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### A REVISION OF *AMMANNIA* (LYTHRACEAE) IN THE WESTERN HEMISPHERE

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*AMMANNIA* L. is a genus of about 25 species of aquatic or marsh-inhabiting herbs distributed in both the Temperate and Tropical zones. It is best represented in Africa (16 species), with a maximum of seven species occurring on each of the other continents. The only monograph of the genus (Koehne, 1903) is outdated because of accumulated changes and additions to the taxonomy and nomenclature and the more extensive collections now available.

Many species of *Ammannia* are distinguished from one another by seemingly minor qualitative differences that are difficult to recognize in practice. In some cases, species limits are based more on geographic disjunctions than on morphological distinctions. Relationships of morphologically similar species occurring on different continents are unknown. The need to resolve the confusion surrounding the variability in species in the New World in order to prepare treatments for several floras now underway has stimulated this revision. The difficulty in obtaining viable seeds necessary for biosystematic investigations of the narrowly endemic African and Asian species also prompted restriction of the study to the species occurring in the Western Hemisphere.

#### MORPHOLOGY

The genus *Ammannia* was divided by Koehne (1880b) into two subgenera and two sections. Subgenus *Cryptotheca* (Blume) Koehne, comprising the single species *A. microcarpa* DC., is unique in the Lythraceae by virtue of its parietal placentation. The remainder of the genus comprises subgenus *Ammannia* (formerly subg. *Euammannia* Koehne), which is further divided into two sections and four series, all highly artificial in nature. Five species, representing both sections of subgenus *Ammannia*, occur in the Western Hemisphere. Section *Ammannia* (formerly sect. *Astyliia* Koehne), with short or included styles, is represented by *A. latifolia* L. and the adventive *A. baccifera* L.; section *Eustyliia*

TABLE 1. Chromosome numbers in *Ammannia*.

SPECIES	HAPLOID NO.	SOURCE
<i>A. auriculata</i> Willd.	15, 16	Graham (1979)
<i>A. baccifera</i> L.	12	Sarkar <i>et al.</i> (1982)
<i>A. coccinea</i> Rottb.	33	Graham (1979)
<i>A. latifolia</i> L.	24	Graham (1979)
<i>A. multiflora</i> Roxb.	9	Sarkar <i>et al.</i> (1980)
<i>A. robusta</i> Heer & Regel	17	Graham (1979)
<i>A. senegalensis</i> Lam.	20 ( $2n = 40$ )	Bir & Sidhu (1975)
<i>A. verticillata</i> (Ard.) Lam.	14 ( $2n = 28$ )	Krishnappa (1971, as <i>A. salicifolia</i> Monti)

Koehne, with long, exserted styles, by *A. auriculata* Willd., *A. robusta* Heer & Regel, and *A. coccinea* Rottb.<sup>1</sup>

All are glabrous annual herbs, mostly 10 dm or less in height, with sessile, linear-lanceolate, decussate, auriculate-based leaves. The flowers, borne in sessile or pedunculate axillary dichasia, are homostylous, 4- (or 5-)merous, 3–6 mm long, with pale pink to deep fuchsia, caducous petals. In *Ammannia latifolia* apetalous forms have been considered distinct species from petalous forms, although petals are absent or vary in number from one to four. In *A. auriculata* stamen number has provided a basis for recognition of varieties, but it too is variable (from two to eight), even in flowers from a single plant. Intraspecific taxa proposed by Koehne for several species of *Ammannia* are based on minor and/or variable morphological characteristics without geographic integrity and are hence taxonomically insupportable.

According to Koehne, the styles of all *Ammannia* species are either filiform and well exserted or short and included. He (Koehne, 1880b, p. 242) concluded that differences in style length are the key to the taxonomy of the genus, without which "species distinction in *Ammannia* becomes impossible." In his taxonomy, species that appear to differ morphologically only in style length are placed in different sections. In the long-styled, nearly cosmopolitan *A. auriculata* and the very similar but short-styled African *A. senegalensis* Lam., the species distinction, which is otherwise suspect, is supported by a difference in chromosome number (see TABLE 1).

The capsule of *Ammannia* is irregularly dehiscent with a microscopically uniform dry wall. The related genus *Rotala* L. frequently grows with *Ammannia* and can be deceptively like it in habit but can be recognized by the microscopically dense transverse striations of its capsule wall and by its 2- to 5-valved septicidal dehiscence. The capsule characters provide the most consistent gross morphological distinction between the genera.

Anatomical features of stems and leaves have been described for eight species

<sup>1</sup>The citation of *A. coccinea* as *A. × coccinea* in S. Graham (1979) was meant to convey recognition of the amphidiploid origin of the species. Following Article H.3.4, note 1, of the International Code of Botanical Nomenclature (Voss, 1983), the amphidiploid is treated as a species and the hybrid sign is now better omitted.



by Panigrahi (1980), and wood anatomy of the genus, based on *Ammannia octandra* L. f., was described and compared to that of other lythraceous genera by Baas and Zweypfenning (1979). In wood anatomy the genus shares a juvenilistic character complex with the herbaceous to semiwoody genera *Nesaea* Comm. ex HBK., *Lythrum* L., *Cuphea* P. Browne, and *Crenea* Aublet.

Embryological characters for the genus are typical of the Lythraceae and generally of the order Myrtales. The ovule is crassinucellate with a two-layered inner integument, and megagametogenesis is of the *Polygonum* type (Tobe & Raven, 1983; Smith & Herr, 1971; Joshi & Venkateswarlu, 1936).

## BIOLOGY

*Ammannia* is a predominantly autogamous genus, although outcrossing occurs, as is evidenced by the hybrid nature of *A. coccinea*. Tests for agamospermy in *A. coccinea*, *A. auriculata*, and *A. robusta* were negative. Flowering time is not a barrier to crossing among these species. Flowering extends from July to October in the North Temperate Zone for all species studied; in subtropical and tropical areas it is prolonged throughout the year as long as the habitat remains favorable for seed germination and new plant development. In warm areas new plants mature continuously from seeds of the prior generation.

Flowers of *Ammannia latifolia* are cleistogamous in some parts of its range. In plants grown from seeds of apetalous specimens (Puerto Rico: *Liogier 10314*, NY), the flowers never opened but a large number of viable seeds was produced. After fertilization the style may elongate to 1 mm, and this elongation together with the enlargement of the maturing capsule causes the senescent stigma to be extruded, but true anthesis does not occur. Petalous and apetalous flowers of *A. latifolia* from Manatee Co., Florida (*Graham 698*, MICH), open to varying degrees, with self-pollination occurring either prior to opening or at anthesis. Both petalous and apetalous flowers may be chasmogamous. The attractant role of the petals, when present in this species, is minimized by their small size, pale color, and brief retention time. The introrse anthers closely surround the stigma and frequently detach from the filaments to adhere to the sides of the papillate stigma at dehiscence.

In *Ammannia auriculata*, *A. robusta*, and *A. coccinea* self-pollination starts at anthesis, with anther dehiscence and stigma receptivity beginning simultaneously when these organs are at the level of the floral tube opening or slightly exerted. The anthers may become attached to the stigma as in *A. latifolia*. In the first three species enlargement of the capsule after fertilization causes the style to extrude prominently from the floral tube, even though the style itself does not elongate significantly. In *A. coccinea* an abscission layer forms 1 mm above the base of the style after fertilization, and the upper style withers and falls away. The remaining short style base has led to misidentification of mature long-styled *A. coccinea* specimens as the short-styled *A. latifolia*.

Plants of *Ammannia coccinea* and *A. robusta* are visited by skippers and small bees for nectar produced by the thickened glandular area surrounding the base of the ovary.



## ECOLOGY AND DISTRIBUTION

*Ammannia* characteristically grows in wet, relatively open habitats from sea level to 1500 m. It is colonial in shallow fresh or brackish marshes, temporal pools, roadside ditches, river banks, and other intermittently wet areas. Soils in which it flourishes vary from nearly pure white sand to heavy gray clay. Appropriate water level and lack of competition appear to be the most important factors in establishment and spread of the plants. *Ammannia coccinea* and *A. robusta* develop extensive populations in fresh water to depths of 0.5 m but are most common in moist or saturated soils. In standing water extensive aerenchymatous tissue develops on the external surface of submerged stem parts. Similar aerenchyma is seen on submerged stems of *Decodon* J. Gmelin, another lythraceous genus. In India, where *A. auriculata* is one of the predominant broad-leaved weeds in rice fields of the Punjab, control is effected by maintaining an optimum (high) water level for rice in the field, since low water levels promote *Ammannia* development (Shetty *et al.*, 1975). Similar ecological requirements are shared among the *Ammannia* species in North America, as demonstrated by numerous herbarium sheets on which more than one species is mounted. Species recorded in this manner growing at the same site are *A. coccinea* with *A. latifolia*, *A. coccinea* with either *A. auriculata* or *A. robusta* (or rarely all three species), and *A. auriculata* with *A. robusta*.

*Ammannia* seeds are well adapted to dispersal in aquatic environments. They are produced in great quantity (an average of ca. 250 seeds per capsule in the species occurring in the Western Hemisphere). They are ca. 1 mm long and are buoyed by the convex-concave shape and by a large aerenchymatous float on the concave side (FIGURE 1B, C). The thin-walled cells of the float dehydrate more quickly than the seed coat proper and consequently are not always visible on older seeds (FIGURE 1D). Seeds without floats retain viability.

The epidermal cells of the seed coat enclose internal unicellular hairs that evaginate upon soaking. The hairs are tuberculate-ribbed and when fully evaginated are more or less erect and ca. 100  $\mu$ m long (FIGURE 1E, F). They lack the internal spirals observed in seed-coat hairs of the lythraceous genera *Cuphea* and *Lafoensia* Vand. (Stubbs & Slabas, 1982; pers. obs.). Corner (1976) has reported seeds of *Ammannia* to be mucilaginous. The hairs may act to increase the flow of water into the seeds, thus hastening germination, and the mucilage produced may act to affix the seeds to objects during dispersal. In the American species mucilage appears on wetted seeds but is not profuse.

Observations of seed germination in the greenhouse suggest further adaptations to intermittently wet habitats. The seeds retain viability for many years, although only about 50 percent are viable after the first year. Retention of some viability for several years enables the species to persist through extensive dry periods. Even after herbarium fumigatory treatments, 5 percent of the seeds of *Ammannia coccinea* from herbarium specimens 27 years old (*Winterringer 9199*, ISM) have germinated. Germination of seeds from herbarium specimens was generally vigorous from collections up to 12 years old.

Under conditions of 100 percent humidity and high light intensity and temperature (28°C) in closed plastic bags, germination begins after six days; the



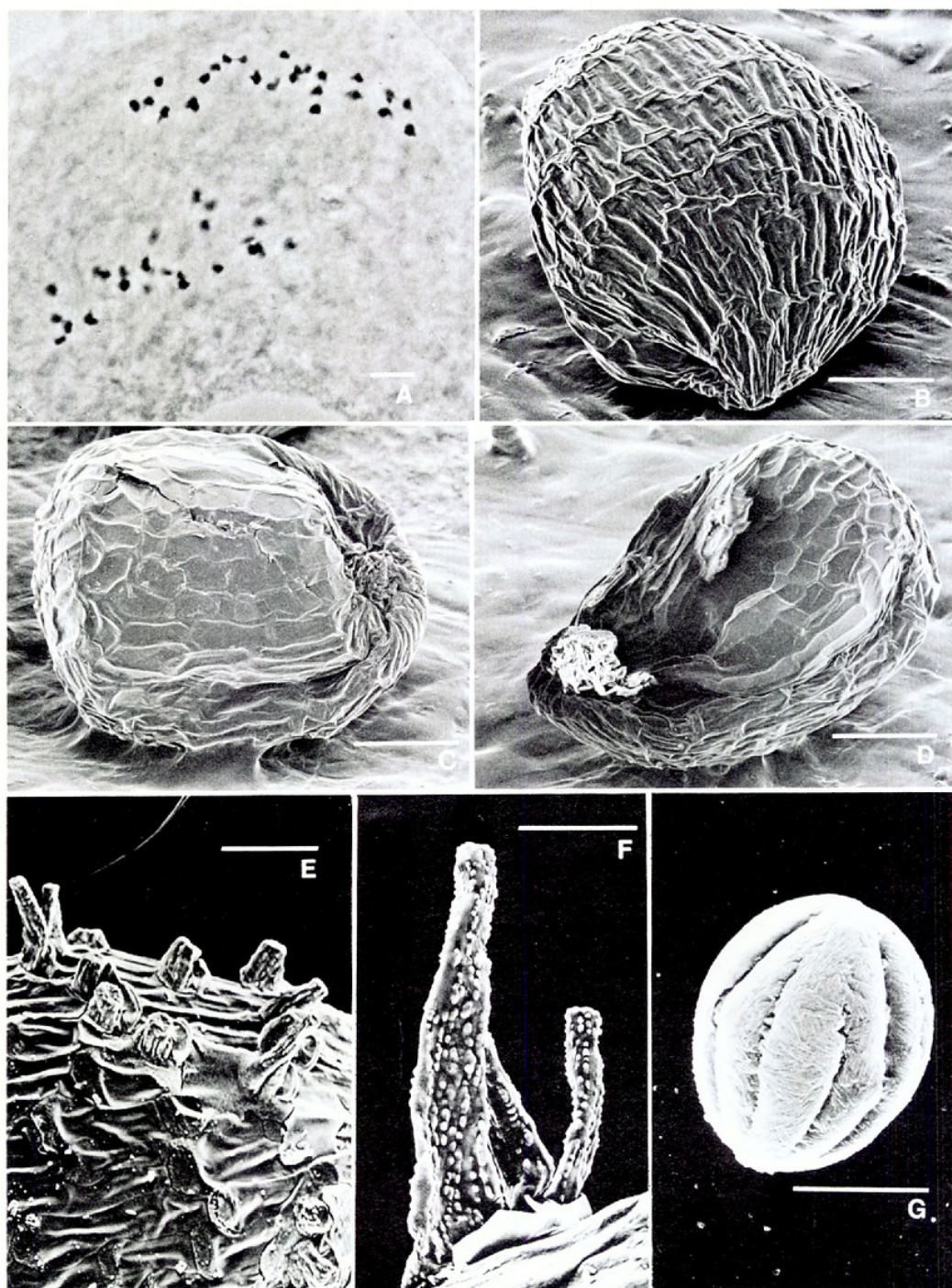


FIGURE 1. Scanning electron micrographs of *Ammannia* chromosomes, seeds, and pollen. A, *A. latifolia* (progeny of Liogier 10314, NY), meiotic chromosomes, metaphase II,  $n = 24$  (scale =  $10\ \mu\text{m}$ ). B–F, seeds of *A. coccinea* (S. Graham 700, MICH): B, convex ventral side, unsoaked (scale =  $100\ \mu\text{m}$ ); C, concave dorsal side, aerenchymatous float occupying concavity (scale =  $100\ \mu\text{m}$ ); D, concave dorsal side, aerenchymatous float collapsed (scale =  $100\ \mu\text{m}$ ); E, surface of soaked seed, partially evaginated epidermal hairs visible (scale =  $50\ \mu\text{m}$ ); F, 1 fully and 1 partially evaginated epidermal hair, tuberculae evident (scale =  $25\ \mu\text{m}$ ). G, *A. latifolia* (progeny of Liogier 10314, NY), pollen, subsidiary colpi central, pore-containing colpi to left and right (scale =  $10\ \mu\text{m}$ ).



majority of seeds germinate within fourteen days. Under natural conditions at 20°C in daylight, germination in pots begins at ten days and continues for ten weeks. Staggered germination time is not correlated with seed size. Establishment of seedlings in areas with fluctuating water levels is surely enhanced by these staggered germination rates: some seeds can be lost without completely eliminating the opportunity for species growth at those sites. The effective dispersal and germination mechanisms and long seed viability have promoted wide dispersal of the genus. This pattern is typical of aquatic plants, whose vagility and wide ranges have long been noted (Darwin, 1859; Arber, 1920).

Adventive stations for several species are known. Introduction of *Ammannia coccinea* through rice culture is recorded from Afghanistan (Shalizan, without collector or number, BM!), Italy (*vide* Abba, 1977), and Spain (*Borja s.n.*, 10 Oct. 1945, F!). It has been introduced in hay at San Blas, Panama (*Johnston 1239*, GH!), where it persists. Both *A. coccinea* and *A. robusta* are now present in the South Pacific (several collections from Guam and Saipan, US!), as well as in Hawaii and the Philippines (Koehne, 1903). The Asian *A. verticillata* has been introduced in Argentina (Molfin, 1926). Presence of *A. auriculata* in southern Patagonia and the spread of *A. robusta* along the coast of Brazil north of Rio de Janeiro are apparently the results of early introductions. Disjunct interior collections of the coastal *A. latifolia* in South America (like those of *A. robusta* in the western United States) are probably the result of accidental introductions by man.

## CHEMISTRY

The leaf flavonoids of *Ammannia coccinea* have been determined (S. Graham *et al.*, 1980). Four flavonols and three flavone glycosides have been isolated: quercetin 3-D-glucoside, rutin, luteolin 7-D-glucoside, isorhamnetin 3-rutinoside, apigenin 7-D-glucoside, vitexin, and kaempferol 3-rhamnoglucoside. The predominance of flavonols is consistent with their occurrence as the major flavonoid type for Lythraceae, and for Myrtales generally.

Analysis of seed composition in *Ammannia auriculata* showed that 15.2 percent of the seed by weight was oil, 16 percent was protein. The predominant fatty acid in the seed oil (78.6% of total fatty-acid composition) was linoleic acid, typical for the family and the most commonly occurring fatty acid in angiosperms (S. Graham & R. Kleiman, unpubl. data).

## PALYNOLOGY

In seven species surveyed, including all those occurring in the Western Hemisphere, the pollen has virtually the same morphology: grain prolate, 30–34  $\mu\text{m}$  (P)  $\times$  24–28  $\mu\text{m}$  (E), tricolporate with 6 pseudocolpi; colpi meridionally elongated, equatorially arranged, equidistant, extending to within 4–5  $\mu\text{m}$  of the pole, the colpus membrane minutely granular; pseudocolpi like colpi but slightly shorter; pores circular; wall finely striate, tectate (FIGURE 1G; A. Graham *et al.*, 1985).



Pollen of *Ammannia* is most similar to that of *Nesaea*, another lythraceous genus of herbs favoring wet habitats, concentrated in Africa and resembling *Ammannia* in habit. Pollen grains of the genera share the same striate exine sculpture pattern and are distinctly 6-pseudocolpate. Pollen morphology indicates a closer relationship between the two genera than is suggested by their placement in different tribes of the family.

The inadequately known genus *Hionanthera* Fernandes & Diniz, from Mozambique, has been described as intermediate in morphology between *Ammannia* and *Rotala* (Fernandes & Diniz, 1955; Panigrahi, 1979). Cook (1974) considered the genus synonymous with *Ammannia*. On the basis of pollen features, *Hionanthera* is distinct: although its pollen is similar to that of *Ammannia* and *Nesaea*, the pseudocolpi are faint to absent. More extensive material needs to be studied to resolve the position of the genus in relation to *Ammannia*.

*Ammannia* and *Rotala* were considered congeneric by many botanists from Linnaeus to Bentham and Hooker, until Koehne (1880a) pointed out the subtle but consistent difference in wall structure of the capsules. An equally striking difference is found in pollen morphology. Pollen of *Rotala* has a scabrate to finely verrucate exine and no pseudocolpi. Pollen characters most closely align *Ammannia* with *Nesaea* and support the distinctiveness of *Ammannia* and *Rotala*.

## CYTOLOGY

Chromosome numbers have been counted for eight species. Although nine different numbers have been reported (see TABLE 1), some have yet to be confirmed. Chromosomes are 1–2.5  $\mu\text{m}$  in length. Their small size precludes karyotypic study; most appear in meiosis as spheres or short rods (FIGURE 1A). Since meiosis is often asynchronous, chromosomes are best counted in diakinesis or early metaphase I, when chromatids cannot be confused with unseparated chromosomes. Lagging and sticky chromosomes are occasionally seen, but meiosis is regular in the species growing in the Western Hemisphere. Aneuploid reduction in at least one population of *Ammannia auriculata* from Egypt probably accounts for the gametic count of  $n = 15$ . Four other counts from the United States and Mexico were  $n = 16$ . *Ammannia coccinea*, with a gametic chromosome number of  $n = 33$ , is believed to have originated as an amphidiploid involving *A. auriculata* ( $n = 16$ )  $\times$  *A. robusta* ( $n = 17$ ) (S. Graham, 1979).

## HISTORIC AND TAXONOMIC CONSIDERATION

William Houston first applied the name *Ammannia* to plants now referred to *A. latifolia* in a 1736 manuscript describing his Caribbean collections. The genus was named in honor of Paul Ammann, 1634–1691, professor of botany at Leipzig (Linnaeus, 1737), and was included by Linnaeus in *Hortus Cliffortianus*, *Hortus Upsaliensis*, and subsequently *Species Plantarum*. In *Species*



*Plantarum*, *Ammannia* comprised three species: *A. latifolia* L., *A. ramosior* L. (now referred to *Rotala ramosior* (L.) Koehne), and *A. baccifera* L. Later, Linnaeus (1771) described *Rotala*, with one species (the East Indian *R. verticillaris* L.), but failed to recognize *A. ramosior* as a member of the genus *Rotala*. The genera were long confused until their differences were finally clarified by Koehne (1880a). The superficial similarities of *Ammannia* and *Rotala*, as well as Bentham and Hooker's (1867) rejection of *Rotala*, have necessitated the transfer of at least 45 epithets from *Ammannia* to *Rotala* (see Cook, 1979). In the Western Hemisphere most of these apply to the common *R. ramosior*, and they account for a large number of excluded specific names cited in this study (see APPENDIX).

In the following taxonomic treatment, I have included all names applied to—and misidentifications of—New World *Ammannia* listed in *Index Kewensis*, the Gray Card Index, and Koehne's monographic works (1880b, 1903). The synonymies are complete for *A. latifolia*, *A. coccinea*, and *A. robusta*, which are native to the New World. I have not attempted to list all later synonyms and misidentifications of *A. auriculata* and *A. baccifera* from Europe, Africa, and Asia; this would have required revision of the entire genus. The few omissions in the synonymy of *A. auriculata* are later names applied to Old World collections. *Ammannia baccifera* is a relatively recent introduction into the Caribbean, and no synonymies have been published based on New World collections. Later names based on Asian and African collections are not included in this study. A list of the exsiccatae studied can be obtained from the exsiccatae depository at A and GH, MO, or NY.

## SYSTEMATIC TREATMENT

***Ammannia* L. Sp. Pl. 1: 119. 1753, Gen. Pl. ed. 5. 55. 1754.**

Annual or possibly short-lived perennial glabrous herbs of aquatic or marshy habitats. Leaves decussate, sessile, linear to lanceolate or oblanceolate, cordate to auriculate (rarely attenuate) at base, membranaceous. Flowers borne in sessile or pedunculate axillary cymes, (1 to) 3 to 15 per node, regular, 4- (or 5-)merous, not heteromorphic; bracteoles 2, at base of floral tube, opposite, linear. Floral tube campanulate to urceolate, becoming globose in fruit, 1.5–6 mm long, greenish to rose, 8-nerved with 4 nerves especially prominent at anthesis; calyx lobes 4 (or 5), short and broad; appendages thick, shorter than to equaling lobes, or lacking; petals lacking or 1 to 4, small, deep rose-purple to pink or white, caducous; stamens 4 (to 8), included to exserted; gynoecium without disc at base, the stigma capitate, the style thin, longer than ovary and exserted, or thick, shorter than ovary and included, the ovary incompletely 2- to 4- (or 5-)locular, upper portion of septa incomplete. Fruit a membranaceous, irregularly dehiscent capsule, the outer wall smooth, not striate. Seeds many, obovoid, concave-convex, ca. 1 mm long, golden brown.

LECTOTYPE SPECIES. *Ammannia latifolia* L.; see Britton & Brown, *Illus. Fl. No. U. S. ed. 2. 2: 577. 1913.*



## KEY TO AMMANNIA IN THE WESTERN HEMISPHERE

1. Style thick, ca. 0.5 mm long or less, much shorter than ovary, included within floral tube at anthesis; petals lacking or 1 to 4, pale pink to white.
  2. Floral tube 4–6 mm in diameter in fruit; calyx lobes broad with minute mucronate to cucullate apex; appendages alternating with calyx lobes short, thick; petals lacking or 1 to 4. .... 4. *A. latifolia*.
  2. Floral tube 1–2 mm in diameter in fruit; calyx lobes triangular with acute apex; appendages alternating with calyx lobes absent; petals lacking. ... 2. *A. baccifera*.
1. Style slender, usually 1 mm or more long, equal to half length of ovary or longer, well exerted at anthesis; petals 4 (or 5).
  3. Inflorescence a long-pedunculate, multiflowered simple or compound cyme; peduncle nearly filiform, 3–9 mm long; flowers 3 or more per axil; petals deep rose-purple; fruits mostly 2.5 mm or less in diameter; plant delicate, slender in aspect. .... 1. *A. auriculata*.
  3. Inflorescence a sessile or short- to long-pedunculate, 1- to many-flowered cyme; peduncle, when present, stout, to 4(–9) mm long; fruits mostly 3.5 mm or more in diameter; plant robust.
    4. Inflorescence sessile; flowers usually 1 to 3 per axil; petals pale lavender, occasionally with deeper purple vein; anthers yellow; fruits 4–6 mm in diameter. .... 5. *A. robusta*.
    4. Inflorescence a short- to long-pedunculate cyme, rarely completely sessile; flowers usually 3 or more per axil; petals deep rose-purple; anthers deep yellow; fruits 3.5–5 mm in diameter. .... 3. *A. coccinea*.

1. ***Ammannia auriculata*** Willd. Hort. Berol. 1: pl. 7. 1803. TYPE: Egypt, near Rosette, *Willdenow Herbarium 3081* (lectotype (here designated), B-w; photo of lectotype, Berlin neg. no. 121413 at B-w!). MAP 1.

*Ammannia racemosa* Roth, Catal. Bot. 3: 25. 1806. TYPE: grown from seeds sent from Royal Botanic Gardens, Copenhagen, origin unknown (existence of type specimen unknown). Description clearly of the Old World, 8-staminate form of *A. auriculata*.

*Ammannia arenaria* HBK. Nov. Gen. & Sp. Pl. 6: 190. 1824. TYPE: Venezuela, Prov. Caracas, near San Fernando (holotype, P; photo of holotype, Field Museum neg. no. 38362 at F! and GH!).

*Ammannia senegalensis* var. *brasiliensis* A. St. Hil. Fl. Brasil. Merid. 3: 135. t. 187. 1833. TYPE: Brazil, Minas Novas, S. Miguel, Jiquitinhonha River (holotype, P!).

*Ronconia triflora* Raf. Aut. Bot. 9. 1840, *nomen illegit. et superfl.*, based on *A. auriculata* Willd.

*Ammannia pusilla* Sonder, Linnaea 23: 40. 1848. TYPE: Senegal or Nigeria, swampy places near Sandrivier, *Zeyher 541* (B, destroyed?).

*Ammannia wrightii* A. Gray, Pl. Wright. 2: 55. 1853. TYPE: Mexico, Sonora, east of Santa Cruz and along the San Pedro, *Wright 1062* (holotype, GH!; isotypes, BM!, GH!, K!, P!).

*Ammannia longipes* Wright in Sauvalle, Fl. Cubana, 53. 1868. TYPE: Cuba, near S. Gabriel, Palacios, Dec. 1865, *Wright s.n.* (holotype, GH!).

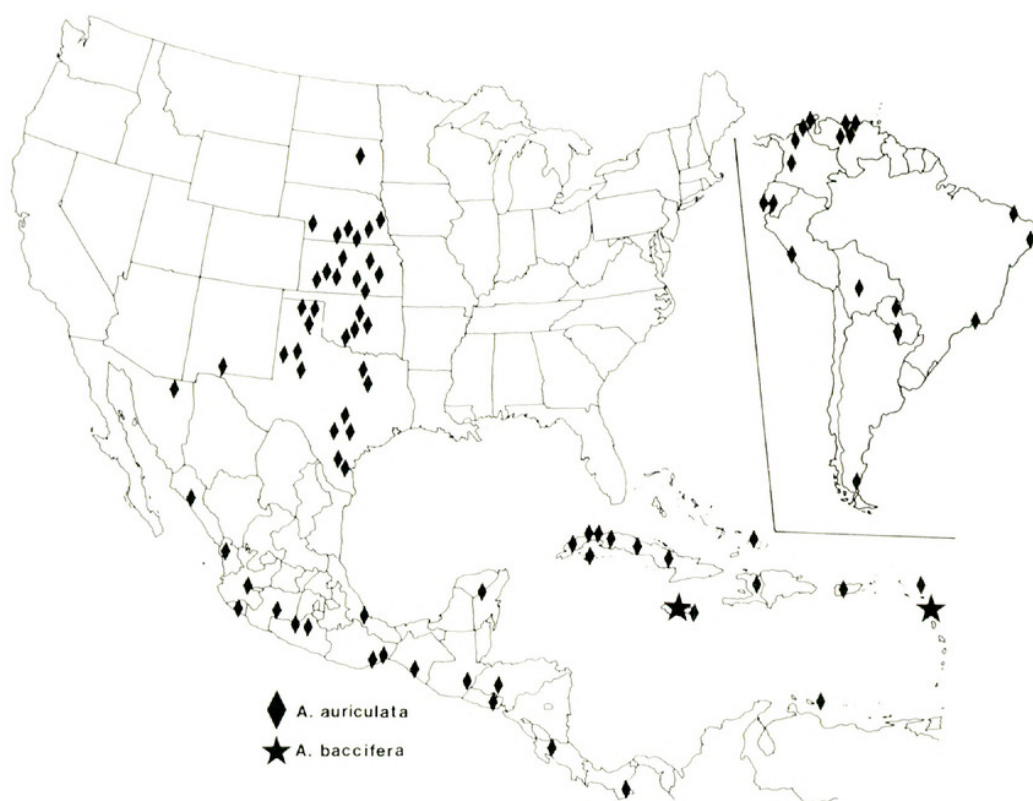
*Ammannia auriculata* Ledeb. ex Koehne, Bot. Jahrb. Syst. 1: 244. 1880, *pro syn.*

*Ammannia auriculata* var. *arenaria* (HBK.) Koehne, *ibid.* 245.

*Ammannia auriculata* var. *arenaria* f. *brasiliensis* (A. St. Hil.) Koehne, *ibid.*

Annual, glabrous herbs 1–8 dm tall, unbranched to pyramidally multi-branched, the branches ascending, generally shorter than stem, progressively shorter toward top of stem. Leaves narrowly linear-lanceolate to linear-oblong,





MAP 1. Distribution of *Ammannia auriculata* and *A. baccifera* in Western Hemisphere. (Symbols on this and subsequent maps may represent more than 1 collection from area covered.)

the largest ones 17–64 by 2–10 mm, equaling or surpassing internode above, the apex acute, the base auriculate-cordate, clasping, occasionally cuneate on lowermost leaves only. Inflorescences axillary, long-pedunculate, simple or compound, multiflowered cymes; flowers pedicellate, (1 to) 3 to 12 (to 15) per cyme, commonly 7; lateral pedicels bibracteolate, 1–3(–6) mm long, emerging from bracteoles of shorter-pedicellate central flower of cyme; peduncle 3–9 mm long; pedicels and peduncle nearly filiform; bracteoles 0.5–1 mm long. Floral tube campanulate to urceolate in bud, globose in fruit, 1–3 mm long at anthesis; calyx lobes triangular, alternating with minute, thickened appendages; appendages to 1 mm long at anthesis, rarely absent; petals 4, obovate, usually ca. 1.5 by 1.5 mm, deep rose-purple; stamens 4 (to 8), well exerted; style filiform, exerted at same level as stamens, as long as to  $\frac{1}{3}$  longer than ovary, ovary incompletely 2- (to 4-)locular. Capsule at maturity equal to or mostly well exceeding calyx lobes, (1–)1.5–3(–3.5) mm in diameter; seeds numerous, ca. 1 mm long.  $n = 15, 16$ .

This species is distinguished by its inflorescence with slender, elongate peduncles and pedicels that bear numerous small, deep rose-petaled flowers. It is the most widely distributed species in the genus, occurring in Africa, Asia (including India and China), Australia, the Americas, and the Caribbean in the wet habitats typical of the genus. In the United States it is sympatric with *Ammannia robusta* and *A. coccinea*. Its appearance is sporadic, however, even in the Central States (where it is most frequent) and depends on the extent of



suitable habitats available in any given year. It is the least collected of the species in the United States. Many collections originally determined as *A. auriculata*, including one state record (Dolbeare, 1973), are long-pedunculate plants of *A. coccinea*. In Mexico it is sympatric with *A. robusta* in the western part of its range and with *A. coccinea* to the east and south. Although geographically sympatric with *A. latifolia* in the Caribbean, it is probably ecologically isolated from that species, which occurs mainly along the coasts and prefers brackish waters to fresh. In South America *A. auriculata* is distributed along the western side south to Peru at elevations from sea level to 600 m.

Three varieties of *Ammannia auriculata* have been recognized: var. *auriculata* and var. *bojeriana* Koehne, restricted to East Africa, and var. *arenaria* (HBK.) Koehne, from Africa, Asia, and the Americas. Variety *arenaria*, in which Koehne further recognized five forms, is defined as having four to eight stamens, a glabrous calyx, and a style 1 to 1.3 times as long as the ovary. It is distinguished with difficulty from the other varieties. The five forms of var. *arenaria* are based on combinations of minor, overlapping characters among which Koehne (1903) claimed there were many intermediates. The American plants have been referred to var. *arenaria* f. *brasiliensis* (A. St. Hil.) Koehne. Forma *brasiliensis* is applied to plants from both the Americas and Africa with calyxes 1.5–2 mm long and four or five stamens. The circumscription is meaningless, given the variation now known for the species.

Koehne (1880b) considered the wide-ranging *Ammannia auriculata* to be the central species of the genus from which the other, more geographically limited species were derived. Recent studies (S. Graham, 1979) suggest the relationship between *A. auriculata* and *A. coccinea*, species frequently confused in the United States, as one of parent and hybrid derivative, with *A. robusta* as the other parent. No evidence of hybridization between *A. auriculata* and *A. latifolia* is suggested by the exsiccatae studied.

The Willdenow herbarium contains one sheet with two plants of *Ammannia auriculata* from Egypt, cultivated in the Berlin Botanical Garden (B-W no. 3081). Neither plant exactly matches the illustration accompanying the description. Both have compound rather than simple cymes and are unbranched or have only a few short branches. Variability in inflorescence complexity and branching, however, is within the limits of the variability of the species. The Code (T.4.b) directs that a specimen be selected over a figure when a lectotype is chosen. Sheet 3081 is thus the obligate lectotype of *A. auriculata*.

2. ***Ammannia baccifera* L. Sp. Pl. 1: 120. 1753. TYPE: China, Savage H 156.4 (lectotype, LINN, IDC 177. 99: III. 4!).<sup>2</sup> MAP 1, FIGURE 2.**

Erect annuals or possibly short-lived perennials to 1 m tall, much branched from near base to top of stem, the branches shorter than stem, ascending.

<sup>2</sup>The Linnaean Herbarium today contains two sheets of *Ammannia baccifera*. One lacks any identifying marks, but the other is probably the Osbeck specimen cited by Linnaeus in the species description even though the penciled Osbeck number that assures this is lacking (Hansen & Maule, 1973). The specimen, Savage H 156.4, bears the inscription in Linnaeus's hand "baccifera 3. india." The number "3" corresponds to the position of the species in the generic treatment in *Species Plantarum*. The term "india" was applied by Linnaeus to include China (Stearn, 1957).





FIGURE 2. *Ammannia baccifera*: a, habit,  $\times 0.16$ ; b, axillary inflorescence,  $\times 2.5$  (from I. Vélez 3609, US).



Leaves lanceolate to oblanceolate, to 50(–70) by 10(–16) mm, usually equaling or surpassing internode above, becoming progressively smaller toward apex of stem, smaller on lateral branches, apex acute, base varying from cuneate to mostly truncate or slightly auriculate. Inflorescences axillary, sessile, densely flowered cymes; flowers 3 to 15 or more per cyme; peduncle to 1 mm long. Floral tube broadly campanulate, narrowly tapering at base, 1–2 mm in diameter, becoming globose in fruit, glabrous; calyx lobes sharply triangular, connivent; appendages lacking; petals lacking; stamens 4, opposite calyx lobes, included to barely exerted; style slender, 0.3 mm long, much shorter than ovary. Capsule barely included to well exerted.  $n = 12$ .

*Ammannia baccifera* is distinguished from other species of *Ammannia* in the Western Hemisphere by its numerous minute, densely clustered axillary flowers that lack petals. This widespread, variable species, native to Africa or Asia, is a relatively recent introduction in the New World. The earliest Western Hemisphere collections, from Guadeloupe, were made in the 1930's. It is now also known from Jamaica, although it is rare and local there (Adams, 1972). Koehne (1880b) recognized three subspecies, six forms, and two subforms, based primarily on differences in shape of the leaf base. The subspecies are not geographically distinct. New World collections are placed with some difficulty in subsp. *aegyptiaca* (Willd.) Koehne, the leaf base varying from the designated auriculate shape to the cuneate base of subsp. *viridis* (Hornem.) Koehne. I prefer not to recognize the subspecies as currently defined. Misidentification of *A. baccifera* is the basis for the incorrect report of the Old World species *A. verticillata* (Ard.) Lam. in the Lesser Antilles (Stehlé, Stehlé, & Quentin, 1948).

3. ***Ammannia coccinea*** Rottb. Pl. Horti Univ. Rar. Progr. (Hafn.), 7. 1773.

TYPE: Jamaica, St. Catherine Parish, 1 mi W of Spanish Town, 15 Nov. 1958, G. Proctor 18339 (neotype (here designated), NY!; isoneotype, A!).

MAP 2, FIGURE 3.

*Ammannia purpurea* Lam. Encycl. Méth. Bot. 1: 131. 1783. TYPE: Carolina, *Fraser s.n.* (neotype (here designated), P-LA!; photo of neotype, Field Museum neg. no. 38365 at F! and GH!).<sup>3</sup>

*Ammannia sanguinolenta* Sw. Nov. Gen. & Sp. Pl. Prodr. 33. 1788, Fl. Ind. Occ. 1: 272. 1797. TYPE: Jamaica, Domingo, 1783–1786, *Swartz s.n.* (s!).

*Ammannia octandra* auct., non L. f., Cham. & Schldl. Linnaea 2: 376. 1827. = *A. coccinea* fide Koehne, who probably saw material, no longer extant, at B.

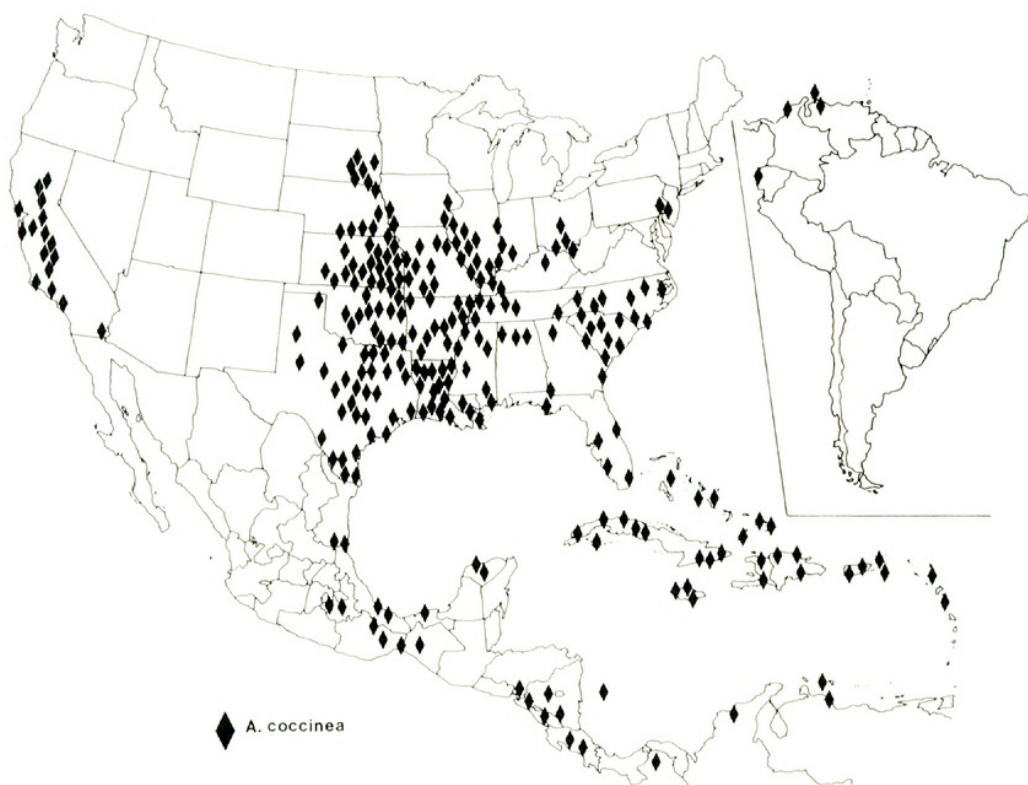
*Ammannia teres* Raf. Aut. Bot. 1: 39. 1840. TYPE: U. S., Delaware, Sussex, *Nuttall s.n.* (lectotype (here designated), P!). This specimen annotated *A. teres* by Rafinesque.

*Ammannia stylosa* Fischer & Meyer, Index Sem. Hortus Imp. Petrop. 7: 41. 1841. TYPE: U. S., Louisiana, New Orleans, *Wiedemann s.n.* (LE!).

*Ammannia sagittata* var. *angustifolia* A. Rich. in Sagra, Hist. Fis. Pol. Nat. Cuba 10:

<sup>3</sup>Lamarck cited *Ammannia ramosior* L. (= *Rotala ramosior* (L.) Koehne) with the Linnaean phrase name and reference to the Clayton type, as if in synonymy with *A. purpurea*. However, his description is of *A. coccinea* and is based on a plant cultivated in the Jardin du Roi. A specimen in the Lamarck herbarium annotated *Ammannia purpurea* is selected as neotype.





MAP 2. Distribution of *Ammannia coccinea* in Western Hemisphere.

252. 1845, Hist. Phys. Pol. Nat. Cuba, Pl. Vasc. 542. 1846. TYPE: Cuba, near San Diego, *Sagra s.n.* (P!).

*Ammannia texana* Scheele, Linnaea 21: 588. 1848. TYPE: near New Braunfels, *Lindheimer s.n.* (holotype not located). Possible type collection: "Tex.," and in A. Gray's hand "Ammannia Texana Scheele in Linnaea 21, p. 588," *Lindheimer 338* (GH!).

*Ammannia latifolia* var. *octandra* A. Gray, Pl. Lind. 2: 188. 1850. TYPE: based on *A. texana* Scheele.

*Ammannia sanguinolenta* subsp. *purpurea* (Lam.) Koehne in Martius, Fl. Brasil. 13(2): 207. 1877.

*Ammannia sanguinolenta* subsp. *longifolia* Koehne in Martius, *ibid.* 208, *pro parte*. Based in part on *A. octandra* Cham. & Schldl., *non* L. f., in part on an *A. coccinea* specimen of Gaudichaud from Hawaii, and in part on an *A. coccinea* specimen of Eschscholtz from the Philippines.

*Ammannia coccinea* subsp. *purpurea* (Lam.) Koehne, Bot. Jahrb. Syst. 1: 250. 1880.

*Ammannia coccinea* subsp. *longifolia* (Koehne) Koehne, *ibid.*

*Ammannia pedunculata* Rusby, Descr. S. Amer. Pl. 68. 1920. TYPE: Colombia, near Ciénaga, 10 Sept. 1898, *H. H. Smith 548* (holotype, NY!; isotypes, CM!, F!, GH!, K!, P!).

Robust annual herbs to 1 m tall, unbranched, or branching mainly above base with branches mostly shorter than main stem, infrequently branching from base with long, semidecumbent branches. Leaves linear-lanceolate to linear-oblong, rarely elliptic to spatulate, largest ones 20–80 by 2–15 mm, apex acute, base auriculate to cordate, clasping, occasionally cuneate on lowermost leaves. Inflorescences varying from sessile (1-) to 3-flowered cymes to



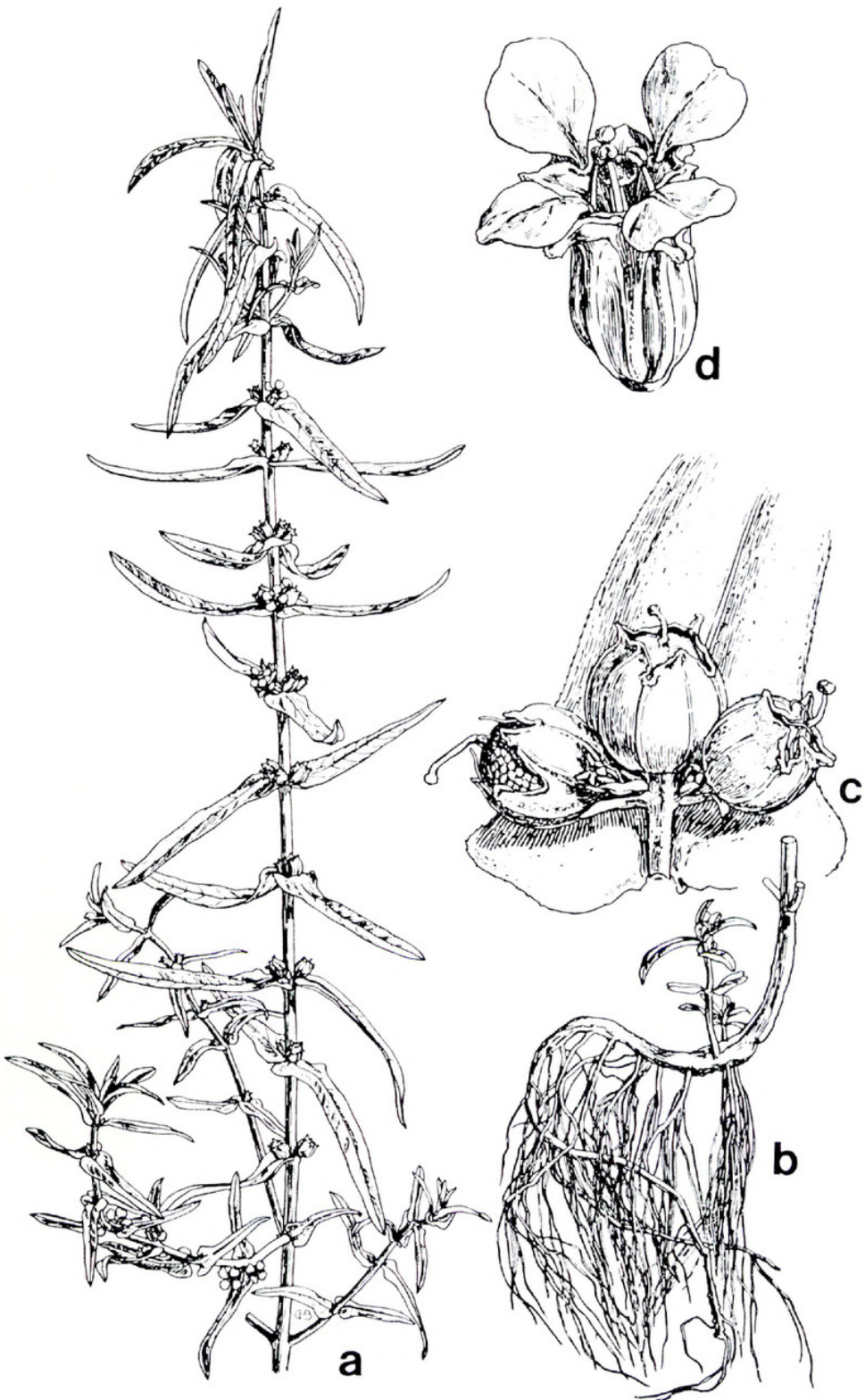


FIGURE 3. *Ammannia coccinea*: a, habit,  $\times 0.4$ ; b, basal part of plant with roots,  $\times 0.4$ ; c, pedunculate inflorescence subtended by auriculate leaf base,  $\times 3$ ; d, flower,  $\times 4$ . (Reprinted with permission from Mason, 1957. FIGURE 4c originally published as *Ammannia auriculata*.)



TABLE 2. Variation in floral features of *Ammannia auriculata*, *A. coccinea*, and *A. robusta*.\*

SPECIES	n	PETAL LENGTH	PETAL WIDTH	PEDUNCLE WIDTH
<i>A. auriculata</i>	42	1.33 ± 0.41	1.42 ± 0.38	7.0 ± 2.70
<i>A. coccinea</i>	37	2.01 ± 0.30	2.03 ± 0.23	1.74 ± 2.13
<i>A. robusta</i>	26	2.50 ± 0.55	2.96 ± 0.40	0.11 ± 0.33
		FLOWERS PER CYME	CALYX LENGTH	CAPSULE WIDTH
<i>A. auriculata</i>		7.12 ± 3.90	1.95 ± 0.22	2.54 ± 0.51
<i>A. coccinea</i>		5.59 ± 2.29	2.86 ± 0.62	3.98 ± 0.18
<i>A. robusta</i>		2.36 ± 1.18	3.50 ± 0.61	4.93 ± 0.61

\*Measurements in mm; first figure = mean, second figure = standard deviation.

short- to long-pedunculate 3- to 5- (to 14-)flowered cymes; peduncle, when present, to 9 mm long, sturdy, bibracteolate; pedicels mostly 2 mm or less, bibracteolate, bracteoles  $\frac{1}{3}$  or less length of floral tube. Floral tube urceolate to slightly campanulate, (2.5-)3-5 mm long, longitudinal ridges present but not conspicuously enlarged; calyx lobes triangular, alternating with thickened appendages; appendages about equal in length to lobes, mostly oriented outward from floral tube in bud; petals 4 (or 5), obovate, usually 2 by 2 mm, deep rose-purple, sometimes with deeper purple spot at base; stamens 4 (to 7), exserted, anthers deep yellow; style long, slender, equal to or longer than ovary, exserted at anthesis; ovary incompletely 2-locular. Capsule 3.5-5 mm in diameter, equal to or exceeding calyx lobes, rarely enclosed.  $n = 33$ .

As a successful amphidiploid derived from *Ammannia auriculata* and *A. robusta*, *A. coccinea* displays a range of morphological variability that, at its extremes, closely approaches the putative parent species. Since species of *Ammannia* on the whole are very similar, distinction between parent species and hybrid derivatives can be subtle. The number of characters separating *A. auriculata*, *A. robusta*, and *A. coccinea* are few and primarily quantitative. TABLE 2 summarizes variation in size of the floral features, and the key characters of the three species are compared in TABLE 3. Most specimens of *A. coccinea* resemble *A. robusta* more closely than they do *A. auriculata*. In the field *A. coccinea* is easily distinguished from *A. robusta* by its deep petal and anther color. On herbarium specimens the species is usually identified by the combination of stout peduncles, 3- to 5-flowered cymes, and mature capsules that are intermediate in size between those of *A. robusta* and those of *A. auriculata*. Occasional specimens that approach *A. auriculata* in peduncle length are best recognized by the usually larger flowers of *A. coccinea*.

No original material of *Ammannia coccinea* is extant (Maule, pers. comm.). Rottbøll (1773) described the species in careful detail from cultivated plants at the Copenhagen Botanical Garden. According to the protolog, these were grown from seeds brought to the Garden by a Belgian gardener, Kaesemaker. The neotype is selected from a Caribbean collection, because the original seeds were most likely collected in that region.

The name *Ammannia teres* Raf. has long been applied to the petal-bearing



TABLE 3. Comparison of major morphological features distinguishing taxa of the *Ammannia coccinea* complex.\*

FEATURE	TAXON		
	<i>A. auriculata</i>	<i>A. robusta</i>	<i>A. coccinea</i>
<b>Chromosome count</b>	15, 16	17	33
<b>Aspect</b>	Delicate	Robust	Robust
<b>Leaves</b>	Membranaceous, narrowly lanceolate	Fleshy, lanceolate, often spatulate at lower nodes	Membranaceous to fleshy, lanceolate
<b>Peduncles</b>	3–9 mm long, fili-form	Lacking	Lacking or to 4(–9) mm long, stout
<b>Flowers</b>	1–3 mm long, usually 3 or more per axil	2.5–5 mm long, usually 1 to 3 per axil	2–3.5 mm long, usually 3 or more per axil
<b>Petal color</b>	Rose-purple	Pale lavender	Rose-purple
<b>Anther color</b>	Deep yellow	Yellow	Deep yellow
<b>Capsules</b>	Usually 2.5 mm in diameter, equal to or exceeding lobes	4–6 mm in diameter, usually enclosed to equaling lobes	3.5–5 mm in diameter, equal to or exceeding lobes

\*Table modified from S. Graham (1979).

form of *A. latifolia* (Merrill, 1949). The correct application, determined by examination of the Rafinesque type located at P, is as a synonym of *A. coccinea*.

4. *Ammannia latifolia* L. Sp. Pl. 1: 119. 1753. TYPE: Savage H 156.1 (lectotype, LINN, IDC 177. 99: II. 7!).<sup>4</sup> MAP 3.

*Ammannia lythrifolia* Salisb. Prodr. Stirp. 65. 1796, *nomen illegit. et superfl.*

*Isnardia subhastata* Ruiz & Pavon, Fl. Peru. & Chil. 1: 66. t. 86, fig. b. 1798.

*Jussiaea sagittata* Poir. in Lam. Encycl. Méth. Bot. Suppl. 3: 198. 1813. Type based on a plant from Santo Domingo, grown in Paris and described from Herb. Desfontaines. Description clearly *A. latifolia*.

*Ludwigia hastata* Sprengel, Syst. Veg. ed. 16 [17]. 1: 446. [1824] 1825. BASIONYM: *Isnardia subhastata* Ruiz & Pavon.

*Ammannia hastata* DC. Prodr. Syst. Nat. Regni Veg. 3: 78. 1828. BASIONYM: *Isnardia subhastata* Ruiz & Pavon, incorrectly cited as "*Isn. hastatum* Ruiz Pav."

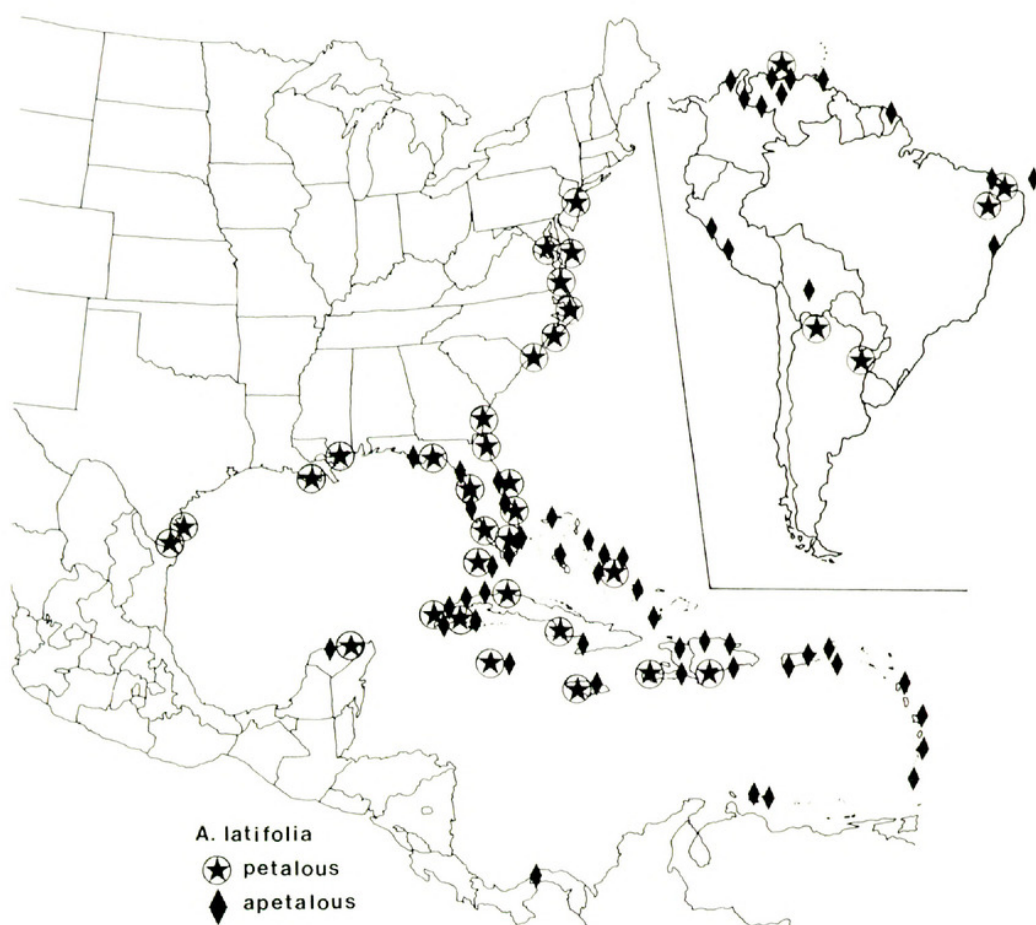
*Ammannia sagittata* DC. *ibid.* 80. BASIONYM: *Jussiaea sagittata* Poir.

*Ammannia lingulata* Griseb. Catal. Pl. Cubens. 106. 1866. TYPE: Cuba, Wright s.n. (probable holotype, GH!—this specimen annotated *Ammannia lingulata* Gr. in Wright's hand, with Wright's original field note attached, and labeled *Ammannia latifolia*; not at GOET or K).

*Ammannia koehnei* Britton, Bull. Torrey Bot. Club 18: 271. 1891. TYPE: U. S., New Jersey, Hackensack Flats, 28 July 1868, W. H. Leggett s.n. (holotype, NY!; isotype, NY!).

<sup>4</sup>This specimen bears the annotation "latifolia 1" in Linnaeus's hand. The number indicates the position of the species in *Species Plantarum*, indicating that it was seen by Linnaeus prior to publication of this work or soon after and is therefore the obligate lectotype (Stearn, 1974, and pers. comm.).





MAP 3. Distribution of *Ammannia latifolia*.

*Ammannia friesii* Koehne in Engler, Pflanzenr. IV. **216**(Heft 17): 50. 1903. TYPE: Argentina, Prov. Jujuy, Quinta, near Laguna de la Brea, R. E. Fries 94 (holotype, B, presumably destroyed; isotype, s!).

*Ammannia koehnei* var. *exauriculata* Fern. Rhodora **38**: 437. t. 449, figs. 4, 5. 1936. TYPE: U. S., Virginia, Princess Co., Fernald, Long, & Fogg 4954 (holotype, GH!; isotypes, MO!, NY!, US!).

*Ammannia teres* var. *exauriculata* (Fern.) Fern. Rhodora **46**: 50. 1944.

Robust erect annuals to 10 dm tall, unbranched or sparsely branching mainly from lower portions of stem, the branches ascending, shorter than stem. Leaves mostly linear-lanceolate to oblong, elliptic, or spatulate, 15–70(–100) by 4–15(–21) mm, usually equal to or longer than internode above, mature leaves mostly uniform in size, not significantly smaller toward apex of stem, the apex obtuse to subacute, the base strongly to moderately auriculate and rarely cuneate on middle and upper leaves, cuneate on lower ones. Inflorescences axillary, short-pedunculate or sessile, closely flowered cymes; flowers (1 to) 3 to 10 per cyme; peduncle, when present, to 3 mm long. Floral tube 4-merous, urceolate in bud, globose and 4–6 mm in diameter in fruit, subtended by linear bracteoles 1–1.5 mm long; lobes of fruiting calyx broad, apex very small or mucronate (occasionally slightly cucullate), disappearing with enlargement of capsule; appendages short, thick; petals lacking or 1 to 4 (to 6), obovate, to 1



mm long, pale pink to white; stamens 4 (to 8), included; style thick, 0.5 mm long, much shorter than ovary. Capsule incompletely 2- to 4-locular, included to barely exerted.  $n = 24$ .

*Ammannia latifolia* is a robust, erect, sparsely branched species in which the flowers are short styled, sessile, and usually three in each axil, with petals lacking or one to four. Broad calyx lobes with minute, mucronate apices are distinctive. The species is distributed in brackish to fresh-water marshes and ditches along the Atlantic and Gulf coasts from New Jersey southward to Florida, west to Texas, throughout the Caribbean, and in widely scattered, primarily coastal localities in South America. The species is not present in California; specimens so identified are *A. coccinea*.

An initial survey of variability in *Ammannia latifolia* in the United States and the Caribbean led me to consider the eastern North American and Caribbean specimens to be a single species. A study of many more collections from throughout the entire range of the species now confirms that decision and leads me also to include *A. friesii* Koehne of northern Argentina within *A. latifolia*. The two have been distinguished weakly at best, but since the recognized species of *Ammannia* are often separated by few characters, an intensive comparison of characters was made. In Koehne's treatment (1903), *A. latifolia* is described as having calyxes 4–5 mm long, flowers apetalous, and lower leaves cordate to auriculate. *Ammannia friesii* differs from *A. latifolia* in having 4 to 6 petals 1 mm long. The eastern North American *A. koehnei* (later incorrectly referred to *A. teres* Raf.; see discussion under *A. coccinea*) is distinguished by its calyxes 5–6 mm long, 4 petals 1.5 mm long, lower leaves cuneate, lobes retuse margined, and bracteoles larger than those of *A. friesii*.

Examination of herbarium specimens indicates that the species are not consistently separable on these or any other characters. When leaves are present at the lowest nodes, they are cuneate based. Calyx length varies from 3.5 to 6 mm throughout the range, mature calyx lobes are the same shape, and bracteole length varies insignificantly.

Petalous and apetalous plants are found throughout most of the range (see MAP 3). Although all specimens collected north of approximately 28°30'N latitude in the eastern United States have petals, 24 percent of the collections studied from south of that latitude also have them, and these collections are from widely separated localities. A previous figure of 30 percent petalous plants (S. Graham, 1975) is based on fewer collections. In a Manatee Co., Florida, population surveyed (Graham 698, MICH) 10 percent of the plants had petals. Flowers from a single plant were either petalous or apetalous, with the single exception of a primarily apetalous plant that bore one-petaled flowers on one branch. Petalous flowers typically bear four fully developed petals, but they may also be found with one to three rudimentary ones. Presence of petals appears to be a sporadic phenomenon in all but the northernmost part of the range, and their presence there is difficult to determine unless mature buds are present. Since no other morphological character is correlated with presence or absence of petals and at least four other species of *Ammannia* have either no petals or one to four of them, maintenance of the species on this basis alone is not justified.



TABLE 4. Geographic variation of selected characters of *Ammannia latifolia*.

REGION	PERCENT PETALOUS PLANTS	MEAN CAPSULE DIAMETER (mm)	MEAN LEAF LENGTH/ WIDTH QUOTIENT
Maryland–North Carolina	100	5.5	4.05
Georgia–Texas–northern Florida	100	4.8	5.97
Florida–Florida Keys	50	4.5	5.61
Bahamas	17	4.5	7.81
Greater Antilles, Yucatan	30	4.2	7.71
Lesser Antilles	0	4.4	6.53
South America, Panama	25	4.3	7.36

Geographic variation in leaf length/width quotient, mature capsule size, and percent petalous specimens is summarized in TABLE 4. Leaves are spatulate to mainly lanceolate in the northern part of the range, and commonly linear-lanceolate from North Carolina southward, with infrequent spatulate-leaved specimens found in the Caribbean area. The spatulate leaf with a cuneate base is a juvenile leaf-form typical of the first set of leaves in the seedling. Collections of *Ammannia latifolia* from Virginia, scattered localities in the Caribbean, and Peru with only this leaf type represent cases of arrested development of the mature leaf-form. *Ammannia teres* var. *exauriculata* (Fern.) Fern. is based on plants with predominantly spatulate leaves and cuneate bases.

Leaf length/width quotients initially increase southward, reaching a maximum in the Bahamas and Greater Antilles, and thereafter decrease slightly, suggesting that vegetative growth for this taxon is optimum in the northern Caribbean region. Capsule size is most variable in the north, but the difference in mean size between the largest and smallest capsule on all specimens is only 1.3 mm.

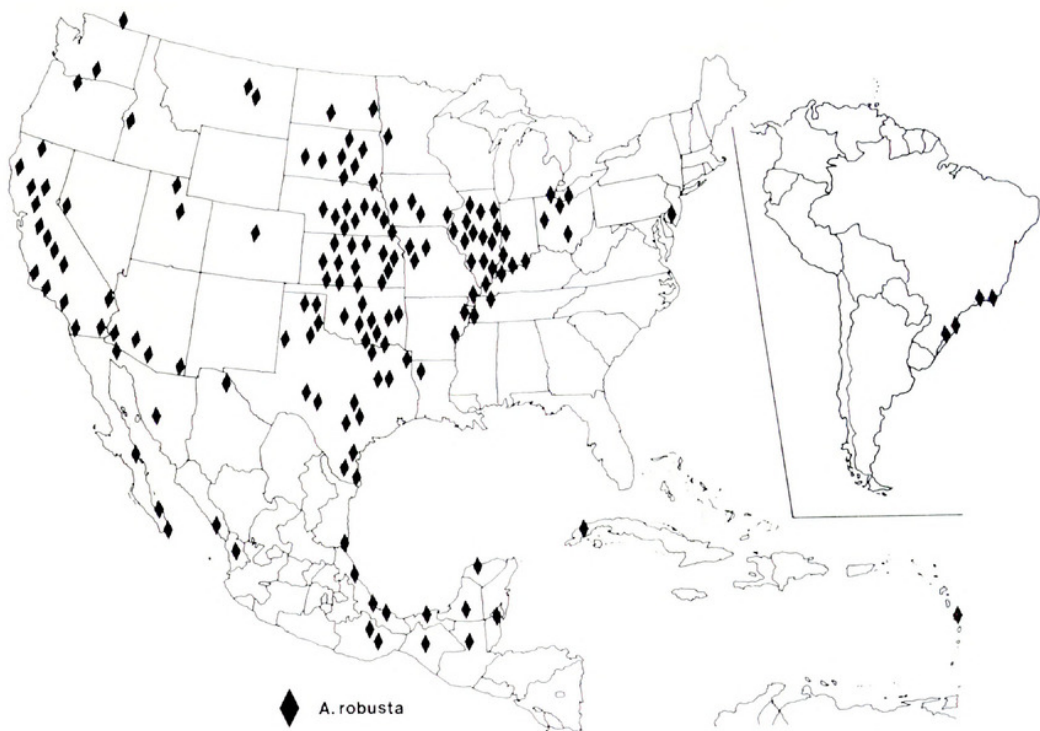
There are no significant discontinuities in morphology over the approximately 7500 km north–south distribution that would justify retention of more than one species. *Ammannia latifolia* is, in fact, remarkably uniform considering its extensive range. Autogamy, particularly cleistogamy (the common mode of fertilization in the apetalous plants), is probably the major factor in maintaining this uniformity.

On the basis of Koehne’s monographic descriptions, *Ammannia latifolia* is most similar to *A. urceolata* Hiern, an African endemic. Koehne’s (1880b) suggestion that *A. latifolia* ( $n = 24$ ) could have been derived from *A. coccinea* ( $n = 33$ ) is discarded due to the difference in chromosome numbers. *Ammannia latifolia*, with  $n = 24$ , is more likely a hexaploid derived from an ancestral  $x = 8$ .

5. ***Ammannia robusta*** Heer & Regel, Index Sem. Horto Bot. Turic. adn. 1. 1842. TYPE: Brazil, Rio de Janeiro, Piratininga, 23 July 1875, *Glaziou* 8340 (neotype (here designated), R!). MAP 4.

*Ammannia sanguinolenta* subsp. *robusta* (Heer & Regel) Koehne in Martius, Fl. Brasil. 13(2): 208. 1877.





MAP 4. Distribution of *Ammannia robusta* in Western Hemisphere. (Collections from LAF, DUKE, and NCU not included.)

*Ammannia coccinea* subsp. *robusta* (Heer & Regel) Koehne, Bot. Jahrb. Syst. **1**: 250. 1880.

*Ammannia alcalina* Blank. Montana Coll. Agric. Sci. Stud., Bot. **1**: 1905. TYPE: U. S., Montana, Lake Bowdoin, near Malta, 25 Aug. 1903, *J. W. Blankinship* s.n. (lectotype (here designated), MONT).

Robust annual herbs to 1 m tall, unbranched or branching from base, the lowest pairs of branches decumbent, often equaling height of main stem, the upper branches fewer, shorter. Leaves linear-lanceolate, less often elliptic to spatulate, 15–80 by 4–15 mm, usually 1–3 times length of internode above, tending to be fleshy, the apex obtuse to generally acute, the base auriculate-cordate, clasping, occasionally cuneate on lowermost leaves. Inflorescences axillary, sessile, 1- to 3- (to 5-)flowered cymes. Floral tube urceolate, frequently prominently 4-ridged or subulate, averaging 3.5 by 2 mm, subtended by 2 linear bracteoles  $\frac{1}{2}$  height of tube; calyx lobes broadly triangular with acute apex, alternating with thickened appendages equal to lobes in length; appendages usually erect in bud; petals 4 (to 8), obovate, usually 2.5 by 3 mm, pale lavender, sometimes with deep rose spot at base of midvein or with rose-purple midvein; stamens 4 (or 5 to 12), exserted, anthers pale yellow to yellow; style long, slender, slightly exserted at anthesis; ovary incompletely 2- (to 4-)locular. Capsule 4–6 mm in diameter at maturity, enclosed in or equal to calyx lobes, rarely exceeding lobes.  $n = 17$ .

*Ammannia robusta* has been overlooked in the North American flora because of its morphological similarity to *A. coccinea* (under which most specimens have been determined). In the field it is easily distinguished from *A. coccinea*



by a combination of features: pale lavender petals and light yellow anthers, one to three large, sessile flowers with four exaggerated ribs, and large, sessile capsules 4–6 mm in diameter. Mature herbarium specimens occasionally pose problems in identification due to change of petal and anther color in drying, but the presence of one to three large, sessile capsules at each axil is generally sufficient for determination. Variability in size of floral parts among *A. robusta*, *A. coccinea*, and *A. auriculata* is summarized in TABLE 3. Mixed collections of these species are not unusual in the herbarium since they may grow side by side at a single site and have been assumed by collectors to represent morphological variability within a single species.

*Ammannia robusta* is widely distributed in North America except in the southeastern United States and is most frequently collected in the Plains States. It is uncommon in the Caribbean, and it is limited to the coast north of Rio de Janeiro in South America, where it is apparently an early, but persistent, introduction.

The species was described from cultivated material of Brazilian origin. A type has not been located. Regel may have taken herbarium and library material with him to St. Petersburg on leaving Zurich (C. D. K. Cook, pers. comm.), but the type material of *Ammannia robusta* has not been located at LE. Since the description leaves no question as to the application of the name, a neotype has been selected from a Brazilian collection.

#### EXCLUDED NAMES<sup>5</sup>

*Ammannia alata* Steudel, Nomencl. Bot. ed. 2. 1: 76. 1840, *nomen nudum*.

*Ammannia auriculata* auct., *non* Willd., Raf. Atlantic J. 1: 146. 1832 = *A. ramosior* sensu Torrey, Ann. Lyceum Nat. Hist. New York 2: 199. 1827 = ***Rotala ramosior*** (L.) Koehne.

*Ammannia catholica* Hooker & Arn. ex Seemann, Bot. Voy. Herald, 284. 1856, *pro syn.* = ***Rotala ramosior*** (L.) Koehne.

*Ammannia catholica* var. *brasiliensis* Cham. & Schldl. Linnaea 2: 379. 1827 = ***Rotala ramosior*** (L.) Koehne; see Van Leeuwen (1974) and Cook (1979).

*Ammannia coccinea* auct., *non* Rottb., Pers. Synopsis Pl. 1: 147. 1805 = ***A. octandra*** L.

*Ammannia coccinea* subsp. *pubiflora* Koehne, Bot. Jahrb. Syst. 1: 250. 1880. TYPE: Iran, *Hohenacher* 2948. Authentic material unknown; not at BM or CAS. Description inadequate.

*Ammannia dentifera* A. Gray, Pl. Wright. 2: 55. 1853 = *Rotala dentifera* (Gray) Koehne, Bot. Jahrb. Syst. 1: 161. 1880 = ***R. ramosior*** var. ***dentifera*** (A. Gray) Lundell, Bull. Torrey Bot. Club 69: 395. 1942.

*Ammannia diffusa* Raf. Aut. Bot. 1: 39. 1840, *non* Willd., 1809, *nomen dubium*. The description is applicable to both *A. auriculata* and *A. coccinea*. Authentic material unknown.

*Ammannia humilis* Michaux, Fl. Bor. Amer. 1: 99. 1803 = *Boykiana humilis* (Michaux) Raf. Neogenyton, 2. 1825 = ***Rotala ramosior*** (L.) Koehne.

<sup>5</sup>Including misidentifications and misapplications listed by Koehne (1903) and *Index Kewensis* for the Western Hemisphere species.



- Ammannia humilis* auct., non Michaux, Chapman, Fl. So. U. S. 134. 1860, *ex descr.* = **R. ramosior**, *pro parte*, and **A. coccinea**, *pro parte*.
- Ammannia hyrcanica* Fischer ex Steudel, Nomencl. Bot. ed. 2. 1: 77. 1840, *nomen nudum*.
- Ammannia latifolia* auct., non L., Wallich, Catal. no. 2096. 1829, *nomen nudum* (not validated by G. Don, Gen. Syst., 1831–1838), *nec* Walp. Rep. Bot. Syst. 2: 102. 1843.
- Ammannia linearifolia* Raf. Aut. Bot. 1: 39. 1840, *ex descr.* = **Rotala ramosior** (L.) Koehne.
- Ammannia longifolia* Raf. *ibid.*, *nomen dubium* (description inadequate), synonym for either *A. coccinea* or *A. robusta*. Authentic material unknown.
- Ammannia mexicana* (Cham. & Schldl.) Baillon in Grandidier, Hist. Nat. Pl. (Madagascar Atlas) 3: t. 363. 1895 = **Rotala mexicana** Cham. & Schldl.
- Ammannia monoflora* Blanco, Fl. Filip. ed. 1. 64. 1837, *nomen dubium* (description inadequate) = **Rotala ramosior** (L.) Koehne (Cook, 1979).
- Ammannia multicaulis* Raf. Aut. Bot. 1: 39. 1840, *ex descr.* = **Rotala ramosior** (L.) Koehne.
- Ammannia nuttallii* A. Gray, Man. Bot. No. U. S. ed. 4. Add. 92. 1863, *ex descr.* = **Didiplis diandra** (DC.) Wood.
- Ammannia occidentalis* DC. Prodr. Syst. Nat. Regni Veg. 3: 78. 1828 = **Rotala ramosior** (L.) Koehne.
- Ammannia occidentalis* var. *pygmaea* Chapman, Fl. So. U. S. 134. 1860. TYPE: U. S., Florida, Key West, Dr. Blodgett s.n., *ex descr.* = **Rotala ramosior** (L.) Koehne.
- Ammannia pallida* Lehm. Index Sem. Horto Bot. Hamburg, 3. 1823, Linnaea 3: 9. 1828, *nomen dubium*. Authentic material unknown, not at K. Koehne followed DC. in regarding *A. pallida* as synonymous with *A. latifolia*, but description inadequate and even country of origin unknown.
- Ammannia racemosa* Hill, Veg. Syst. 11: 14. 1767. An erroneous citation in *Index Kewensis* for *A. ramosior* L.
- Ammannia ramosior* L. Sp. Pl. 1: 120. 1753, ed. 2. 175. 1762, *non sensu* L. Mant. Pl. Alt. 332. 1771. TYPE: U. S., Virginia, Clayton 774 (Savage H 156.2, LINN). = **Rotala ramosior** (L.) Koehne.
- Ammannia ramosior* auct., non L., Elliott, Sketch Bot. S. Carolina & Georgia 1: 219. 1817, *ex descr.* = **A. latifolia** L.
- Ammannia sanguinolenta* auct., non Sw., Cham. & Schldl. Linnaea 5: 568. 1830 = **A. auriculata** *fide* Koehne, who probably saw this specimen at B.
- Ammannia sanguinolenta* auct., non Sw., Heyne ex Steudel, Nomencl. Bot. ed. 2. 1: 77. 1840, *pro syn.*
- Ammannia sanguinolenta* auct., non Sw., Hooker & Arn. ex Seemann, Bot. Voy. Herald, 284. 1856, *pro syn.*
- Ammannia wormskioldii* Fischer & Meyer, Index Sem. Hortus Imp. Petrop. 7: 42. 1841. Not from Brazil as cited by Koehne in Martius, Fl. Brasil. 13(2): 205. Type (LE!) bears notation "C[ult.] e semina Congo allatis." A specimen from Koehne's herbarium (GH!) initially determined by him as *A. wormskioldii* was corrected by him to *A. latifolia* and may be the basis for the erroneous report of this species in the New World.



*Ludwigia scabriuscula* Kellogg, Proc. Calif. Acad. Sci. 7: 78. 1876. Equated by Koehne with *Ammannia latifolia*, but *A. latifolia* does not occur in California, and by description, the species (with scabrous, small-toothed leaves, clawed petals, and a 4-lobed stigma) does not belong to the genus *Ammannia*. Authentic material unknown; not at BM.

*Lythrum apetalum* Sprengel, Syst. Veg. ed. 16 [17]. 2: 454. 1825. Erroneously equated with *Ammannia latifolia* in *Index Kewensis, ex descr. non Ammannia*. = *Heimia myrtifolia* fide Koehne, 1903.

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## APPENDIX. Index of cited plant names.\*

- Ammannia alata* Steudel = excl  
*A. alcalina* Blank. = rob  
*A. arenaria* HBK. = aur  
*A. auriculata* Ledeb. ex Koehne = aur  
*A. auriculata* Raf. = excl  
*A. auriculata* Willd. = aur  
*A. auriculata* var. *arenaria* (HBK.) Koehne = aur  
*A. auriculata* var. *arenaria* f. *brasiliensis* (St. Hil.) Koehne = aur  
*A. baccifera* L. = bac  
*A. catholica* Cham. & Schldl. = excl  
*A. catholica* Hooker & Arn. = excl  
*A. coccinea* Pers. = excl  
*A. coccinea* Rottb. = coc  
*A. coccinea* subsp. *longifolia* (Koehne) Koehne = coc  
*A. coccinea* subsp. *pubiflora* Koehne = excl  
*A. coccinea* subsp. *purpurea* (Lam.) Koehne = coc  
*A. coccinea* subsp. *robusta* (Heer & Regel) Koehne = rob  
*A. dentifera* A. Gray = excl  
*A. diffusa* Raf. = excl  
*A. friesii* Koehne = lat  
*A. hastata* DC. = lat  
*A. humilis* Chapman = excl  
*A. humilis* Michaux = excl  
*A. hyrcanica* Fischer ex Steudel = excl  
*A. koehnei* Britton = lat  
*A. koehnei* var. *exauriculata* Fern. = lat  
*A. latifolia* L. = lat  
*A. latifolia* Wallich = excl  
*A. latifolia* var. *octandra* A. Gray = coc  
*A. linearifolia* Raf. = excl  
*A. lingulata* Griseb. = lat  
*A. longifolia* Raf. = excl  
*A. longipes* Wright = aur  
*A. lythrifolia* Salisb. = lat  
*A. mexicana* (Cham. & Schldl.) Baillon = excl  
*A. monoflora* Blanco = excl  
*A. multicaulis* Raf. = excl  
*A. nuttallii* A. Gray = excl  
*A. occidentalis* (Sprengel) DC. = excl  
*A. occidentalis* var. *pygmaea* Chapman = excl  
*A. octandra* Cham. & Schldl. = coc  
*A. pallida* Lehm. = excl  
*A. pedunculata* Rusby = coc  
*A. purpurea* Lam. = coc  
*A. pusilla* Sonder = aur  
*A. racemosa* Hill = excl  
*A. racemosa* Roth = aur  
*A. ramosior* Elliott = excl  
*A. ramosior* L. = excl  
*A. robusta* Heer & Regel = rob  
*A. sagittata* DC. = lat  
*A. sagittata* var. *angustifolia* A. Rich. = coc  
*A. sanguinolenta* Cham. & Schldl. = excl  
*A. sanguinolenta* Heyne ex Steudel = excl  
*A. sanguinolenta* Hooker & Arn. ex Seemann = excl  
*A. sanguinolenta* Sw. = coc  
*A. sanguinolenta* subsp. *longifolia* Koehne = coc  
*A. sanguinolenta* subsp. *purpurea* (Lam.) Koehne = coc  
*A. sanguinolenta* subsp. *robusta* (Heer & Regel) Koehne = rob  
*A. senegalensis* var. *brasiliensis* St. Hil. = aur  
*A. stylosa* Fischer & Meyer = coc  
*A. teres* Raf. = coc  
*A. teres* var. *exauriculata* (Fern.) Fern. = lat  
*A. texana* Scheele = coc  
*A. wormskioldii* Fischer & Meyer = excl  
*A. wrightii* A. Gray = aur  
*Isnardia subhastata* Ruiz & Pavon = lat  
*Jussiaea sagittata* Poir. = lat  
*Ludwigia hastata* Sprengel = lat  
*L. scabriuscula* Kellogg = excl  
*Lythrum apetalum* Sprengel = excl  
*Ronconia triflora* Raf. = aur

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\*Explanation of abbreviations: aur = *Ammannia auriculata*, bacc = *A. baccifera*, coc = *A. coccinea*, excl = excluded name, lat = *A. latifolia*, rob = *A. robusta*.





Graham, Shirley A. 1985. "A revision of Ammannia (Lythraceae) in the Western Hemisphere." *Journal of the Arnold Arboretum* 66(4), 395–420.

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