THE DIOSCOREACEAE IN THE SOUTHEASTERN UNITED STATES[1]

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DIOSCOREACEAE R. Brown, Prodr. **1**: 294. 1810, "Dioscoreae," nom. cons.

(YAM FAMILY)

Twining [rarely erect] herbs [lianas or subshrubs] with rhizomes or fleshy [rarely woody or corky] tubers, the tubers derived from the hypocotyl, the internode above it, or both; plants with raphides in mucilaginous idioblasts, frequently rich in steroidal sapogenins, and usually accumulating chelidonic acid and lactone alkaloids. Stems smooth, winged [or spiny]; vascular bundles closed, arranged in 2 [or 1] ring(s), the vessels restricted to the roots, stems, and petioles, with scalariform perforation plates; sieve-tube plastids with cuneate, proteinaceous inclusions. Leaves alternate, rarely opposite or whorled, long petiolate, simple [rarely palmately compound, with 3–7 leaflets], usually cordate, entire, undivided [or palmately lobed], often with embedded mucilaginous pits or nectaries, the tips usually with a distinct pore; venation palmate, with 3–13 converging main veins and anastomosing lateral veinlets; stomata anomocytic, rarely different; trichomes unicellular, eglandular, simple [sometimes peglike, furcate (T-shaped), or stellate], often confined to the abaxial surface and along the veins, rarely occurring on the petiole or stem. Inflores-

[1]Prepared for the Generic Flora of the Southeastern United States, a long-term project made possible by grants from the National Science Foundation and currently supported by BSR-8415769 (C. E. Wood, Jr., principal investigator), under which this research was done, and BSR-8415637 (N. G. Miller, principal investigator). This account, the 124th in the series, follows the format established in the first paper (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. The references that we have not verified are marked with asterisks.

We are most grateful to Carroll Wood for his support and continuous help during the preparation of this paper, and particularly for his critical review of the manuscript. We should also like to thank Norton Miller for reviewing the paper, Rogers McVaugh for help in lectotypifying *Dioscorea*, Charles E. Jarvis for notes and photographs of the type of *D. villosa*, and Barbara Nimblett for typing the manuscript. We are also grateful to Elizabeth B. Schmidt and Stephen A. Spongberg for their editorial advice.

FIGURE 1, b and k, were drawn by the late Dorothy H. Marsh (DHM), e and m–o by Ihsan Al-Shehbaz (IAS), and the remainder by Karen Stoutsenberger (KS) under earlier grants. Carroll Wood and Kenneth R. Robertson prepared the material and supervised the illustrations. Preserved material, as well as herbarium specimens in the Arnold Arboretum and the Gray Herbarium, was used as the basis for the drawings.

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Journal of the Arnold Arboretum **70**: 57–95. January, 1989.

cences axillary racemes, spikes, panicles, or cymes, many flowered, usually bracteate. Flowers trimerous, actinomorphic [very rarely zygomorphic], imperfect (the plant dioecious [rarely monoecious]) [or perfect], subtended by 1 small [to large] bract and 1 [rarely 2] bracteoles. Tepals 6, in 2 whorls, distinct [or connate], the perianth rotate [tubular to campanulate]. Stamens (absent in the carpellate flowers but often represented by staminodia) 6, in 2 whorls [the inner 3 sometimes staminodial or obsolete]; filaments distinct [connate at base, or fused into a tube]; anthers 2-locular and the lobes contiguous or separated, tetrasporangiate, dehiscing by longitudinal slits, introrse [or extrorse]; microsporogenesis simultaneous; pollen grains binucleate, 2- to 4- [rarely 1-]sulcate [or 4- or 5-foraminate]. Gynoecium (rudimentary in the staminate flowers) 3-carpellate; ovary inferior, 3-locular, the placentation axile, septal nectaries usually present; styles 3, connate at base [or distinct]; ovules 2 [to many] in each locule, anatropous, bitegmic, crassinucellate, endosperm development nuclear, the megagametophyte (embryo sac) of the Polygonum type. Fruits triangular, 3-winged capsules [1-seeded samaras, or berries]. Seeds flattened [or globose], winged [or wingless]; embryos small, well differentiated, with a subterminal plumule and a broad, flat, nearly lateral cotyledon embedded in the hard, copious endosperm that contains lipids and aleurone, as well as hemicellulose deposited in its thick cell walls. Base chromosome numbers 9, 10, 12. (Including Androsynaceae Salisb., Cladophyllaceae Dulac, Stenomeridaceae J. G. Agardh, Tamaceae Gray.) TYPE GENUS: *Dioscorea* L.

A family of seven genera and approximately 900 species of tropical, subtropical, or rarely warm-temperate plants. *Avetra* Perr. (monotypic) is endemic to Madagascar, while *Borderea* Miégeville (two species; Heywood) is restricted to the Pyrenees. See, however, Miège (1986; reference under *Dioscorea*) for assignment of *D. Gillettii* Milne-Redhead (Kenya, Ethiopia) to *Dioscorea* sect. BORDEREA (Miégeville) Bentham. *Epipetrum* Phil. (three species; Reiche) is confined to Chile, *Rajania* L. (25 species) is native to the West Indies, *Stenomeris* Planchon (two species) is indigenous to Malaysia (Borneo, Malay Peninsula, Philippines, Sumatra), and *Tamus* L. (five species) is widespread in the Mediterranean area (southwestern Asia; southern, central, and western Europe; northwestern Africa) and Macaronesia. *Dioscorea,* the largest genus of the family, has approximately 850 species distributed on all continents except Antarctica.

The limits of the Dioscoreaceae are controversial, and Knuth (1930) and Burkill (1960) recognized ten and six genera, respectively. Both authors and Cronquist have retained *Trichopus* Gaertner (monotypic; Sri Lanka, southern India, Malaysia) in the family, while Ayensu (1966, 1972), Hutchinson (1973), Dahlgren (1980, 1983), and Dahlgren, Clifford, & Yeo placed it in a monotypic family, the Trichopodaceae Hutchinson, assigned to the Dioscoreales, a view with which we agree. *Trichopus* differs from genera of the Dioscoreaceae in having an erect (nontwining) herbaceous stem with one or a few flowers borne opposite the leaf, glandular hairs, successive microsporogenesis, and long-appendiculate anthers. It also differs in nodal anatomy and chromosome number (see below). The monotypic *Petermannia* F. Mueller (New South Wales and Queensland, Australia), which was retained in the Dioscoreaceae by Knuth

(1924, 1930), is now believed to represent a unigeneric family, the Petermanniaceae Hutchinson, somewhat related to the Dioscoreaceae (Conran; Dahlgren, Clifford, & Yeo; Tomlinson & Ayensu). However, Hutchinson (1973) assigned this family to the Alstroemeriales, while Cronquist placed *Petermannia* in the Smilacaceae Vent. We prefer to associate the Petermanniaceae with the Dioscoreales for reasons discussed by Conran.

Burkill (1960) reduced both *Borderea* and *Epipetrum* to sections of *Dioscorea*. The presence in *Borderea* of wingless seeds, nontwining stems, unbranched leaf veins, and a base chromosome number of 12 supports its recognition as a distinct genus. Furthermore, in *Epipetrum* the lack of wings around the seeds, the presence of well-developed stylar rudiments in the staminate flowers, and the spiral twisting of pedicels of the carpellate flowers are sufficient grounds for its maintenance at the generic rank.

On the basis of their perfect flowers, prominent staminal appendages, and thin, nonfleshy rhizomes, both *Avetra* and *Stenomeris* were considered to be anomalous in the Dioscoreaceae. *Avetra* was placed in the Trichopodaceae by Hutchinson (1973), but the climbing habit, three-winged fruits, and nodal anatomy (Ayensu, 1972) strongly support its retention in the Dioscoreaceae, as was initially recognized by Perrier de la Bâthie. *Stenomeris* also deviates from the rest of the Dioscoreaceae in having linear fruits with numerous seeds. It was placed in the Stenomeridaceae by many authors, but the overwhelming anatomical evidence favors its placement in the Dioscoreaceae. Dahlgren, Clifford, & Yeo assigned *Avetra* and *Stenomeris* to subfam. Stenomeridoideae and suggested that they should perhaps be treated in two unigeneric subfamilies or even in an independent family. Knuth's (1924, 1930) division of the Dioscoreaceae into the tribes Dioscoreae and Stenomerideae Planchon may be useful only after the exclusion of *Petermannia* and *Trichopus* from the latter tribe. *Avetra* may represent a monotypic tribe. However, reorganizing the subfamilial classification of the Dioscoreaceae is beyond the scope of this flora.

The remaining genera of the Dioscoreaceae are easily distinguished by their fruits. *Rajania* has one-seeded samaras, *Tamus* has berries, and *Dioscorea* has three-winged, few-seeded capsules like those of *Borderea* and *Epipetrum*. *Higinbothamia* Uline, a monotypic genus described from the Yucatán, was said to differ from *Dioscorea* in having four instead of two seeds per locule. It is now recognized as a section of *Dioscorea* with two species, one of which is endemic to Belize (see Schubert (1966) under references for *Dioscorea*).

The evolutionary relationships among the genera of the Dioscoreaceae have not been fully resolved. Because of their perfect flowers and long-appendiculate stamens, *Avetra* and *Stenomeris* are probably basal (Burkill, 1960). The remaining genera of the family have imperfect flowers (the plants dioecious), and with the exception of *Dioscorea* they all have a restricted distribution. According to B. W. Smith (see under *Dioscorea*), these small genera have arisen from *Dioscorea*. However, this view implies that *Dioscorea* is paraphyletic. The development of one-winged fruits in *D. cyphocarpa* Robinson ex Knuth and *D. tacanensis* Lundell may suggest a closer relationship between *Rajania* and *Dioscorea*. It is possible, however, that samaroid fruits evolved independently in the two genera.

The ordinal disposition and familial relationships of the Dioscoreaceae are controversial. A few authors (e.g., El-Gazzar & Hamza) advocated that the family be placed in the dicotyledons near the Aristolochiaceae Juss. because of its twining stems, petiolate, exstipulate leaves, trimerous, epigynous flowers, anatropous ovules, loculicidal capsules, endospermous seeds, and binucleate pollen. Furthermore, the presence in both families of PIIC-type sieve-tube plastids, which is universal in the monocotyledons, may be considered as evidence supporting this view. However, because of the presence of other plastid types in the family, Dahlgren & Rasmussen believe that the occurrence of these plastids in only two genera of the Aristolochiaceae is by convergence. Similarities between the Dioscoreales and the Magnoliales were summarized by Dahlgren & Clifford, who suggested (p. 342) that the extant forms of these orders do not represent "missing links or relicts of the common ancestors of the monocotyledons."

Lawton & Lawton, who studied the seedlings of five species of *Dioscorea*, suggested that the first seedling leaf is homologous to a modified second cotyledon, whereas the first cotyledon remains in the seed as an absorbing structure. However, P. M. Smith (reference under *Dioscorea*) did not find any structure comparable to a second cotyledon in the Dioscoreaceae. The slightly lateral position of the cotyledon in the family is considered to be ancestral among the monocotyledons, which otherwise have terminal cotyledons (Dahlgren, Clifford, & Yeo).

The close relationship between the Dioscoreaceae and the Smilacaceae was pointed out as early as 1810 by Brown. Most recent authors (e.g., Cronquist; Dahlgren, Clifford, & Yeo; Takhtajan) accept such a relationship. They and Thorne also associate the Dioscoreaceae closely with the Stemonaceae Engler (see Rogers), the Taccaceae Dumort., and the Trichopodaceae. However, these authors have variously placed the Dioscoreaceae under the Dioscoreales, the Liliales, or the Smilacales. The Dioscoreales (*sensu* Dahlgren, Clifford, & Yeo) are somewhat homogeneous and are apparently monophyletic. On the other hand, raising the Trilliaceae Lindley, the Taccaceae, and the Smilacaceae-Petermanniaceae to three orders, as suggested by J. W. Walker (pers. comm.), may be more appropriate. Evidently, the placement of the Dioscoreaceae with 14 other families in the order Liliales (Cronquist) needs further study.

The Dioscoreales have been considered to be the most central order in the monocotyledons (Dahlgren, Clifford, & Yeo). However, since various families of the Dioscoreales have several specialized features, particularly tetramery, epigyny, complex nodal anatomy, and fleshy fruits, a critical evaluation of the order is needed.

According to Coursey (1967; see under *Dioscorea*), the Dioscoreaceae likely evolved before the end of the Cretaceous, and *Dioscorea* was probably widespread before the separation of America from Africa. Pax listed *Majanthemophyllum petiolatum* O. Weber from the Miocene of Germany and *Dioscorites resurgens* Saporta from the Tertiary of southern France. Daghlian suggested that fossils described as *Dioscorites* Saporta from the Upper Cretaceous (Maastrichtian), as well as from many other Tertiary sediments, are disputable as to

familial and generic identity. Pollen of *Rajania* described from the Miocene of Veracruz (Graham), if indeed dioscoreaceous, may well belong to *Dioscorea*. The identity of the North American fossil *D. cretacea* Lesq. is questionable.

Pollen of the Dioscoreaceae is heterogeneous. *Tamus* has reticulate, 2-colpate pollen (Clarke & Jones). In *Dioscorea* pollen is monocolpate in the presumably primitive sect. STENOPHORA Uline and 2-colpate in four other sections (Su; see under *Dioscorea*). Monosulcate, multiaperturate pollen has been found in *D. polygonoides* Humb. & Bonpl. (Zavada). *Avetra* deviates strongly from the rest of the Dioscoreaceae in having spinulose, 4- or 5-foraminate pollen.

Cytology of the Dioscoreaceae has not been surveyed adequately, and chromosome numbers are known for only about nine percent of the entire family. *Petermannia* ($x = 5$) and *Trichopus* ($x = 7$), which are now placed in monotypic families, are evidently different not only in base number but also in chromosome size (Ramachandran, 1962, 1968). Diploid counts of $2n = 24$ in *Borderea* support its separation from *Dioscorea*, a genus uniformly based on either nine or ten. The closely related *Rajania* is apparently a polyploid based on nine, but only *R. cordata* L. ($2n = 36$) has been studied cytologically. Polyploidy based on $x = 12$ probably played an important role in the evolution of *Tamus*, as is evidenced by its occurrence in the tetraploid *T. communis* L. ($2n = 48$) and the octoploid *T. edulis* Lowe ($2n = 96$).

Goldblatt (1980) suggested that the base chromosome number for the Dioscoreaceae may be seven and that such a number is found in the relict *Trichopus*, as well as in the families Stemonaceae and Taccaceae. As indicated above, however, *Trichopus* does not belong to the Dioscoreaceae, and it is more appropriate to assume that the base number for the family is ten. No chromosome counts are known for *Avetra* or *Stenomeris*.

The Dioscoreaceae are characterized by three anatomical peculiarities that are unusual among the monocotyledons. First, xylem and phloem glomeruli are present at the nodes. These represent an interlacing mass of prosenchymatous xylem that encloses one to many phloem glomeruli, each with interlacing sieve tubes and sieve plates of various sizes (see Behnke (1965) for further details). Karnick (1970; see under *Dioscorea*) believed that this "nodal plexus" is the site of various chemical activities, including the biosynthesis of diverse constituents. Second, vascular bundles of the stem are often arranged in two circles. Those of the outer circle have a V-shaped group of metaxylem vessels and tracheids, with two phloem units terminating the flanges and a third one at the converging ends of the V. Bundles of the inner circle have an elliptic arrangement of metaxylem vessels and tracheids, with one or two large phloem units on the inner side of the innermost pair of the larger metaxylem vessels and at least one at the outer end (Ayensu, 1972). Third, the sieve tubes are rather large and have highly oblique, compound sieve plates and numerous sieve areas. Because of their size, sieve elements could easily be mistaken for vessels.

The presence of these three anatomical features in *Avetra* and *Stenomeris* supports their placement with *Dioscorea*, *Rajania*, and *Tamus* in the Dioscoreaceae, instead of in two other families (Ayensu, 1972). Furthermore, *Tri-*

chopus and *Petermannia* have nodal and vascular-bundle anatomy quite different from that of the Dioscoreaceae and are therefore appropriately assigned to monotypic families (Ayensu, 1966, 1972; Tomlinson & Ayensu).

Vessels of the Dioscoreaceae have scalariform perforations; these are present in the roots, aerial stems, and petioles but absent in leaf blades, bulbils, rhizomes, and tubers. Although most fibers of the Dioscoreaceae have tapered ends, a large proportion have square ones (Ayensu, 1972).

Stomata of the Dioscoreaceae are anomocytic and are not associated with morphologically differentiated subsidiary cells. Furthermore, the contiguous epidermal cells have no distinctive arrangement (Ayensu, 1972; Stebbins & Khush). However, Patel and others (e.g., Ekundayo; Ling *et al.*; Purnima & Srivastava; G. L. Shah & Gopal; references under *Dioscorea*) have indicated that other types of stomata may also be found. The stomata are distributed primarily on the abaxial leaf surface, but in a few species (e.g., *D. bulbifera* L.) they are present on both surfaces.

Dispersal in the Dioscoreaceae is primarily by wind. In *Rajania* and *Dioscorea,* which produce samaras and variously winged seeds, respectively, short-distance dispersal is usually accomplished by seeds or fruits gliding or whirling from carpellate plants that can climb to heights of more than 30 feet. The red berries of *Tamus* are dispersed in the Mediterranean region by birds (Burkill, 1937), whereas in species of *Epipetrum* the capsules become buried in the vicinity of the mother plant.

Numerous species of *Dioscorea* are important medicinal or food plants. They are discussed in some detail under the generic account. The remaining genera of the Dioscoreaceae have little or no economic value.

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Dioscorea Linnaeus, Sp. Pl. **2:** 1032. 1753; Gen. Pl. ed. 5. 456. 1754.

Twining [rarely erect] herbs [or lianas]; glabrous or with unicellular, eglandular, simple [or variously branched] trichomes. Underground organs rhizomes, woody corms, or usually fleshy, single or clustered, edible [or poisonous], smooth [or spiny] tubers with thin [or thick to corky] skin. Stems almost always produced annually from underground structures, smooth, winged [or armed], terete or angled, dextrorse or sinistrorse. Leaves alternate, opposite, or whorled, petiolate, simple [or palmately compound, with 3–7 leaflets], cordate to nearly deltoid, undivided [or palmately lobed]; main veins 3–13, converging, the lateral ones reticulate, usually horizontal; petioles usually with a pulvinus at both ends, sometimes with a bulbil at the axil. Inflorescences axillary, many-flowered, bracteate racemes, panicles, spikes, or cymes. Flowers imperfect (plants dioecious or—abnormally—monoecious), actinomorphic, with rotate [funnelform or campanulate] perianth; tepals 6, in 2 similar [or sharply differentiated] whorls, distinct or variously connate; staminate flowers usually grouped in cymes borne on racemes, often with stylar rudiments, the stamens usually 6, in 2 whorls, all fertile [or the inner 3 either staminodial or absent], the filaments free [or connate], very short [or as long as the tepals]; carpellate flowers usually in spikes or spikelike racemes, epigynous, with 6 [3 or 0] staminodia; styles 3, branched. Fruits dehiscent, 3-winged, leathery or membran-

aceous capsules. Seeds flattened [or not], reticulate or smooth, broadly [to narrowly] winged all around [or only at 1 end, rarely wingless], 2 [or 4] per locule. Base chromosome numbers 9, 10. (Including *Androsyne* Salisb.; *Botryosicyos* Hochst.; *Elephantodon* Salisb.; *Hamatris* Salisb.; *Helmia* Knuth; *Higinbothamia* Uline; *Hyperocarpa* (Uline) Barroso, Guimarães, & Sucre; *Merione* Salisb.; *Nanarepenta* Matuda; *Polynome* Salisb.; *Rhizemys* Raf.; *Sismondaea* Delponte; *Strophis* Salisb.; *Testudinaria* Salisb.; *Ubium* Cothenius.) LECTOTYPE:[3] *D. bulbifera* L.; see Green in Hitchcock & Green. (Name commemorating the Greek Pedanios Dioscorides (fl. ca. A.D. 40–80), naturalist, physician, and officer in the army of Nero. His *De Materia Medica,* which was published in five volumes during the period A.D. 50–70 (Riddle), was the leading text on pharmacology for 16 centuries and contained medicinal properties of more than 1000 drugs derived primarily from plants.)—YAM.

A genus of approximately 850 species, of which the majority grow in the humid tropical and subtropical areas of the world, and only several occur in the warmer parts of the temperate zones. Small's estimation of 160 species for *Dioscorea* is well below the mark. As was suggested by B. W. Smith, nearly 50 percent of the species of *Dioscorea* are found in South America. There are approximately 130 species in Brazil, 120 in Central America and Mexico, 160 in Africa, and 250 in Asia (authors' compilation). The genus is poorly represented in Europe and adjacent Asia (three species), Australia (four), and the United States and Canada (three). Three of the six species growing in the southeastern United States are naturalized weeds of Asiatic origin.

The sectional classification of *Dioscorea* is controversial. About 75 sections, including 60 in Knuth (1924), have been recognized by various authors. Knuth

[3]The lectotypification of *Dioscorea* has not been fully resolved. Britton & Brown, who were the first to lectotypify the genus, chose *D. sativa* from the eight species described by Linnaeus (Sp. Pl. **2:** 1032, 1033. 1753). Prain & Burkill (1919) clearly demonstrated that Linnaeus, in his citations under *D. sativa,* included elements now believed to belong to five species of *Dioscorea,* as well as one each of *Cardiopteris* Wall. ex Blume (Cardiopteridaceae Blume) and *Tinospora* Miers (Menispermaceae Juss.). Hooker's suggestion (p. 291) that "the plant figured in *Hortus Cliffortianus* must be accepted as [*D.*] *sativa* Linn." was followed by Prain & Burkill (1919), who also argued that the name *D. sativa* must be abandoned because the figure in *Hortus Cliffortianus* represents a plant with leaves from *D. villosa* L. and fruits from another species. The single specimen (*1184.4*) in the Linnaean herbarium, which was annotated by Linnaeus as *D. sativa,* was collected by Kalm from eastern North America and is generally agreed (Prain & Burkill, 1919) to belong to *D. villosa.* As indicated by Jackson's letter to Bartlett (see Bartlett, p. 8), "I do not find any specimen named by Linné "*villosa*" in his herbarium, but as *sativa* is an East Indian species, and the specimen is of Kalm's collection, it is patent that there is a blunder." If *D. sativa* is lectotypified on Kalm's specimen above, we would be forced to replace the well-known North American *D. villosa* by *D. sativa.* This, however, would be a serious mistake because Linnaeus had indicated in his original description of *D. sativa* that the plant grows in the "Indiis" (East Indies; see Bartlett) and implied that it is a cultivated plant. *Dioscorea villosa* is neither cultivated nor edible. Evidently *D. sativa* was based on materials inadequate and highly controversial with respect to citations, diagnosis, illustrations, and specimens. No matter how the species is typified, there would still be several unresolved problems. On the basis of these facts, *D. sativa* could be maintained as the lectotype of the genus only if it is satisfactorily typified. It is doubtful, however, that this will ever be accomplished. In fact, the report of the Standing Committee on Stabilization of Species Names (Taxon **24:** 171–177. 1975) listed *D. sativa* as a nomen ambiguum to be rejected under Article 69 of the ICBN. Therefore, we are accepting *D. bulbifera* L. as the lectotype of the genus, as was proposed by Green (in Hitchcock & Green).

has often been criticized for his narrow sectional concept, particularly with respect to the New World taxa. Burkill (1960) assigned the Old World species to 23 sections (including *Borderea*) and placed particular emphasis in his keys on aspects of the underground parts. On the other hand, Knuth (1924, 1930, family references) divided *Dioscorea* into four subgenera based on the position of the seed wing, relying heavily on characters of the staminate flowers and fruits in his sectional divisions of subgenera. Some of the sectional realignment proposed by Ayensu (1972) on the basis of anatomy should be taken into consideration. In our opinion, the number of New World sections accepted by Knuth (1924) should be reduced. However, it is beyond the scope of this flora to do that.

Burkill (1960) and Prain & Burkill (1939) suggested that *Dioscorea* evolved during the Cretaceous in what are now the temperate areas of the Far East, where the presumably primitive sect. STENOPHORA Uline is primarily distributed, and that the genus later migrated to the tropics. Burkill (1960) believed that the formation of the Atlantic rift was responsible for the separation of the range of *Dioscorea* into two portions, each of which evolved independently because no sections or species are now common to the New and Old worlds. Section STENOPHORA is considered primitive on the basis of having primarily diploid taxa, monocolpate pollen, and rhizomatous underground organs (Burkill, 1960; Pei *et al.*).

The assignment of the eastern North American species of *Dioscorea* to sect. STENOPHORA by Burkill (1960), Coursey (1967), and Prain & Burkill (1936) is unacceptable because seeds of these species are broadly winged all around, while those of sect. STENOPHORA are winged above (distally). We follow Uline (1897) and Knuth (1924) in placing these species in sect. MACROPODA Uline but disagree with the latter author on the sectional limits. Uline admitted only three species in this section: *D. villosa* and two unnamed ones that were said to grow in the Caucasus and the Himalayas. Therefore, *D. villosa* has to be considered as the sectional type. Coursey (1967) has suggested that the eastern North American taxa evolved from ancestors that migrated from eastern Asia across the Bering Strait land bridge. However, there is no evidence at present that supports this speculation.

Section MACROPODA Uline (stems sinistrorse; staminate flowers grouped in verticillate to subcapitate cymes borne on racemes; fertile stamens 6, inserted at base of perianth, the filaments short; capsules large, obovate) is represented in the United States and Canada by three species that also grow in the Southeast.

Dioscorea quaternata J. F. Gmelin (*D. villosa* L. subsp. *quarternata* (J. F. Gmelin) Knuth, *D. paniculata* Michx., *D. villosa* subsp. *paniculata* (Michx.) Knuth, *D. paniculata* var. *glabrifolia* Bartlett, *D. villosa* subsp. *paniculata* var. *glabrifolia* (Bartlett) Knuth, *D. villosa* var. *glabrifolia* (Bartlett) Blake, *D. villosa* f. *glabrifolia* (Bartlett) Fern., *D. glauca* Muhl., *D. villosa* subsp. *glauca* (Muhl.) Knuth, *D. quaternata* var. *glauca* (Muhl.) Fern., *D. villosa* var. *glabra* C. G. Lloyd, *D. Lloydiana* Krause), $2n = 36, 54, 60$, is the most variable and widely distributed of the North American species. It is distributed primarily east of the 95th meridian and between 27 and 45° north latitude. It does not grow in New England and is very rare in New Jersey, New York, Wisconsin, Minnesota,

Iowa, Kansas, Oklahoma, and Texas, but is quite common in the remaining states that fall within its geographic range. It is sporadic in southern Ontario, Canada. *Dioscorea quaternata* grows in moist, rich or rocky woods and thickets, on limestone or talus slopes, in creek bottoms, and along roadsides, railroad tracks, and borders of swamps, ponds, and marshes.

Dioscorea villosa L. (*D. hirticaulis* Bartlett, *D. villosa* subsp. *hirticaulis* (Bartlett) Knuth, *D. villosa* var. *hirticaulis* (Bartlett) Ahles) is distributed from southwestern Massachusetts (Bristol County), Rhode Island (Washington County), and western Connecticut (Fairfield, Hartford, Middlesex, New Haven, and New London counties) southward along the Coastal Plain of all states to northern Florida. We have not seen any material from Delaware, and the records from New York and New Jersey are based on old collections. Furthermore, *D. villosa* is disjunct and probably introduced to Kentucky; it is first recorded here (*Beckett 651*, GH; Clark County). The species is common in Virginia and the Carolinas, where it grows in bogs, peaty depressions, and swamps. Linnaeus (Sp. Pl. **2:** 1033. 1753) stated that it occurs in Florida, but this has not previously been confirmed. We are recording *D. villosa* from Alachua (*Arnold s.n.*, 1931; FLAS), Jackson (*Godfrey 76493*; FSU), and Leon (*Lazor 922*; FSU) counties, Florida.

Dioscorea villosa is easily recognized by its narrowly winged, polygonal (8- to 14-angled) stems (FIGURE 1m), alternate lower leaves, and densely grouped glomerules on short (usually 2–4 cm) staminate inflorescences. The closely related *D. quaternata* has terete, wingless stems, whorled lower leaves (three to nine per node), and lax, longer inflorescences. Field notes on the phyllotaxy of lower nodes are useful for separating the two species. *Dioscorea quaternata* is the earliest published binomial for the North American dioscoreas with whorled lower leaves.

The identities of *Dioscorea hirticaulis, D. quaternata,* and *D. villosa* have been confused. A few authors (e.g., Ahles, 1968; Gleason; MacRoberts; E. B. Smith) suggested that the first and/or second be reduced to synonymy of the last. As shown above, however, *D. quaternata* and *D. villosa* are very distinct and should therefore be maintained at the specific rank.

Dioscorea villosa was typified by Blake on *Clayton 94* (BM) from Virginia. Charles E. Jarvis (pers. comm.) has indicated that there are two Clayton sheets in the British Museum (photos, A!), one bearing staminate material and the other a carpellate plant. The staminate material, annotated as *Clayton 94* and with a handwritten note by Gronovius that male and female flowers are borne on separate plants, is the type. It has narrowly winged, 8- to 14-angled, very sparsely pubescent stems and alternate lower leaves. Previously these features have been attributed to *D. hirticaulis*. Therefore, what has been called *D. hirticaulis* by all North American authors is in fact *D. villosa*. Accordingly, the range of *D. villosa* becomes restricted to only the coastal states above, and all records from the other states should belong to *D. quaternata*. Evidently, Deam's record of *D. villosa* (as *D. hirticaulis*) from six counties in Indiana belongs to *D. quaternata*.

Both *Dioscorea villosa* and *D. quaternata* are highly variable in stem and leaf pubescence. Forms with densely pubescent to completely glabrous leaves that are either glaucous or nonglaucous occur in populations of both species.

Bartlett's recognition of four species in this complex was based primarily on differences in the branching of rhizomes and in pubescence, color (green vs. glaucous), and number of leaves per node. These alleged distinctions are far from being realistic. In fact, characters of rhizome branching, thickness, and surface configuration can be modified by soil texture, habitat, and environment. Furthermore, petiole length, leaf pubescence and glaucescence, and fruit length show continuous variations of no taxonomic value.

Dioscorea floridana Bartlett (*D. villosa* subsp. *floridana* (Bartlett) Knuth, *D. villosa* var. *floridana* (Bartlett) Ahles) is the most distinctive of the North American species. It is readily distinguished by its two or three staminate inflorescences in the axils of upper leaves, longer (ca. 0.4 mm), inwardly curved filaments, connate anther lobes (see FIGURE 1n, o), and oblong tepals. Both *D. quaternata* and *D. villosa* have single staminate inflorescences in the axils of upper leaves, shorter (ca. 0.2 mm), straight filaments, separated, didymous anther lobes (see FIGURE 1e), and ovate tepals. Differences in the anthers of these species were first observed by Bartlett (see p. 18), but they have been overlooked by subsequent workers.

Dioscorea floridana grows in moist thickets and swamps, as well as in moist to dry woods and hammocks in South Carolina (Berkeley, Charleston, Dorchester, Orangeburg, and Williamsburg counties), Georgia (Baker, Chatham, Clarke, Dougherty, Jenkins, Lowndes, Sumter, and Tattnall counties), and Florida (Alachua, Calhoun, Columbia, Duval, Hernando, Hillsborough, Jackson, Levy, and Santa Rosa counties). It has been mapped from Bamberg and Beaufort counties, South Carolina (Ahles, 1968), but we have not seen any material from either.

No chromosome counts are available for either *Dioscorea floridana* or *D. villosa*. The few counts for *D. quaternata* are inconsistent, and more studies are needed before any meaningful conclusions can be reached.

Dioscorea bulbifera L. (*Helmia bulbifera* (L.) Kunth; see Coursey (1967) for ten additional synonyms), aerial or potato yam, $2n = 36?, 40, 54?, 60, 70, 80, 100$, is the only edible yam believed to be native to both Asia and Africa (Prain & Burkill, 1936). Introduced to the New World during the slave trade, it is a widespread weed in Florida, where it grows in disturbed woods and thickets (Wunderlin), but is uncommon in Mississippi. Edible and poisonous forms are known, but the Florida populations produce bulbils that remain inedible and nauseating even after repeated washing and boiling (Ward). Prain & Burkill (1934) recognized ten varieties primarily on the basis of the shape and taste of both bubils and tubers. It is doubtful, however, that these entities are significant taxonomically. Tubers of *D. bulbifera*, if produced, are very small, bitter, and usually hard. The bulbils, on the other hand, may weigh up to 2 kg. The species is easily distinguished from the other introduced dioscoreas that grow in the Southeastern States by its sinistrorse, terete, wingless stems; large, alternate, broadly cordate, acuminate leaves with rounded lobes; large, smooth, subspherical bulbils; and auriculate petiolar bases.

The sectional disposition of *Dioscorea bulbifera* is problematic. If the species is accepted as the lectotype of the genus, as is done here, it should be assigned to sect. DIOSCOREA. Accordingly, sect. OPSOPHYTON Uline, to which *D. bulbifera* is assigned by nearly all students of the Dioscoreaceae, should be reduced to

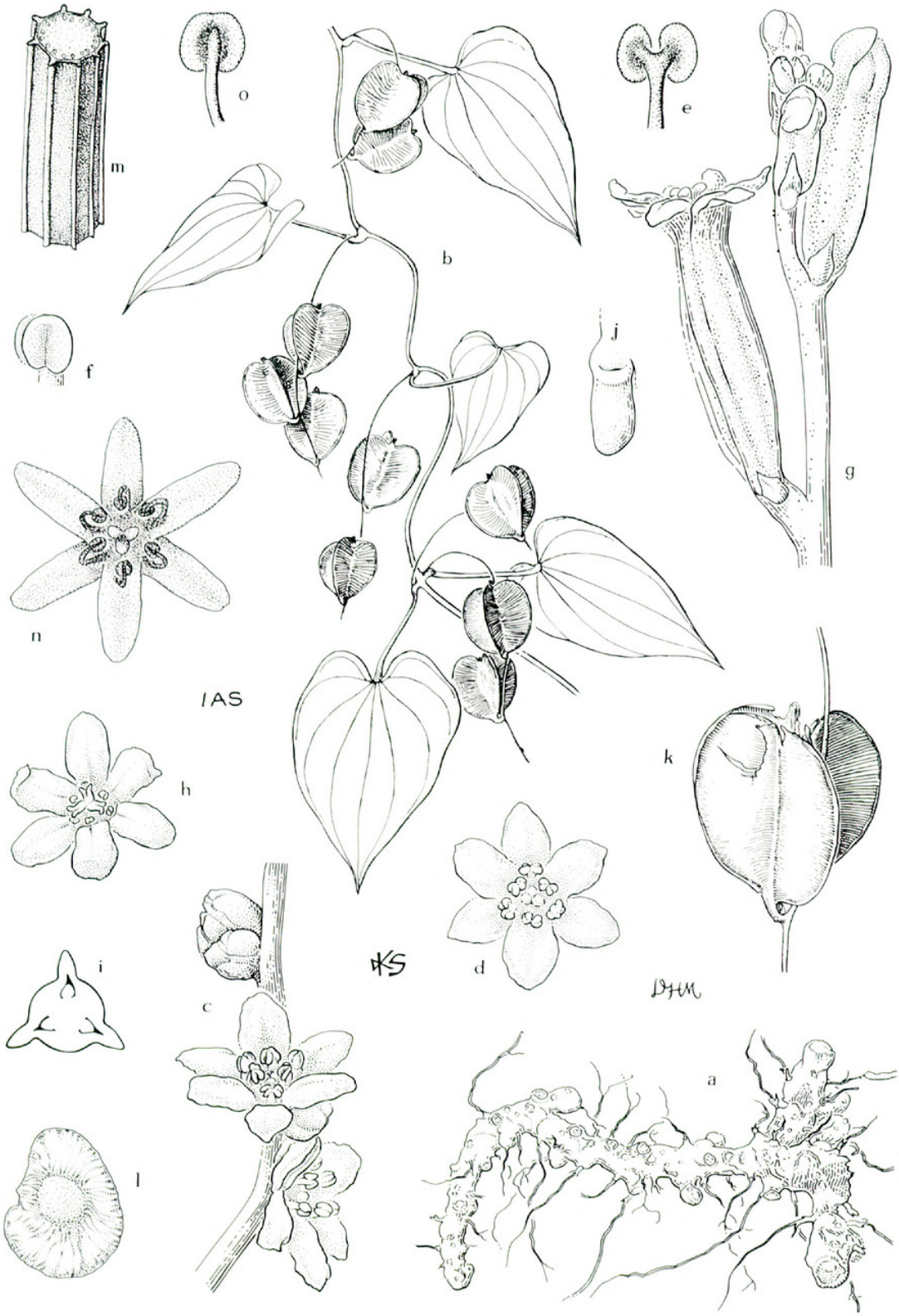

FIGURE 1. *Dioscorea.* a–l, *D. quaternata:* a, rhizome, × ½—note scars left by annual aerial stems; b, portion of mature plant with fruits, × ½; c, flowers and buds from staminate plant, × 6; d, staminate flower from above, × 6; e, abaxial view of anther, × 40; f, lateral view of anther, × 40; g, tip of carpellate inflorescence with buds and 1

a synonym of sect. DIOSCOREA. Knuth (1924) recognized 26 species and three subsections in sect. OPSOPHYTON and placed *D. bulbifera* in subsect. *Euopsophyton,* which also included three other species believed to be of hybrid origin. Prain & Burkill (1936), on the other hand, defined the section to include only *D. bulbifera* and its putative hybrids with three members of sect. ENANTIOPHYLLUM Uline.

The two remaining species of *Dioscorea* that are naturalized in the Southeastern States are *D. alata* L., white yam, greater yam, $2n = 20, 30, 40, 50, 60, 70, 80$, and *D. oppositifolia* L. (*D. batatas* Dcne.; *D. opposita* Thunb., see Taxon **24:** 173. 1975), Chinese yam, cinnamon vine, $2n = 138, 140, 142, 144$. They belong to sect. ENANTIOPHYLLUM Uline (tubers nonpoisonous, stems dextrorse, leaves alternate or opposite, filaments as long as the anthers, seeds winged all around). This section, the largest in *Dioscorea,* includes about 120 species restricted to Africa and Asia, none of which is common to both continents (Prain & Burkill, 1939).

Dioscorea alata, a native of southeastern Asia not known to grow in the wild state (Coursey, 1967), is the most widely cultivated edible species in the genus. It has escaped from cultivation in several counties in Florida (Ward; Wunderlin) but is not naturalized in the other Southeastern States. *Dioscorea alata* is highly variable, and many cultivars with different ploidy levels are grown. It resembles *D. bulbifera* in the production of bulbils and in having auriculate petiolar bases but differs in having dextrorse, quadrangular, broadly winged stems.

Dioscorea oppositifolia, which is naturalized in North and South Carolina, Georgia, Tennessee, Alabama, and Arkansas, is native to China and is widely cultivated in eastern Asia for its edible tubers. It is grown in the United States primarily as an ornamental (Bailey *et al.*) and has escaped from cultivation in many parts of the country. It is a weed of thickets, alluvial woods, waste places, flood plains, roadsides, limestone outcrops, slopes, and fence rows. According to Purseglove, *D. oppositifolia* (as *D. opposita*) was cultivated experimentally in Europe during the mid-nineteenth century as a substitute for potatoes (*Solanum tuberosum* L.) that were threatened by blight. *Dioscorea oppositifolia* is most likely a 14-ploid based on ten, and the aneuploid counts above are probably approximations of $2n = 140$. It is readily distinguished from the other bulbil-producing species by its terete, dextrorse, wingless stems, nonauriculate petiolar bases, and somewhat hastate, usually opposite leaves.

Hooker's statement (p. 288) that "the species of *Dioscorea* are in a state of indescribable confusion" may be justified because of the inadequacy of material for many tropical species. It is often difficult, if not impossible, to identify specimens that lack well-developed staminate flowers or mature fruits. Because of dioecism, there are many cases in which the carpellate and staminate plants of a given species were described as two species assigned to different sections.

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opened flower, × 6; h, carpellate flower from above, showing 3 styles and 6 staminodia, × 6; i, cross section of ovary of carpellate flower, × 10; j, ovule, × 25; k, mature capsule, × 1; l, winged seed, × 2. m, *D. villosa,* stem, × 6. n, o, *D. floridana:* n, staminate flower from above, × 10—note stylar rudiments and 6 inwardly curved filaments; o, abaxial view of anther, × 40.

A case in point is *D. hondurensis* Knuth: carpellate material was described in sect. TRIANGULARES Knuth, while staminate material of the same species was described as *D. tabascana* Matuda in sect. MACROGYNODIUM Uline. According to Schubert (1966), *D. hondurensis* probably belongs to the South American sect. SARCANTHA Uline.

The reproductive biology of *Dioscorea* has been poorly studied. Although all species are dioecious, monoecism is known in at least 17 species (Burkill, 1960; Hawley). It is not known, however, if the carpellate flowers of monoecious plants are fertile. The flowers of *Dioscorea* are generally small, and their diameter in the great majority of species is 2–4 mm. The smallest flowers (ca. 1 mm wide) are found in the Madagascan *D. nako* Perr. (Burkill, 1960), while the largest (tepals more than 3 cm long) belong to the Mexican *D. insignis* Morton & Schubert (see Schubert & Morton).

Because of their reduced size and dull colors (usually dirty white, creamy, greenish, or brownish), the flowers of *Dioscorea* were believed to be wind pollinated. However, this is highly unlikely because the pollen is glutinous. Furthermore, Coursey (1967) suggested that the flowers are sweetly scented and are likely to be pollinated by night-flying insects. Sadik & Okereke observed thrips of the genus *Larothrips* carrying pollen from the staminate to the carpellate flowers of *D. rotundata* Poiret. The flowers of *D. composita* Hemsley and *D. floribunda* Martens & Gal. are said to be inefficiently wind pollinated in Puerto Rico (Martin, Cabanillas, & Ortiz).

Chromosome numbers have been reported for about 90 species (ca. 9.5 percent) of *Dioscorea*. Apparently all of the Old World species are either diploids or polyploids based on ten, while most of the New World ones are polyploids based on nine (Martin & Ortiz, 1963a). However, only about three and 17 percent, respectively, of the New and Old World species have been surveyed, and more counts are needed to confirm these cytological observations.

Aneuploidy has been well documented in *Dioscorea alata, D. bulbifera, D. cayenensis* Lam., *D. dumetorum* (Kunth) Pax, and *D. oppositifolia*. All of these species are among the principal food yams, and it is not unusual to encounter variations in chromosome numbers of crop plants that have been propagated vegetatively for hundreds or perhaps thousands of generations. A continuous ploidy series (2–8x) is known in *D. alata* (Bolkhovskikh *et al.*), and higher ploidy counts (10–14x) based on ten are known in at least 12 species. The lowest chromosome number ($2n = 20$) in the genus characterizes most species of sect. STENOPHORA, the most primitive group in *Dioscorea* (Chin *et al.*; Pei *et al.*), while the highest ($2n = 140$) has been reported for *D. cayenensis, D. oppositifolia,* and *D. pentaphylla* L. Onwueme's conclusion (p. 3) that "the highest chromosome numbers and the smallest chromosome sizes occur in the more tropical *Dioscorea* spp., while the smallest numbers and largest sizes occur in the more temperate species" needs further study. It is evident, however, that polyploidy has played a major role in the evolution of *Dioscorea* (Ramachandran, 1962).

Except for a few aberrant cases, species of *Dioscorea* are always dioecious, and within a given population staminate plants usually outnumber the car-

pellate ones by three to five times. The mechanism of sex determination in *Dioscorea* is controversial. Nakajima, Ramachandran (1962), and B. W. Smith have all suggested that the staminate plant is heterogametic and that the "male-determining" genes are borne on the Y chromosome. On the other hand, Bhat & Bindroo concluded that in *D. deltoidea* Wall. staminate plants have homomorphic chromosomes and carpellate ones have heteromorphic. Furthermore, Jensen could not find any evidence of sex chromosomes in *D. quaternata,* and Martin & Ortiz (1963a) and V. R. Rao & Murty reached similar conclusions for four Central American species. The presence of an extra chromosome in *D. alata* and *D. brachybotrya* Poeppig (as *D. reticulata* C. Gay) was considered to be responsible for "male" expression in an XO sex-determining mechanism (B. W. Smith).

Because of their high numbers and small sizes, the chromosomes of *Dioscorea* are very difficult to distinguish morphologically. As suggested by Martin (1966), however, the cytological evidence supports the staminate plant as heterogametic, and therefore an XO sex-determining mechanism is highly unlikely. It is possible that the staminate plants are produced by different mechanisms. Sex ratios of progeny from a carpellate parent vary according to the staminate plant, and such ratios are constant among the progeny of a staminate parent. On the basis of these facts, Martin (1966) concluded that in tetraploid taxa the staminate plants have XXYY or XXXY genotypes.

Natural interspecific hybridization is very rare in *Dioscorea.* The origin of one such hybrid (*D. composita* × *D. floribunda*) has been supported by chemical, cytological, and morphological data (Martin & Cabanillas, 1963). Artificial crosses among some of the New World species (*D. composita, D. floribunda, D. Friedrichsthalii* Knuth, and *D. spiculiflora* Hemsley) are successful in all possible combinations (Martin & Cabanillas, 1966; V. R. Rao *et al.*; V. R. Rao & Murty). The reduction of hybrid fertility is caused by some meiotic abnormalities (univalent and multivalent formations), high percentage of abnormal pollen, low crossability of hybrids, and poor seed set. Crosses between the Old and New World species, as well as between *D. alata* and *D. deltoidea,* have been unsuccessful (V. R. Rao *et al.*).

Alkaloid production in the tubers is apparently restricted to some of the Old World species of *Dioscorea* that belong to sects. LASIOPHYTON Uline, PARAMECOCARPA Prain & Burkill, and TESTUDINARIA (Salisb.) Prain & Burkill. The principal compounds are dioscorine and its stereo isomer dihydrodioscorine. These highly toxic alkaloids cause general paralysis of the central nervous system. The African *D. Dregeana* (Kunth) Durand & Schinz and *D. dumetorum* and the Asiatic *D. hispida* Dennst., which are rich in alkaloids, are used locally to poison animals (see below). No attempts have been made to determine the chemotaxonomic significance of these compounds in the genus.

A few Asiatic species accumulate in their tubers relatively high concentrations of tannins that are economically important. *Dioscorea cirrhosa* Lour. (= *D. rhipogonoides* Oliver) contains between six and 13 percent tannins per dry weight and is widely used in Taiwan and Indochina for tanning leather and for fishing cordage and nets (Burkill, 1966).

More than 20 steroidal sapogenins have been isolated from some 70 species

of *Dioscorea*. Diosgenin is found in all the saponin-containing species. Its content in the tropical dioscoreas is generally much higher than in those of other regions (Takeda). The distribution of sapogenins in *Dioscorea* supports certain sectional groupings and is therefore of some chemotaxonomic value (Akahori, 1965a; Kadkade *et al.*; Takeda). For example, sect. ENANTIOPHYLLUM, which contains the most important food crops of the genus, lacks the steroidal sapogenins. These compounds are also lacking in a few sections that produce bulbils and have sinistrorse stems. On the other hand, sections with alternate leaves, sinistrorse stems, and no bulbils are often rich in sapogenins. Takeda concluded that the chemical data tend to support Prain & Burkill's (1936, 1939) sectional classification of the eastern Asiatic *Dioscorea*. However, the chemistry of the genus is far from being adequately studied, and the great majority of the New World sections have not been surveyed.

Using polyacrylamide-gel electrophoresis of tuber proteins, Ikediobi & Igboanusi have found significant differences in the locations and intensities of certain bands in five species. They were also able to distinguish among nine cultivars of *Dioscorea rotundata*. Several authors (e.g., Rašper & Coursey) observed that differences in the viscosity, size, and shape of the tuber starch grains are useful in separating several edible species of *Dioscorea*. Only a few species, however, have been surveyed for tuber proteins and starch grains.

Ayensu (1972, 1973) observed that stems of the Old World species have two distinct phloem units below the innermost pair of metaxylem vessels, whereas those of the New World species have only one. This anatomical differentiation between the two groups of *Dioscorea*, however, requires further study to assess its phylogenetic value.

On the basis of stem anatomy, Ayensu (1972) concluded that the anatomical data are very useful taxonomically at the intersectional level but have little value within sections. He proposed several alterations to the sectional classification of Knuth (1924), including the reduction of many sections to synonymy and the elevation of a few subsections to sectional rank. In general, stem anatomy supports the sectional subdivision of the genus as accepted by Prain & Burkill (1936, 1939) and Matuda (1953b) but not by Knuth (1924).

Extrafloral nectaries of certain species (e.g., *Dioscorea rotundata*) are embedded in the leaf blade and open on the lower leaf surface. Each gland consists of small cells with dense cytoplasmic contents and is surrounded by a layer of cells with apparently little or no cytoplasm. The secretions of these nectaries contain fructose, glucose, and sucrose, as well as ninhydrin and traces of galactose (Grout & Williams). Leaf glands of the West African *D. macroura* Harms form enlarged pockets within the mesophyll and are connected to the upper leaf surface by slits or ducts. The pockets are lined with multicellular glandular "trichomes" that secrete mucopolysaccharide, on which nitrogen-fixing bacteria grow (Orr). As shown by Behnke, however, these bacteria are parasitic, and in response to their presence the plant produces an abundance of simple trichomes that fill the pockets and cause the bacteria to disintegrate.

In the African *Dioscorea praehensilis* Bentham and the Asiatic *D. esculenta* (Lour.) Burkill and *D. piscatorum* Prain & Burkill, roots produced on the tuber

surface are modified into thorns or spines. Such modified roots apparently evolved independently several times within the genus.

Tubers of *Dioscorea* originate primarily from the seedling hypocotyl following the initiation of a cambial zone around the vascular tissue. The intensive activity of the cambium produces the storage parenchyma. These tubers differ from stem tubers of other genera in lacking both scale leaves, buds, or eyes that identify nodal positions and a terminal bud that marks the growing point of the tuber. Furthermore, most tubers of *Dioscorea* exhibit positive geotropism.

The corky outer portion of the tuber is derived from successive cork cambia each originating beneath another. The ground tissue, which is derived from the vascular cambium, forms the bulk of the tuber and consists of thick-walled parenchyma densely packed with starch grains. The vascular bundles are collateral and have xylem comprising tracheids and parenchyma but no vessels.

Some species of *Dioscorea* develop enormous tubers: up to 365 kg in *D. elephantipes* (L'Hér.) Engler (Purseglove) and up to 110 kg and 3.5 m long in *D. alata* (Haynes & Coursey).

Species of *Dioscorea* can be propagated by tubers, bulbils, vine cuttings, tissue cultures, or seeds. A leaf cutting with the complete pulvinus dipped in "hormone powder" is capable of producing new plants (Blunden, Hardman, & Trease). Bulbil production, which is reduced by the increase of day length (Allard), promotes dispersal, particularly in habitats that are subjected to floods or rain washes. Because of their occurrence in many species of unrelated sections, bulbils probably evolved independently a few times within *Dioscorea*. Murty & Purnima, who studied 11 species, suggested that bulbils develop as composite structures from the diffused growth of accessory buds that arise on the abaxial side of the axillary bud. Ayensu (1972) and Burkill (1960) define the bulbil as a modified branch of the aerial stem. They stated that it resembles the tuber anatomically.

Little is known about the ecology of *Dioscorea*. Although the majority of species are tropical, many rhizomatous taxa grow in temperate areas. In general, most species require more than 1 m of annual rainfall and temperatures higher than 25°C (Purseglove). The effect of photoperiodism has not been studied adequately. According to Purseglove, long days apparently favor the development of aerial parts, whereas short days promote the growth of tubers.

Food crops of the genus *Dioscorea*, which are known as yams in most parts of the world but are often confused with the sweet potatoes (*Ipomoea Batatas* (L.) Lam., Convolvulaceae) in the United States, provide the staple foodstuff for millions of people in many subtropical and tropical countries, particularly in West Africa (Coursey, 1967). The dietary position of yams in the tropics, however, has declined substantially due to socioeconomic reasons, introduction of better crops, and higher costs and greater labor needed for the cultivation and preparation of yams for food. The so-called "yam zone," which extends from the Cameroun Mountains west into central Ivory Coast, is the area where most of the world's yams are grown. In fact, Nigeria alone produces nearly half of the world's crop (Ayensu & Coursey; Coursey, 1967). Yams are eaten

baked, boiled, fried, mashed, pounded, or roasted. They are also used to prepare chips, flakes, and flour.

Although about 50 species of *Dioscorea* are collected from the wild or cultivated as food crops, only ten are considered to be of major importance. These are associated with three independent centers of domestication. In southern China and southeastern Asia *D. alata, D. bulbifera, D. esculenta, D. japonica* Thunb., *D. oppositifolia,* and *D. pentaphylla* were first domesticated, while in the Caribbean region *D. trifida* L. and in the West African forest belt *D. cayenensis, D. dumetorum,* and *D. rotundata* were first brought into cultivation. It has been suggested that the domestication of *Dioscorea* probably took place ca. 10,000 B.P. in Asia and ca. 11,000 B.P. in Africa (Coursey, 1976a).

The West African *Dioscorea cayenensis* and *D. rotundata* were described from plants cultivated in Jamaica and French Guiana, respectively. Both species were introduced to the New World during the slave trade (Ayensu & Coursey). There is some controversy whether *D. rotundata,* the most important African yam that is not known to grow in the wild, is a distinct species or a subspecies of the earlier-published *D. cayenensis.* It has been suggested that *D. rotundata* probably evolved from hybridization between *D. cayenensis* and *D. praehensilis,* although the second parent may have been either *D. abyssinica* Hochst. or *D. togoensis* Knuth (Akoroda & Chheda; Coursey, 1976a).

The medicinal value of various species of *Dioscorea* has increased dramatically following Marker's (see Tyler *et al.*) pioneering research on the conversion of diosgenin to precursors of steroidal drugs. These drugs include the sex hormones androgen, estrogen, and progestogen, as well as oral contraceptives and anti-inflammatory compounds such as the systemic corticosteroids and topical hormones. Diosgenin is commercially extracted mainly from the tubers of the Mexican *D. composita, D. floribunda,* and *D. spiculiflora,* the South African *D. sylvatica* Eklon, and the Himalayan *D. deltoidea* and *D. Prazeri* Prain & Burkill. Sapogenin content in the tubers of the Mexican species above can be as high as 10–15 percent of the dry weight. Although the use of *Dioscorea* tubers in traditional medicine is likely based on superstition and magic rather than on actual physiological effects, some of the sapogenins and other steroidal components may have certain medicinal properties. In fact, preparations from the tubers of various species have been prescribed to cure colic, dysentery, ulcers, syphilis, sore throat, swellings, pulmonary complaints, diarrhea, hemorrhoids, boils, tumors, corns, diabetes, cuts, superficial lesions, and hysteria (Hartwell; Karnick, 1969; Perry; Sastri; Watt & Breyer-Brandwijk).

Tubers of numerous species of *Dioscorea* are highly toxic. The poisonous substances are alkaloids, sapogenins, or tannins. Because of their hemolytic properties, sapogenins are highly toxic if introduced into the bloodstream. Therefore, the tubers have been widely used as a source of poison for fishing, hunting, or criminal purposes. Fish poisons are obtained from *D. deltoidea* in India, *D. hispida* in Java, *D. piscatorum* in Malaya, *D. Poilanei* Prain & Burkill in Vietnam, *D. Prazeri* in Sikkim, *D. sansibarensis* Pax in tropical East Africa, *D. tokoro* Makino in China, *D. composita* in Mexico, and *D. bulbifera, D. Dregeana,* and *D. rupicola* Kunth in various parts of Africa. The placement of

grated tubers into a stream can stupefy fish at a considerable distance. Arrow or dart poisons are prepared in Malaysia and Sikkim by mixing the juice of *Antiaria toxicaria* Lesch (Moraceae Link) with that of the tubers of *D. hispida,* and in Africa by using the tuber extracts of *D. dumetorum* or *D. sansibarensis* with extracts of *Strophanthus* DC. (Apocynaceae Juss.). These poisons are employed to kill tigers and monkeys. In India tigers are hunted by placing pounded tubers of *D. hispida* in carcasses (Karnick, 1969).

Because of their high saponin content, tubers of various species, particularly *Dioscorea deltoidea* and *D. Prazeri,* are used in Burma, southwestern China (Yunnan), and northern India as soap for washing hair, silk, or wool. Decoctions of the tubers are also used in these countries to kill lice in human hair and clothing. In Malaysia tubers of *D. piscatorum* are used in the preparation of an insecticidal powder and are employed to destroy rice parasites (Coursey, 1967), while in Tanzania the tubers of *D. dumetorum* are used as a remedy for schistosomiasis (Watt & Breyer-Brandwijk). A paste prepared from the bulbils of *D. bulbifera* is said to cure scorpion stings and snake bites (Karnick, 1969). Bulbils of the last species are also used as a fish bait in Kashmir (Sastri).

Other minor uses of *Dioscorea* include extracting starch from *D. alata,* distilling alcohol from certain species (Sastri), brewing beer from *D. dumetorum* (Corkill; Irvine), substituting *D. polygonoides* Humb. & Bonpl. (as *D. lutea* G. F. W. Meyer) for coffee (Uphof), tanning leather and making fishing nets (see above), dyeing clothes and cotton threads with tubers of *C. cirrhosa* (Karnick, 1969; Uphof), coloring ice cream with phenolic pigments extracted from *D. alata* (Ingram & Greenwood-Barton), feeding livestock (Bailey *et al.*), and utilizing stems as cordage (Burkill, 1966). A drink prepared by the Meskwakis from the rhizomes of *D. villosa* is said to relieve the pain of childbirth (Lewis & Elvin-Lewis). The juice of a certain *Dioscorea* is used in Tanganyika for tattooing (Watt & Breyer-Brandwijk).

Several species of *Dioscorea* are grown as outdoor twining ornamentals, and forms of *D. alata* and *D. oppositifolia* with variegated foliage or colored younger parts are highly desirable (Hawley). *Dioscorea elephantipes,* elephant's foot, is occasionally grown in Europe and North America as an indoor plant for its large, curious, above-ground tubers with corky bark.

Yams have played a central role in the social and religious life of people in the tropics, particularly in West Africa. Cultural, social, magic, and religious practices associated with almost every aspect of yam planting, harvest, and storage are especially evident in Nigeria and neighboring countries (Ayensu & Coursey; Coursey, 1967, 1972; Purseglove). The cultivation of *Dioscorea pentaphylla* has been intimately associated with priesthood and has therefore been considered sacred in various parts of Malaysia and Indonesia (Coursey, 1967). The poisonous properties of many species form the basis of several magical beliefs in West Africa. Many of the highly toxic species (e.g., *D. dumetorum* and *D. hispida*) are used during famine for food. The tubers are peeled, sliced, boiled, pounded, and placed in running water for a few days to remove the toxins before they are consumed (Irvine; Karnick, 1969). Different tribes, however, follow different procedures to detoxify the tubers.

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The literature on *Dioscorea* is too voluminous to be presented fully here. The interested reader should consult Lawani & Odubanjo and the indexes of the *Bibliography of Agriculture* for additional leads. The references listed below were selected from a file containing more than 3500 entries.

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