

THE GENERA OF THE ARALES IN THE SOUTHEASTERN UNITED STATES¹

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THE ARALES (Spathiflorae), in the view of most authors, include only the families Araceae and Lemnaceae, the latter representing highly reduced plants of aroid ancestry. A much broader interpretation of the order is the one of Wettstein, who included in his "Spadiciflorae" not only the Araceae and Lemnaceae, but also the Palmae and Cyclanthaceae. Other authors (e.g., K. Fritsch, *Ber. Deutsch. Bot. Ges.* **50a**: 162-184, 1932) have interpreted this group as including also the families Pandanaceae, Sparganiaceae, and Typhaceae. Such an interpretation of the order is subject to considerable disagreement, and these families may indeed not be very closely related to each other. The Arales are here interpreted in the Englerian sense to include only the families Araceae and Lemnaceae, which are generally agreed to be closely allied.

ARACEAE (ARUM FAMILY)

Tuberous or rhizomatous, terrestrial or aquatic (rarely floating) herbs with watery, milky or acrid sap. Leaves simple or compound, basal and solitary or clustered, or cauline and alternate. Inflorescence a spadix (an axis with small, sessile, tightly grouped flowers), subtended by an herbaceous spathe (or spathe absent). Flowers bisexual, with a perianth (in ours), or unisexual, without a perianth (the plants then monoecious or dioecious); perianth, when present, of 2-6 parts; stamens 1-6, free or united into a synandrium; gynoecium completely syncarpous, the ovary 1(-many)-locular, superior or inferior (i.e., embedded in the spadix); ovules 1-many in each locule. Fruit usually a berry. Seeds with or without endosperm, the embryo large. (Including Pistiaceae.)

A large family, primarily tropical or subtropical in its distribution, of over 100 genera grouped into eight subfamilies by Engler (18 tribes by

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Hutchinson) with about 1500 species. Eight genera, representing five sub-families, are native to the United States, while at least two exotic genera, *Colocasia* and *Pinellia*, are becoming established. All but three of these (*Calla* L., *Lysichitum* Schott, and *Pinellia* Tenore) are represented in our area.

The family may be recognized by the inflorescence, a spadix, which usually is subtended or enveloped by a spathe. Great diversity exists with respect to the nature, position and distribution of the flowers on the spadix, the habitat, habit, leaf morphology, flower structure and other morphological characters. The subdivision of the family is based not only on floral but also on anatomical characters, such as the presence or absence of raphides and the occurrence of latex.

Although there appears to be no doubt that the family represents a natural group, much speculation exists with respect to its origin and phylogenetic relationships. Engler considered the Araceae to be derived from the Palmae through the Cyclanthaceae. Hutchinson, on the other hand, thought the group to be monophyletic and derived from the stock of the tribe Aspidistreae of the Liliaceae. Other authors have considered it as having evolved from the ancestors of the Liliaceae through various phylogenetic lines.

The Araceae as a group are notable for the occurrence of the needle-like crystals of calcium oxalate (raphides) in "packets" which occur in small capsules in almost all tissues. These account for the immunity of most Araceae to herbivorous mammals and for the intense irritation or "burning" sensation which is experienced when raw or improperly cooked corms of *Colocasia*, *Xanthosoma*, or *Arisaema* are eaten. In *Dieffenbachia*, the dumb-cane, widely grown as an ornamental foliage plant, the irritation is so severe as to produce temporary inability to speak. When the cells of the plant are broken in chewing, the capsules absorb water and the needles are discharged with sufficient force to penetrate the tissues of the mouth. The prolonged cooking which is necessary with the "edible" Araceae renders the capsules inactive. (Cf. *Colocasia*.)

Many genera are popular in cultivation as ornamentals, some, such as *Philodendron*, *Syngonium*, *Pothos*, *Scindapsus*, and *Caladium*, for their decorative foliage, others, such as *Zantedeschia* and *Anthurium*, for their showy spathes. Some of these may possibly escape sparingly in subtropical areas.

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KEY TO THE GENERA OF ARACEAE

- A. Perianth present; flowers (at least the basal) bisexual, frequently proterogynous.
- B. Spadix lateral on a leaf-like axis; leaves sword-shaped; perianth segments 6; fruit a berry. 1. *Acorus*.
- B. Spadix terminal on peduncle; leaves cordate, ovate, or oblong-elliptic.
- C. Spathe fleshy, enveloping the subglobose spadix; perianth segments 4; fruit embedded in swollen spadix (multiple fruit.) 2. *Symplocarpus*.
- C. Spathe bract-like, ensheathing base of peduncle of oblong spadix; perianth segments (in lower flowers) 6; fruit a berry, not embedded in spadix. 3. *Orontium*.
- A. Perianth wanting; flowers unisexual.
- D. Plants rooted in soil; spadix free from spathe.
- E. Leaves simple; stamens united into a peltate synangium.
- F. Leaves sagittate or hastate; spadix almost completely covered by flowers. 4. *Peltandra*.
- F. Leaves ovate-cordate and peltate; apex of spadix naked or covered with sterile flowers; plants spreading by runners. 5. *Colocasia*.
- E. Leaves palmately or pedately divided; stamens 2-4-locular, subsessile. 6. *Arisaema*.
- D. Plants floating; spadix adnate to spathe. 7. *Pistia*.

Subfam. POTHOIDEAE Engl.

1. *Acorus* Linnaeus, Sp. Pl. 1: 324. 1753; Gen. Pl. ed. 5. 151. 1754.

Plant herbaceous, with a thick, creeping rhizome. Leaves equitant, sword-shaped. Spadix borne laterally on an axis resembling a foliage leaf, spathe absent (the prolongation of the fertile axis often interpreted as an open spathe). Flowers bisexual, 3-merous, greenish; perianth of 2 whorls of 3 concave tepals; stamens 6, filaments linear; gynoecium with a 2- or 3-loculed superior ovary, each locule with several orthotropous ovules apically attached. Fruit a gelatinous, few-seeded berry. TYPE SPECIES: *Acorus Calamus* L. (*Acorus*, an ancient Latin name for an aromatic plant.) — SWEET-FLAG.

A genus of two or three species, as currently interpreted, from the northern temperate regions of the world. It is represented in our area by the widespread *Acorus americanus* Raf. which grows in low, wet areas, marshes and along the banks of quiet streams. Although generally known as *A. Calamus* and considered to have been introduced into the United States from Europe, recent cytological evidence indicates that the American plant is most likely a native one. The American plants are diploid ($2n = 24$) and fertile, while the European plants, which were introduced from southern Asia, are triploid ($2n = 36$) and sterile. Whether or not the European sterile triploid has been introduced into North America still remains to be shown. The plants of "*A. Calamus*" from Siberia and Asia are tetraploid ($2n = 48$) and fertile. Various characters have been found to be corre-

lated with the degree of polyploidy in *A. Calamus*. These include the blade width/length ratio, the angle of the spadix insertion, the oil content of the rhizome (greater with polyploidy), water content, and also the amount of calcium oxalate (decreases in polyploids). It has been suggested that each polyploid group be considered a variety of *A. Calamus*, but perhaps each might better be regarded as separate species. The American diploid (*A. americanus* Raf., *A. Calamus* var. *americanus* (Raf.) Wulff) needs further study to establish the possible validity of separation of northern and southern plants as was done by Rafinesque.

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Subfam. CALLOIDEAE Engl.

2. *Symplocarpus* Salisbury ex Nuttall, *Gen. N. Am. Pl.* 1: 105, 106. 1818, nom. cons.²

Herbs with a stout, erect rhizome bearing numerous large, clustered leaves; entire plant with a strong odor, often compared with that of a

² Conservation unnecessary; see *Taxon* 8: 230. 1959.

skunk. Leaves entire, ovate or cordate, conspicuously veined. Spathe thick, fleshy, purple spotted, ovoid, with a tapering, arched tip, the margin inrolled. Spadix ellipsoid or globose, completely covered by the crowded flowers. Flowers bisexual, proterogynous, maturing basipetally; perianth segments 4, fleshy; stamens 4, opposite the perianth segments, the filaments slender, flattened, the anthers 2-loculed, extrorse; gynoecium with a 1 (-seldom 2)-loculed ovary imbedded in the spadix, the solitary ovule pendent, orthotropous; style 4-angled, subulate. Fruits embedded in the spongy tissue of the globose spadix which is roughened by the persistent perianth parts and styles. Seeds naked, without endosperm or seedcoat, subspherical, depressed on the funicular side. (*Spathyema* Raf., nom. rejic.) TYPE SPECIES: *S. foetidus* (L.) Nutt. (Name from Greek, *symploce*, connection, and *carpos*, fruit, in allusion to the multiple fruit.) — SKUNK-CABBAGE.

Symplocarpus foetidus, is known from two widely disjunct areas: eastern Asia (the Japanese plant has been named *S. nipponicus* Makino), and eastern North America, where it ranges from Quebec and Nova Scotia, south to

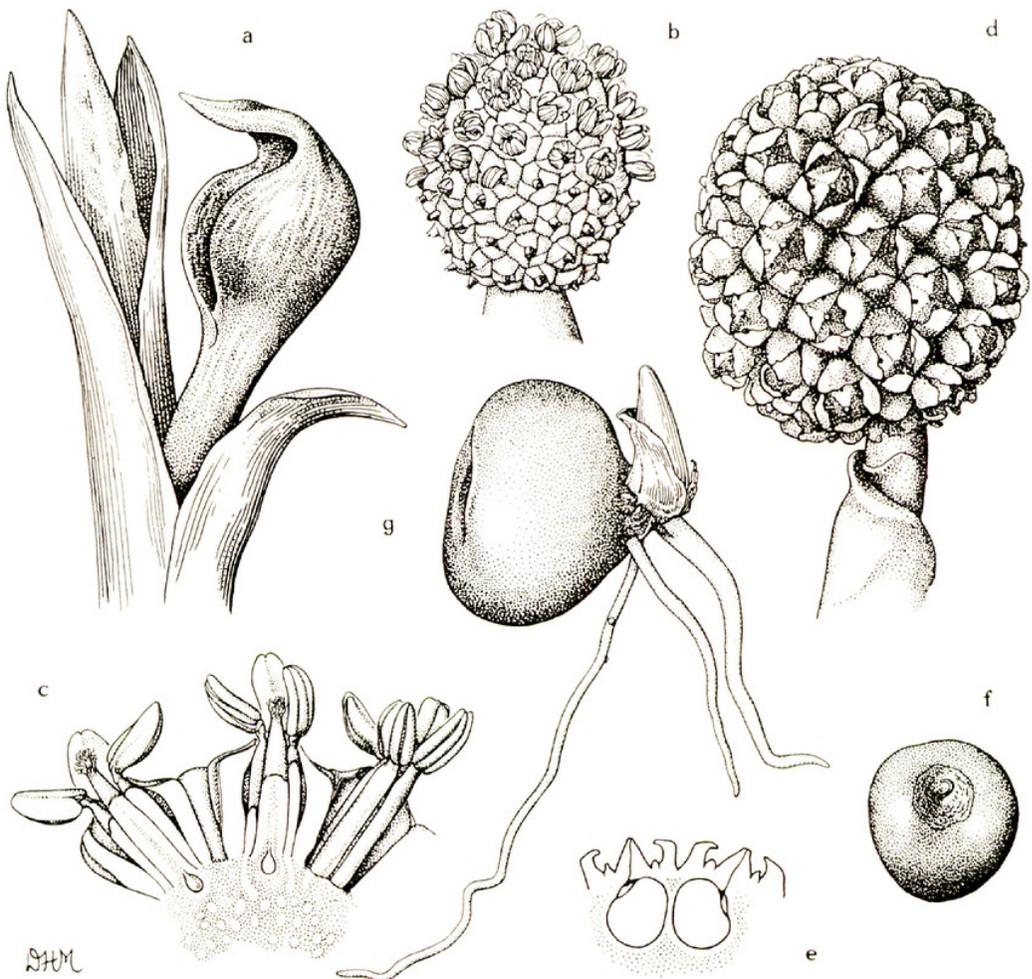


FIG. 1. *Symplocarpus*. a-g, *S. foetidus*: a, habit, showing inflorescence, $\times \frac{3}{8}$; b, spadix, $\times 1\frac{1}{2}$; c, section through spadix, showing flowers in vertical section, $\times 4$; d, fruiting spadix, $\times 1$; e, section through fruiting spadix, showing seeds in vertical section, $\times 1$; f, seed, $\times 1\frac{1}{2}$; g, seedling, $\times 2$.

New England, North Carolina, Georgia, and Tennessee and west to Ontario, northern Michigan, Minnesota, and Iowa. (It has also been recorded from Florida and Missouri.) It occurs in swamps, wet meadows, and woods, where it often forms dense stands. *Symplocarpus* is one of the earliest plants to flower in the spring. The inflorescence appears barely above the surface of the ground, long before the leaves appear. The flowers are all perfect and proterogynous and mature basipetally on the inflorescence. As the embryo develops it absorbs both endosperm and integuments, so that when mature it possesses no seed coat. Except in the younger stages, during which it has a monopodial branching system, the plant is sympodial, each branch producing two leaves and a terminal inflorescence, although many of the inflorescences do not mature (Shull). The roots are contractile and function in pulling the plant into the soil.

The closest relative of *Symplocarpus* apparently is *Lysichitum*, a western American and Asiatic genus of two species, although Hutchinson, primarily on the basis of the more differentiated spathe of *Symplocarpus*, placed these two genera in different tribes. This view, however, does not seem to be supported by the morphology of the flowers, of the inflorescence, and of the vegetative body (including odor!), which are similar enough to indicate a close relationship between the two.

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3. *Orontium* Linnaeus, Sp. Pl. 1: 324. 1753; Gen. Pl. ed. 5. 151. 1754.

Perennial aquatic herbs with stout, deeply sunken rhizomes. Leaves simple, oblong-elliptic, prominently nerved and long petioled, usually floating. Spadix on an elongated scape, oblong, golden yellow, the scape green, with a band of white below the flowers. Spathe obscure, forming a sheath at the base of the scape, the blade bract-like. Flowers variable: perfect at the base of spadix, with 6 tepals, 6 stamens and a 3-carpellate gynoecium, gradually becoming staminate towards the tip; tepals yellow, 6 in two whorls to 2 in a single whorl; stamens 6-1, 1 or 2 staminodia sometimes present; gynoecium 3- or 2-carpellate; ovary 1-locular with a single basal, anatropous ovule. Fruit a 1-seeded berry with thin pericarp. TYPE AND SOLE SPECIES: *Orontium aquaticum* L. (*Orontium*, an ancient name for a plant which is said to have grown in the Syrian river Orontes.) — GOLDEN CLUB.

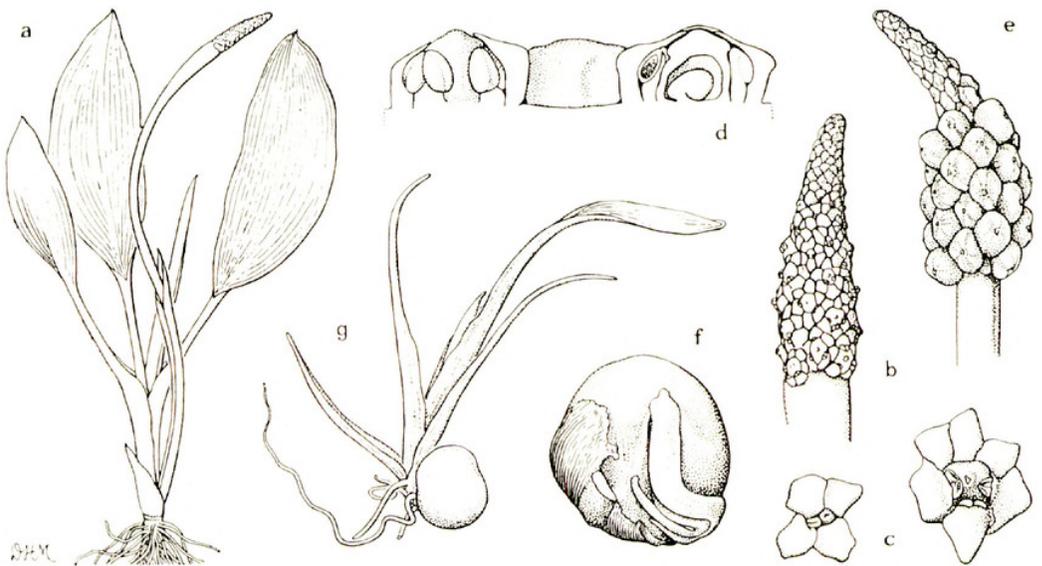


FIG. 2. *Orontium*. a-g, *O. aquaticum*: a, habit, $\times \frac{1}{8}$; b, spadix, $\times 1$; c, flowers, $\times 4$; d, spadix, longitudinal section, showing flowers in lateral view and in vertical section, $\times 4$; e, fruiting spadix, $\times \frac{1}{2}$; f, seed with seed coat partially removed to show embryo, $\times 2$; g, seedling, $\times 1$.

Orontium aquaticum L. is known only from the eastern United States, primarily on the Coastal Plain, where it occurs growing in the shallow water of pools or streams and on their moist banks or shores, from Florida, north to Massachusetts, and west to Louisiana and Kentucky. The flowers, which are crowded on the spadix, show a remarkable amount of variation, ranging from those with six perianth segments, six stamens and a 3-carpellate gynoecium, to those with only two perianth segments, one stamen, and one staminodium and no pistil. Numerous intermediate or transitional

conditions may also be found on the spadix. The morphological and biological details of this plant merit further investigation.

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Subfam. PHILODENDROIDEAE Engl.

4. *Peltandra* Rafinesque, *Jour. Phys. Chem.* 89: 103. 1819, nom. cons.

Herbs with long, stout-petioled, clustered leaves. Leaf blades sagittate or hastate with 3 prominent palmate nerves. Scape about as long as the petioles. Spathe convolute throughout or dilated and spreading above. Spadix completely covered with flowers, or with the apex naked. Flowers unisexual, a perianth wanting; staminate flowers covering apical portion of spadix, sessile, consisting of 4-8 two-loculed anthers embedded in the margin of a peltate shield-like scale; anthers dehiscing by terminal pores. Car-

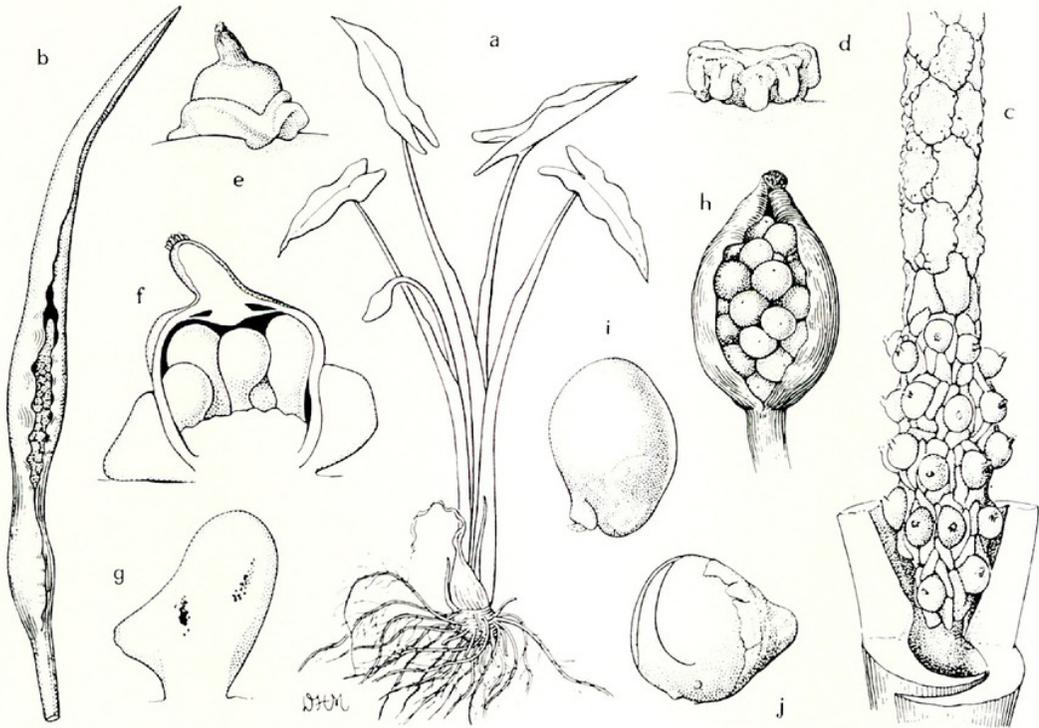


FIG. 3. *Peltandra*. a-j, *P. virginica*: a, habit, $\times \frac{1}{8}$; b, inflorescence, $\times \frac{1}{2}$; c, spadix, basal portion, showing staminate and carpellate flowers, spathe removed, $\times 2$; d, staminate flower, lateral view, $\times 5$; e, carpellate flower, lateral view, $\times 5$; f, carpellate flower, vertical section, showing ovules, $\times 10$; g, ovule, $\times 20$; h, fruiting spadix enveloped by base of spathe, $\times \frac{1}{2}$; i, seed, $\times 2$; j, seed, apical view, seed coat partially removed to show embryo, $\times 2$.

pellate flowers covering basal portion of spadix, consisting of the 1-loculed gynoecium surrounded by 4 or 5 white, fleshy staminodia; ovules 1-few, basal, amphitropous. Fruits 1-3-seeded berries aggregated in a fleshy head inclosed by the leathery base of the spathe; scape recurved at maturity. (*Houttinia* Necker, nom. rejic.) TYPE SPECIES: *P. undulata* Raf. = *P. virginica* (L.) Schott & Endl. (The name from Greek, *pelta*, a small shield, and *andros*, of a man, in reference to the peltiform stamens.) — ARROW-ARUM.

Three species, all of which occur in our area, of wet soils or shallow water along stream and pond borders, marshes, swamps, and wet woods in the eastern areas of North America. The best known and most widespread species is *Peltandra virginica* ($2n = c. 44, 88$), which is exceedingly variable in the shape of the blades, having seven named forms. The northern and southern extremes of this species also differ in the shape of the spathe and in the undulation of the margin of the spathe. *Peltandra sagittifolia* (Michx.) Morong (*P. glauca* (Ell.) Feay ex Wood), with an entirely white spathe and red fruits, is found from southeastern North Carolina to Florida, entirely on the Coastal Plain. The third species, *P. luteospadix* Fern., has a white-bordered spathe and yellow spadix and occurs from southeastern Virginia, southward to Florida. It has been suggested that *P. luteospadix* may have arisen as a hybrid of *P. virginica* and *P. sagittifolia* but no investigations have been made either to confirm or refute this hypothesis.

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Subfam. COLOCASIOIDEAE Engl.

5. *Colocasia* Schott, Meletemata Bot. 18. 1832.

Perennial herbs with starch-filled corms and tubers. Leaves ovate-cordate and peltate, dark velvety green above. Plants monoecious; inflorescence

stoutly peduncled, shorter than the petioles; spathe ovate-lanceolate, constricted below the middle; the spadix inclosed by the spathe, with pistillate flowers on the basal portion and staminate flowers above, the two groups separated by a group of sterile flowers, the terminal portion of the spadix naked (or covered by sterile flowers). Perianth wanting. Staminate flowers of several stamens united into a peltate body, the anthers elongate, laterally adnate or partially free and pendent, dehiscing by an apical slit. Carpellate flowers consisting of the short-styled gynoecium, the ovary 1-locular, with numerous orthotropous ovules on the ovary wall. Fruit a berry. TYPE SPECIES: *Colocasia antiquorum* (L.) Schott, *C. esculenta* (L.) Schott, or *C. acris* (R. Br.) Schott, a lectotype apparently not yet chosen. (An old Greek name derived from the Arabic *colcas* or *culcas*.) — DASHEEN, TARO.

A genus of tropical Asiatic herbs, variously interpreted as consisting of seven or more species. *Colocasia esculenta* (L.) Schott is widely cultivated throughout the tropics for its starchy, edible tuber. Numerous cultivars occur, and several have been introduced into the United States, where the species has been grown in the lowlands of the Coastal Plain from South Carolina to eastern Texas. *Colocasia esculenta* var. *aquatilis* Hasskarl has escaped cultivation and is an aggressive weed which forms large clones spreading vegetatively by slender, rapidly growing stolons. This plant has been poorly collected in the southeastern United States, and herbarium material is rare. It has been reported to be spreading in southern Louisiana, and it is known also from several localities from central to southern Florida growing along streams, marshes, and roadsides. The leaves of naturalized plants observed in southern Florida have a purple centrum and a purple band at the summit of the petiole. No flowering material of this form has been collected in our area. Other clones may well occur, however, and a form lacking purple markings, locally naturalized at Tallahassee, Florida, flowers in September and October (Godfrey).³

Care must be taken to cook the starchy corm thoroughly before it is eaten. Small capsules containing calcium oxalate raphides are found in abundance in all tissues of the plant. If improperly cooked, the capsules discharge the raphides with such force that they penetrate the tissues of the mouth causing great irritation. Prolonged cooking renders the capsules inactive.

³ A plant grown from a corm collected in Dade County, Florida, in May, 1958, flowered in the greenhouse at the Arnold Arboretum on October 28, 1959. The firm, fleshy spathe was 28 cm. long and light orange in color, except for the green basal portion inclosing the carpellate region of the spadix. The erect, cream-colored staminate region and the sterile appendix of the spadix were exerted from the spathe which was inclined backward above the carpellate region at an angle of about 45 degrees and which was open for about 10 cm. between this and the strongly convoluted terminal 18 cm. Flowering lasted two days: the carpellate flowers were receptive the first day and the pollen was shed on the second. The leaves of these plants bore purple markings when collected, but those produced in the greenhouse lacked this coloring.

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Subfam. AROIDEAE Engl.

6. *Arisaema* Martius, Flora **14**: 459. 1831.

Perennial herbs with globose or subglobose corms each bearing a simple scape sheathed by the leaf petioles. Leaves palmately or pedately divided. Spathe convolute below, spreading and arched above. Spadix obovoid and fertile at the base, above sterile (appendix) and cylindrical, clavate or long attenuate. Plants dioecious or at times monoecious with both staminate and carpellate flowers in an inflorescence. Flowers without a perianth. Staminate flowers of numerous 2-4-locular, subsessile anthers opening by a slit or a pore. Carpellate flowers consisting of a gynoeceium with a unilocular ovary containing 5 or 6 erect, orthotropous ovules. Fruits 1-few-seeded red berries, few to many borne on the enlarged, ovoid base of the spadix. (Including *Muricauda* Small). TYPE SPECIES: *A. nepenthoides* Mart. (Name from Greek, *aris*, an ancient plant name, and *haima*, blood, in reference to the red-spotted leaves of some species.) — JACK-IN-THE-PULPIT, INDIAN TURNIP.

A genus of over 100 species in 15 sections, of eastern Asia, Africa (Ethiopia), North and Central America; represented in our area by three to five species in two sections.

Section TORTUOSA Engl., with seven eastern Asiatic and one eastern American and Mexican species, is represented in our flora by *A. Dracontium* (L.) Schott ($2n = 28, 56$), green dragon or dragon root, widespread from Florida to Texas, north to southern Quebec and Ontario, and also

with disjunct stations in eastern Mexico. The pedately divided leaves and the long-exserted, slender, tapering appendix are characteristic.

Our other species belong to sect. *PISTILLATA* Engl., which includes about eight species of eastern Asia and three or four of eastern North America. The species of this section have a distinctly stipitate appendix which is more or less cylindrical and shorter than the spathe. *Arisaema quinatum* (Nutt.) Schott ($2n = 28$), of rich woods from Florida north to North Carolina and west to Louisiana, is a well-marked plant with a curved spadix and leaves generally with five leaflets. *Arisaema Stewardsonii* Britton ($2n = 28$), with the back of the spathe fluted, occurs primarily to the north of our area (Nova Scotia and southern Quebec, southward along the Appalachians at higher elevations in cold, wet woods) reaching its

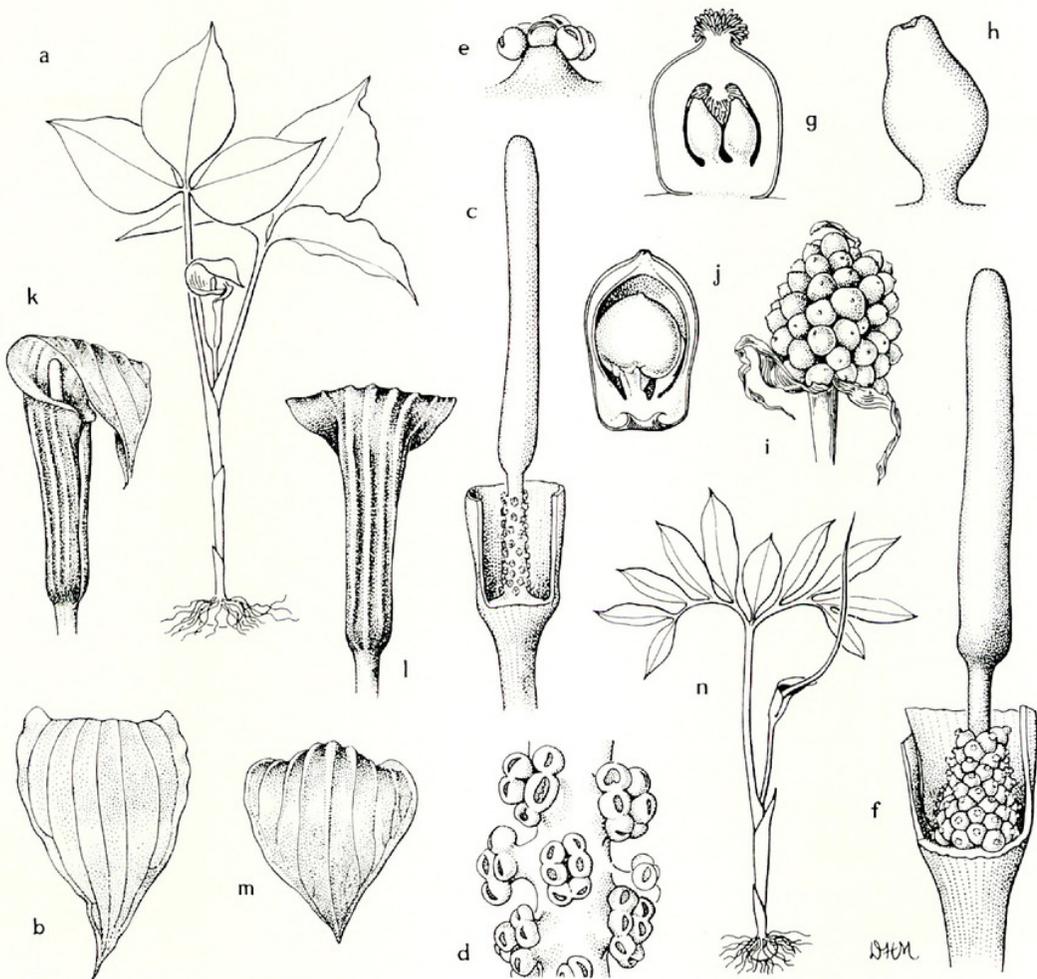


FIG. 4. *Arisaema*. a-j, *A. atropurpureum*: a, habit, $\times \frac{1}{8}$; b, spathe, apical view, $\times \frac{1}{2}$; c, staminate inflorescence, spathe removed, $\times 1$; d, portion of staminate spadix, $\times 6$; e, staminate flower, lateral view, $\times 8$; f, carpellate inflorescence, spathe removed, $\times 1$; g, carpellate flower, vertical section, showing ovules, $\times 8$; h, ovule, $\times 20$; i, fruiting spadix, unusually large, $\times \frac{1}{2}$; j, fruit, vertical section, showing seed, $\times 2$. k-m, *A. Stewardsonii*: k, inflorescence, lateral view, $\times \frac{1}{2}$; l, inflorescence, back view, $\times \frac{1}{2}$; m, spathe, apical view, $\times \frac{1}{2}$. n, *A. Dracontium*: habit, $\times \frac{1}{8}$.

southern limit in western North Carolina. Most of the taxonomic difficulties in the genus in our area center around the widespread *A. atrorubens* (Ait.) Blume (*A. triphyllum* sensu Huttleston) ($2n = 28, 56$), a plant primarily of woodlands in the northeastern United States, southward to South Carolina and Tennessee, and its close relatives. The status of this familiar and abundant plant and that of the smaller, later-flowering *A. triphyllum* (L.) Schott (*A. triphyllum* subsp. *pusillum* (Peck) Huttleston) ($2n = 28$) are still unsettled. Although the two are quite distinctive in some areas, in others forms of intermediate morphology occur; *A. acuminatum* Small, of the southeastern Coastal Plain, is perhaps one of these latter.

All of these species have been distinguished on morphological grounds and, for the most part, appear to be distinct ecologically. In instances in which *Arisaema atrorubens* and *A. Stewardsonii* come in contact (to the north of our range), hybrid colonies may occur. Such local hybridization and intergradation has led to the interpretation of the latter as a subspecies of the former. However, with local exceptions, these plants appear to represent distinct groups which maintain themselves as natural units.

Further careful population studies are essential. Collectors should note conformation (especially fluting of *A. Stewardsonii*), coloration and markings of the spathe, width of flange at the upper margin of the spathe, and diameter of fruits. Careful notes on habitat, flowering time, and variability of colonies should be taken.

Apart from the differing taxonomic interpretation, the nomenclatural application of the name *A. triphyllum* L. has been a matter of controversy. It is used here in the sense of Fernald (1940) for the plant formerly known as *A. pusillum* Peck; almost all literature references to *A. triphyllum* prior to 1940 apply to the plant here called *A. atrorubens*.

Numerous morphological studies have been made of *A. atrorubens* (mostly as *A. triphyllum*) and *A. Dracontium*. The factors influencing the sex of the flowers in the inflorescence of *A. atrorubens* apparently are environmental or nutritional. By manipulating the growth conditions it is possible to control the sex of the flowers that will be produced. Thus, in rich soil with an abundant water supply, carpellate flowers are produced, while staminate flowers are produced with the reduction of the root system and leaf surface of the plant.

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Subfam. PISTIOIDEAE Engl.

7. *Pistia* Linnaeus, Sp. Pl. 2: 963. 1753; Gen. Pl. ed. 5. 411. 1754.

Floating, aquatic, stoloniferous herb with a short stem bearing a rosette of leaves and numerous branching, adventitious roots. Leaves sessile, with simple, ovate to obovate-cuneate, densely pubescent blades, 3-15 cm. long,

each surrounded at its base by a membranous sheath. Spathe 2–4 cm. long, tubular at its base, but free and spreading above, slightly constricted above the middle. Plants monoecious, the spadix both staminate and carpellate; spadix fused to the median line of the spathe, free at its distal end. Flowers without a perianth, the carpellate solitary on the lower part of the spadix, the staminate whorled above; stamens 2–8, appearing to terminate the spadix. Staminate flowers subtended by a membranous collar surrounding the free portion of the spadix, this in turn subtended by a short-stalked, cordate, membranous flap. Gynoecium 1-carpellate with a 1-locular ovary containing numerous orthotropous ovules. Fruit green, ovoid to ellipsoid, many-seeded, crowned by the persistent style. Seed with a rugose, thick testa, a minute embryo, and abundant endosperm. TYPE AND SOLE SPECIES: *P. Stratiotes* L. (Generic name from Greek, *pistos*, liquid, in reference to the aquatic habitat.) — WATER-LETTUCE.



FIG. 5. *Pistia*. a–g, *P. Stratiotes*: a, habit, $\times \frac{1}{2}$; b, inflorescence, $\times 3$; c, inflorescence, lateral view, portion of spathe removed, $\times 3$; d, gynoecium, vertical section, showing ovules, $\times 4$; e, ovule, $\times 12$; f, mature fruit, $\times 3$; g, seed, $\times 6$.

A genus of a single species, *Pistia Stratiotes* L. ($2n = 28$), found floating in ponds and streams of tropical and subtropical Africa, Asia, and America. In our area it occurs in Florida and the Gulf States where it frequently forms dense mats on the water. *Pistia* is of considerable biological importance not only because of its weedy nature, which frequently results in the clogging of waterways, but also because it may represent the evolutionary line through which the Lemnaceae developed. The embryo-sac development is of the *Polygonum* (normal) type.

At least in Florida, *Pistia* does not seem to produce seeds, although the ovary tends to enlarge and to become somewhat inflated. When the plant is pollinated artificially, seeds and fruit develop normally. Whether the failure of seed development is a result of the absence of suitable pollinating agents must still be established, but the evidence at present seems to favor such an interpretation.

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LEMNACEAE (DUCKWEED FAMILY)

Small aquatic plants, floating on or below the surface of the water, consisting of a highly reduced, fleshy or membranaceous plant body (frond), lacking distinct stems and leaves, and either rootless or with one or many roots. Plants monoecious, the flowers borne in marginal pouches or in pouches on the upper surface of the frond. Staminate flower consisting of a single stamen, borne singly or in pairs; anther 2-locular. Carpellate flowers solitary, consisting of a single carpel; ovary 1-locular with 1 or 2 basal ovules. Fruit a 1- or 2-seeded utricle.

This family, generally considered to be composed of four genera and 26 species, is distributed in streams and other bodies of fresh water in most parts of the world. All four genera occur in our area and are represented by a total of 11 species which are of considerable economic and biological importance. Species of the Lemnaceae have been reported to serve as an important food for wild fowl, marsh birds, and aquatic animals, such as fish and snails.

The small plant body of the Lemnaceae is oval or elongate, and bears at its basal margin one or two reproductive pouches where the buds (and in two genera the flowers) develop. Reproduction is primarily vegetative; a single plant may multiply to several million in one season. It has been

estimated that compact floating mats of *Spirodela* contain from 100,000 to 200,000 plants per square yard of water, and mats of *Lemna* 300,000 to 800,000 plants, while those of *Wolffia* may have 1,000,000 to 2,000,000 plants per square yard.

It is generally accepted that the Lemnaceae represent a group derived from the Araceae and that the genera exhibit a reduction and simplification series from *Spirodela* to *Lemna* to *Wolffiella* and *Wolffia*. Lawalrée, however, considered the Lemnaceae to be related to the Helobiales with a close affinity to the Najadaceae.

The frond of the Lemnaceae has been interpreted as a stem functioning as a leaf, as a modified leaf, and as a structure partly foliar and partly axial. Arber compared the structure of *Pistia* with that of *Spirodela* and considered the lemaceous frond to be axial at the base and foliar at the distal region. She interpreted the distal part of the frond as a "petiolar phyllode," and considered the pockets of *Spirodela* on the lower side as being formed by "wings of the leaf-sheath, terminating in two minute ligular flaps" and on the upper side by the axis. A somewhat different point of view was expressed by Brooks who interpreted the plant body of *Spirodela* as a single sympodial branch bearing a prophyllum, a leaf, and a bract and terminating in an inflorescence, all somewhat reduced and fused to each other.

In the fall, modified fronds or "bulblets" (turions) are produced which sink to the bottom of the water where they overwinter, rise again in the spring, and begin to grow. These bulblets may also be produced during other unfavorable growth periods.

The flowers of *Spirodela* and *Lemna* are enclosed in a membranaceous spathe within the reproductive pouch. This spathe is absent in *Wolffia* and *Wolffiella*. The flowers of a single plant mature at different times. When two staminate flowers and a carpellate flower are produced by the plant the sequence of their maturation is basipetal: the distal stamen matures first, then the carpel, and finally the second stamen. This difference in the time of the maturation of the flowers doubtless promotes cross pollination. Apparently pollination may result from direct contact of the flowers as the plants float and also by the agency of insects and other small aquatic animals which are associated with these plants. The pollen grains are spherical, monocolpate and generally have spiny projections on the exine. These grains show some characters in common with certain types of the Araceae, while they are less similar to those of the Najadaceae.

The ovule is bitegmic and the inner integument forms the operculum, which persists, resembling a stopper at the micropylar end of the seed. The endosperm is cellular and forms a chalazal haustorial process, the "caecum." The monocotyledonous embryo has a short suspensor and, in some genera, lacks a radicle.

These genera have been the subject of numerous laboratory experiments dealing with the physiology of flowering and the effects of minerals, light, temperature and other factors on growth and development. Very few physiological races have been found to be present within the Lemnaceae. The small number of races has been interpreted to be a result of the mor-

phological specialization and antiquity of the Lemnaceae, their extreme reduction, and their ability to reproduce vegetatively.

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KEY TO THE GENERA OF LEMNACEAE

- A. Plant with 2 marginal reproductive pouches; segments with 1-many roots; inflorescence of 2 staminate and 1 carpellate flower surrounded by a membranaceous spathe.

- B. Fronds with 2 or more roots; conspicuously 5–18 nerved. 1. *Spirodela*.
 B. Fronds bearing a single root; obscurely 1–3 nerved. 2. *Lemna*.
 A. Plant with a single marginal reproductive pouch; segments rootless; inflorescence of 1 staminate and 1 carpellate flower without a spathe.
 C. Frond elongate, thin; stipe-attachment on one side of the reproductive pouch. 3. *Wolffiella*.
 C. Frond ellipsoid or ovoid, thick; stipe-attachment within reproductive pouch (not evident). 4. *Wolffia*.

1. *Spirodela* Schleiden, *Linnaea* 13: 391. 1839.

Plants solitary or in groups of 2–5. Frond round or obovate, thick, purple beneath and green above with 5–18 palmately arranged nerves radiating from the node (centrum). Roots 2–16 to each frond. Each frond with 2 marginal reproductive pouches at the basal region. Inflorescence of 1 carpellate and 2 (rarely 3) staminate flowers, inclosed within a membranaceous spathe. Stamens 2-locular, dehiscing longitudinally. Gynoecium with a 1-locular ovary and 1 campylotropous or 2 anatropous ovules. Utricle with winged margins. TYPE SPECIES: *S. polyrhiza* (L.) Schleid. (Name from Greek, *speira*, a cord, and *delos*, evident, alluding to the conspicuous roots.)

A genus of three species, represented throughout our area by *S. polyrhiza* ($2n = 40$) in aquatic habitats. While *Spirodela* is one of the most abundant and widely distributed of the Lemnaceae it seldom occurs in pure stands but is usually found growing in association with species of *Lemna* and *Wolffia*. *Spirodela oligorrhiza* (Kurtz) Hegelm. has been reported from two collections in Missouri and may possibly be found to occur in our area. It has oblong or narrowly obovate fronds with only four to six nerves and two or three (rarely more) roots.

Spirodela, the least reduced of the Lemnaceae, frequently has been compared to *Pistia*, of the Araceae.

Jacobs, in a morphological study of *Spirodela polyrhiza*, interpreted the lower flap of the reproductive pouch as "bracts which were derived by phylogenetic reduction from leaves." The plant was considered to be a "greatly reduced type of rosette in which the vertical axis has been reduced to three highly compacted nodes." Brooks has shown that the flowers of the plant are always produced in the larger, usually left-hand reproductive pouch, while the smaller, right-hand reproductive pouch produces only vegetative buds. This led him to interpret the right-hand pouch as being formed by the prophyllum and the basal part of the foliage leaf, and the left-hand, flowering pouch by the bract and foliage leaf. Occasional plants may be found, however, in which this arrangement is reversed.

The embryo sac was described by Brooks as being of the "Polygonum" (normal) type. This is the same type found in *Pistia* but differs from the other known types in the Lemnaceae, all of which are bisporic and of the "Allium" type. However, in contrast to *Pistia*, which forms four megaspores, three of which disintegrate, *Spirodela* forms two megaspores and one dyad cell; the dyad and one megaspore degenerate. The mature ovule is

campylotropous when only one is present in the ovary; when two are present they are almost completely anatropous.

In addition to its possession of numerous roots, *Spirodela* differs from the other genera of the Lemnaceae by the presence of vascular tissue in the roots, the formation of two ovules in the ovary (*L. gibba* L. is described as having as many as 7 ovules), and by the "Polygonum" type of development of the embryo sac. Brooks reports the presence of a root in the embryo of *Spirodela*, but this needs confirmation, since *Lemna* has recently been shown not to form one during its development within the seed.

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2. *Lemna* Linnaeus, Sp. Pl. 2: 970. 1753; Gen. Pl. ed. 5. 417. 1754.

Fronds solitary or in groups of 2-5, each frond with 1-3 nerves and a single root without vascular tissue. Marginal reproductive pouches 2, of unequal size, at the basal region of each frond, the flowers, when produced, always appearing in the smaller pouch, the vegetative buds in both. Inflorescence of 1 carpellate and 2 staminate flowers surrounded by a membranaceous spathe. Anther 2-loculed, dehiscing transversely. Gynoecium with a 1-loculed ovary and 1 campylotropous ovule. Utricle ovoid and smooth. TYPE SPECIES: *L. minor* L. (Name from Greek, *lemna*, an aquatic plant, possibly *Callitriche*, mentioned by Theophrastus.) — DUCKWEED.

A genus of about ten species, five of which occur within our area. By far the most common is *Lemna minor* L. ($2n = 40, 42$), which frequently forms dense covers over quiet waters. *Lemna trisulca* L. ($2n = 44$), although less conspicuous because it floats beneath the surface of the water, occurs almost as frequently as *L. minor*. Three other species known from our area are *L. valdiviana* Phil., *L. minima* Phil., and *L. perpusilla* Torr.

Several of the species of *Lemna* have been used extensively in physiological studies, although *L. minor* and *L. gibba* L. have been the subject of the greater number of the papers on the subject. (Reports of experiments on *L. major* Griff. refer to *Spirodela polyrhiza*.) Recently Kandler has been able to induce flowering in *Lemna gibba* ($2n = 64$); under controlled conditions it has a day-length requirement of 12–14 hours. (See also Hillman, 1959).

Lemna usually is described as having one to seven ovules in the ovary; Hegelmaier described *L. gibba* as possessing one to six. It appears that our species have only a single ovule per carpel, but a careful investigation of the various species should be made to determine this accurately.

During the development of the embryo sac most of the nucellus disappears, but a few cells persist as the nucellar or micropylar cap. The endosperm is cellular and has a chalazal haustorial outgrowth or "caecum." According to Maheshwari, no radicle is formed in the embryo. However, both Lawalrée and Brooks describe the development of a root in the embryo. Brooks has also shown that the embryo of *Lemna* has only one pouch, the vegetative pouch. These embryological characters of *Lemna* seem to agree much more closely with those of Araceae than with those of the Helobiales, which differ in the nature of their endosperm, the absence of a caecum, and in the absence of a nucellar or micropylar cap.

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3. *Wolffiella* Hegelmaier, Bot. Jahrb. 21: 303. 1895.

Fronds thin, linear-attenuate or curved, solitary or in groups of several cohering generations, forming a star-shaped colony, rootless, each with a single, triangular vegetative pouch at the base from which arise the daughter fronds; each frond held to its parents by means of a “stipe.” Flowering reproductive pouch developing on the upper surface of the frond to one side of the stipe, thus resulting in a tendency toward asymmetry of the frond. Vegetative fronds floating just beneath the surface of the water, but in flowering the inflorescence-bearing portion of the frond breaking the surface. Inflorescence proterogynous and consisting of a single stamen with a 2-loculed anther and a single carpel with one orthotropous ovule, without a spathe. Utricle spherical. TYPE SPECIES: *W. oblonga* (Phil.) Hegelm. (Name a diminutive of *Wolffia*.)

A genus of about five species, primarily of the New World. It is represented in our area by *Wolffiella floridana* (J. D. Sm.) Thompson, which is known in the area from Michigan and Ontario south to Louisiana, Texas, Florida, and Mexico, and by *W. lingulata* (Hegelm.) Hegelm., which has been reported from Louisiana.

The flowers of *Wolffiella* were first found and described in *W. oblonga* (Phil.) Hegelm., from Argentina, in 1935. In 1938, flowering plants of *W. lingulata* were discovered in California, and, in 1948, a report of the discovery of the flowers of *W. floridana* was published. The flowers of the three species are remarkably similar, and their resemblance to the flowers of *Wolffia* is also striking. The flowering plants of *Wolffiella floridana* are slightly shorter, but wider and thicker at the base, than the vegetative plants. Furthermore, individuals are separated from the colonies during flowering time. Stomata are found only on the emergent portion of the frond during flowering.

The carpellate flower of both *Wolffia* and *Wolffiella* matures before the staminate flower. The position of the inflorescence and the structure of the flowers of the two genera are alike in all essential features. Thus, the primary basis for maintaining *Wolffiella* as distinct from *Wolffia* is the position of the vegetative shoot axis with respect to the vegetative pouch. In *Wolffiella* the vegetative pouch is formed on one side of the stipe which

attaches it to the parent plant, while in *Wolffia* the stipe and the bud develop on the lower side of the pouch near the apex of the cavity. *Wolffia* tends to be bilaterally symmetrical, while *Wolffiella* tends to be asymmetrical. This vegetative difference is presumably a very fundamental one in the morphology of the two genera.

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4. *Wolffia* Horkel ex Schleiden, *Linnaea* 13: 389. 1839.

Fronds solitary or in pairs, globose or ellipsoid, without roots or veins. Frond with a single funnel-shaped, basal vegetative pouch from within which arise the young fronds, which soon become detached. Inflorescence of a single stamen with a 2-loculed anther and a single carpel containing 1 orthotropous ovule. Spathe absent. Utricle spherical and smooth. (*Horkelia* Reichb., 1830, not Cham. & Schlect., 1827; *Bruniera* Franch.; *Bruneria*, Small.) TYPE SPECIES: *W. Delilii* Schleid., not Kurtz. = *W. hyalina* (Delile) Hegel. (Name in honor of J. F. Wolff, 1788-1806, who wrote on *Lemna* in 1801.) — WATER-MEAL.

A genus of about 15 species, primarily of the tropics and subtropics, represented in our area by *W. columbiana* Karst., *W. punctata* Griseb. ($2n = ca. 40$), and *W. papulifera* C. H. Thompson. These are the smallest and simplest (by reduction) of the flowering plants, resembling small dots or grains floating in the water. Because of their minute size and the rarity of flowers these plants have been a subject of considerable botanical controversy. Dried, pressed plants are usually so shriveled and distorted that their natural shape is impossible to determine, with consequent taxonomic difficulties. The dots which are described for *W. punctata*, for instance, are apparent in dried material, but not in living plants. It has been recommended that plants of *Wolffia* be preserved in formalin-acetic alcohol and placed in flattened glass ampules which can be mounted on herbarium sheets.

Recent studies of the flowers and embryo development indicate that the anther is two- rather than one-loculed as has been previously reported. In *Wolffia* the carpel matures before the stamen, and pollination probably is effected through the agency of wind or rain.

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