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

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URTICACEAE A. L. de Jussieu, Gen. Pl. 400. 1789, "Urticae," nom. cons.
(NETTLE FAMILY)

Taprooted and rhizomatous annual and perennial herbs [or shrubs, rarely large trees], with watery [rarely milky] sap, generally provided with a vesture of some kind, sometimes with stinging hairs. Stems often fluted, mostly nonsucculent, but sometimes fleshy or translucent. Leaves alternate or opposite, sometimes anisophyllous, simple, usually petiolate, blades mostly ovate to lanceolate [rarely lobed]; punctiform, linear [or stellate] cystoliths borne in cells of the adaxial (upper) or abaxial (lower) epidermis or both; margins serrate, dentate, entire, or rarely incised, venation pinnate or palmate; stipules present or absent, if present, either paired at the petiole base or intrapetiolar and partly to entirely connate, fugacious or not. Plants monoecious, dioecious, or polygamous; flowers imperfect, rarely perfect; inflorescences basically cymose, axillary, bracteate, the flowers arranged in loose to tight clusters, or inflorescence sometimes racemose or paniculate [or flowers aggregated on a flat or campanulate to figlike receptacle]; if monoecious, staminate and carpellate flowers in different inflorescences or intermingled. Staminate flowers small, greenish or whitish, rarely otherwise, with short pedicels or sessile, caducous after shedding pollen; tepals 4, 5 [6], equal, valvate, or partly fused

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before anthesis [sometimes appendaged]; stamens of equal number and opposite the perianth segments [or a single stamen and a subtending involucre]; filaments initially inflexed, slightly flattened, pollen dispersal explosive as the stamens free themselves from the partially surrounding tepals; anthers 2-locular at anthesis, medifixed, thin walled, reniform, oriented with the concave sides inward, dehiscence longitudinal; pollen with 2, 3, or 4[–6] pores, ± suboblate, exine stratification obscure, equatorial diameter ca. 15 μ; rudimentary gynoecium prominent, conical, obovoid, globose, or cup-like, hyaline or not, glabrous [or woolly]. Carpellate flowers minute, sessile or subsessile, greenish or reddish; tepals 3 or 4 or perianth ± tubular [or rarely absent]; staminodia present or absent; gynoecium unicarpellate; style 1, present or absent, if present, apical at anthesis and rarely becoming laterally displaced in fruit; stigma penicillate, linear, or style prolonged into a filiform stigma; ovule 1, basal, usually orthotropous, sometimes hemianatropous, bitegmic, crassinucellar. Perfect flowers with 4 basally fused tepals and 4 opposite stamens, gynoecium with a penicillate or linear stigma. Fruits mostly laterally compressed or ovoid, symmetrical to asymmetrical achenes, rarely drupaceous, generally either loosely or tightly surrounded by the accrescent perianth [which becomes fleshy in some], achene and perianth sometimes dispersed as a unit; style and stigma persistent or not. Seed 1, seed coats thin, brownish, membranaceous; endosperm thin, fleshy or mealy, completely surrounding the embryo; embryo straight, radicle pointing toward the ovary apex and shorter to longer than the orbicular to ovate, sometimes emarginate, cotyledons. Embryo sac development of the Polygonum type; embryogeny of the Asterad type. TYPE GENUS: *Urtica* L.

A natural family of about 40 genera and 800 species (ca. 1900 according to Hutchinson), largely confined to tropical and subtropical latitudes of both New and Old Worlds, rarer in temperate regions, and represented by only a few species still farther poleward. Of the six genera native to the United States (excluding Hawaii with four additional genera, two of which, *Neraudia* Gaud., with milky sap, and *Touchardia* Gaud., are endemic), five have one or more species in our region. Closely related to *Urtica*, but differing in the continuous, appressed perianth of the carpellate flower, *Hesperocnide* Torr. occurs in California (*H. tenella* Torr.) and Hawaii (*H. sandwicensis* Wedd.; however, see W. Hillebrand, Fl. Hawaii. Is. 408. 1888, who regards the Hawaiian plants as probably unintentionally introduced from California at an early date).

The family has traditionally been divided into five tribes. Four have representatives in North America. Floral morphology in the exclusively Old World tribe Forskohleeae Gaud. is somewhat atypical for the family as a whole, in that staminate flowers are comprised of a single stamen and a subtending perianth (or involucre), while carpellate flowers may either have a perianth or lack one altogether. The other tribes are distinguished mainly on the nature of the perianth in both staminate and carpellate flowers. Only members of the Urticeae have stinging hairs. As has been

recently suggested, *Cecropia* L., *Coussapoa* Aubl., and *Musanga* C. Sm. ex R. Br., which generally have been placed in subfam. Conocephaloideae of the Moraceae, are better treated as a separate tribe of the Urticaceae on account of their basal, orthotropous ovules (cf. Chew, Corner). The oldest tribal name available for these genera would seem to be Cecropieae Gaud.

Wind pollination is characteristic of the family, and the staminate flowers are accordingly reduced and of a relatively simple form. However, the presence of vestigial nectaries, at least in flowers of *Urtica dioica*, is suggested by Stäger's work. Pollen is hurled into the air by an abrupt and often simultaneous extension of the inflexed filaments, which prior to anthesis are held in place by the tepals. Associated with the extension is a sudden bursting of the anther-sacs that may be related to the short longitudinal slit observed in the wall of the young anther (Eames), although the precise mechanism is not known. The uniseriate anther-sac walls of the Urticaceae seem to represent the endpoint of a reduction series in which epidermal and fibrous layers have been successively lost. Intermediate stages in the series are encountered in other members of the Urticales.

Anatomically, the family has been studied from several standpoints. Laticiferous canals have been found in stems and roots (sometimes both) in certain species of *Dendrocnide* Miq. and *Urera* Gaud., both members of tribe Urticeae. Mucilage cells similar to those occurring in the Tiliaceae are abundant in the stems and leaves of many genera. Bechtel's identification of aborted vascular bundles in gynoecia of *Laportea canadensis* and *Urtica gracilis* suggests that the unicarpellate ovary, which is usually cited as a family character, may have been derived through abortion of a second (and anterior) carpel. He has also presented evidence for a shift in ovule position from either the side or apex of the locule to its base. In *Boehmeria cylindrica* the vascular bundle supplying the ovule ascends the carpel wall for a short distance and later reverses direction to enter the ovule at the base of the ovary. Anatomical study of the tubular perianth of this species shows it to be comprised of two segments. Development of zygomorphic flowers (weakly expressed in *Urtica*, but obvious in *Laportea*) is a notable specialization of floral structure.

The occurrence of cystoliths (generally mineralized with calcium carbonate) supported by a cellulose stalk in enlarged epidermal cells of leaves and sometimes elsewhere is a characteristic feature of the Urticaceae, although similar ones are known in other families of the Urticales and in the Acanthaceae. Spherical, bacilliform, and fusiform (curved or straight) types are most common; stellate or vermiform shapes occur rarely. Cystoliths are difficult to see in living plants but are apparent in dried specimens as elevated markins.[2] Ashed leaf fragments containing cystoliths, calcium oxalate crystals, and calcified or silicified cell walls, have been studied

[2] Sreemadhavan *et al.* (Taxon 17: 17, 18. 1968) have introduced the term "furuncle" (*adj.* furunculate) to describe elevations in dried material arising from either cystoliths or raphides.

microscopically, either embedded in celloidin to preserve their original orientation and arrangement in the leaf (a spodogram), or as simple mounts of the ash residue. Cystoliths may be diagnostically useful at various taxonomic levels. There is a general correspondence between cystolith shape and tribes of the Urticaceae (e.g., members of the Elatostemeae Gaud. for the most part have linear cystoliths), and different species within a genus may have markings of distinctive shape.

Chromosome counts reported for 17 genera are $2n = 14, 16, 20, 22, 24, 26, 28, 32, 42, 48, 52, 60$, and 76–78.

The Urticaceae, Moraceae, Cannabaceae, and Ulmaceae (and perhaps the Barbeyaceae) are generally taken to comprise the Urticales whose derivation from the Magnoliales through the Hamamelidales is postulated by many workers. A relationship between the Urticaceae and certain families of the Malvales has been suggested also.

Apart from ramie (*Boehmeria nivea*), a fairly important fiber plant in the Orient, the family is of little importance economically. Several species of *Pilea* and *Pellionia* Gaud. are grown as ornamentals, and *Soleirolia soleirolii* (Req.) Dandy (*Helxine soleirolii* Req.), baby tears, $2n = 20$, a native of Corsica and Sardinia, is a favored houseplant.

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KEY TO THE GENERA OF THE URTICACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *monoecious, dioecious, and polygamous annual or perennial herbs, with or without stinging hairs; leaves stipulate or exstipulate, mostly opposite, but sometimes alternate, always with cystoliths; inflorescences cymose, axillary; flowers either staminate or carpellate, rarely perfect; staminate flowers with 4 or 5 tepals and an equal number of opposite stamens, rudimentary gynoecium present; perianth or carpellate flowers accrescent, either tubular or of 3 or 4 separate, equal or unequal tepals, staminodia rarely present; perfect flowers with 4 equal, mostly fused tepals, perianth accrescent; gynoecium unicarpellate, ovule one, basal, generally orthotropous; style one or absent, stigma generally*

penicillate or linear; fruits mostly achenes (rarely drupaceous), loosely to tightly surrounded by the persistent perianth or not.

A. Plants with stinging hairs; perianth of carpellate flowers at fruiting stage comprised of four separate tepals, 1 pair large, the other small.
  B. Leaves opposite; style absent, stigma apical, penicillate; achene erect, symmetrical, nonstipitate; pedicel supporting mature fruit short and wingless. ..... 1. *Urtica.*
  B. Leaves alternate; style and stigma awl-shaped, at first apical but displaced to a lateral position during fruit maturation; achene deflexed, asymmetrical, stipitate; pedicel supporting mature fruit long and bearing lateral wings. ..... 2. *Laportea.*

A. Plants without stinging hairs, otherwise pubescent or not; perianth of carpellate flowers at fruiting stage either tubular or of three separate tepals.
  C. Perianth of carpellate flowers with 3 equal or 1 hooded and 2 non-hooded tepals; staminodia present, inflexed beneath the maturing ovary. ..... 3. *Pilea.*
  C. Perianth of carpellate flowers either continuous or comprised of 4 mostly fused segments; staminodia absent.
    D. Perianth of carpellate flowers (perfect flowers absent) continuous, tightly covering the mature fruit; style apical and flexed near the tip, stigma linear; plants generally tall, fibrous perennials, stem nonsucculent; stipules or stipule scars present. .... 4. *Boehmeria.*[3]
    D. Perianth of carpellate and perfect flowers accrescent, segments mostly fused; style short or absent, stigma penicillate; plants mostly delicate annuals, stems watery and usually translucent; stipules absent. ..... 5. *Parietaria.*

Tribe URTICEAE [Urereae Gaud.]

1. **Urtica** Linnaeus, Sp. Pl. 2: 983. 1753; Gen. Pl. ed. 5. 423. 1754.

Tall, erect or sometimes ascending, fibrous annual or perennial herbs of diverse habitats, including thickets, bottomlands, damp forests, roadsides, shell middens, other waste places, and sometimes fields. Roots in annual species fibrous but usually with a short taproot, or, in perennials, with a horizontal rootstock bearing adventitious roots and aërial branches. Stems generally fluted, mostly hollow, greenish or sometimes purple or red, in certain species bearing numerous stinging hairs on short [or long] pedestals, particularly at nodes. Leaves simple [rarely deeply incised], petiolate, opposite, blade mostly ovate or lanceolate, margins serrate, often with stinging hairs on both upper and lower surfaces; punctiform, rarely linear cystoliths visible on upper surfaces of dried leaves; stipules lanceolate, generally paired at the petiole base, membranaceous, green [or brown], sometimes ciliate, free [or connate], usually persistent. Plants monoecious or dioecious; inflorescences bracteate, basically cymose, flowers organized into lax racemes or aggregated into loose [or tight] clusters that originate from axils of stipules and leaves, in some species zones of stamin-

[3] *Pouzolzia zeylanica* (L.) J. Benn. (tribe Boehmerieae) from Asia, collected once as a weed in Seminole County, Florida, would key out here. For its separation from other members of the family see footnote 5.

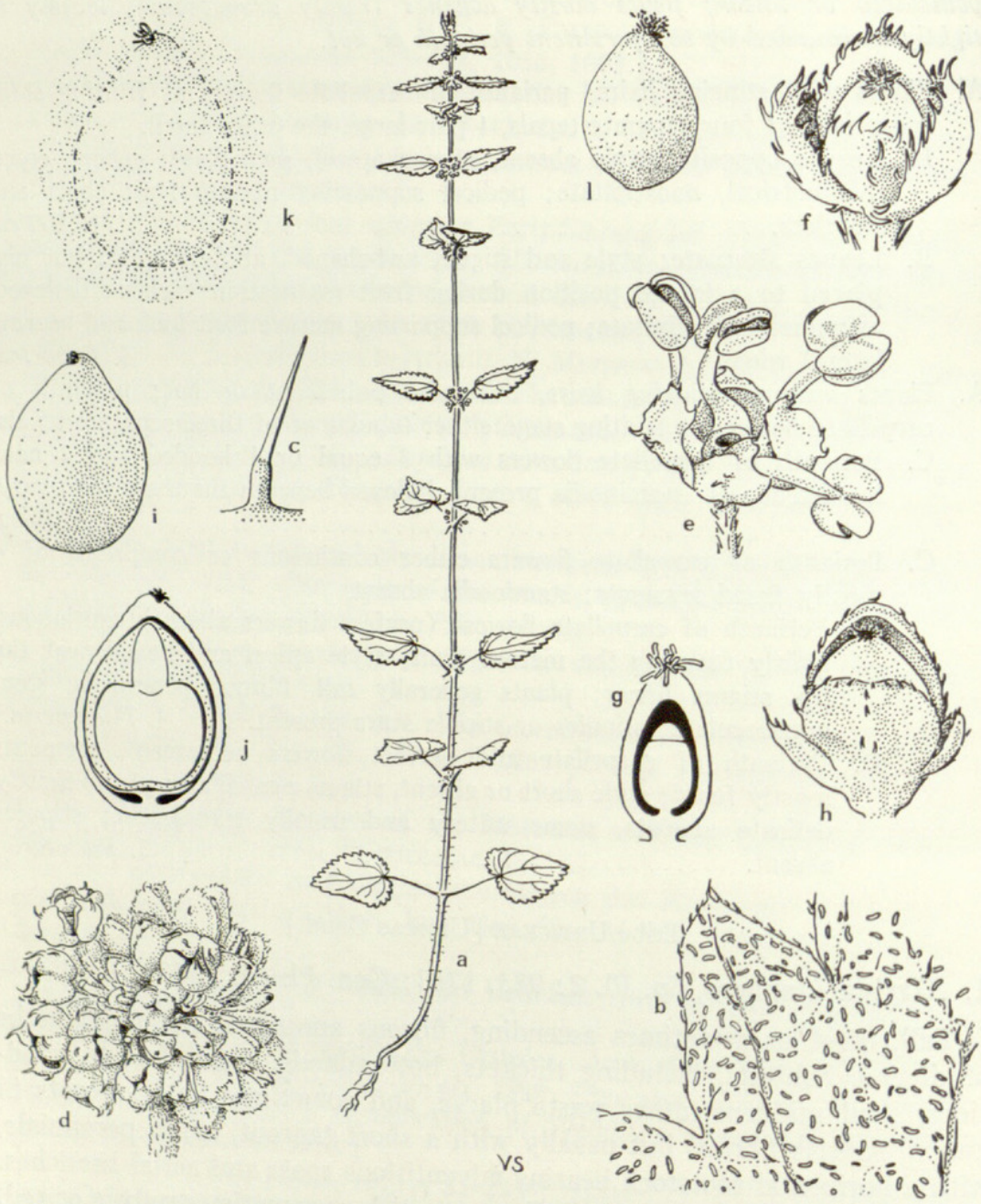

FIGURE 1. **Urtica.** a–k, *U. chamaedryoides*: a, habit of young plant, × ½; b, portion of adaxial leaf surface with cystoliths, × 12; c, stinging hair from petiole, × 12; d, inflorescence with staminate flowers and young fruits, × 6; e, post-anthesin staminate flower, × 12; f, carpellate flower, × 40; g, longitudinal section of ovary with orthotropous ovule, × 50; h, achene and accrescent perianth, × 15; i, mature achene, × 20; j, mature achene in longitudinal section showing embryo, endosperm stippled, × 20; k, wet achene, mucilage halo dotted, × 20. l, *U. dioica*: mature achene, × 20.

ate and carpellate flowers alternating along the axis. Staminate flowers small, pedicellate, greenish or yellowish, with 4 equal, saccate, pubescent tepals sometimes bearing stinging hairs; stamens 4; rudimentary gynoecium small, cuplike. Carpellate flowers minute, subsessile, greenish; tepals 4, decussate, ± equal, pubescent; style absent; stigma apical, central, penicillate; ovule orthotropous, micropyle formed from the inner integu-

ment. Fruit a thin-walled, compressed, ovoid achene, loosely inclosed by enlarged inner tepals, outer tepals remaining small; apical stigmatic tuft persistent or not. Seed coats thin; endosperm fleshy, forming a thin layer around the embryo, some species with a chalazal endosperm haustorium; embryo straight, radicle generally shorter than the ± orbicular, emarginate cotyledons. LECTOTYPE SPECIES: *U. dioica* L.; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. 1: 634. 1913. (Classical Latin name, from *urere*, to burn, surely in reference to the stinging hairs.) — NETTLE.

A genus of about 45 species, mostly indigenous to temperate parts of the Northern and Southern Hemispheres, but a few species in the New and Old World tropics, usually in the mountains at middle and upper elevations. *Urtica dioica* L. and *U. urens* L. are exceptionally widespread weeds. In North America *U. gracilis* Ait. extends northward through the Boreal Forest to the edge of the subarctic (also in central Alaska).

The genus is badly in need of monographic study, especially in North America where regional floristic treatments of the perennial species vary dramatically. About 10 species of *Urtica* generally have been recognized on this continent north of Mexico, and of these, seven are perennials. *Urtica californica* Greene, *U. holosericea* Nutt., and *U. Lyallii* S. Wats. occur in western North America; *U. serra* Blume is a species of the Southwest; *U. dioica*, *U. procera* Muhl. ex Willd., and *U. viridis* Rydb. are generally northern and mostly restricted to the central and eastern sections (strictly dioecious plants of *U. dioica* may be entirely introduced from Europe); and *U. gracilis* is northern and transcontinental. *Urtica dioica*, *U. gracilis* (sensu Small, Man. Southeast. Fl. 433. 1933), and *U. procera* (sensu Fernald) have ranges that include a portion of the southeastern United States. The latter two species are often treated as *U. dioica* var. *procera* (Muhl. ex Willd.) Wedd. (Hermann; however, see Hitchcock for a different interpretation). *Urtica dioica* in the broad sense seems clearly to be a circumpolar species complex. The temperate Asian representative of the complex is *U. angustifolia* Fisch. ex Hornem.

Two annual nettles occur in the southeastern United States. The Eurasian *Urtica urens* is sporadically naturalized in Florida, South Carolina, and probably elsewhere in the region. The native *U. chamaedryoides* Pursh, generally a plant of flood plains and rich woods often over limestone, occurs from central Florida west to Texas and Mexico. It is native northward to South Carolina, West Virginia, and Missouri, and occasionally is found as an adventive beyond these states. Disjunct populations have been reported from Argentina. A third annual, *U. gracilenta* Greene, occurs in Arizona, New Mexico, and Texas.

Cystoliths are prominent in the leaves of many *Urtica* species, and both punctate and bacilliform types are present. The effervescence of those in *U. chamaedryoides* and *U. urens* when dilute hydrochloric acid is added indicates that the cystoliths are probably mineralized with calcium carbonate. Specimens of *U. chamaedryoides* generally have bacilliform cystoliths, although a few collections from Texas have been seen with punctiform markings.

Stinging hairs are present or absent on leaves, stems, inflorescence axes, and tepals, and occur on both annual and perennial species. Each hair consists of a single, long, narrow, tapering stinging cell with a sac-like base embedded in a multicellular emergence. The hair is closed at the tip by a small bulb that, when pressure is applied, breaks off along a predetermined line of fracture producing an extremely sharp, bevelled point. Hair cells are reported to be both silicified and calcified. Upon contact with the skin, the hair punctures the surface and compression of the base forces the contained fluid into the wound. Contact with nettles results in a three-phase reaction involving formation of a wheal (associated with itching), reddening, and pain. The chemical basis of these responses has not been fully determined but experimental data obtained from the hairs of *Urtica urens* indicate that in this species histamine and acetylcholine are responsible for the itching and burning sensations, respectively.

Base chromosome numbers for the counted species are $x = 11$, 12, and 13. Diverse chromosome numbers appear to be documented in *Urtica dioica, sensu lato*, $2n = 22$, 52 (*U. kioviensis* Rogowitch = *U. dioica*?), 48, 52 (Löve & Löve), and 52, 76–78 (*U. platyphylla* Wedd. = *U. dioica*?); diploid and tetraploid races occur in *U. urens*, $2n = 24$, 26, and 52. Sex chromosomes tentatively identified in *U. dioica* by Meurman have not been confirmed subsequently (Westergaard).

Little has been written about the dispersal of *Urtica* species. According to Ridley, the achene and perianth (which surrounds the fruit to maturity) may be transported as a unit by passing animals. In some species the stiff, curved, downward-pointing hairs that cover outer tepal surfaces provide the means of attachment. Achenes from the annuals *U. chamaedryoides* and *U. urens* become mucilaginous upon wetting, but those of the perennial nettles *U. dioica*, *U. gracilis*, and *U. procera*, in contrast, do not develop mucilage when placed in water (Miller). Annual and perennial species from other parts of the world should be examined to document this difference further.

The genus is of little importance economically. Young leaves and shoots of *Urtica* species are sometimes made into soup, or, after boiling, are used as a substitute for spinach by the Scots and Irish and in parts of continental Europe. Nettles find similar use in the Canadian Maritime Provinces. In Great Britain, until about 1860, the strong phloem fiber from *U. dioica* was made into cloth. This species was extensively used by the Germans during both World Wars as raw material for certain chemical, food, paper, and textile industries.

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2. **Laportea** Gaudichaud-Beaupré in Freycinet, Voy. Monde Bot. 498. 1830 ('1826'), nom. cons.

Erect, perennial herbs [or shrubs] of moist forests, stream banks, and ravines. Roots tuberous, plants spreading by rhizomes. Aërial branches fluted, covered with stinging hairs. Leaves alternate, petiolate, ovate, serrate [dentate, or shallowly incised], puberulent or not, generally with stinging hairs; cystoliths punctiform (calcium carbonate?), restricted to upper leaf surface; stipules intrapetiolar, bifid toward the apex, fugacious. Plants monoecious; inflorescences axillary, lax bracteate cymose panicles; carpellate and staminate flowers in separate inflorescences [rarely together], the carpellate inflorescences borne higher on the axis than the staminate. Staminate flowers small, greenish, pedicellate [or sessile] with 5 [4] saccate, longitudinally ridged tepals; stamens 5 [4]; rudimentary gynoecium large, obovoid, hyaline. Carpellate flowers small, zygomorphic, borne on a thick pedicel that develops lateral [or dorsi-ventral] wings as the fruit matures; tepals 4, free, the inner pair lateral, green, the outer pair smaller, ciliate, sometimes reddish, the abaxial tepal becoming hood-like and covering part of the pedicel apex; ovary situated on a short disk; style apical, stigma elongate, subulate [sometimes trifid], covered with short hairs; ovule hemi-anatropous, funiculus lengthening during maturation of fruit so that the embryo comes to occupy a horizontal position with respect to the base of the carpel. Fruit a laterally compressed, stipitate achene, partly covered by enlarged lateral tepals, adaxial tepal small,

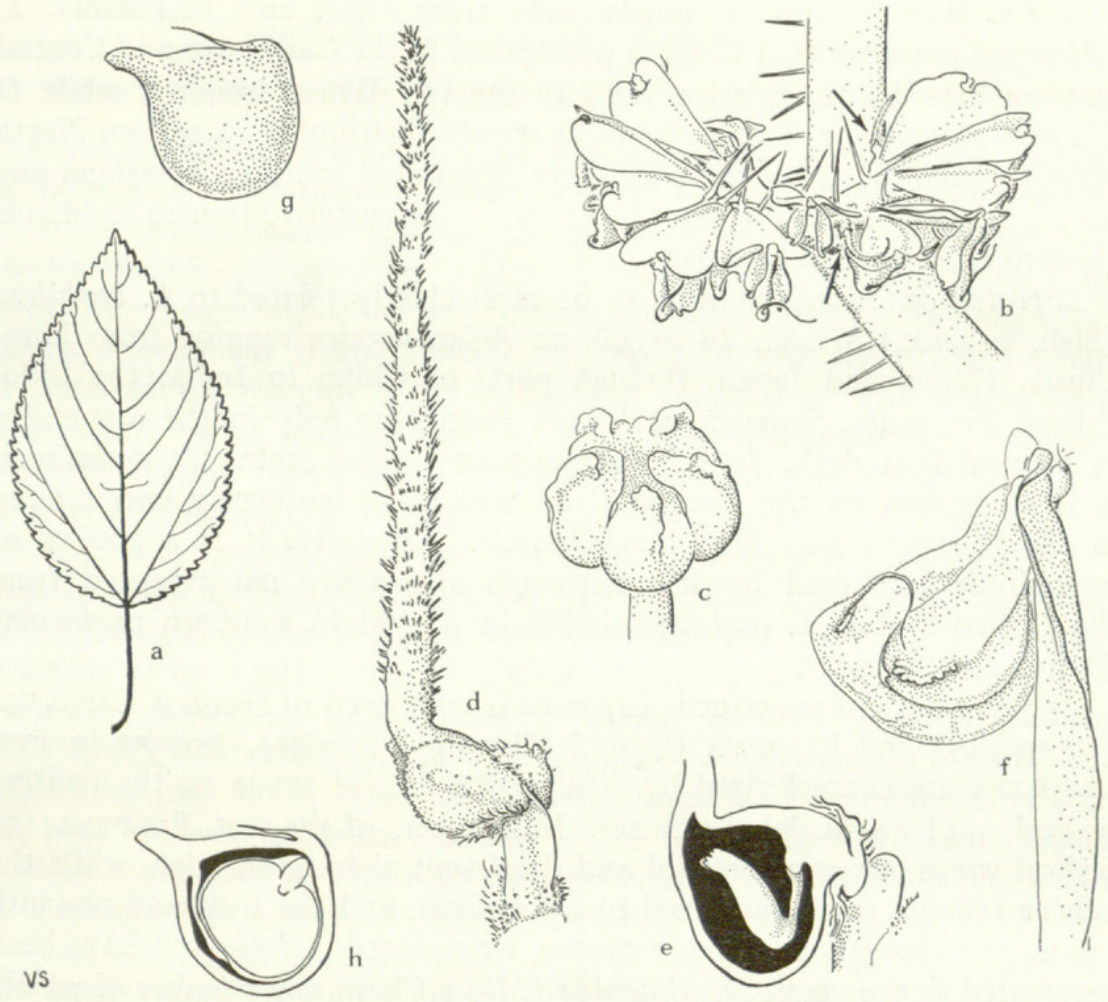

FIGURE 2. **Laportea.** a–h, *L. canadensis*: a, leaf, adaxial surface, × ¼; b, portion of carpellate inflorescence, cymules containing both flowers (at arrows) and fruits, × 3; c, staminate flower bud, × 30; d, carpellate flower, × 25; e, young fruit in longitudinal section showing position of ovule shortly after fertilization, stigma mostly removed, × 25; f, enlarged perianth with mature achene and winged pedicel, × 10; g, mature achene, × 8; h, mature achene in longitudinal section showing embryo, endosperm white, × 8.

mostly hidden by the mature fruit, abaxial tepal only slightly larger than at anthesis, base of style persistent and displaced laterally by unequal development of the achene and embryo. Seed coats thin; endosperm mealy, sparse; cotyledons large, orbicular, radicle short. (*Urticastrum* Heister ex Fabr., nom. rejic.) LECTOTYPE SPECIES: *L. canadensis* (L.) Wedd.; see Hitchcock & Greene, Prop. Brit. Bot. Int. Bot. Congr. Cambridge, England, 1930. 101. 1929. (Named for François L. de Laporte, a 19th century French entomologist.) — WOOD-NETTLE.

A predominantly Old World genus of 22 species, 12 restricted to either the Malagasy Republic (5 species endemic) or Africa south of the Sahara (Chew, 1969). Other Laporteas occur in Asia (4 species), Polynesia and/or Malesia (2 species), and widely throughout the Old World tropics (1 species). Of those in the Western Hemisphere, *Laportea* (*Fleurya*) *cun-*

eata (A. Rich.) Chew, is known only from Cuba and Hispaniola, *L.* (*Fleurya*) *aestuans* (L.) Chew is widespread in the Caribbean and Central and northern South America (also in the Old World tropics), while *L.* (*Laportea*) *canadensis* (L.) Wedd. is widely distributed in eastern North America from Nova Scotia to southern Manitoba, south to Louisiana and northern Florida. Disjunct stations occur in the eastern Mexican highlands (Nuevo León and Tamaulipas).

Laportea canadensis appears to be most closely related to *L. bulbifera* (Sieb. & Zucc.) Wedd., $2n = 60$, an Asian species ranging from Manchuria, Korea, and Japan, through parts of China to India, the Indochinese Peninsula, Sumatra, and Java (occurring only in the mountains in tropical latitudes). In the southeastern United States, *L. canadensis* is less common on the Coastal Plain and more frequently encountered in the Piedmont and Mountain districts. Typically, it is a species of mesophytic hardwood forests. Although apparently not reported from the United States, *L. aestuans* should be sought in southern peninsular Florida and the Keys.

As presently circumscribed, *Laportea* is composed of sections LAPORTEA (10 species) and FLEURYA (Gaud.) Chew (12 species). Species in sect. LAPORTEA are characterized by symmetrical lateral wings on the fruiting pedicel and by articulated achenes. In members of the sect. FLEURYA, the pedicel wings are asymmetrical and dorsi-ventral in orientation, while the achene remains firmly attached to the pedicel, and the fruit and perianth are dispersed together. Woody species, long placed in *Laportea*, have been segregated as the genus *Dendrocnide* (Miq.) Chew, one member of which, *D. excelsa* (Wedd.) Chew, an endemic of Queensland and New South Wales, Australia, attains a height of 35 m.

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Tribe ELATOSTEMEAE Gaud. [Procrideae Wedd.]

3. **Pilea** Lindley, Collect. Bot. *ad pl. 4.* 1821, nom. cons.[4]

Erect, ascending, or repent [sometimes scandent or suffrutescent] annual or perennial herbs of rich, moist forests, swampy ground, and weedy habitats. Roots mostly fibrous, but plants often with a short taproot; repent species rooting from nodes. Stems translucent and watery, or fleshy and succulent, or neither. Leaves opposite, equal or anisophyllous; blades ± orbicular, ovate, obovate, or lanceolate, with one strong midvein or triplinerved, margins entire or serrate, glabrous or with sparse, long nonstinging hairs; petioles short or long; cystoliths prominent, linear or fusiform [rarely punctiform], restricted to the adaxial epidermis or occurring in enlarged cells of both the adaxial and abaxial surfaces; stipules intrapetiolar, connate, persistent or not. Plants monoecious [or dioecious]; inflorescences axillary, bracteate, lax or tight compound cymes, carpellate and staminate flowers borne at the same node, but generally on separate branches of the inflorescence. Staminate flowers small, white or sometimes purplish, pedicellate, ± compressed laterally in bud; perianth crowned with short protuberances in bud, the segments initially mostly connate, but separating into 4 (3) tepals at anthesis, segments remaining fused near the base following anthesis; stamens 4 (3); rudimentary gynoecium small, conical. Carpellate flowers with short pedicels, zygomorphic or not; tepals 3, identical, linear, and all slightly expanded at the apex, or, 1 strongly hooded, and 2 identical, lanceolate, and nonhooded; staminodia 3, opposite the tepals, adaxially flexed during fruit maturation and ejecting the fruit from the perianth at maturity; stigma penicillate, mostly falling away after pollination; ovule orthotropous. Fruit a ± symmetrical, laterally compressed, light brown to black achene, surface smooth and mottled, or papillose, or covered with prominent bosses. Endosperm fleshy; cotyledons ovate, not emarginate. (*Adicea* Raf. ex Britton & Brown.[4]) TYPE SPECIES: *Pilea mucosa* Lindl.; see Collect. Bot. *ad pl. 4.* 1821, nom. illeg. = *P. microphylla* (L.) Liebm. (Name from Latin, *pileus*, a felt cap, in reference to the hooded tepal in the type species.) — RICHWEED, CLEARWEED.

A much ignored genus, primarily pantropical, with a few species in temperate parts of the Northern and Southern Hemispheres; absent from Europe, Australia, and New Zealand. *Pilea* is by far the largest genus of the Urticaceae, with over 600 species described, but the actual number probably considerably less than this. The American tropics, especially the Caribbean region, are rich in species. Killip records 112 species from northern and western South America; León & Alain report that of the 64 species occurring in Cuba, 51 are endemic. Four species are found in

[4] Conservation unnecessary because *Adicea* Raf. was not validly published until after 1821 and *Adike* Raf. dates from 1836 (see Taxon 8: 262. 1959). *Adicea* exists as a name only in several of Rafinesque's publications. Britton and Brown (Illus. Fl. No. U. S. 1: 533. 1896) were apparently the first to supply the missing generic description, although several botanists used *Adicea* in the mid-1800's.

eastern North America. The genus is not represented in the western half of this continent.

Weddell's two outdated treatments (1856, 1869; 136 and 159 spp. recognized, respectively), in which *Pilea* is artifically broken down into three sections and a number of lesser categories, mainly on the basis of leaf characteristics, are the only monographs of the entire genus. Killip has recognized 12 informal species-groups based similarly on vegetative traits. Our native species fall into two, perhaps more, natural categories according to the presence or absence of a hooded third tepal.

Section PILEA (*Integrifoliae* Wedd.), containing species with entire leaves, is represented in the Southeast by *Pilea microphylla* (L.) Liebm., artillery plant, $2n = 36$, and *P. herniarioides* (Sw.) Wedd., both restricted to the southern parts of our area but fairly widespread in the American tropics. The former, a plant of pinelands, forests, hammocks, and sometimes weedy places, has been found sporadically throughout Florida (in part escaped from cultivation) and may occur at climatically favorable places elsewhere in the Southeast. It is present in the Old World tropics, probably also as a garden escape, and is grown commonly in greenhouses in temperate regions. *Pilea herniarioides* is known from damp ground and hammocks in southern peninsular Florida and the Keys. It differs from the more fleshy and ascending *P. microphylla* in being repent and in having filiform stems and deltoid to ± orbicular leaves with petioles as long as or longer than the blades (vs. obovate or lanceolate leaves with short petioles). Specimens of *P. herniarioides* from Florida, the West Indies, and South America seem to include several elements, one of which approaches *P. microphylla*. The small, entire-leaved pileas are in need of further study, as a comparison of the descriptions of *P. herniarioides* in Killip (1939, 1960) and Fawcett and Rendle shows. Small (Man. Southeast. Fl. 434. 1933) lists a third member of the section, *P. serpyllifolia* (Poir.) Wedd., from southern Florida and coastal Louisiana, but specimens so-named by Small lack the ciliate leaves characteristic of the type (see Killip, 1939, pp. 479, 480) and appear to be only robust plants of *P. microphylla*.

Species in sect. HETEROPHYLLAE Wedd. have distinctly anisophyllous paired leaves. Both New and Old World members are cited by Weddell (1869), but anisophyllous species of *Pilea* are especially abundant in the American tropics.

Our other two species belong to sect. DENTATAE Wedd., members of which have neither entire nor anisophyllous leaf-pairs. *Pilea pumila* (L.) Gray (including var. *Deamii* (Lunell) Fern.), $2n = 16$, a plant of moist, shaded woods, occurs widely from New Brunswick to North Dakota, south to Texas, Louisiana, Mississippi, Alabama, Georgia, and northern Florida. The less frequently collected *P. fontana* (Lunell) Rydb., in contrast, usually grows in open, swampy or marshy habitats. Although perhaps of wider distribution, literature reports and specimens examined establish its presence from Prince Edward Island westward to North Dakota and south to Nebraska and Indiana in the Midwest, and to the Ridge and

Valley Province of Virginia, and along the Coastal Plain of North and South Carolina, southeastern Georgia, to northeastern Florida in the East. These species are of similar aspect and differ mainly in fruit characters. In *P. fontana* mature achenes (FIGURE 3, o) are black or dark brown, only slightly less broad than long, and often have a narrow, translucent edge and prominent low bosses that do not coincide with a color pattern, should one exist. Fruits of *P. pumila* (FIGURE 3, n) are much narrower, light brown in color, and have a contrasting mottling that appears only slightly raised in relation to the unmottled achene surface.

Pilea has a unique type of fruit dispersal in which the achene is forcefully ejected from the enlarged, but non-adhering, perianth by staminodia. This phenomenon has been investigated in two tropical species, *P. Spruceana* Wedd. (Mosebach) and *P. stipulosa* Miq. (Goebel) and should be studied in our native species as well. For example, the distance the achene is propelled from the parent plant is a critical yet unknown fact in our plants. The mechanism (Mosebach) involves the simultaneous build-up of tension in the three inflexed staminodia, a result both of their anatomy and their being restricted to the confined space beneath the developing fruit. The central cells of the staminodia are larger (to 560 μ long) than the cubical cells of the adaxial epidermis (90 μ) and the longer spindle-shaped abaxial epidermal cells (ca. 275 μ long). When intercell pressure reaches the critical point during the elongation phase of growth, the fruit breaks off the receptacle and is hurled out of the perianth as the staminodia pop outward. (See FIGURE 3, e, k-m.) An adhesive substance produced at the tips of the staminodia apparently helps to hold them under the fruit and prevents their premature extension.

Only a few chromosome counts (9 spp., $2n = 16$, 24, 36, 48, and 52) have been reported for the genus, and, with two exceptions, all for species occurring beyond our region.

At least five species, including *P. Cadierei* Gagnep. & Guillaumin, $2n = 48$, the aluminum plant, are cultivated as ornamentals.

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Under family references see BERNBECK, HEYWOOD, HOLM, KILLIP, LAKELA & CRAIGHEAD, MARTIN, MOSEBACH, RIDLEY, SATAKE, SAYEEDUD-DIN & SALAM, SHARMA, SOLEREDER, TARNAVSCHI *et al.*, THORNE (1954), WEDDELL (1856, 1869), and WERNER.

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FAWCETT, W., & A. B. RENDLE. Flora of Jamaica. Vol. 3. xxiv + 280 pp. *5 pls.* London. 1914. [42 spp. of *Pilea*, 60–81, including *P. herniarioides*, *P. microphylla*, 61–64, *pl. 1.*]

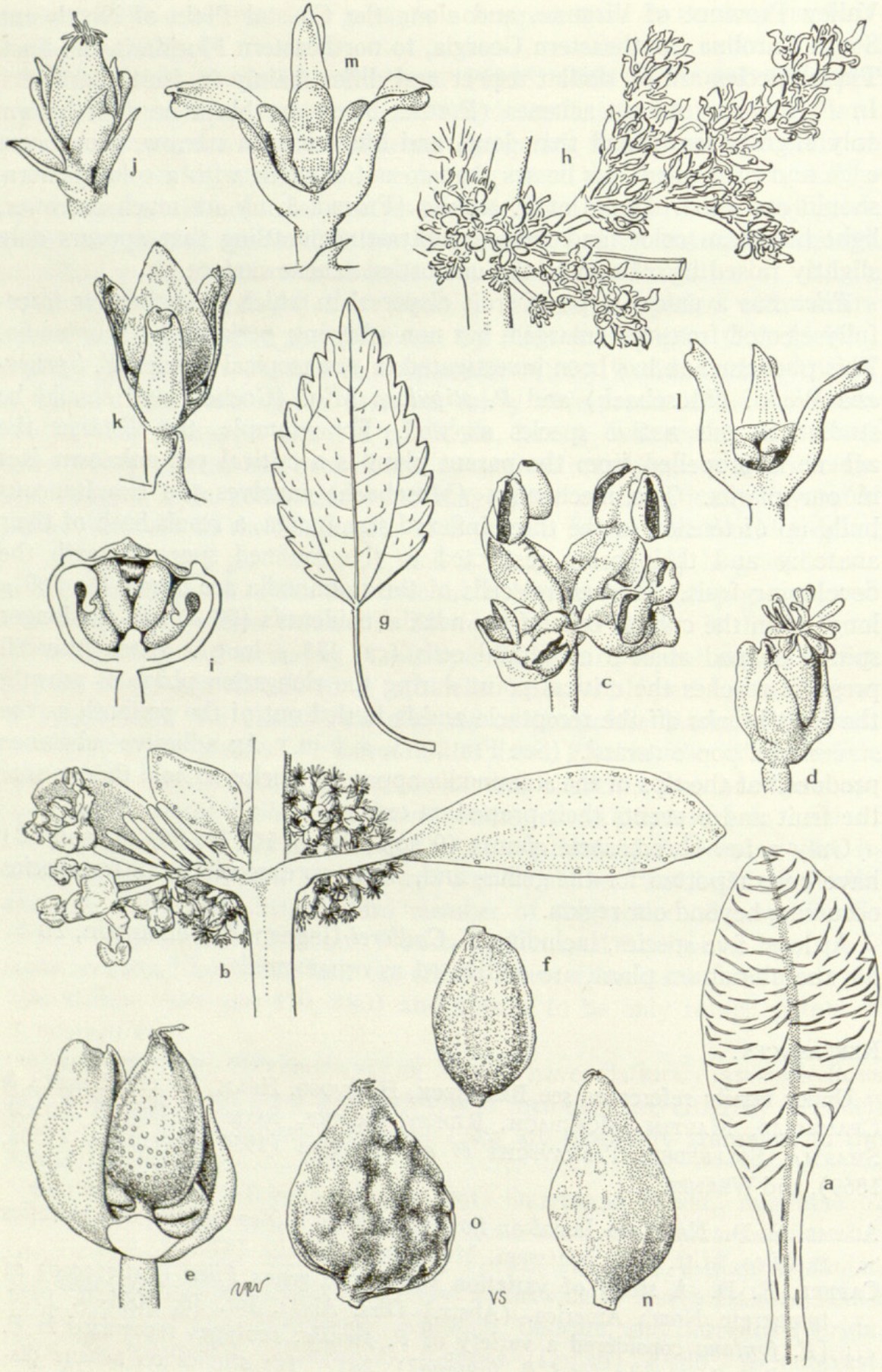

FIGURE 3. **Pilea.** a–f, *P. microphylla*: a, partially cleared leaf with cystoliths, midvein stippled, × 18; b, axillary staminate and carpellate inflorescences, leaves with inframarginal hydathodes, × 10; c, post-anthesin staminate flower, × 25; d, carpellate flower, × 40; e, nearly mature achene and enlarged perianth (one

FERNALD, M. L. Contr. Gray Herb. **113.** II. *Pilea* in eastern North America. Rhodora **38:** 169, 170. *pl. 413.* 1936. [*P. pumila* var. *Deamii.*]

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RADFORD, A. E., H. E. AHLES, & C. R. BELL. Manual of the vascular flora of the Carolinas. lxi + 1183 pp. Chapel Hill, North Carolina. 1968. [*P. fontana* in North and South Carolina, 395.]

Tribe BOEHMERIEAE Gaud.
Subtribe **Euboehmeriineae** Wedd.

4. **Boehmeria** Jacquin, Enum. Syst. Pl. Ins. Carib. 9. 1760.

Erect, fibrous, perennial herbs [or shrubs to small trees] of swamps, marshes, lake margins, stream banks, and, less frequently, drier situations. Roots fibrous, sometimes thick and fusiform; plants spreading by rhizomes. Stems weakly fluted, glabrous to densely pilose. Leaves decussate or alternate, if decussate, then sometimes alternate on branches, blades broadly ovate to narrowly elliptic, triplinerved, margins serrate or dentate [or shallowly incised], upper surface smooth to strongly scabrous with rigid, forward-pointing hairs, lower surface pilose to white tomentose; cystoliths punctiform, restricted to upper epidermis; stipules lanceolate, brown, usually caducous, and either paired at the petiole base, or intrapetiolar with the apex bifid. Plants monoecious [or dioecious]; inflorescences axillary and bracteate, either ± erect and spicate with carpellate and staminate flowers occurring mixed in remote to congested clusters borne along the main inflorescence axis, the individual staminate flowers surrounded by groups of carpellate flowers within one cluster, or, paniculate

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tepal removed), × 40; f, mature achene, × 40. g–n, *P. pumila*: g, leaf, adaxial surface of blade, × 1; h, axillary infructescence, staminate flowers represented only by pedicels, × 3; i, staminate flower bud in longitudinal section showing inflexed stamens and central, basal, rudimentary gynoecium, × 25; j, carpellate flower and two subtending bracts, × 40; k, nearly mature achene and enlarged perianth, × 15; l, carpellate flower before ejection of achene by staminodia (achene removed), × 15; m, carpellate flower after ejection of achene, × 15; n, mature achene, × 20. o, *P. fontana*: mature achene with bosses on surface, × 20.

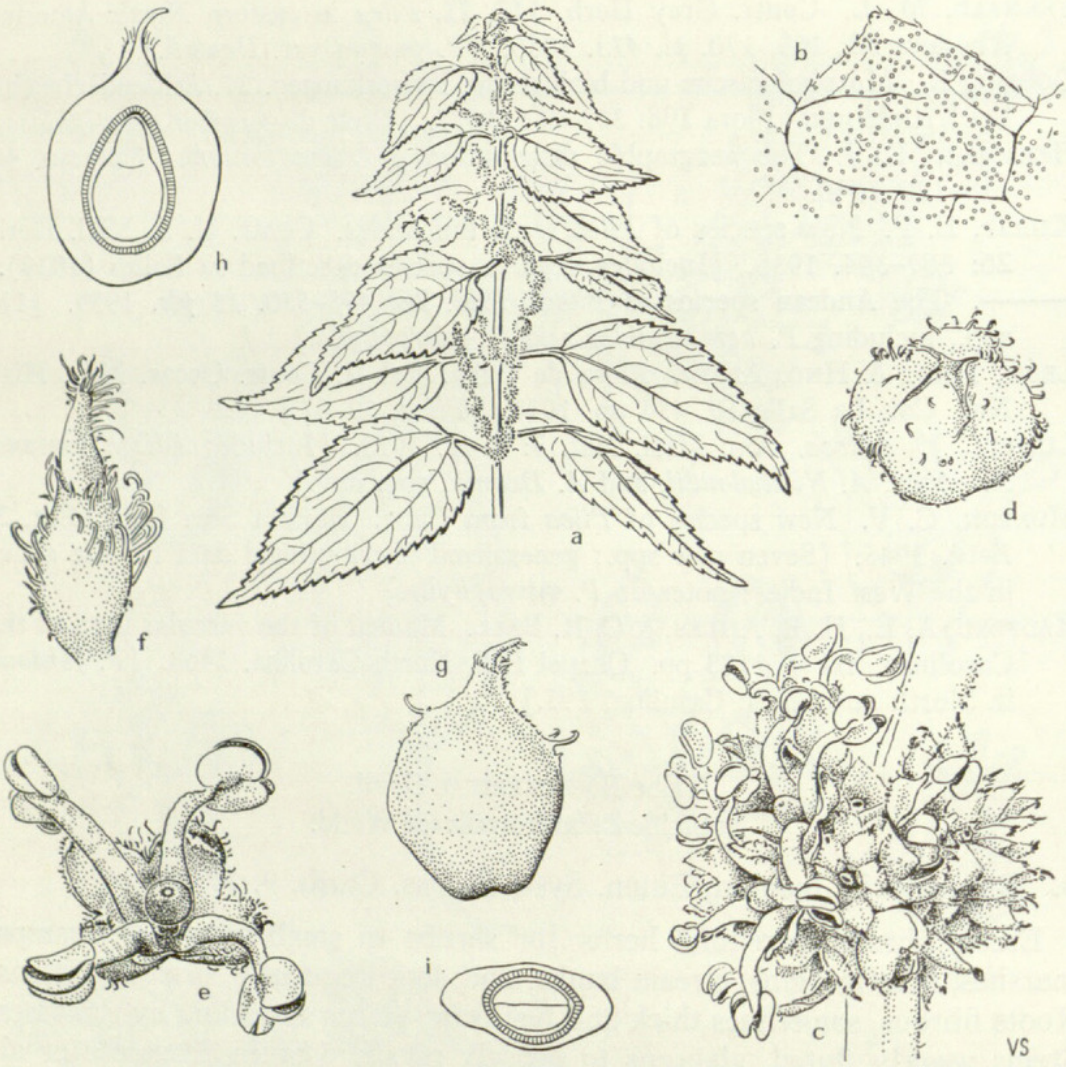

FIGURE 4. **Boehmeria.** a–i, *B. cylindrica*: a, plant apex with axillary inflorescences, × ½; b, cystoliths at edge of adaxial leaf surface, × 10; c, cluster of carpellate and staminate flowers from inflorescence, × 8; d, staminate flower bud showing valvate tepals, × 15; e, post-anthesin staminate flower, × 12; f, carpellate flower, × 40; g, mature fruit covered by persistent perianth, × 20; h, fruit in longitudinal section, endosperm white, endocarp hatched (semidiagrammatic), × 20; i, fruit in cross section, endosperm and endocarp as in *h* (semidiagrammatic), × 20.

and composed of either staminate or carpellate flowers, the staminate inflorescences borne lower on the axis than the carpellate and caducous soon after anthesis. Staminate flowers with short pedicels; tepals 4, valvate, abaxial surfaces bearing numerous hooked and straight hairs; stamens 4; rudimentary gynoecium globose, hyaline to brownish. Carpellate flowers red or brown, sessile; perianth continuous, appressed to the ovary and extending to the base of the style, ciliate or toothed at the apex and bearing hooked or unhooked hairs on the outer surface; ovary stipitate or not; style central, prolonged into a short or long filiform, linear stigma which is flexed near the apex and densely covered along one side with soft trichomes. Fruit either drupaceous and laterally compressed, with the endocarp hard and the outer layers fleshy and thin on two faces but thick

around the edge, or, a ± ovoid, hard-walled achene; in both cases the perianth and withered style persistent [perianth strongly inflated in some]. Endosperm fleshy, sparse; cotyledons ovate, longer than the radicle, not emarginate. (Including *Ramium* Kuntze.) TYPE SPECIES: *B. ramiflora* Jacq.; see Enum. Syst. Pl. Ins. Carib. 31. 1760; Select. Stirp. Am. Hist. 246, 247. *pl. 157*. 1763. (Named in honor of George Rudolph Boehmer, 1723–1803, professor of anatomy and botany at Wittenberg University, Saxony.) — FALSE NETTLE.

A genus of about 100 species, mostly confined to tropical and subtropical latitudes in both New and Old Worlds (poorly represented in Africa), but with species native also to temperate portions of the Northern and Southern Hemispheres; absent from Europe; Australia and New Zealand with one species each. Two species occur in the southeastern United States. *Boehmeria* (subg. TILOCNIDE) *nivea* (L.) Gaud. (*Ramium niveum* (L.) Kuntze), ramie, $2n = 22$, 28, and 42, a native of China, has been widely introduced in the tropics and subtropics as a source of fiber. It has been found as an escape in South Carolina, Florida, and parts of the Gulf Coastal Plain (also near Washington, D. C.), and may be naturalized in some of these areas. The native *B.* (subg. DURETIA) *cylindrica* (L.) Sw., bog-hemp, $2n = 28$, is readily distinguished from ramie by its glabrous to weakly pilose lower leaf surfaces (*vs.* densely white tomentose) and spicate inflorescences (*vs.* paniculate). *Boehmeria cylindrica* (including var. *Drummondiana* (Wedd.) Wedd., and probably *B. decurrens* Small described from specimens collected in northern Florida) ranges from southern Quebec and Ontario west to Minnesota, south to Florida (throughout) and across Nebraska, Kansas, and Oklahoma to Texas. It is known also from southeastern New Mexico and Arizona, Mexico (Coahuila and Tamaulipas to Morelos and Tabasco), Guatemala, Honduras, Costa Rica, Panamá, the Greater Antilles, Bermuda, Trinidad, and as a disjunct in southeastern Brazil, Uruguay, Argentina, and Paraguay.

In North America, *B. cylindrica* is extremely variable in petiole length, leaf blade shape, roughness of upper blade surface, and character of the inflorescence. Forms with rigid, strongly scabrous leaves and short petioles are sometimes separated as var. *Drummondiana*. Although apparently less frequent in the north, it is largely coextensive with var. *cylindrica* but seems to prefer more open habitats. Transplant studies would help to establish whether the variety is merely a sun-form, as has been suggested.

Subgenera were defined by Blume (Mus. Bot. Lugd. Bat. 2: 194–227. 1857) on the basis of a combination of vegetative, floral, and fruit characters, especially the form of the perianth surrounding the mature fruit. In a treatment of the Asiatic members of subg. DURETIA Blume, Satake proposed seven sections based on shape and pubescence of the perianth. The usefulness of this classification on a world-wide basis remains to be determined by monographic study.

Chromosome numbers for species investigated to date are $2n = 22$, 28, 42, and 52, with 28 and 42 the most frequently reported counts. Okabe

(1963) has found apomixis to be widespread in Japanese species of subg. DURETIA. Sixteen (84 per cent) of the nineteen species he investigated were triploids ($2n = 42$) which, upon embryological study, were found to reproduce through generative apospory. In this type of apomixis the megaspore mother cell does not undergo meiosis, but develops into an embryo sac containing diploid nuclei resulting from mitotic divisions of the mother cell nucleus. The egg cell subsequently gives rise to an embryo without fertilization. Since staminate flowers are rarely produced by most of the investigated species, pollination apparently is not required to stimulate embryo development, in contrast to certain other apomictic plants. The several species studied in subg. TILOCNIDE Blume (including *B. nivea*) were normal, sexually reproducing diploids ($2n = 28$). In Japan, where *Boehmeria* is regarded as a difficult genus, taxonomic treatments have not taken into account the occurrence of apomixis (cf. Satake, who recognized 28 species in subg. DURETIA, many of which are geographically restricted endemics, with Ohwi, who accepts only 10).

Hooked hairs on the outside of the fruiting perianth in *B. cylindrica* probably facilitate dispersal. The fleshy, drupaceous fruits of this species may also be eaten by birds.

The genus is of little economic importance except in China, Formosa, Japan, and the Philippines, where ramie or China grass is grown commercially. Among the several cultivated varieties, *B. nivea* var. *tenacissima* (Roxb.) Miq., rhea, is characterized by sparsely white tomentose to greenish lower surface of the leaves. Propagation is mainly by rhizome cuttings, and varieties high in fiber content have been selected. Ramie is the strongest plant fiber known. Individual fiber cells are exceptionally long (to 5.5 cm. and probably greater, according to Aldaba), and they are reported to absorb water and to dry more quickly than flax. Further, ramie is claimed to be nearly equal to silk in luster and brilliance. But in spite of its many qualities, ramie is not widely utilized because pure fibers are difficult to separate from abundant associated gums. Willimot gives the following uses for ramie: table and household linens, lace, furnishing and bedding textiles, filter cloths, fabric for rubber tires, sewing thread for leather goods, ropes, gas mantles, paper for bank notes, and packing material.

Before the introduction of cotton, ramie was the principal fiber plant in the Far East where its use dates back several millenia. It was introduced into the United States in 1855, but since then, crops have been raised mainly on an experimental basis, mostly at places on the Gulf and southern Atlantic coastal plains and in California. Only a few tons of fiber for commercial use were obtained between 1935 and 1943 from this region. Until better methods of fiber-preparation are devised, high labor costs will keep ramie a minor fiber plant in the United States.

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Tribe PARIETARIEAE Gaud.

5. **Parietaria** Linnaeus, Sp. Pl. 2: 1052. 1753; Gen. Pl. ed. 5. 471. 1754.

Erect, ascending, sometimes decumbent, often multi-stemmed, taprooted annual or perennial herbs [or subshrubs] of moist forests and shaded ground. Stems in annual species translucent, watery, sparsely to densely pubescent with soft, sometimes hooked hairs; stems usually somewhat woody in perennial species. Leaves petiolate, pinnately to ± palmately veined, opposite in seedlings, alternate in mature plants; blades lanceolate, ovate, or deltoid, generally pubescent, margins entire; cystoliths dense, punctiform [rarely otherwise], restricted to the upper leaf epidermis; stipules absent. Plants polygamous; inflorescences few-flowered axillary cymes, one cymule borne on each side of the petiole base, flowers subtended by 1 to 3 green, linear [or deltoid and somewhat foliar], often ciliate [and sometimes basally-fused] bracts, usually bearing cystoliths; basal (first opening) flower in each cymule often bisexual, others generally carpellate; staminate flowers also said to occur, but apparently rare or absent (?) in American species. Carpellate flowers sessile with 4 equal, pubescent tepals, fused toward the base, but free above; ovary short-stipitate or not, attached to a small disklike receptacle; style central, apical or slightly displaced from the ovary tip, short or long, stigma penicillate [or linear]; ovule orthotropous (?), micropyle formed by both integuments. Bisexual flowers apparently proterogynous; tepals 4, equal; stamens 4, anther sacs falling off after anthesis, but filaments persisting inside enlarged perianth; gynoecium as in carpellate flowers. Fruit a shiny, light to dark brown or black, hard-walled, symmetrical or slightly asymmetrical, ovoid achene, with or without a short stipe; style completely caducous or persisting as a small apical or subapical papilla; perianth accrescent and often becoming tubular, dry, brown, of a different shape and size in carpellate and bisexual flowers; achene and perianth apparently dispersed together. Endosperm white, abundant; radicle equal or often longer than the cotyledons. LECTOTYPE SPECIES: *P. officinalis* L.; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. 1: 637. 1913. (Name from Latin, *paries*, a wall, the habitat of the species first described.) — PELLITORY.

A genus of about 20 species in two subgenera, occurring mainly within temperate and subtropical latitudes, but occasionally also in the tropics, where often restricted to montane habitats. Subgenus PARIETARIA (subg.

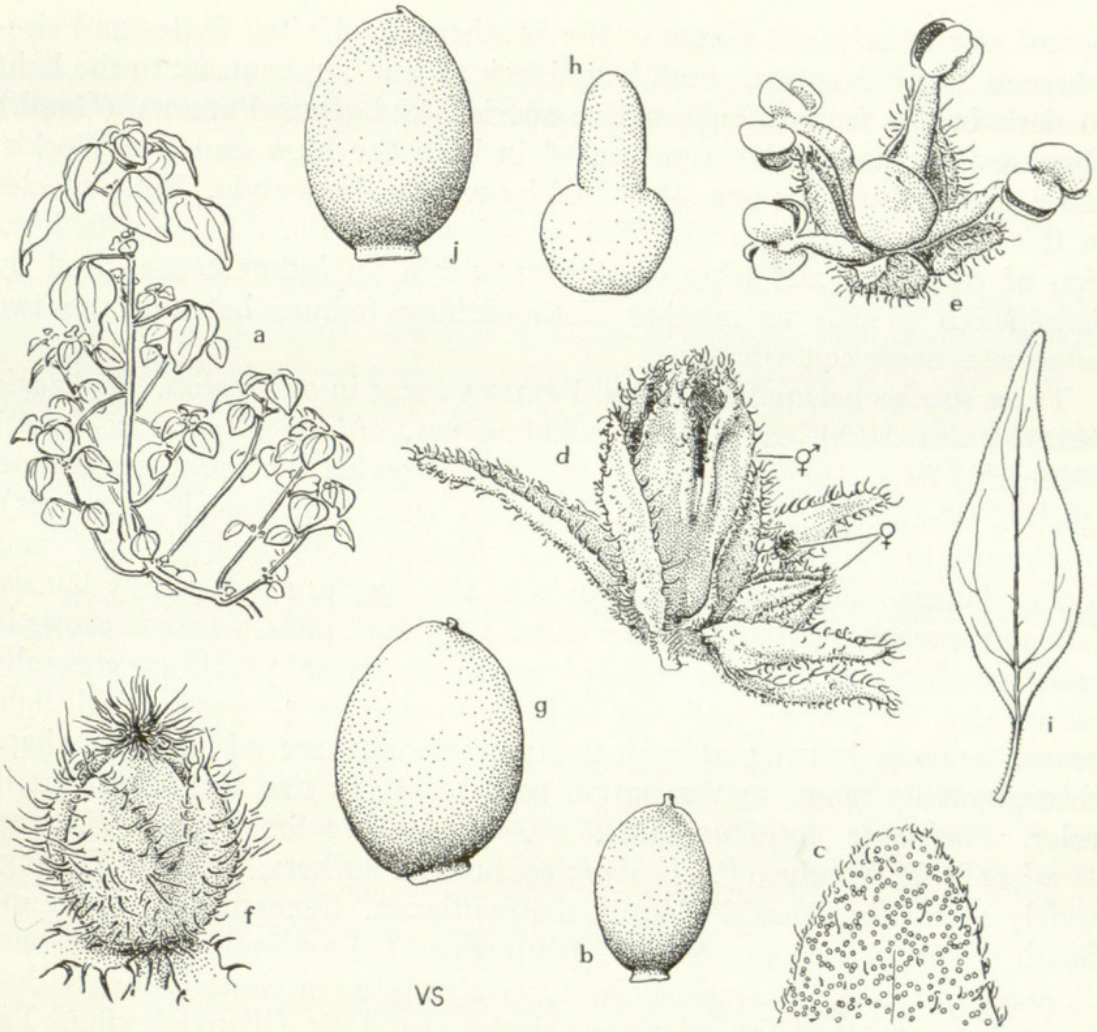

FIGURE 5. **Parietaria.** a, b, *P. floridana*: a, habit of young plant, × ½; b, achene (note flanged stipe), × 25. c–h, *P. praetermissa*: c, adaxial surface of leaf apex with punctiform cystoliths, × 10; d, inflorescence with perfect flower, the perianth accrescent, and two carpellate flowers, × 10; e, perfect flower just after pollen discharge (note absence of stigma, cf. f), × 12; f, carpellate flower, × 25; g, mature achene, × 25; h, embryo, × 25. i, j, *P. pensylvanica*: i, leaf, × 1; j, mature achene, × 25.

Euparietaria Komarov ex Jarmolenko) has long, filiform styles supporting a brush-like stigma, and is comprised mostly of perennials that occur from western Europe and northwestern Africa eastward to central Asia (although *Parietaria macrophylla* Robins. & Greenm., a species of southwestern Mexico, would seem to belong here also). Two members of this subgenus, *P. officinalis* L.[5] and *P. judaica* L., have been infrequently re-

[5] Specimens named *Parietaria officinalis* from Sanford, Seminole County, Florida [shaded places, *Rapp*, April 11, 1929 (NY), sandy, waste places, *Rapp*, July 1929 (NY)] on which Small probably based his statement, "sandy pinelands, old fields, and roadsides, pen. Fla." (Man. Southeast. Fl. 435. 1933), actually represent an apparently unreported adventive in the United States, *Pouzolzia zeylanica* (L.) J. Benn., a native of Asia that ranges from Japan to Formosa, China, Indochina, Malaysia, and India. Although similar in aspect to certain shrubby *Parietaria* species, *Pouzolzia zeylanica* has stipulate leaves and typically a large taproot. Carpellate and staminate flowers subtended by small, scarious bracts are aggregated in tight axillary clusters, and the

ported as adventives at places in the Southeastern United States and elsewhere in North America. Both have black achenes, in contrast to the light to dark brown fruits of our native species. Subgenus FREIREA (Gaud.) Komarov ex Jarmolenko, represented in both the New and Old Worlds, has a sessile stigma or one supported by a very short style. Most species in this subgenus are annuals. The significance of the difference in location of carpellate and bisexual flowers within an inflorescence, used by Jarmolenko (1936) as another distinguishing feature between the two subgenera, needs confirmation.

Three species belonging to subg. FREIREA occur in our region. *Parietaria pensylvanica* Muhl. ex Willd. (including var. *obtusa* (Rydb. ex Small) Shinners), $2n = 16$, occurs widely in North America from southern Maine, Quebec, Manitoba, and British Columbia (not continuously, however), southward to North Carolina, Florida, Alabama, Mississippi, Louisiana, Texas, Mexico, and California. Leaves of this species are typically lanceolate and sparsely pubescent in the eastern United States, where it grows in moist woodlands and other shaded places, but westward plants are generally more hairy, the leaves smaller and often ovate. The ± symmetrical, light brown achenes bearing an apical style remnant are of uniform shape throughout its range, and variation occurs only in size and somewhat in color. *Parietaria floridana* Nutt. (*P. nummularia* Small) and *P. praetermissa* B. D. Hinton (*P. floridana* sensu most authors, not Nutt.[6]) range widely across the Coastal Plain in the Southeast. Occurring in North and South Carolina, Georgia, Florida (throughout), Louisiana, and Missouri, *P. praetermissa* is distinguished by its relatively large (usually longer than 1 mm.), asymmetrically apiculate achenes that lack a flanged stipe. The smaller (usually shorter than 1 mm.), symmetrically apiculate achenes of *P. floridana*, which occurs from Delaware to Florida to Texas, and also in Cuba, are provided with a flanged stipe.

In general species of *Parietaria* are vegetatively polymorphic, and those defined mainly on leaf or bract shape, pubescence, or degree of woodiness may be partly open to reinterpretation (e.g., see Hedberg, who includes the three species described from plants collected in the mountains of East Africa within the range of variation of the widespread *P. debilis* Forst. f.). The most reliable taxonomic characters appear to be shape of the achene and form of the accrescent perianth of both carpellate and bisexual flowers.

Dispersal of certain European species by ants attracted to the achenes by the contents of the basal stipe, which they utilize as a food source, is mentioned by Ridley.

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filiform styles of carpellate flowers drop off soon after anthesis (*vs.* persisting in *Boehmeria*). At maturity, the black, shiny, ovoid achenes (similar to those of *Parietaria officinalis*) are tightly enclosed by a thick, dry, continuous perianth bearing conspicuous ribs. Whether the Sanford plants have persisted, and therefore can be considered naturalized, remains to be determined, as does the status of Small's report of *P. officinalis*.

[6] Treatment of these two species follows Hinton (1968). The type specimens of *P. nummularia* and *P. floridana* represent the same species.

Chromosome counts of $2n = 14$, 16, and 26 have been reported.

The genus is of no economic importance, except possibly for the infrequent use of *P. officinalis* medicinally. Expressed juice and boiled extracts obtained from this species have been used as diuretics and to lower fevers.

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