

THE ZANNICHELLIACEAE IN THE SOUTHEASTERN UNITED STATES¹ROBERT R. HAYNES² AND LAURITZ B. HOLM-NIELSEN³

ZANNICHELLIACEAE Dumortier, Anal. Fam. Pl. 59, 61. 1829, "Zanichelliaceae," nom. cons.

A small family of annual [or perennial], glabrous, monoecious, aquatic herbs, growing entirely submersed in fresh or brackish waters, rooting at the lower nodes. Roots unbranched, 1–7 at a node, nonseptate. Stems slender, dimorphic, the lower often stoloniferous, the upper erect and leafy, without teeth along internodes; turions and tubers absent. Leaves alternate, opposite, or pseudo-whorled, scalelike, without vascular tissue or foliaceous, linear, 1- [or rarely 3-] veined, subterete, sessile, with basal sheaths, the sheath adnate to or free from the blade, the infravaginal scales membranaceous. Inflorescences axillary, with 2 [to several] imperfect flowers. Staminate flowers short-pedicellate, perianth absent [rarely minute and 3-lobed], androecium consisting of 1 stamen, the connective extended into a blunt appendage, the anthers (2–)4(–8)[–12]-loculate, dehiscing by longitudinal slits; pollen inaperturate, globose, often in a gelatinous matrix. Carpellate flowers short-pedicellate, often enclosed in a membranaceous, spathe-like envelope; perianth absent [or a small cuplike sheath; or segments 3, separate]; carpels (1–)4 or 5(–8), separate, short-stipitate, 1-loculate; ovule solitary, bitegmic, pendulous, anatropous, placentation apical; style short [long], stigma enlarged, $\pm$ funnel shaped [feathery or peltate]. Fruit drupaceous, with a membranaceous exocarp, fleshy mesocarp, and stony endocarp. Seed solitary; embryo curved; endosperm helobial in development, absent in mature seed. (Zannichelliaceae *sensu stricto*, excluding genera that

¹Prepared for the Generic Flora of the Southeastern United States, a long-term project currently made possible through the support of National Science Foundation grants BSR-8415769 (Carroll E. Wood, Jr., principal investigator) and BSR-8415637 (Norton G. Miller, principal investigator). The 117th in the series, this paper follows the format established in the first one (Jour. Arnold Arb. 39: 296–346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of a family or genus in brackets []. References that we have not verified are marked with an asterisk.

We are indebted to Drs. Wood and Miller for their advice, suggestions, and help with the literature during the preparation of the manuscript.

The illustration was drawn by Karen Stoutsenberger at the Arnold Arboretum under Haynes's direction from material he collected in Alabama.

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are better placed in the Potamogetonaceae, Cymodoceaceae, and Posidoniaceae.) TYPE GENUS: *Zannichellia* L.

Four genera and ten to twelve species; represented in the southeastern United States by one species of *Zannichellia*, a nearly cosmopolitan genus consisting of four or five species. *Zannichellia* differs from *Pseudalthenia* Nakai, *Althenia* Thouars, and *Lepilaena* Drumm. ex Harvey in lacking a creeping rhizome, in having mostly four- or five-carpellate flowers (rarely fewer than four-carpellate), and in having warty fruits. Tomlinson & Posluszny indicated that no clear lines of evolution are recognizable in the family.

Pseudalthenia Aschersoniana (Graebner) Den Hartog (*Vleisia Aschersoniana* (Graebner) Tomlinson & Posluszny) is an endemic of the Cape Southwest region of South Africa, where it grows in vleis (depressions in which water collects during the wet season). The species is unique in the family in having leaves with a submarginal vascular strand and transverse strands continuous with the midvein. The staminate flower lacks a perianth, is eight-sporangiate, and has a pair of vestigial appendages on the connective. The carpellate flower is always unicarpellate and produces a papillate fruit, with the papillae not arranged in lines.

Althenia, with two species in northern Africa, the west-central Mediterranean region, and the Atlantic coasts of Morocco, Spain, Portugal, and France, is characterized by peltate stigmas and styles about 3 mm long.

Lepilaena consists of three species endemic to Australia and a fourth occurring in New Zealand and Australia. Diagnostic features of the genus include two- or twelve-sporangiate staminate flowers and carpellate flowers with short styles and funnel-shaped or feathery stigmas.

Cronquist placed the Zannichelliaceae in the Najadales, whereas Dahlgren, Dahlgren & Clifford, and Thorne (1976, 1983) put the family in the Zosterales. The Zannichelliaceae as here interpreted have been combined variously with members of the Potamogetonaceae, Najadaceae, Zosteraceae, and Cymodoceaceae under the names Zannichelliaceae (Taylor), Zosteraceae (Fernald), Najadaceae (Gleason & Cronquist), and Potamogetonaceae (Ascherson & Graebner). Miki considered *Najas* L. to be closely related to the Zannichelliaceae, especially *Althenia*, less so to *Zannichellia*.

Pollen is mostly dispersed as single grains but is occasionally contained in a gelatinous matrix (as in *Zannichellia palustris*). The grains are spherical, nonaperturate or rarely monosulcoidate, binucleate, and sparsely and unevenly verrucate. Adjacent verrucae are often in contact. The endexine, according to Pettitt & Jermy (see generic references), is very indistinct, and the intine is thin.

The family is known to have secondary compounds, including flavonoid bisulphates, flavones (Gornall *et al.*), and apiose (Van Beusekom).

Cytological data are incomplete for the family, but the reported chromosome numbers include $2n = 12, 24, 28, 32$, and 36 ($x = 6$ or 8).

The Zannichelliaceae are all aquatic herbs and grow clonally in shallow, generally brackish coastal waters or in inland freshwater lakes.

The roots are all adventitious and unbranched; they arise from nodes of the

creeping and sympodially branched rhizomes or from those of the erect and richly branched leafy stems. The leaves are linear, sheathing at the base, and with rounded, pointed, truncate, or toothed apices. Pairs of inconspicuous, filiform squamules (nonvasculated scales) occur laterally at the nodes.

The unbranched roots have a thin-walled epidermis of large cells and conspicuous root-hairs that arise from short trichoblasts. The outer cortex is compacted into an exodermis of one or two layers of narrow, slightly lignified, thick-walled cells, while the inner part is lacunose, the endodermis uniseriate and thin walled, and the stele narrow, surrounding a metaxylem lacuna.

The stems are nearly without mechanical tissue, and the epidermis, cortex, endodermis, and stele resemble those of the roots. Vascular bundles supporting lateral organs diverge directly from the stele, and there is no cortical vascular system.

The leaf blade is glabrous, with the epidermis uniform, thin walled, and chlorophyllous. The epidermis mostly lacks stomata, although they do occur in the apices of leaf blades of certain species of *Zannichellia*. The mesophyll is lacunose either throughout or only on each side of the midvein. The vascular system is reduced to a single median vascular bundle surrounded by a uniseriate endodermis. The leaf blades have submarginal fibers.

The plants are monoecious, with complex, terminal, sympodial inflorescences of reduced, specialized flowers subtended by reduced bractlike leaves. Each inflorescence usually has one staminate flower terminating the first-order meristem and one to several carpellate flowers terminal on branches of higher orders.

The staminate flowers are short-pedicellate, reduced to one stamen, and with or without a short, three-lobed, scalelike perianth. The anther consists of one or more bisporangiate units, sometimes with a short connective appendage; dehiscence is longitudinal. The tapetum is of the periplasmodial type, microsporogenesis is of the successive type, and the pollen grains are three-celled at dispersal.

The carpellate flowers are short-pedicellate and have one to eight separate, short-stalked, slightly asymmetric carpels. The carpels are surrounded by a biseriate perianth that consists of a closed tubelike structure in *Zannichellia* and *Pseudalthenia*, and of three separate segments in *Althenia* and *Lepilaena*, with the segments opposite the carpels. The styles are more or less elongate and are terminated by enlarged peltate or funnel-shaped stigmas that have more or less lacerate margins or are occasionally feather shaped. Each of the stipitate carpels contains a solitary, pendulous, anatropous, bitegmic ovule. The embryo sac is of the *Allium* type, with embryo formation of the caryophyllad type. Endosperm is of the helobial type but is absent in the mature seed.

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1. **Zannichellia** Linnaeus, Sp. Pl. 2: 969. 1753; Gen. Pl. ed. 5. 416. 1754.

Annual or rarely perennial, monoecious plants of fresh or brackish waters. Roots single or in pairs at the nodes. Leaves in pseudowhorls of 3 but usually also alternate and opposite on same plant, entire, stipulate, mostly less than 1 mm wide, 1 veined. Inflorescence usually consisting of 2 flowers, 1 staminate and 1 carpellate. Flowers without a perianth. Staminate flowers with a single usually 4-loculate [2–8-loculate] stamen, the connective prolonged into a blunt appendage. Carpellate flowers with (1–)4 or 5(–8) carpels surrounded basally by a membranaceous envelope, the style less than 1 mm long, the stigma asymmetrically funnel shaped. Fruit endocarp often coarsely papillose. TYPE SPECIES: *Z. palustris* L., the only species of the genus in *Species Plantarum*. (Named after Gian Girolamo Zannichelli, 1662–1729, a Venetian apothecary and botanist.)—HORNED PONDWEED.

A nearly cosmopolitan genus of perhaps five species, represented in the southeastern United States only by *Zannichellia palustris* L. The genus has been variously interpreted as consisting of one highly variable species (e.g., Dandy) or as many as five species (e.g., Holm-Nielsen & Haynes; Van Vierssen, 1982a). We recognize the genus to comprise at least one near-cosmopolitan species (*Z. palustris*) and four others of restricted distribution, of which three (*Z. major* Boenn., *Z. pedunculata* Reichb., and *Z. peltata* Bertol.) are in northern Europe and one (*Z. andina* Holm-Nielsen & Haynes) is in the high Andes of South America.

Zannichellia has an unusual pollination system in which the anther of the staminate flower arches over the funnel-shaped stigmas of the carpellate flower. Pollen transfer is entirely underwater: it is released from the anther in a gelatinous mass and falls directly into the stigma. Such a system limits outcrossing but is valuable for a submersed annual aquatic since pollination is essentially assured.

Reported chromosome numbers for *Zannichellia* are $n = 12$, $2n = 24$, 28,

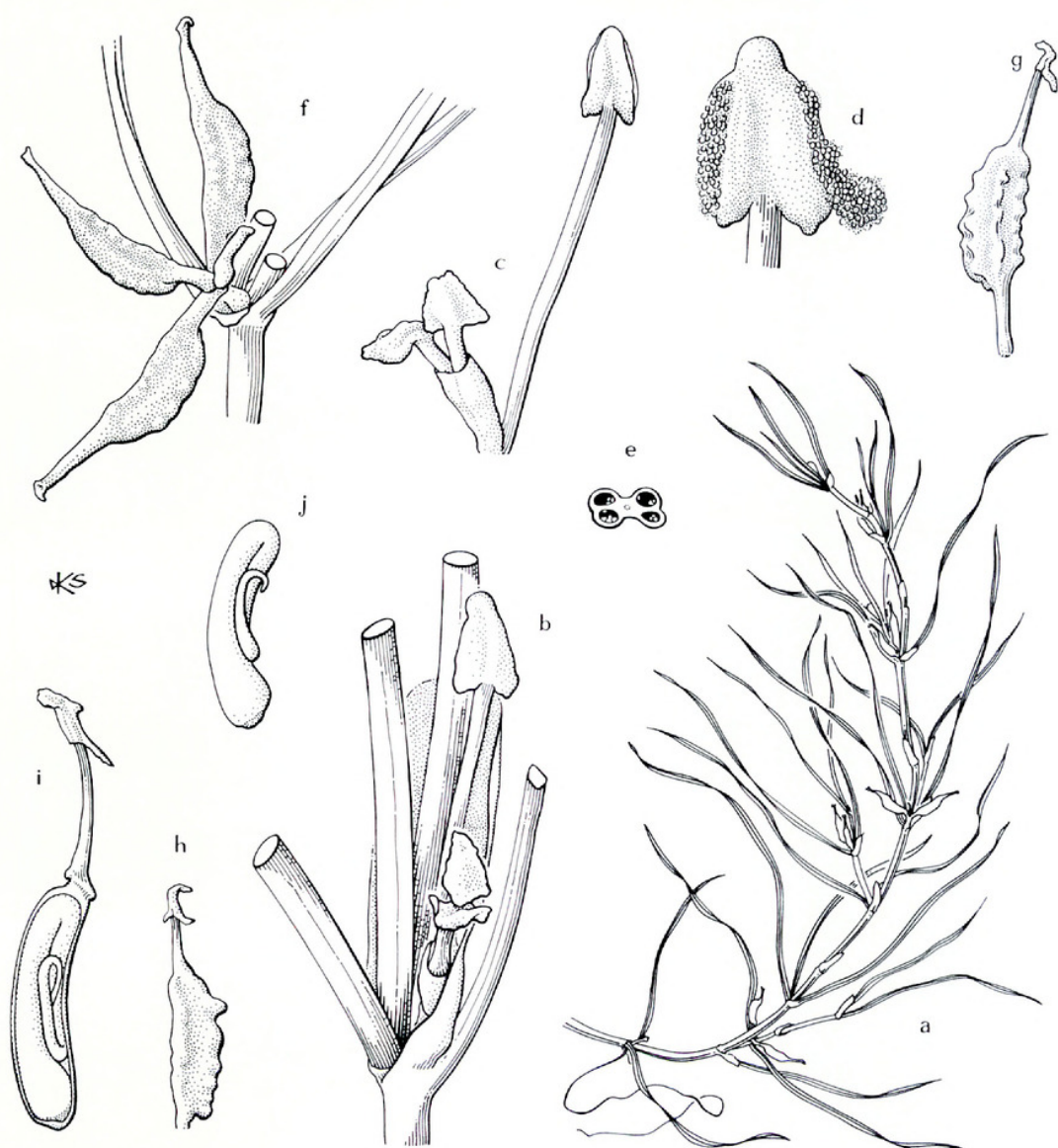


FIGURE 1. *Zannichellia*. a-j, *Z. palustris*: a, branch of plant with fruit, $\times 1$; b, node with staminate and carpellate flowers, base of leaf (to right), portion of stem, and base of 2 branches, $\times 12$; c, staminate flower (a single stamen) and carpellate flower with 2 carpels, $\times 12$ —note expanded stigmas; d, anther shedding pollen, $\times 25$; e, cross section of anther before dehiscence, showing 4 locules, a few pollen grains indicated diagrammatically, the vascular bundle dotted, $\times 25$; f, nearly mature fruits of a 4-carpellate flower, 1 carpel undeveloped, $\times 6$; g, h, endocarps of 2 fruits, with tip of style still covered by outer part of pericarp, $\times 6$; i, fruit, the ovary in longitudinal section to show embryo, $\times 12$; j, embryo, $\times 12$.

32, 36 for *Z. palustris* (Bolkhovskikh *et al.*), $2n = 36$ for *Z. pedunculata* and $2n = 12, 36$ for *Z. peltata* (Van Vierssen & Van Wijk).

Daghlian did not report the Zannichelliaceae in the fossil record, although Katz and colleagues listed three species from the Quaternary in the Soviet Union. Miller reported *Zannichellia* from lateglacial deposits in western New

York, and Pierce & Tiffney have reports from the postglacial Holocene in Connecticut.

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<https://doi.org/10.5962/bhl.part.11934>.

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