are two-nucleate in *Justicia*, as in *Beloperone* and *Adhatoda*. No significant embryological differences were found between the three genera. *Dicliptera* and the African genus *Barleria* also resemble *Justicia* in the morphology of the chalazal haustoria, but *Blechum*, *Ruellia*, and *Hemigraphis* produce four-nucleate haustoria. The broad basal apparatus characteristic of the three latter genera is represented by a rudimentary, few-nucleate structure in *Justicia*.

Palynological and cytological investigations of taxonomic relationships have generally been inconclusive. Raj was not able to find any differences between the pollen grains of *Justicia* and *Dianthera*. However, Bhaduri concluded that Lindau subordinated *Adhatoda* as a section in *Justicia* because he misconstrued the morphology of the pollen of *A. vasica* (*J. Adhatoda*) and further concluded that the two genera should be separate. Bentham & Hooker maintained *Adhatoda* as a separate genus on the basis of other morphological grounds, but Leonard (1958), apparently on similar bases, submerged *Adhatoda* in *Justicia*. Grant concluded there is sufficient evidence to retain *Adhatoda* as a separate genus because the somatic chromosome number typically is $2n = 54$. *Justicia* species are known with $2n = 28, 32,$ and 36 , suggesting three basic numbers: $x = 7, 8,$ and 6 or 9 . The same numbers are also found in *Beloperone* and *Jacobinia*. Grant suggested that aneuploidy is a probable cause for the diversity in chromosome number in *Justicia* and that possibly related groups, such as *Adhatoda*, arose through allopolyploidy. The discovery of "B" chromosomes in *J. ovata* var. *lanceolata* (cf. Lewis *et al.*) may be evidence of the occurrence of aneuploidy that perhaps was caused by fragmentation of chromosomes or is a vestige of reduction from higher ploidy levels. Additional

cytological studies should be useful in any future intrageneric studies, but crossing experiments might be more helpful at this point.

Unlike many *Ruellia* species, *Justicia* populations may be largely if not entirely allogamous. Although no hybridization studies have been made, there is some evidence that outbreeding occurs regularly in *J. simplex*. Jain & Joshi conducted a genetic analysis of gene frequencies at a petal-color locus in local populations and concluded that the tendency for markedly local differentiation in these polymorphic plants could best be explained by considering them as partially isolated, panmictic populations. Additional investigations of causes of variation in the genus ought to include artificial hybridization experiments to ascertain whether barriers to crossing occur between species. It is possible that some of the observed patterns of variation in our species are caused by natural hybridization.

Future work on *Justicia* may result in additional evidence that would provide a basis for splitting up the genus into two, three, or more segregate genera. At the present time the evidence for this course of action is equivocal, but it seems clear that most of our southeastern species are more closely related to one another than they are to other taxa outside of the range of the Flora. If segregate genera are to be recognized they would be *Dianthera* L. (based on *D. americana* L.), *Adhatoda* Nees (based on *Justicia Adhatoda* L. = *A. vasica* Nees), and *Justicia* (based on *J. hyssopifolia* L.).

Justicia species have also been used in various other biological and chemical investigations. Anatomical and morphological studies have been reported by Sterling, Jones, *et al.*; studies of toxins, alkaloids, and other chemical constituents have been carried on by Munakata *et al.* and Bhatnagar & Popli; and pollination studies by Buxbaum. Many of the attractive cultivated plants that pass under the name *Justicia* properly belong to the tropical American genus *Jacobinia* Nees ex Moric.

REFERENCES:

- Under family references see BAILLON (pp. 440, 442, 445), BENTHAM & HOOKER, BREMEKAMP (1948, 1965), ELLIS, HARTMANN, JOSEPH, LEONARD (1958, 1959), LINDAU (1895), NEES (1847), PAL, RAJ, and SOLEREDER.
- BENOIST, R. Contribution à la connaissance des *Justicia* de Madagascar. Not. Syst. Paris 13: 118–131. 1947. [Describes 13 new spp.]
- BHATNAGAR, A. K., & S. P. POPLI. Mass fragmentation of the alkaloids of *Adhatoda vasica* Nees. Indian Jour. Chem. 4: 291, 292. 1966. [Spectroscopic characteristics of vasicine and vasicinol.]
- BREMEKAMP, C. B. E. Philippine Acanthaceae, I. Philip. Jour. Sci. 80: 11–21. 1952. [*Drejerella* vs. *Beloperone*, 13, 14.]
- BUXBAUM, F. Die Biene als Honigdieb bei *Justicia Adhatoda* L. Biol. General. 2: 104–106. 1926.*
- FERNALD, M. L. *Justicia umbratilis*, sp. nov., *J. humilis* Michx., *J. americana* var. *subcoriacea*, var. nov. In: Another century of additions to the flora of Virginia. Rhodora 43: 639–642, pl. 693. 1941. [See also Rhodora 44: 92. 1942; *J. umbratilis* Fern. = *J. mortuifluminis* Fern., nom. nov., not *J. umbratilis* S. Moore, 1913.]

- & B. G. SCHUBERT. Studies of American types in British Herbaria. Part IV. Some species of Thomas Walter. *Rhodora* **50**: 190–208, 217–229. *pls.* 1103–1115. 1948. [*Dianthera ovata* Walt., 224–226; *J. ovata* (Walt.) Lindau replaces *J. humilis* Michx.]
- HOLM, T. *Ruellia* and *Dianthera*: an anatomical study. *Bot. Gaz.* **43**: 308–329. *pls.* 11, 12. 1907. [General description of vegetative structures; *Ruellia* has monostelic structure, *Dianthera* polystelic.]
- JAIN, S. K., & B. C. JOSHI. Local differentiation in some natural populations of *Justicia simplex*. *Genetics* **47**: 789–791. 1962.
- JONES, W. R. The development of the vascular structure of *Dianthera americana*. *Bot. Gaz.* **54**: 1–30. *pls.* 1–4. 1912. [Seedlings are monostelic at first, later peripheral meristemes develop.]
- LAMMERS, W. T. Accumulation of radioisotopes by *Justicia americana* L. in the Clinch River. (Abstr.) *ASB Bull.* **8**: 23. 1961.
- LEWIS, I. M. A black knot disease of *Dianthera americana* L. *Mycologia* **4**: 66–70. 1912. [*Bagniesiella Diantherae*, sp. nov., an Ascomycete.]
- LEWIS, W. H., H. L. STRIPLING, & R. G. ROSS. Chromosome numbers for some angiosperms of the southern United States and Mexico. *Rhodora* **64**: 147–161. 1962. [*J. ovata* var. *lanceolata*, $n = 14$; $n = 14 + 1$, $2n = 29$.]
- MOHAN RAM, H. Y., & P. P. SEHGAL. The life-history of *Justicia simplex* Don. *Phytomorphology* **8**: 124–136. 1958.
- MONACHINO, J., & E. C. LEONARD. A new species of *Justicia* from Florida. *Rhodora* **61**: 183–187. 1959. [*J. Cooleyi*.]
- MUNAKATA, K., S. MARUMO, K. OHTA, & Y. CHEN. Justicidin A. and B., the fish-killing components of *Justicia Hayatai* var. *decumbens*. *Tetrahedron Lett.* **47**: 4167–4170. 1965.*
- NAG, N. C., & K. N. BOSE. Chemical examination of some Indian medicinal plants. *Trans. Bose Res. Inst. Calcutta* **6**: 201–211. 1931. [Includes *J. Gendarussa*.]
- PENFOUND, W. T. The biology of *Dianthera americana* L. *Am. Midl. Nat.* **24**: 242–247. 1940. [In connection with mosquito control.]
- RAJ, B. Pollen morphology of two species of Acanthaceae. *Curr. Sci. Bangalore* **34**: 319, 320. 1965. [*J. prostrata* (Clarke) Gamble and *Rungia repens* Nees.]
- ROBERTSON, C. Flowers and insects. VII. *Bot. Gaz.* **17**: 65–71. 1892. [*J. americana* (as *Dianthera*), 65, 66; pollinated by Apidae and Andrenidae, but also visited by syrphid flies and by butterflies.]
- SCHULTES, R. E., & B. HOLMSTEDT. De plantis toxicariis e Mundo Novo tropicale commentationes II. *Rhodora* **70**: 113–160. 1968. [*J. pectoralis* Jacq. var. *stenophylla* Leonard used in preparation of a narcotic snuff from *Virola theiodora*.]
- SEN, P. K., T. BOSE, & R. N. BOSE. Effects of boron and molybdenum on rooting of semi-hardwood cuttings of *Justicia Gendarussa* L. *Indian Jour. Pl. Physiol.* **2**: 21–28. 1959.
- SHINNERS, L. H. *Dianthera americana* L. var. *subcoriacea* (Fern.) Shinners, comb. nov. *Field Lab.* **25**: 79, 80. 1957. [Accepts Bremekamp's circumscription of *Justicia*.]
- SIMS, J. *Justicia americana*. *Bot. Mag.* **50**: *pl.* 2367. 1822.
- SMALL, J. K. *Dianthera crassifolia*. *Addisonia* **3**: 79, 80. *pl.* 120. 1918. [Plant illustrated is *J. ovata* var. *angusta*.]
- . *Justicia Runyonii*. *Ibid.* **15**: 29, 30. 1930. [From Texas.]

- SMITH, E. B. I.O.P.B. Chromosome number reports VII. *Taxon* **15**: 155-163. 1966. [*J. americana*, $2n = 26$.]
- STERLING, C. The primary body of the shoot of *Dianthera americana*. *Am. Jour. Bot.* **36**: 184-193. 1949. [Developmental anatomy with reference to stelar concept; includes references.]
- TURNER, B. L. *Justicia Warnockii* (Acanthaceae), a new species from Trans-Pecos Texas. *Field Lab.* **19**: 100, 101. 1951. [Shrubby perennial, vegetatively unlike any other sp. of *Justicia* in U.S.]

DEPARTMENT OF BOTANY & BACTERIOLOGY
UNIVERSITY OF SOUTH FLORIDA
TAMPA, FLORIDA 33620